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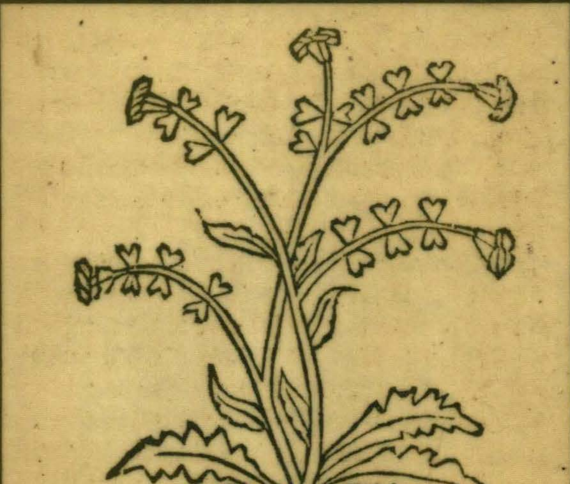

History of Botanical Science

an account of the development of botany from ancient times to the present day

A. G. Morton

Julius Sachs (1832–97)

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Preface

History needs to be constantly re-written—not in order to supersede the work of earlier historians, itself a permanent part of history—but to enlarge their vision with the new material and the unique illumination provided by later experience.

When trying to give university students of botany an inkling of the history of their subject, as an adjunct to the more serious business of teaching its latest developments, I was struck by the lack of a history of botany as seen from the standpoint of today. The histories of E. F. H. Meyer (1854) and Julius Sachs (1865) are indispensable but are now classics, whilst the *Short History of the Plant Sciences* by H. S. Reid (1942) and the *Short History of Botany* (in Russian, Moscow 1968) by N. A. Basilevskaya, I. P. Belokon and A. A. Tscherbakova, and the *Geschichte der Botanik* (1973) by K. Mägdefrau, although useful, are not entirely adequate to fulfil this need. It was with much misgiving that I began writing a general history of botany, prompted by the suggestion of a colleague, and encouraged to proceed by others to whom I spoke of my intention. My only qualification for the task, which has proved far more laborious and time-consuming than I anticipated, is a deep and life-long interest in the science of plants and in its history. The only merit I would claim for this interpretation of botanical history is that it is based on first-hand study of as many of the primary sources as time and my own limitations permitted.

The distinctive feature of science as a human activity is the attempt to find a structure of causal laws, a guiding theory, in the relations between the particular phenomena it is concerned with. This is true of the science of botany, even though it necessarily contains a large descriptive element. In tracing its history I have therefore taken as my central theme the evolution of botanical theory, of what men at different times have thought about plants as a class of beings. The growth of specifically botanical concepts from the existing knowledge of plants, and the influence of these concepts on the further course of discovery, are the twin threads of a long and fascinating story. Choice of the term botanical science in the title is deliberate; it gives emphasis to the viewpoint adopted, and also happens to be a closer rendering of the older name for the science of plants.

The history of botany has many colourful facets, the study of which throws light on the sources of its movement. Botany is indeed embedded in human history, from its origins in two of the most ancient sciences of all, magic and medicine, through its long association with pharmacology, agriculture and horticulture, to its part in the exploration of the world, and in ensuring the supply of food and raw materials for the rise and maintenance of modern industrial society. Botany has drawn strength from other sciences, and contributed to them in return; and at various stages has reflected in its thought the philosophical currents of the time. Before everything, botany is the creation of botanists: knowledge of their lives and tribulations, their characters and motives, are part of the fabric of its history. All these aspects have some place in our chronicle in so far as they contribute to deeper understanding of the causes and the course of botanical progress.

My aim has been to write in a form sufficiently concise and uncluttered by detail to be comprehensible to readers who are not botanists and have no more than a general interest in the history of science, whilst at the same time giving botanists an adequate account of the development of the principles and the factual basis of their science. The text is a continuous story, complete in itself, which can be read without any reference to the notes. The copious and sometimes discursive apparatus of notes is intended for those readers, and particularly for those botanists, who may be interested in additional facts, comments, and source material, which amplify the interpretation presented in the text. Reference to the primary literature and to many secondary sources will be found in the text or in the notes, but I have not included a bibliography of all the works consulted in the preparation of this book, as it could well exceed in length the notes already included.

Technical terms have been kept to a minimum but obviously cannot be excluded from a work of this nature. Some explanation is indicated for most of them, but others, whose meaning is not easily conveyed to the non-botanist, can probably be taken by most readers in their stride.

I have freely quoted actual words of many botanists of the past in order to bring their thoughts as vividly as possible to modern readers. Translations from Greek, Latin, French, German and Russian are generally my own, but where there exist scholarly translations of Greek and Latin sources I have naturally made grateful use of them.

The naming of a specific plant referred to in the older literature often presents grave difficulties due to doubts about its identity, and to the absence of systematic nomenclature before the Linnean reform. For older plant references I have used the nearest English vernacular name, or occasionally the contemporaneous Latin name (not italicized), when these give as close an identification as is attainable; sometimes the italicized Latin name of a modern genus or species is used, if identification is fairly certain. For post-Linnean references the author's Latin designation (when one is given) is quoted in italics, but no account is taken of subsequent taxonomic changes. I hope this rough and ready system will sufficiently indicate the likely identity in most cases, without being either misleading or too repugnant to strict taxonomic canons.

I am deeply grateful to Dr Joseph Needham, FRS, Director of the East Asian History of Science Library, and to Mr D. M. Henderson, Regius Keeper, Royal Botanic Garden, Edinburgh, for their helpful comments on the manuscript. Needless to say, I alone am responsible for all the inevitable errors of ignorance and inadvertence which remain, as I am for the opinions expressed.

My thanks are due to the Governing Body of Chelsea College, University of London, for the award of a Professorial Fellowship, during the tenure of which this history was begun, and to the Leverhulme Trust for the award of an Emeritus Fellowship, which greatly assisted me in gathering together much of the necessary material for bringing it to completion.

Edinburgh
July 1981

A. G. MORTON

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A. G. M.

1

The Beginnings of the Knowledge of Plants

To know . . . the diversities of plants, and the virtues of roots.
Wisdom of Solomon, VII, 20 (first century BC).

Man's vital interest in plants as a source of food goes back to the very origins of human society. Long before recorded time men had gained by trial and error a close acquaintance with those plants in their environment that were either good to eat or useful in some other way. The inhabitants of Australia, at least before their society was wrecked and decimated by civilized immigrants, lived in a way not essentially different from most of mankind during the thousands of years of the Old Stone Age. Their hunting and gathering activities were socially organized and based on detailed familiarity with the life histories of the various kinds of plants and animals available to them; for each plant the habitat, the nature of the edible parts, and the right season for gathering, were well known.[1] This type of traditional knowledge is pre-scientific, as is shown by the absence from their language,[2] as from other primitive languages, of any word for the concept of plant, although there may be a wealth of special names for particular plants, and even for parts of a particular plant or for a plant at different stages of growth. Such knowledge became part of the indispensable equipment for the slow advance of society. Early men and women in the search for food must have carried out an immense exploration of the vegetable kingdom, accompanied by some hazardous experimentation; they habitually ate many wild plants which today are not thought of as sources of food.[3] The last meal of the Tollund Iron Age man, whose well-preserved body was found in a Danish bog, consisted of the seeds of several plants now counted as weeds and kept out of our fields by unrelenting effort.[4]

The process of discovering food plants also revealed others not nutritious in themselves but useful in increasing the palatability, digestibility and keeping quality of the primary foods, and still other plants having more or less powerful effects on the functioning of the human body and mind, including some which could be dangerous and fatal poisons. Long before it could be consciously analysed, men must have established the distinction between plants useful for medicinal purposes, in the widest sense, and plants which could be eaten or could be used in making tools, utensils, dwellings and other social products. This basic dichotomy in the use-value of plants has been, through many vicissitudes of time and history, and in many varied and complex ways, a twin stimulus and influence in the development of plant science.

Evidence of anything that may truly be called systematic knowledge of plants only becomes apparent, however, in the period after the discovery and increasing practice of agriculture had caused profound technological, social and intellectual changes in human society.[5] This transformation of the way of life of a large part of mankind has been called the Neolithic revolution. It was the foundation from which the arts of civilization grew, and its decisive feature was the discovery, selection and bringing into effective cultivation of essentially those plant species which, modified and improved, are still today the main food resources of the world. The domestication of sheep, goats, cattle and pigs probably followed soon after the earliest stages of cultivation of the first crop plants. Even if, in some communities, animal husbandry originated independently of plant cultivation, its full development was ultimately dependent on the growth of crops, and the two activities soon became linked in a balanced and productive farming economy. It was the use of oxen for ploughing which set the seal on the establishment of agriculture, the cultivation of fields as distinct from garden plots, and led to a rapid and relatively enormous increase in food production, an increase that cost much less expenditure of time and energy than had been required to live by hunting and fishing, supplemented by the laborious collection of wild roots and seeds. For the first time in history men were able to ensure themselves a regular sur-plus of food, which could be stored in order to maintain a steady supply between one season and the next, and to protect society against natural disasters, but which could also be appropriated by some members of society at the expense of others, or used as an article for exchange or for trade. A new life was created which included, at least for some, the opportunity for leisure and for thought, and which was pregnant with new technical advances, and with far-reaching changes in social structure and in mental attitudes to the world around.

The first attempts at plant cultivation, probably in small hoed plots near human dwellings, are believed to have been made shortly before 10,000 BC in Western Asia: by 6000 BC Neolithic agricultural societies were widely established in the Old World, and highly developed agriculture based on the ox-drawn plough was established in fertile parts of the Middle East after about 4500 BC. In the New World the plot cultivation of pumpkins, squashes and peppers began probably as early as 7000 BC, and agriculture based on maize was established in Central America by about 2500 BC. The ancient civilizations arose on the material achievements of agriculture. The pictorial and written records which they left for posterity are a witness to the fact that men had in consequence begun to be consciously aware of plants and to consider them in a way that marks the first step to scientific study. Symptomatic is the appearance of plants in artistic representations, in wall paintings and sculpture. The lively and brilliant productions of Palaeolithic art show almost exclusively animals or human beings, in very few are plants represented and then only as fragments, perhaps a leaf or a few grains of wild wheat.[6] Presumably this reflects the much greater social organization and effort involved in hunting than in gathering, possibly also the fact that gathering was strictly the function of women. There is indeed abundant archaeological evidence that the discovery of plant cultivation was made by women and continued to be women's work until the use of the plough led to the involvement of men in agricultural labour. Only after the cultivation of plants had become the mainstay of society were they elevated to the realm of art. In ancient Egypt the earliest plant portrayed is the date-palm, its stem, leaves and fruiting branches being clearly depicted before 3200 BC whilst carvings of awned cereals (wheat and barley)[7] are found on monuments about 3000 BC. Thereafter plants are frequently shown in carvings and grave-paintings, often affording graphic evidence of the methods of agriculture and of sundry technical processes connected with plants. The plants depicted are chiefly economic, although coronary flowers whose appeal was purely aesthetic are also shown in many scenes. Representation of plants tends in general to be less accurate and more conventionalized than that of people and animals, but the species are often recognizable nevertheless. At about the same time as in Egypt, economic plants such as date-palms, vines and cereals begin to be represented in Mesopotamian art, although usually in a rather stylized way.

About 1800 BC craftsmen of the Minoan civilization in Crete painted frescoes in the great king's palace at Knossos and introduced the images of a number of plants which evidently interested them. Some of the delineations are imaginative and not recognizable with certainty but others are quite accurate, show keen and close observation, and leave no doubt of the identity of the species shown.[8] The pictures include a group of native-grown plants of economic importance, barley, olive, fig, lupin (*Lupinus alba*), wheat, saffron crocus, and, with less certainty, pomegranate; some purely decorative plants such as lily, sword lily, narcissus, rose and myrtle,[9] and two foreign plants, date-palm and papyrus, the products of which must have been imported. This interesting selection reflects two historical developments which contributed to the beginning of systematic enquiry into plants, in the first place, the rise of trade in plant products, and secondly, stimulated thereby, attempts to introduce alien plants, and the establishment of gardens for their acclimatization and propagation, which at a very early date acquired a second, and even an exclusive, function as pleasure gardens, where plants were grown for their beauty and intrinsic interest as well as for use.[10]

That the ancient Egyptians imported timber is shown by the use of non-native wood, readily identified by its microscopic characteristics, in tombs and shrines. Cedar, cypress and juniper, which must have been brought from Syria or Asia Minor, and ebony,[11] *Dahlbergia melanoxylon*, from various regions of tropical Africa lying south of Egypt, are found in quantity from before 3000 BC onwards. An inscription from the Palermo stone records the arrival, in the time of King Snefru (about 2900 BC), of forty ships laden with cedar wood, some of which was used two years later, according to the chronicler, for making the doors of the great palace. Some twenty-four different kinds of wood, native and foreign, are distinguished in the records of the time, but the names in many cases cannot be equated with definite species owing to the lack of any description.[12] The oldest epic poem in the world, the story of Gilgamesh of Sumer, written fragments of which go back to 2000 BC, contains passages which are clearly records of expeditions or sorties in search of timber in the hill country to the north of Mesopotamia, showing that the Sumerians were equally interested in exotic timbers.

An early plant expedition from Egypt is described and pictured on reliefs at the great terrace temple at Deir-el-Bahari. This expedition was sent by Queen Hatshepsut about 1480 BC to the land of Punt (modern Somaliland) and returned with not only vast quantities of resins, ivory, gold, scented woods and incense, but also with "many fine plants and green myrrh trees". About thirty trees are pictured, each carried complete with roots in soil, in a large basket, by two men. Most of the trees have foliage and are almost certainly specimens of *Boswellia carteri*, native in S. Arabia and Somaliland and the source of frankincense,[13] but some trees are without foliage and may be different species. The trees were planted in the gardens at Thebes and are represented growing in tubs, but whether they were successfully acclimatized is not known: three hundred years later Rameses III boasts of sending a similar expedition to Punt in search of living trees. Only a few years after Queen Hatshepsut's expedition her successor Thotmes III brought back a number of rare plants from Palestine, following a military excursion against that region, and a catalogue of these is carved on bas reliefs at Karnak. Flowers and leaves are indicated but definite identification is not possible for most of the plants.

The earliest description of an Egyptian garden comes from a grave-inscription of the Third Dynasty (shortly after 3000 BC) and gives a picture which, as many later grave-paintings show, became the pattern for thousands of years. Within an enclosing wall stand trees, including date palms, figs and trellised vines, around a rectangular pond with water-lilies, the edges adorned with flower-beds. This is clearly a fruit and pleasure garden, the vegetables and herbs were grown elsewhere. The owner of such a garden must have enjoyed wealth and privilege that can only have been the lot of the fortunate few.

The cult of the garden seems to have reached great heights in ancient times in Mesopotamia, in the practice of the Assyrian and Babylonian kings—a tradition that was continued in the succeeding Persian empire and so impressed the contemporary world that the Persian word for an enclosed garden entered the Greek language,[14] and being used by the translators of the Hebrew books of the Old Testament became, in slightly varying forms, the designation in many languages of the

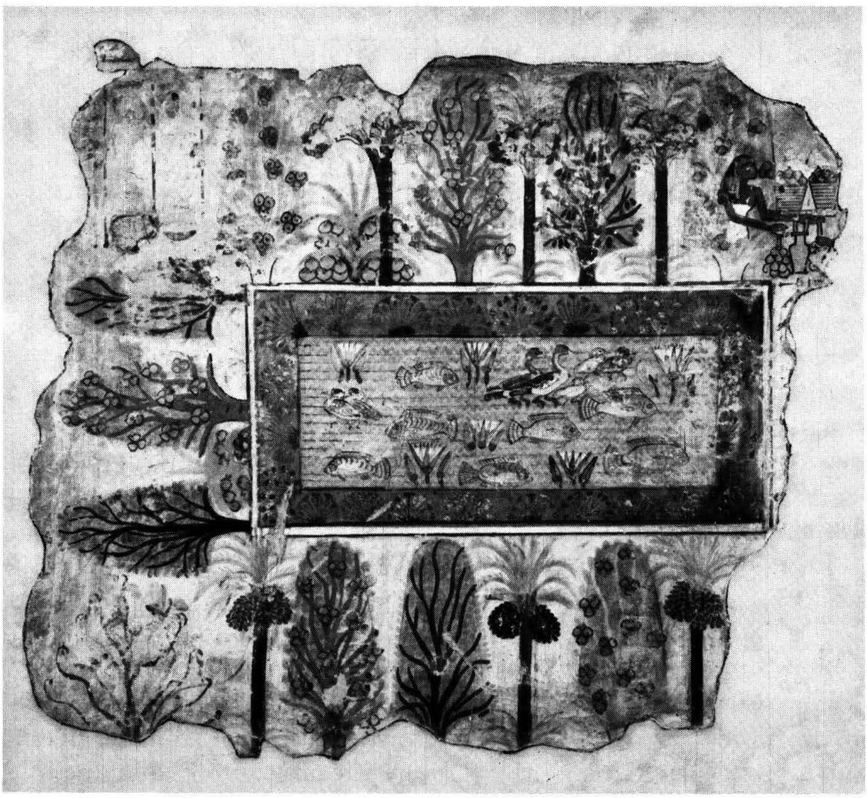


Figure 1 Wall-painting of an Egyptian garden about 1400 BC. Reproduced by permission of the Trustees of the British Museum.

heavenly pleasure garden or paradise. King Tiglath-Pileser I, about 1100 BC, records that he planted cedars and "precious garden plants not known in my country" in the gardens of Assyria, and both Sargon, who reigned from 722 to 705 BC, and his son Sanherib boast that they laid out parks specifically to grow foreign plants. The latter says "I made gardens above and below the city with plants of surrounding lands, spice plants of the vines of the mountains, myrrh trees which flourish better than in their native lands, and fruit trees—all these I planted for my subjects". The gardens of the Assyrian queen Sammuramat (Semiramis) constructed about 800 BC became so famous that Alexander is said to have turned aside from his campaigns to see them. From the description given by Diodorus Siculus a notable feature of these gardens was the elaborate construction of roofed arcades and terraces, and the installation of a complete system of irrigation.

All these developments created the conditions for the first systematic and recorded knowledge of plants, which began in the old centres of civilization, in the first place as an adjunct of medicine: the recording of plants considered to be useful in treating disease or injury. The primitive dichotomy in the use of plants has already been mentioned: it now finds expression in a recognized division of knowledge. So in the Babylonian creation hymn, dating from the second millenium BC, the god Marduk is celebrated as the controller of irrigation and cultivation, who fills the store-room with emmer and sesame, and holds in his palm a healing herb as he goes to battle.[15] The invention of writing was stimulated by the more complex requirements and organization of communities based on advanced agriculture. It seems quite likely that writing actually began with the need to record the stored harvest and from attempts to devise means of doing this. Once invented, writing rapidly became the tool of government and trade and of organized communication and knowledge. Only after the invention and general use of writing could science in the sense of an accepted and accurately transmitted body of knowledge really begin, and it is at this stage that the outlines of the history of botanical science can first be sketched.[16]

In antiquity the Egyptians were renowned for their knowledge of medicinal plants. Homer refers to the many herbs produced by the rich corn-bearing soil of Egypt, and tells how Helen of Troy had been given many useful drugs by an Egyptian lady.[17] There is documentary evidence that this tradition is well-founded. The Ebers papyrus, found in a tomb at Thebes, and which can be dated about 1500 BC, is a compilation of Egyptian medicine containing prescriptions for a variety of conditions and diseases, systematically arranged under the condition to be treated. The recipes contain many specific drugs, the majority of plant origin, and about 150 of the plants concerned are said to have been identified with reasonable accuracy. Since the text is medical, no botanical descriptions are given and the plants must be identified principally by philological comparison of the names with the vernacular names in related languages or by indirect evidence from the medical usage. The difficulties of identification are increased by the habit of the Egyptian physicians, who were priests or linked with the priesthood, of assigning invented "sacred" names to plants in order to conceal their art from the profane.[18] Thus a drug believed to be *Ambrosia maritima* is mentioned twenty-eight times in the Ebers papyrus under the cover name of vulture's heart.

The Ebers papyrus contains material drawn from much earlier sources: reference is made to "old writings" and to dynastic dates as early as 3000 BC. Although these ascriptions may be symbolical rather than literal, they are indicative of a very ancient and authoritative traditional body of written knowledge (doubtless derived from still older oral tradition), the existence of which is confirmed by the appearance of many prescriptions almost unchanged in other, even older, medical papyri. In these Egyptian texts plants are treated as materia medica and not as objects of botanical interest.

There is evidence that the Babylonians, too, possessed a considerable store of drug plants. A collection of medical tablets from the library of King Asshur-bani-pal at Nineveh were studied by R. Campbell Thompson.[19] The tablets date from early in the first millenium BC, but contain prescriptions which indicate a herbal tradition of much earlier times. By listing those vegetable drugs which appear more than five times in the 660 tablets studied, Campbell Thompson showed the existence of a Babylonian herbal corpus of at least 150–160 plants, of which he considered that about 100 could be identified. This closely parallels the state of medical plant knowledge in Egypt: some of the most frequently used drugs are in fact common to both herbals. Of even greater botanical interest is a collection of plant lists, which also comes from the royal library at Nineveh. This treasure-house of literature and learning was buried under the ruins of the city after its capture and destruction by the allied Medes and Babylonians in 610 BC. Fortunately the contents, inscribed on almost indestructible brick tablets, survived for centuries beneath the sand and rubble until their discovery early in the nineteenth century.

The plant lists form a remarkable document, amounting to a dictionary of plants. They were compiled by the order of King Asshur-bani-pal himself, who reigned from 669 to 626 BC, from at least four pre-existing works which the king (or perhaps his scribe) apparently claims as lacking in logical arrangement and failing to explain difficult names. This may well be considered the earliest truly botanical work at present known that has come down to us. It is more than a medical herbal, for it includes a wide range of plants useful to man in various ways, and is thus a treatment of plants as plants. In addition, one of its aims is evidently to clarify the naming—as we would say the synonymy—of the plants concerned, and such an effort may perhaps be considered the beginning, although it is not the end, of botanical wisdom. The list does not contain, however, any general botanical concepts or theory, nor even any attempts at description of the plants, except an occasional illuminating comment by the scribe; thus colocynth is "like a ball" (the spherical fruits) or the red poppy "is like the mandrake, its young female shoots holding the juice" (i.e. it is narcotic and the juice is extracted from the soft, unripe capsules).

The intention of the work was to equate the old Sumerian names of the plants with their popular names, including synonyms, in Akkadian, the language of Babylonia and Assyria. Sumerian was no longer spoken but continued as the learned classical language, taught to boys in school, much as Latin continued in use during the Middle Ages in Europe. Sumerian and Akkadian are not linguistically related although both were written in the cuneiform script. The dictionary contains about 400 Sumerian names which correspond to about 200 distinct plant species. About 800 Akkadian names and synonyms are equated with the plants. The work is not a local flora either in fact or intention: it is a systematic list of many plants that were of interest because used as food, textiles, drugs or timber, and it even included a few which appear to be weeds or ornamentals.

From his study of the tablets Campbell Thompson suggested botanical identifications for many of the plants, based on comparative philology together with his reading of the medical tablets, and supported by his knowledge of the flora, customs and technology of the Middle East. In so far as the non-expert is capable of weighing this erudition, it seems to me that 140–150 of the 200 plants can be identified with considerable probability. This is a remarkable achievement of the scholar and also a tribute to the careful labours of the Assyrian botanist–scribe who drew up and collated the list of names and synonyms.

The plants are listed in sixteen groupings founded on usage or properties rather than on botanical features. Thus the basic food plants, cereal and legumes, form a group, as do vegetables and cucumbers, trees and fruits. Other groups apparently embrace alkali plants (used for washing), plants which provide dyes, purgatives, narcotics, textiles, and plants (both trees and herbs) exuding gum or resin. There are at least five groupings of which the basic principle is uncertain but in three of them, containing respectively, grasses and reeds (but including *Convolvulus*), thorny plants, climbing plants, the delimitation may be based on general similarity of habit. It seems to be the only faint suggestion of any feeling for botanical grouping, although Campbell Thompson pointed to a few instances where plants seem to have been listed together on account of some morphological resemblance.[20] The plant names are normally preceded by a determinative sign showing whether they are trees or herbs, but this is an ancient feature of the system of writing and is not always employed consistently even for the same plant.

The principal species of cereals and legumes were evidently carefully designated, although we cannot now be sure of the correct equivalent in all cases. In other groups, too, the nomenclature of the various plants is detailed. The list of cereals includes barley, wheat, emmer, einkorn, millet (*Panicum miliaceum*), and rice. It is interesting to find that rice was well known in Babylonia in the seventh century BC, although probably not yet widely cultivated. The inclusion of sesame with the cereals, no doubt because of the edible grain-like seeds, shows that the grouping of plants was not primarily botanical.

There is a chapter on plants in the Persian Būndahišn, a compilation from the Zoroastrian religious writings dealing with the creation of the world.[21] The Middle Persian manuscript was not written before AD 300 but it derives from a tradition several centuries earlier. Although without any botanical significance, the work shows a feature worthy of remark. Whilst but few plants are individually named, fourteen classes of plants on the earth are spoken of, most of which correspond fairly closely to the groupings of the Babylonian plant lists. This suggests that the Babylonian classification of plants was probably already an accepted and oft-repeated scheme, with which the Zoroastrians would be familiar and which it would therefore be natural for them to adopt in their teaching.

In the other centres of ancient civilization the earliest records of systematic plant knowledge also show that attention was given in the first place to plants as materia medica. In China[22] the oldest study of plants was herbalist in character and was contained in the Classical Pharmacopeia of Tzu-I (*Tzu-I Pên Tshao Ching*),* dating from the time of Confucius or a little later, perhaps about 500 BC. Although this work was lost about AD 500, it was available to the writer of the Classical Herbal of Shen Nung[23] (*Shen Nung Pên Tshao Ching,* known as the *Pên Ching*) and embodied in this work. The earliest text of the Classical Herbal was produced at some time between 300 and 100 BC, and although not extant as such, the substance is known from the collected commentaries thereon (*Shen Nung Pên Tshao Ching Chi Chu*) written by Tshao Hung-Ching about AD 492. There were 365 distinct entries of medicinally useful herbs in the Classical Herbal, to which nearly 200 more were added by Tshao Hung-Ching in his commentary some 700 years later. Almost all these plants were subsequently included in the first national pharmacopeia of China (probably the first official pharmacopeia of any civilization, according to Needham[24]), which was produced by a committee of experts in AD 659 and issued by imperial decree. This continuity of content shows the existence in China of an established body of herbal knowledge from very early times. The classification of the drugs of the Classical Herbal was pharmacological, not botanical, and was at the same time a curious reflection of social stratification, since drugs were classed as princely, ministerial or adjutant. Princely drugs were those which preserved general health but did not contain dangerously active principles. Adjutant drugs on the other hand were used against acute conditions and contained potentially dangerous principles, whilst ministerial drugs were intermediate in their properties. The social criticism implied in this classification is a fascinating subject for meditation.

* Romanization of Chinese according to the modified Wade–Giles system adopted in *Science and Civilization in China.*

The Vedic writings of India, of which the oral sources come down from at least the middle of the second millennium BC, and possibly from much earlier, contain many references in hymns, invocations and charms to various plants possessing medical or magical properties. Evidence of systematic herbal knowledge, however, is first found in the oldest medical texts of India, the *Susruta-Samhita*[25] (the collection of Susruta), a compendium traditionally associated with the great surgeon and physician Susruta who flourished at Benares about the time of Gautama Buddha (BC 560–480). The extant text was edited in the late third century but probably dates from several centuries earlier and certainly includes even older material. The *Susruta-Samhita* witnesses to a state of medical knowledge and practice comparable in quality to that of ancient Egypt, and particularly notable for the bold and original techniques of the Indian surgeons and of the range of instruments available to them. It shows in addition that the Indian physicians possessed a very large armoury of herbal materia medica: about 700 plants are named, placed in thirty-seven groups according to the disease or condition to be treated. Food plants are classed according to the part of the plant used and also according to taste and to their dietetic and physiological properties. No botanical information is included apart from the occasional comment on habitat or type of foliage to aid in distinguishing similar species: in consequence, the names cannot in most cases be linked with specific plants.[26] It is evident, however, that plants were being closely looked at, as shown for example by the naming of many varieties of sugar cane or the listing of fungi in four classes in accordance with the substrate on which they grow (stacks of straw or bamboo, sugar cane, the earth, dung).

In addition to the basically pharmacological grouping of the plants, reference is also made to a type of botanical classification which seems to have been widely recognized since it is found with variations and refinements in other later writings (e.g. the medical collection of Charaka, the *Charaka-Samhita*). This classification was based on certain botanical characteristics, such as habit (tree, herb, creeping, grass-like), the presence or absence of flowers (referring, naturally, to coloured petaloid flowers only), whether withering after fruiting, the mode of propagation (seed, cuttings from tops, roots, etc.), combined to give curiously formal divisions and subdivisions, which inevitably suggest a quasi-botanical reflection of the complex caste-divisions of

Indian society, already established centuries before the Susruta was written.[27]

In the civilized centres of the New World, which arose after the indigenous invention of agriculture in Central America and Peru, the medicinal virtues of plants were doubtless discovered and treasured from early times. Unfortunately we are ignorant of any early records, if such existed, owing to the senseless destruction wrought by the European conquerors, breaking the precious continuity of tradition and thereby losing, among other things, the key that might readily have opened the secrets of the script, which today's scholars are vainly labouring, even with the despairing aid of the computer, to recover. Thousands of manuscripts, written on paper made from the bark of *Ficus cotonifolia*, and treasured in great libraries and in the private houses of individuals, were committed to the flames by the authorities of the Christian Church or by the Inquisition, on the grounds that they were full of "superstition and lies of the devil". The reverend instigator of one such burning of books remarks that the Indians regretted it to an amazing degree and that it caused them great anguish. The destroyer of the library of Texcoco notes that the burned codices "contained figures and characters that represent rational and irrational animals, herbs, trees, stones . . .", a glimpse of what has been irretrievably lost which rekindles even today something of the anguish of the unfortunate Indians.[28]

The independent testimony of many contemporary Spanish observers concurs that at the time of the conquest the Mexicans had a number of botanical and zoological gardens, which in extent and arrangement were said to be far in advance of any then existing in Europe.[29] The gardens of Montezuma at Tenochtitlan were irrigated and contained medicinal herbs, flowers, and aromatic and scented plants, from parts of his dominions, but vegetables and food plants were expressly excluded. In a letter to the Emperor Charles V, Cortez reported that herbs were sold in the market places and that apothecaries sold herbal medicines from their own houses.

When Francisco Hernandez, the private physician of Philip II of Spain, was sent to Mexico in 1570 to study the natural resources, he made full use of the collection of medicinal herbs in the celebrated botanical garden at Huaxtepec, which had escaped destruction by the conquerors owing to its lucky proximity to a newly established

Spanish hospital. Hernandez's manuscripts, unpublished at his death in 1580, three years after his return to Spain, had a chequered history which need not concern us, some being lost by fire, the remainder ultimately being published in Naples in 1651 by the Accademia Lyncei. The significant fact is that he was able to enumerate some 1200 Mexican plants esteemed for their medicinal or other useful qualities, information that must have been drawn from indigenous sources.

An exciting glimpse of Aztec herbal and medical knowledge was offered by the discovery early in the century of a manuscript which had long lain unnoticed in the Vatican library.[30] This proved to be an illustrated herbal published in Mexico in 1552 and written, originally in the Nauhuatl (Aztec) language, by a native physician, Martin de la Cruz, who speaks of himself modestly as having no theoretical learning but being well taught by experience alone. The text of the manuscript is in Latin, having been translated by another Aztec, Juan Badanio, Reader in Latin at the College of Santa Cruz and presumably a colleague of Martin de la Cruz. Appearing only thirty years after the conquest, this work probably represents the level of herbal medicine attained by the ancient inhabitants of America. The coloured illustrations depict 184 plants, about four-fifths of which can be identified with reasonable likelihood. It is a herbal and not a botanical work. The plants are grouped in relation to the medical condition to be treated, whilst the illustrations, although beautiful in colour and elegant in form, are not accurate in detail and often too stylized for recognition. The text refers only to the medical usage of the plants but gives the vernacular name of each plant mentioned and pictured. One noteworthy botanical feature is the illustration of the roots of most of the plants, accompanied by a symbolic representation of their environment (aquatic, rocky, stony, etc.), apparently to convey simple ecological information for each species, perhaps as an aid in collecting them.

In all the old civilizations there must also have existed, in addition to herbal lore, a store of plant knowledge embodied in the traditional techniques and practices of agriculture and horticulture. At the early period of which we have been speaking, however, this knowledge did not find systematic expression: there seem to be no agricultural treatises as early as the earliest works on medical plants. The Egyptian tomb paintings by their vivid and accurate observation can inform us of the minutiae of Egyptian agricultural operations but they were not designed to instruct. This difference between the attitude to medicine and to agriculture springs no doubt from the fact that agriculture was the occupation, at once laborious and full-time, of the poor and lowly, the peasant or the slave, whilst medicine, apart from a substratum of folk medicine, persisting like a palaeolithic memory among the common people, developed as the speciality of certain of the more privileged and more leisured, just as it ministered primarily to the needs of the more fortunate members of society.

The evidence is clear that men's first scientific awareness of plants was awakened by their medicinal properties, real or supposed, and by the consequent need to recognize, to distinguish and to record the plants in question. The botanical content of this knowledge was little more than the delimitation of plants as a distinct class of being, but with it went the practical aim of ensuring a consistent nomenclature of plants among the herbalists themselves, as a condition for preserving and transmitting herbal lore. These simple yet fundamental conceptual advances mark the first beginnings of a science that was eventually to play a vital and indispensable part in the development and sustaining of human society.

Notes

1. G. Clark and S. Piggott: *Prehistoric Societies* (1965).
   It may be noted that plants, equally with animals, gave names to totem groups.
2. V. G. Childe: *Man Makes Himself* (1941).
3. G. W. Dimbleby: *Plants and Archaeology* (1967).
   Compare Pliny: "It is impossible sufficiently to admire the pains and care of the ancients, who explored everything and left nothing untried." (*Naturalis Historia* 23,112).
4. H. Godwin: In *Essays on Plant Evolution* (Ed. J. B. Hutchinson) (1965).
   It is possible that in Iron Age times some of these wild plants may have been cultivated as a side-line to the cereals and pulses which were becoming the main crops, just as silverweed (*Potentilla anserina*) was sometimes cultivated for its nutritious rhizome in the Western Highlands of Scotland even as late as the eighteenth century. Economically less developed communities still know and eat many wild plants that agriculture and horticulture do not make use of.
5. G. Clark and Piggott (see Note 1).
   S. Cole: *The Neolithic Revolution* (1970).

F. M. Heichelheim: *Wirtschaftsgeschichte des Altertums*. Leiden (1938).
P. J. Ucko and G. W. Dimbleby, Eds. *The Domestication and Exploitation of Plants and Animals* (1969).

6. C. Singer: *From Magic to Science* (1928).
7. *Triticum dicoccon* (Emmer) and *Hordeum hexastichum*. Grains of these cultivated cereals have been found dating more than 1000 years earlier than the first representation of them. Varieties of emmer were the only type of wheat grown in Egypt for many millennia. Bread wheat (*Triticum aestivum*) only became widely grown during the first millennium BC, although occasional finds were much earlier.
8. M. Möbius: *Jahrbuch der deutschen archäologischen Instituts* **48,** 1–39 (1933).
9. It should be emphasized that probably all decorative plants were also, and indeed primarily, used medicinally. This was so in ancient as it was in mediaeval times; modern garden plants such as roses, paeonies, lilies and many others started their association with man as herbs in medicine.
10. D. Hennebo: Gärten und Pflanzenexpeditionen im frühen Altertum. *Altertum* **2,** 151–61 (1956).

    A list of the plants in the garden of King Merodach-baladan of Assyria (overthrown in 710 BC) was drawn up by a scribe who claims to have seen them with his own eyes. Judging from the translation by B. Meissner (Babylonische Pflanzennamen. *Zeitschrift für Assyrologie* **6,** 289–98 (1891)) this was a herb and kitchen garden. Over sixty plants are named but relatively few can be identified with certainty: these include onion, garlic, leek, lettuce, cabbage, radish, saffron, houndstongue, beans, and a number of aromatic and spicy herbs. G. Coutenau says that the four groups under which the plants are listed correspond to definite types of use (vegetables, aromatics, etc.) but this is not obvious to me. An interesting inclusion in the list is alfalfa, *Medicago sativa* (Babylonian "aspasti", Old Persian "aspast" = horse-fodder), which is native to Persia and adjoining regions, where it became important as a fodder plant for breeding superior horses, and whence it was introduced in the fifth century BC to Greece and the Mediterranean countries, and in the second century BC to China. (See B. Laufer: *Sino-Iranica*. Chicago (1919).)
11. Ebony, called hebeng by the ancient Egyptians, was *Dahlbergia melanoxylon* which they imported from various parts of tropical Africa. The "true" ebony of today is *Diospyros ebenum* and other *Diospyros* species, native in S. India and Ceylon. There is one record of *Diospyros ebenum* from Fifth Dynasty Egypt (*c.* 2500 BC) but this needs confirmation. However, Theophrastus (*Historia Plantarum* 4,4,6) describes ebony (*D. ebenum*) from India.

    A. Lucas: *Ancient Egyptian Materials and Industries* (1934).
12. J. H. Breasted: *Records of Ancient Egypt* (1906).
13. The harvesting of frankincense in Arabia was described in detail by Theophrastus about 1500 years later (*Historia Plantarum* 9,4,1).

14. Greek παράδεισος, Latin paradisus.
 In his *Oeconomicus,* written some time about 360 BC, Xenophon refers to "gardens called paradises" set up by the Persian king and containing all the good and beautiful things which the soil produces. This statement shows that they were to some extent botanic gardens and not just pleasure parks.
 In later classical times it was the ambition of every wealthy snob to have a paradise of his own in imitation of oriental despots.
15. N. K. Sanders, Trans: *Poems of Heaven and Hell from Ancient Mesopotamia.* Penguin Classics (1971).
16. Writing was first invented in Sumeria in the fourth millenium BC and in Egypt at almost the same time. The Egyptians may have got the idea of writing from Sumeria, but their system of writing was certainly their own invention. The still undeciphered script of the Indus-valley civilization was possibly derived from Sumeria, but the Chinese invention of writing (although perhaps 2000 years later than Sumerian) was probably independent, as was the invention of writing in the New World, by the Olmec people about 1000 BC.
17. *Odyssey* 4,221 ff. Quoted by Theophrastus (*Historia Plantarum* 9,15,1).
18. B. Ebell, Trans: *The Papyrus Ebers: The Greatest Egyptian Medical Document.* Copenhagen and London (1937).
 H. Schelenz: "Geschichte der Pharmazie". Berlin (1904).
 There is a Greek papyrus from 200 BC which aimed to give a translation into the vernacular of "the sacred writings as the holy scribes use them, for owing to the curiosity of the lay public about plants they name them after divine personages".
19. R. Campbell Thompson: *The Assyrian Herbal.* London (1924).
 A Dictionary of Assyrian Chemistry and Geology. Sections XVI–XVIII on Assyrian Botany. Oxford (1936).
 A Dictionary of Assyrian Botany. London (1949).
20. Thus poppy, cucumber and colocynth are placed together, possibly because of similarity in the form of the ovary.
21. B. T. Aklesaria, Trans: *Zand-Akasih: Iranian or Greater Bundahisn.* Bombay (1956).
 Another translation by E. W. West will be found in Vol. V of *Sacred Books of the East* (edited by Max Müller).
22. China. A full history of botany in China will appear in Vol. 6, pt 1, of J. Needham's *Science and Civilization in China.* I am deeply indebted to Dr Needham for generously allowing me to read and make use of much of this material in advance of publication.
 It should be made clear that I only refer to the plant materials included in the Chinese pharmacopeias: they also contained animal and mineral materia medica.
23. The invention of agriculture and the plough is attributed to the semi-

legendary Emperor Shen-Nung (traditionally dated about 2700 BC). In fact, agriculture in China dates from at least two millennia earlier.

It is interesting that an Anglo-Saxon herbal also contained a symbolical 365 entries. See W. Bonser: *Medical Background of Anglo-Saxon England* (1963).

24. *Hsin Hsiu Pên Tshao* (The Newly Improved Pharmacopeia) was richly illustrated with pictures in red and black of plants, animals and minerals. In addition to almost all the plants of the *Pên Ching* and of Tshao Hung-Ching it contained 114 new drugs.
25. K. K. Bhishagratna: *Susruta-Samhita* (English Trans.). Bombay (1963).
26. A study of the herbs of the Susruta by Indian scholars with the requisite botanical and linguistic knowledge, would be extraordinarily valuable. The botanical identification of the plants could possibly throw light on the extent to which the Aryan conquerors brought herbs and herbal knowledge with them into India, and on the origins of Hindu medicine. For a discussion of the identity of the mysterious soma of the Rg-Veda see R. Gordon Wasson, *Soma: Divine Mushroom of Immortality*, who produces cogent evidence that it was the fly agaric, *Amanita muscaria*.
27. There seems to be some resemblance in principle between the Indian classificatory methods and those of Speusippus (head of the Academy from 339 to 337 BC), which were criticized by Aristotle (*Parts of Animals* I,2 ff.)
28. F. Peterson: *Ancient Mexico* (1959).
29. W. H. Prescott: *History of the Conquest of Mexico*.
    Z. Nuttall: *Gardens of Ancient Mexico*. Smithsonian Institute Annual Report (1922).
30. E. W. Emmart: *The Badianus Manuscript: An Aztec Herbal*. Baltimore (1940).

2

The Origin of Botany as a Science

We must understand that human nature has been taught many different things by force of circumstance itself, and that reason subsequently worked on these discoveries and made fresh ones, the rate of progress being quicker or slower among different peoples at different times.

Epicurus (quoted by Diogenes Laertius X.75).

The true scientific study of plants—in the sense that we would accept the term today—began as a consequence and a part of the great intellectual movement which was born in the sixth century BC in Asia Minor, in the Greek-speaking cities of Ionia. Spreading to mainland Greece and the Greek colonies of southern Italy, the impetus culminated in Athens in the teaching of Aristotle and Epicurus.[1] Few periods in history have had deeper or more lasting effects on human thought, or have evoked, understandably, a richer harvest of commentary, study and analysis. For our purpose, in trying to comprehend the environment in which botany arose and the influences reflected in its development, it will suffice to consider in only the barest outline the nature of this intellectual quickening and the reasons why new and germinal ideas were born at this time and place.[2]

The first millennium BC was a period of economic and social change, brought about by the discovery, in Asia Minor about 1200 BC, of the smelting and working of iron. Slowly at first and then with increasing speed, the use of iron, cheaper and far more serviceable than copper or bronze, liberated forces which began to disturb and destroy old-established social relations and to induce in men's minds fresh ways of looking at the world. The process rapidly involved the old centres of civilization as well as neighbouring peoples previously unrecorded by history. Iron draws all men to itself, said Homer, catching the essence of the time in memorable words.[3] The availability of iron had many far-reaching results but the effect on agriculture was the most fundamental and revolutionary. Iron-tipped ploughs and iron tools caused a very significant rise in agricultural production, partly no doubt by greater efficiency of cultivation, but mainly by making productive large areas of land which could not previously be cleared, drained or cultivated with tools of wood and stone or the rare bronze.[4]

The growth of agriculture, accompanied by various crafts and industries connected with it, stimulated a great expansion of trade, already well under way by the opening of the sixth century BC. This commercial activity led to the rise of a new social class of merchants and traders, recruited partly from individuals of the ruling landed aristocracy who took to trade, partly from individuals of other classes whom good fortune or unusual initiative impelled to embark on an adventurous but often profitable way of life. The assertion of common interests, generally against the established land-owning ruling class, tended to unite and differentiate the merchants as a bustling bold-thinking class whose activities brought them into daily contact with the down-to-earth techniques of crop growing and manufacture at home as well as with techniques, ideas and cultures from abroad.

New modes of thought, free, or at least freer, from long unquestioned assumptions and superstitions of more static societies, naturally arose where the merchants were most successful in establishing themselves as an independent class.[5] A pregnant combination of causes and circumstances determined that this happened uniquely in the ports and trading cities of Ionia, and it was here that Greek philosophy started its astonishing period of florescence.[6] Two other phenomena, closely connected with the emergence of an independent merchant-trading class, acted as a profound stimulus to new developments in thought. Democracy—in the ancient, not the modern, connotation—was the political system corresponding to the greatest degree of hegemony of the merchant class. The establishment, however temporary, of democracy in the Greek city-states, even the struggles towards it, liberated men's thinking and strengthened their confidence in their ability to master their own destiny through the unfettered power of reason. At the same time the recent introduction of metal coinage, first minted in Ionia in the eighth century BC, as a generalized form of exchange-value, must have been a powerful influence in the growth of conceptual thought and the search for connections behind the multifarious appearances of nature.[7]

The Ionian philosophers will always be honoured as the pioneers who broke the ground for the growth of natural science.[8] What was new in their outlook has become part of our mental fabric: we can easily fail to appreciate their originality and boldness, and forget the permanent break with old ways of thinking that they accomplished. For the first time in the records of thought, people tried to explain the origin and constitution of the world, including themselves, as the rational result of movement or forces inherent in the nature of things, without the intervention of supernatural influences, whether exercised by gods or by the stars. This meant in essence the recognition of one universe with causal interconnections between all its parts. It was a rejection of priestly authority and religious myth, and a remarkable turn to observation and reason, even though the form of these first general scientific theories was clearly influenced by prevailing myths and by concepts which betray their social origin.[9] An essential element in forming the new outlook was keen and close observation of natural events and of the technical operations of human arts and crafts. The theories of the early philosophers, however speculative, were founded on rational interpretation of observed or generally accepted material facts, not on divine revelation or unrestrained imagination: it was at least implicit that the theories must be consonant with observation and might have to be revised in the light of fresh evidence, a requirement later explicitly stated and accepted by Aristotle and Theophrastus. Because they built on observation, these early thinkers were able to glimpse generalizations which can still be recognized as valid and fruitful representations of important aspects of reality, and which in this sense truly anticipate, although they did not give rise to, later theories. Their appeal to observation also led them to the first serious analysis of the nature and significance for knowledge of sense perception, and to establish in principle the basic assumption of scientific investigation: that sense data, when critically interpreted by reason, provide true and reliable knowledge of the world.[10]

Interest in wide-ranging generalization combined with heightened curiosity about natural phenomena were two aspects of the same intellectual stirring. During the sixth century arose both a practical and a theoretical interest in living organisms, animals and plants, that was keener in observation and broader in viewpoint than anything that had gone before and that marks the beginning of real biological investigation. The first philosopher to devote attention to living things was Anaximander of Miletus, who flourished about 520 BC, and was a younger contemporary and pupil of Thales, the traditional founder of Greek philosophy. A more powerful thinker than Thales, he foreshadowed many concepts which others later developed further. Of profoundly original mind, and familiar with the most advanced techniques of the time—he is said to have introduced the gnomon from Babylonia, and to have drawn the first map of the world, subsequently improved by Hecataeus—he put forward the first complete cosmological theory, according to which the universe was composed of a single sensible substrance, endowed with ceaseless self-motion, the material principle of existing things. He has the further distinction of being the first theoretician of biology—and a very remarkable one. He held the materialist view that living creatures, including man, originated as part of nature, arising either from the moist element or from a mixture of water and earth as it was heated and evaporated by the sun.[11] The first living creatures, produced in the moist element, were covered with thorny integument or bark.[12] In the course of time they came out upon the drier part and, the bark breaking off, they changed their manner of life. Man, said Anaximander, was originally like another animal, fish; in another quotation he says man was born from animals of a different species, since man alone requires a prolonged period of suckling and hence could not have survived had he been as he is now. Unfortunately only fragments from Anaximander survive, in the form of quotations or ascriptions in later writers, but they show that he reached astonishing biological insight and attained the conception, in however primitive a form, that living organisms evolve and change, and are adapted to their way of life or would otherwise be weeded out. Such ideas were not just lucky hits: they certainly reflect the rapid evolution and intense conflicts within the society in which Anaximander lived. On the other hand Anaximander was not just naively or unconsciously transferring social concepts to the world of nature. It is evident that he must have looked closely at living organisms as such and tried to interpret their development in a generalized way.

Apparently Anaximander did not treat of plants as distinct from animals. The first philosopher clearly to do so, perhaps because he was a physician or at least had medical knowledge, was Empedocles of Akragas in Sicily who flourished fifty or sixty years after Anaximander. An enigmatic figure, of whose career little is known, his powerful intellect exerted an influence for many centuries. Luckily sufficient fragments of his actual writings, parts of two long poems, survive to give a distinct outline of his views. His traditional reputation as an uncompromising democrat indicates a close connection with the new merchant and trading class, and he was clearly influenced by the Ionians, Anaximander and Heraclitus, and probably also by Pythagoras, who originated in Ionia but had migrated to Croton, an Ionian colony in Southern Italy.[13]

Empedocles is best known for his systemization of the unitary view of the world, which he held to consist of four fundamental elements (water, earth, air, fire), interacting in response to the principles of love and strife (attraction and repulsion). His biological ideas are integrally connected with this view and are bold and original. He was the first to consider the question of how the organic substance of living bodies arose from inorganic matter, teaching that bones and blood and the forms of flesh arose from varying combinations of the four elements under the influence of attraction and repulsion. Plants are specifically included as having arisen in this way, along with men and animals. In connection with this he developed a theory of plant nutrition and of the movement of food within plants, which will be discussed later. Like Anaximander, he taught that living things evolved from the non-living "by the contrary movement of earth and fire". The first living things to appear were plants, and these, being not yet sexually differentiated, combined the two sexes in one organism: the seeds of plants are therefore homologous with eggs.[14]

Empedocles considered that living organisms changed in course of time and were subject to a process of selection of those better adapted to their environment. He conceived the first organism as morphologically unorganized, having odd mixtures of bodily parts in various combinations; only those well organized were able to persist.[15]

In spite of the rather strange form, this theory expresses more clearly than Anaximander, the transformation of living organisms as a result of variation and selection. The monstrous deformities envisaged by Empedocles as stages in evolution are neither so mythological nor so fanciful as sometimes suggested, since they probably derive from his medical experience of embryonic malformations which are usually not viable. It is noteworthy that he specifically mentions plants as subject to the same process of change and selection as animals. Empedocles evidently developed a coherent body of botanical theory as part of his general biological teaching.[16]

A great surge of interest in plants occurred in the second half of the fifth century BC, in the period after Empedocles, who was probably active about the middle of the century. Anaxagoras, who spent most of his life in Athens, shared the evolutionary views of the Ionian philosophers, saying that animals arose in the first place from moisture and later from one another. He observed the dispersal of seeds by wind and is credited with the view, adopted by Aristotle, that plants are animals fixed in the earth. The first who seems to have studied plants exclusively and has therefore been claimed as the first botanist, was Menestor from Sybaris in Italy, said to have been a Pythagorean. He was interested in the physiology of plants, particularly in what determined fruit-bearing or its failure and the time of budding or fruiting, and in the reason for the deciduous or the evergreen habit and for the ability of plants to grow in definite kinds of soil or climate, as well as in those properties of plants, such as taste and flammability, which made them useful to man—all problems of practical bearing. He interpreted his systematic observations in terms of the hot or cold constitution of different plant species, clearly an application of Pythagorean medical theory.[17] The biological writings of Democritus are unfortunately lost, but references in Theophrastus suggest that he was concerned with explaining plant behaviour on mechanical principles.[18]

Contemporary with the theoretical work of the philosophers there was taking place in medicine a vigorous growth of practical inductive science, which markedly stimulated enquiry into the nature and way of life of plants.[19] Two influential schools of medicine had become established in Ionia, at Cos and at Cnidos, and a third in southern Italy where there were Greek colonies originating from Ionia. An extensive collection of medical writings, preserved at Alexandria, was traditionally ascribed to the physician Hippocrates of Cos. This Hippocratic corpus consists in fact of miscellaneous treatises of various dates, the remnants of an early Greek medical library. The contents give a patchwork but immensely valuable picture of Greek medicine in the late fifth and early fourth centuries BC. Characteristic and impressive is the consistently rational approach to healing, founded on careful observation and records and on tested experience: the theories of the Ionian philosophers form the accepted scientific basis, but over-emphasis on pure theory is explicitly criticized.[20]

From our point of view, it is the references to plants that must be considered. As would be expected, vegetable medicaments are preponderant and over 230 plants are named (without descriptions) as ingredients in the remedies for various ills, whilst in the section on diet—held to be a vital method of therapy—about 100 plants are listed, roughly grouped according to whether the grains, seeds, leaves, roots or fruits are the parts consumed. The botanical content goes far beyond medicinal herbs and food plants, however. It is a mark of the new age of enlightenment that these primarily medical treatises contain frequent comparisons and analogies between the physiology of animals and plants. There are clear descriptions of the germination of seeds and the growth of roots and fruits, evidently derived from experiments deliberately undertaken, in parallel with observations on animal embryogeny, in order to throw light on animal development.[21] The growth and nutrition of plants were interpreted in terms of the four humors which were believed to play the essential role in human and animal physiology.[22] Although this view was based on speculative and superficial analogy, it had the merit of directing attention both to the important concept of common physiological principles in plants and animals, and to the specific qualities of plants as a distinct class of living organisms.

The origin of cultivated plants began to exercise men's minds at this time. Both the philosopher Hippon[23] and the writer of the Hippocratic treatise *On Disease* expressed the opinion that all cultivated plants were produced from wild plants as the result of the care bestowed on them by man. Since cultivated plants were previously held to be the special creation and gift of the gods, this was a rational and revolutionary view which gave, as will be seen, a fruitful impetus to botanical thought. The interest in agricultural plants was a sign of the great economic changes taking place in agriculture in the fifth and fourth centuries, changes which proved a powerful stimulus to botany and to its establishment as an independent science by Aristotle and Theophrastus in the latter half of the fourth century.

As the merchant class gained political ascendancy the old forms of tribal and aristocratic land tenure were destroyed and replaced by free buying and selling of land. In Athens, now becoming the leader and recognized centre of the Greek world, land had become freely alienable as early as 594 BC, when the democratic reforms of Solon put political power into the hands of the wealthier merchants, and measures were taken actively to encourage commercial expansion. The same process was at work, with local variations, throughout Greece. Land became a mobile and profitable form of capital investment, and at the same time traditional agriculture was increasingly transformed into a branch of commodity production: wine, oil and corn became articles of overseas trade,[24] whilst the growth of towns led to the establishment of market gardens in the neighbouring countryside, growing fruit and vegetables and flowers for sale in town. The typical landed estate of the period was fairly small, and though worked mainly by slaves with some hired hands, was not of the latifundia type which came later, and the owner would usually be a gentleman farmer personally concerned with running it. These conditions created strong incentives to efficient operation:[25] a scientific interest in agriculture was awakened and considerable technical advances were made, reflected in greatly increased production. Methods of manuring and fallowing, and the forms of crop rotation, were improved and rationalized: better varieties of agricultural plants were developed and were carefully distinguished according to quality and suitability for particular situations; and the first attempts were made to differentiate between types of soil.[26] Trade and travel—even the movements of war—stimulated intense curiosity for exotic plants, several of which were introduced into Greece during this period.[27] The first systematic treatises on agriculture now began to be written, designed to instruct landowners how to organize their estates and make them productive and profitable, but containing information on crops and on crop production. The writings on agriculture of Democritus, and of Chares of Paros and of Apollodorus of Lemnos, referred to by Aristotle, are not extant, and the earliest works we possess in the *Oeconomicus* of Xenophon (about 360 BC), which is primarily concerned with estate management. A considerable technical literature on agriculture was thus coming into existence and was available to writers and philosophers of the time.

These technical and social changes motivated and influenced the biological activity of Aristotle and Theophrastus. The kind of study of animals and plants which had its origin in medicine was now rejuvenated and refashioned by a host of economic pressures and problems, demanding a many sided exploration of the living world previously unattempted. Aristotle and Theophrastus set out to satisfy this demand, as part of the programme of the Lyceum,[28] although Aristotle had undoubtedly begun the systematic study of animals several years earlier during his sojourn in the Troad and in Lesbos between 347 and 342 BC.[29] His discussions on the nature of science (*Physics* I,1) and on the theoretical limations of earlier scientists (*Parts of Animals* I,1,642a, ff.) show that Aristotle fully understood that the collection of facts must be linked with establishing the causal connections underlying them, and that he was rightly conscious of creating, in his biological work, a new science.[30]

Aristotle had already been a member of Plato's Academy for over ten years when Theophrastus arrived as a young student from Lesbos.[31] Although sixteen years older, Aristotle evidently took to the highly intelligent, industrious, and good-natured young man, who became his close friend and life-long collaborator. In biology there appears to have been a rough division of labour between them—perhaps depending on personal predilection—with Aristotle taking animals, Theophrastus plants as his province. Theophrastus is, however, credited by Diogenes Laertius with six books on animals, and the same author attributes two books on plants to Aristotle: indeed several passages in Aristotle make reference to his own writings on plants. Since it has been argued tht Aristotle did not write on plants and that botanical references in his work are either late glosses or come from Theophrastus,[32] the extent of his contribution to botany must be considered. A study of all the scattered references to plants in Aristotle[33] shows a perfectly consistent pattern of principled comparisons between plants and animals, reflecting his conception of a single natural kingdom of living organisms, a profoundly scientific view derived from the Ionian philosophers and in marked contrast to the ideas of

Plato. He defines the specific properties of life as nutrition, growth, movement and feeling; by movement he meant the process of development, not simply spatial movement; feeling included thinking and desire in addition to sense perception. Plants are living things because they have the properties of nutrition, growth and movement (development), but are lower than animals because they lack feeling and thought.[34] All life, including plants, contains soul (ψυχή), but plants are less fully "souled" than animals, since, for example, they can often be cut in pieces and each piece will continue to live as a complete plant. It should be noted that Aristotle here (and generally in biological contexts) uses soul in a simple materialist sense to describe either the total organized unity of a living thing or some aspect of that organization. He is saying in fact that the organization of plants differs only in degree of complexity from that of animals. Aristotle repeatedly compares animals and plants, emphasizing that they show the same basic properties but in different degrees. His famous discussion of embryonic development (*Generation of Animals* 2,1,733b, ff.), in which he argues for epigenesis and rejects preformationism, is based on arguments from observation of animals, yet plants are mentioned at the outset and are, by implication, included with animals as subject to the same principles. In another passage the seed in plants is held homologous with the egg, because each consists of an embryo together with a supply of food. Furthermore Aristotle applies his concepts of morphological organization to plants and animals alike: both consist of uniform (homoiomerous) and non-uniform parts, an analysis discussed later. He held, as Empedocles had done, that in plants the two sexes are combined, instead of being embodied in distinct individuals as in animals. He said that plants were rooted animals[35] and considered that, since plants feed by the roots, the root is functionally and morphologically equivalent to the mouth and head in animals. On plant nutrition his ideas were similar to those adumbrated in the Hippocratic writings.

Since almost all the isolated references to plants in Aristotle are expressions of general principles, it seems likely that they are based on genuine works that have been lost,[36] but in any case they show clearly that Aristotle was concerned with fundamental problems about the place of plants in the scheme of things and not with specialized plant studies. The counter-suggestion that Aristotle wrote the botanical works ascribed to Theophrastus can certainly be rejected. Not only is the attribution to Theophrastus contemporary—and universal and unquestioned throughout classical times—but the works themselves provide, as will be seen, overwhelming evidence that Aristotle could not have been the author, however much they owe to the mental framework he provided.[37]

The first sentence of Theophrastus' *Enquiry into Plants* proclaims that the study of plants has become a science. "We must consider the distinctive characters and the general nature of plants from the point of view of their morphology, their behaviour under external conditions, their mode of generation, and the whole course of their life." I use a more modern terminology than Sir Arthur Hort in his standard English translation (Loeb Edition, 1916), but one which I believe reflects as accurately and perhaps more sharply the meaning of the original Greek. The new outlook could not be expressed more fully or precisely. No study of plants of such breadth and quality had previously been conceived: botany now first appears as a distinct science with a comprehensive yet clearly defined field of enquiry. The social and economic events that contribute to the birth of biological science at this time have already been outlined. To the general stimulus of enlarging trade and commercially oriented agriculture must be added certain immediate political changes in Athens. The era of the small independent city-states was nearing its end in an imperialist drive to create, by war and colonization, a larger trading area under a single political centre, whether a confederacy under Athenian hegemony, or a tributary area under the Macedonian monarchy, as Aristotle and the realist politicians at the Lyceum were prepared to accept. Whatever the political means, the material measures involved increasing the productivity of agriculture, the study of native and colonial plant resources, the acclimatation of plants in new habitats, an intense interest in the production of timber and tar for shipbuilding, especially for the navy, linen for sails, charcoal for metallurgy and metal-working. Thus botany acquired a powerful economic purpose. Theophrastus, the son of a fuller, whose craft was closely linked to commerce, agriculture and the primitive chemistry of the alkalis used in cleaning wool, was profoundly interested in what may be called applied botany, and gives detailed descriptions of several branches of plant technology (forestry, charcoal burning, extraction of tar and resin, etc.), based on informa-

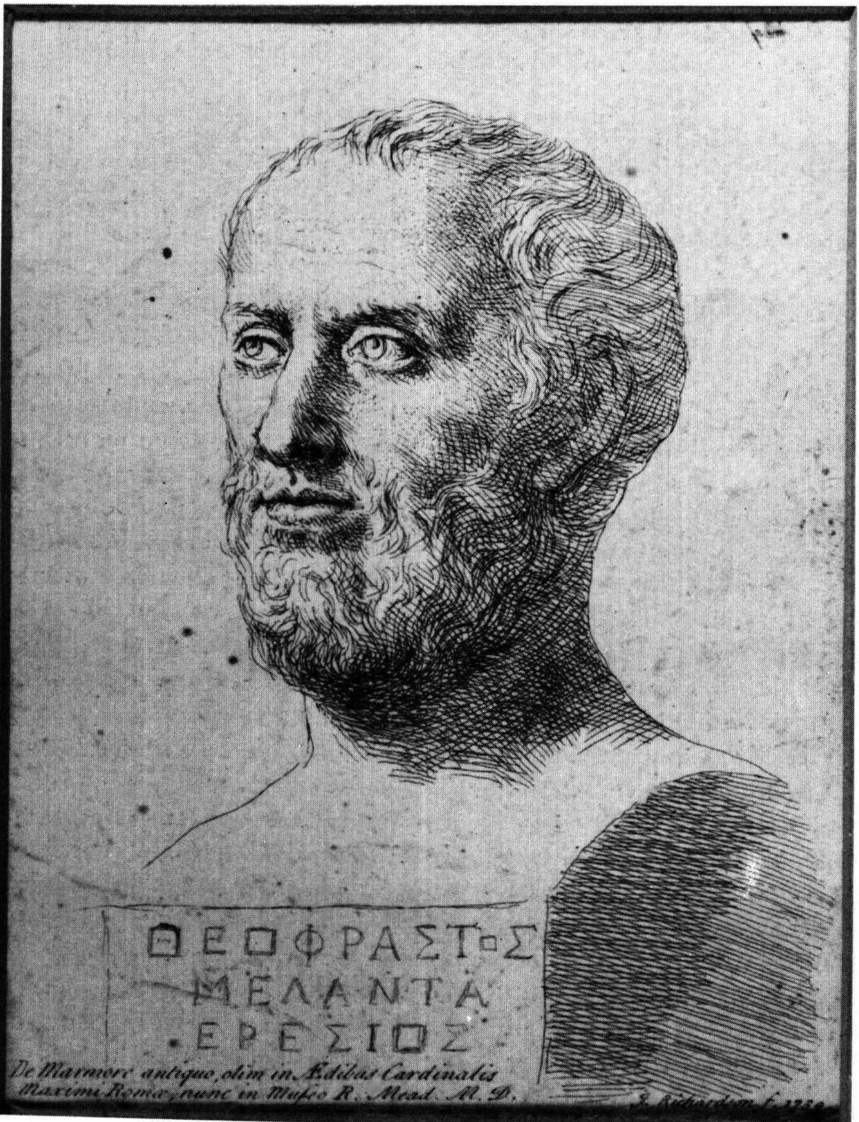


Figure 2 Theophrastus (370–285 BC). Engraving by J. Richardson (1739), courtesy of the Hunt Institute, Carnegie-Mellon University, Pittsburgh, PA.

tion from the mouths of woodcutters, carpenters, charcoal burners and farmers themselves.[38] At the same time the theoretical sweep of Theophrastus' botanical investigations far transcended the practical problems which gave immediacy to them.

We are fortunate in possessing the botanical teaching of Theophrastus almost complete, in the form of two works, the *Enquiry into Plants* (9 books) and the *Causes of Plants* (6 books). The titles may be those of a later editor, but there is good reason to think that the groupings of the books and their arrangement are the author's, and that the *Causes* was intended to follow the *Enquiry*.[39] The contents show Theophrastus thoroughly acquainted with, and making masterly use of, the scientific and technical literature of his own and earlier times. He incorporates information about the plants of several foreign regions, some of it derived from reports of individuals who accompanied Alexander on his military conquests,[40] some from merchants and travellers abroad, some possibly from Babylonian and Egyptian documentary sources. In addition, Theophrastus undoubtedly made original observations, in which his pupils may also have taken part.[41] This store of information was summarized by Theophrastus in a logical and well-balanced manner, placing the facts in a coherent theoretical framework, and creating a true science of plants. He carried out this task with profound originality, whilst acknowledging the guiding philosophic and scientific influence of Aristotle.

Much ingenuity has been expended on attempts to date the *Enquiry* and the *Causes* from internal textual evidence but the question seems misconceived. Allowing for the vicissitudes of time, copying and editing, the extant text is a faithful transcript of Theophrastus' botanical lectures as delivered in the Lyceum at a time when they had acquired substantially their final form. The lectures were given every year and, like a conscientious teacher, Theophrastus no doubt continually brought them up to date. He is indeed recorded as saying that a lecturer must do this, and that shirking revision and ignoring criticisms would not be tolerated by the present generation of students. It is not really surprising therefore that the text shows evidence of interpolations of varying dates or that a very few passages are inconsistent or contradictory.[42] The amazing thing is that we can learn from these two works almost exactly what botany was taught to students in 300 BC and can appreciate the quality of the teacher.

Broadly speaking, the *Enquiry* deals with the morphology and classification of plants, and with descriptive and economic botany, whilst the *Causes* deals with problems of growth and reproduction which now would fall within plant physiology, a division of subject matter that is distinctively Aristotelean. The attempt to develop basic theoretical concepts is what so clearly entitles Theophrastus to be considered the founder of botany. It is worth remarking, however, that his teaching was equally clearly directed to giving his students, the future administrators of the new Hellenistic monarchy, their money's worth. Of about 550 identifiable plants mentioned by Theophrastus the majority are of agricultural or economic importance, and much information is given on the techniques of agriculture and horticulture and plant industries, whilst carefully avoiding undue specialization, so that the subject is presented as a balanced whole. Theophrastus was emphatically teaching botany and was not trying to provide a local flora, a herbal[43] or a treatise on agriculture. Nearly three centuries later Varro made this point when he remarked that Theophrastus was less suited for practical farmers than for those wishing to study science.[44]

The magnitude of Theophrastus' achievement can best be shown by considering the most important theoretical questions discussed by him, or arising directly from his work, and by a glance at some of the topics which he included in his survey of the plant kingdom.* The first book of the *Enquiry* is a closely reasoned discussion of the principles of plant morphology: what are the fundamental parts of plants, how they are to be defined, the relations between them, to what extent they correspond to the parts of animals. Theophrastus firmly rejects any complete or formal correspondence between plant and animal parts, because plants have the power of growth in all their parts, that is, in modern terminology, they have indeterminate growth. With remarkable insight he thus established a fundamental difference of organization between plants and animals, concluding that in consequence their parts must be different *sui generis*. Plants do not, for example, have a mouth and stomach as all animals do. He takes the opportunity to dis-

* When citing particular passages the works of Theophrastus will be referred to by their customary Latin titles (*Historia Plantarum (HP)*, for the *Enquiry into Plants*, and *Causae Plantarum (CP)*, for the *Causes of Plants*).

cuss the use of analogy in science, reaching the view that rational, properly investigated analogies are valuable but superficial ones are dangerous. This passage is an almost explicit rejection of Aristotle's more fanciful analogies between plants and animals, and of his conception of a plant as an animal upside-down with its mouth in the earth.

Having cleared the ground in this characteristically balanced way, Theophrastus proceeds to a systematic analysis of the composition, structure and parts of plants, and to establish his own descriptive terminology. It should be remarked that the general morphological scheme, including the distinction of uniform and non-uniform parts,[45] follows Aristotle, but is critically modified by Theophrastus in applying it to plants. The principal persistent and larger parts are root, stem, branch, twig, which are distinguished from the annual or ephemeral parts, leaf, flower, fruit, stalk (of leaf or fruit). The fruit is made up of the seed or seeds, the pericarpion (the parts, fleshy or otherwise surrounding the seed or seeds), and the fruit-wall. All the foregoing are non-uniform parts according to Aristotle's definition and are called by Theophrastus parts (τὰ μέρη) or limbs (τὰ μέλη). They themselves are composed of the uniform parts, bark, wood, pith, and these again consist of the initials (ἀρχαί), sap, fibre veins, flesh. Finally these initials are composed of the four fundamental elements, of which Theophrastus specifically mentions only moisture and warmth, but which would also include earth and air.

Theophrastus explains that he has borrowed some of his technical terms for plants from analogous parts in animals but carefully warns against assuming, without further investigation, that there is any functional or structural correspondence. His advances in morphological analysis, expressed in new, defined technical terms, are typified by his divisions of the fruit and his recognition of the leaf petiole (equated with the fruit stalk) as a distinct organ.[46]

Not all the plant parts named are actually defined in the text, perhaps owing to losses in transmission: the extent to which Theophrastus approached the concepts of comparative morphology is nevertheless very striking. Although morphological differentiation arose in organisms during their evolution originally from physiological (functional) differentiation, morphological parts are not defined by function but from their mutual relations in space and time, since these express, in the last analysis, certain persisting regularities of a common evolutionary development. For Aristotle, however, an organ or part was defined primarily by its final cause, by "that for the sake of which it is present", or less abstrusely, by the function it performed or was thought to perform in the living creature. As would be expected, Theophrastus shows the influence of this point of view: the stem of plants (ὁ καυλός) is defined by its function of conducting food from the root, or again, as existing for the sake of the ultimate seed. Branches and twigs, however, are defined by their mutual relations to the stem, and in many places throughout the work morphological relationships are expressed with extreme clarity. In grasses Theophrastus comes very close to recognizing the rhizome as a stem because, although underground and apparently a root, it has nodes and bears adventitious roots (*HP* I,6,7). He also correctly questions whether the underground parts of certain other plants are really roots, implies that it is characteristic of roots not to bear leaves, suggests that the spines in some plants may be homologous with leaves, and recognizes the compound pinnate leaf as equivalent to a simple leaf. Many other observations show his keen perception of the essential basis of morphology.

In a famous discussion in his *Parts of Animals* (*PA* I,2 ff.) Aristotle expounded the methods to be used in classifying animals, both at the level of major groupings and of individual species. He realized that the essential basis for a logical (as we should say, a natural) classification of living organisms was the use, at each level, of numerous differentia (parts, characteristics, properties). He saw and emphasized that this method can yield a classification having stability, since additional and qualitatively variant characters or the absence of particular characters can at any time be included without overthrowing the whole scheme or leading to the forcible separation of clearly related groups. Theophrastus follows Aristotle in applying these principles to the classification of plants, but he is more concrete in his approach, scarcely referring to the metaphysical final causes of the latter. For Aristotle the primary fact about a living organism is its substance or essence (οὐσία), which—like Kant's thing-in-itself—is mysteriously more than, and distinct from, its parts and properties. Theophrastus adopts the more direct and practical attitude of the scientist–investigator, repeating, almost defiantly, that the essence of plants consists in their parts, that the parts taken together make up the whole, and that the differential characters of the parts manifest the complete form (*HP* I,1,8–11). He points out the element of relativity in classification and, more explicitly than Aristotle, the importance of definition in terms of the typical (τῷ τύπῳ), thus adumbrating a method that later was of cardinal importance in the development of systematics (*HP* I,1,6; 3,5). The practical procedure for striving towards a classification, already outlined by Aristotle, is formulated fully and precisely by Theophrastus. The essential features are to consider a large number of parts common to many plants, to note their presence or absence, and when present, differences in size, number, quality, function, and mutual relations in space. This is essentially the method by which the classification of plants and animals was to develop and by which it still continues to advance. Theophrastus thus laid great weight on classification as one of the fundamentals of botany and his contributions in this area are therefore worthy of close study.[47]

After his discussion of the principles of morphology and classification, Theophrastus gives a classification of plants which, he says, covers most if not all of them. According to this scheme plants are divided into four classes: tree, shrub, under-shrub, herb.[48] One of the most learned historians of botany, E. H. F. Meyer, remarked that this classification of Theophrastus was a deliberately popular one, a response to the fact that there was not at that time a botanically-minded public to address. In his interpretation Meyer showed remarkable perception and in my opinion came close to the correct explanation. Theophrastus was in fact giving a classification which, like the four-element theory of Empedocles or corresponding ideas that grew up in China, was essentially a tribal classification, reflecting the most primitive, originally functional, division of the tribe into two, later four, and then more numerous, moieties—an organization of human society that left a profound and persistent impression in the thought of early men.[49] It will be recalled that Babylonian writing included traces of such a gentile division in its tree and herb determinatives, long before any botanical analysis existed. If such is the origin of Theophrastus' plant groups, it would explain the necessity for having four fundamental groups and therefore having to include the highly artificial class of under-shrubs in addition to trees, shrubs and herbs, which have at least a rough and ready basis in common observation. Many commentators have observed that Theophrastus abandons under-shrubs almost completely from the start, and in practice speaks mainly of trees and herbs, with occasional references to shrubs. It has not generally been noticed, however, that Theophrastus himself immediately warns his students of the limitations and the provisional nature of his classification, proceeding to give examples of how the various classes intergrade and even herbs assume tree-like forms, proving that the distinction between them is one of convenience and not of principle.

Theophrastus' subsequent treatment shows that he never made the fundamental separation between trees and herbs with which he was credited in later times, an idea which was later picked up by Renaissance botanists and became an obstacle to the development of a natural system of classification. One cannot fail to be impressed with the scientific way he repeatedly applies concepts and descriptive terms—in dealing, for example, with methods of reproduction, types of flower, course of seed germination, position of fruits—to trees, shrubs and herbs alike, demonstrating the absence of any real gulf between them.[50] It is surprising that later botanists were so blind to the inescapable conclusion from his arguments, especially as, having pointedly emphasized the lack of sharp separation between trees, shrubs and herbs, Theophrastus at once embarks on a discussion of alternative ways of differentiating plants, with the clearly implied purpose of developing a more rational classification. That he did not succeed in arriving at a comprehensive natural scheme was inevitable with the existing knowledge of plants, but in his approach to the problem he nevertheless shows evidence of quite extraordinary systematic flair.

In the first place he spotted a whole series of characters which subsequently proved to have high systematic value. Among these were (using modern terminology): mono- and dicotyledony; the distinction, in flowers, between sepaloidy and petaloidy, hypogyny and perigyny and epigyny, radial and bilateral symmetry, polypetaly and gamopetaly; the form of the leaf and its mode of insertion on the stem; annual or perennial habit; and many more.[51] Equally impressive are the indications of his feeling for fundamental taxonomic groupings. He suggested the distinction between flowering and flower-less plants although he did not develop this further, doubtless because of uncertainty about the nature of the flower, discussed below. He delimited the fungi as a class by their lack of the organs of higher plants,[52] noted the absence of roots in marine algae, and almost certainly recognized seedlessness as characteristic of ferns. Within higher plants he had a more than intuitive appreciation of several natural groupings, such as liliaceous, umbelliferous, leguminous plants; grasses and reeds; conifers; catkin-bearing trees; thistles; palms. Some of these groupings he designated by special adjectival terms that pre-figure the families of modern taxonomy.[53] At a lower taxonomic level Theophrastus treats related species in a manner closely corresponding to the modern distinction of genus and species (even including variety in some instances). He discusses this fundamental conception with great clarity and applies it, not of course universally but to a few groups of species, in a remarkable way.[54] He used in some cases a simple, logical system of naming related species which can be said to have remained in scientific use for centuries until, adapted and improved by Linnaeus, it conquered the field in the form of the modern binomial.[55]

Although Theophrastus was not offering a flora, he was deeply interested in descriptive botany, and the *Enquiry* contains details of many individual species. Some of these descriptions were probably taken from contemporary literature[56] but others bear the vivid impress of personal observation. A few of the descriptions that have been most fully preserved in the text are masterpieces of botanical recording, of a quality and detailed accuracy not again approached in Europe for many centuries.[57] The originality of Theophrastus in this field is further shown by his conscious efforts to build an adequate descriptive terminology. For this purpose he coined a copious vocabulary of technical terms, using existing words in combinations and senses new to the Greek language.[58]

Several other fundamental questions were raised, directly or indirectly, by Theophrastus. In relation to the flower he made penetrating morphological observations which were not taken further for centuries. He recognized that the inconspicuous structures of grasses and reeds and of some trees are no less flowers than the brightly petalled flowers of pomegranate or rose, and that seed formation took place after and within the flower; but the true nature of the flower, like the answer to the related problem of sex in plants, eluded him. The failure to understand sexual reproduction in plants is not surprising: what is so obvious and easily seen in most animals and in man is much harder to observe and interpret in plants. In fact Theophrastus was frustrated by his very reliance on observation and logic. He knew and described (*HP* II,8,4; *CP* III,18,1) the age-old practice of fertilizing date palms by bringing male flowers to the female tree and shaking the male dust over them: the analogy with the union of two sexes in animals was not unremarked. But equally well known was the cultivated fig, which to all appearance produced fruit without antecedent flowers (the inconspicuous male and female flowers are actually completely enclosed in the hollow receptacle of the inflorescence), and where swelling of the fruit was "helped" by hanging near them the developing fruits of wild figs, whence insects emerged that caused the figs to swell and become purple, which otherwise remained pale and sickly.[59] Then there were cucumbers and other plants that had both sterile (i.e. male) and fertile flowers on the same plant, and finally there was the most numerous class of plants in which fruit and seed followed the flower. Theophrastus makes it perfectly clear that he could not fit these observations into a coherent theory; he states the facts known to him and suggests that further investigations should be made.

In his account of methods of reproduction in plants Theophrastus mentions seeds as the primary and most typical form, and then describes with his usual accuracy the principal types of vegetative reproduction observed, comparing the adaptive advantages of seed and vegetative reproduction in the life of the plant (*HP* II,8,4; *CP* III,18,1). He also includes spontaneous generation as a possibility in plants—it was accepted by Aristotle as occurring in animals—but is himself extremely cautious and stresses the need for more accurate enquiry. On balance he is obviously against the theory. He thinks the arrival of seeds carried by wind or rivers is the more likely cause of the apparently spontaneous growth of plants and trees on mud banks, and cites Anaxagoras in support of this view.

The relation between wild and cultivated plants, which was of intense interest to the ancient botanists (partly for religious reasons as noted above), is discussed at some length by Theophrastus. He accepts Hippon's view that man's special care, not divine intervention, produced cultivated plants from wild, and he defined "care" objectively in terms of soil, climate, food and the techniques of cultivation (pruning, weeding, dunging, irrigation, field drainage), that is, the factors with which agriculture is concerned. He had an inkling of the limits of culturally induced changes and of the importance of genetic constitution

(*HP* III,2,2; *CP* I,9,3). Considerable attention is given to the fact that cultivated varieties of fruit trees usually degenerated if propagated by seed, but naturally Theophrastus could not even guess at the true cause.[60]

Inevitably Theophrastus' treatment of plant physiology (mainly in the *Causes of Plants*) has seemed less interesting to later times, since in this field simple observation, without experiment, can make little progress, and his explanations of fact may well seem boring or absurdly speculative. Yet one must appreciate how thoroughly he tried to explain the behaviour of plants materialistically, in terms of what were then accepted scientific theories. Moreover it is in treating the facts of plant behaviour as known to him that Theophrastus shows most sharply the advance he made towards modern scientific method and thought, an advance going far beyond even the conceptions of Aristotle. In this connection four topics are particularly relevant.

In plant nutrition Theophrastus started from the commonsense view, which observation and practice appeared to confirm, that plants get their food from the earth through their roots.[61] In some form this idea was probably as old as agriculture, but by the time of the Hippocratic school it had been elaborated, by analogy with animals, into a quite complex theory, according to which the earth contained many different mixtures of the four elementary humours, from which each species of plant selected those suitable to itself. If the required humour is present, the plant flourishes, if present in the wrong amount, the plant grows poorly, but if absent, then the plant will not grow at all. Thus was explained both why plants varied in growth and quality when grown in different soils and why particular plants were confined to certain localities. Aristotle modified this theory in order to explain why plants have neither stomach for digestion (pepsis or concoction) nor excretion of the unwanted products of digestion. According to him plant food was elaborated in the earth itself under the influence of heat (thus the soil was the site of both digestion and of the separation of excreta), and the elaborated food was taken up, pre-digested, by the root of the plant. Theophrastus does not give a systematic account of plant nutrition but comparison of many passages makes his standpoint clear. Nowhere is there any indication that he entertained these theories. His statements leave little doubt that he thought that the primary food absorbed by the roots consisted of varying amounts of the elements, earth, water, air and, probably, warmth, although warmth could also come directly from the sun (*CP* I,17,1). He knew the value of dung as a manure, apparently regarding it as a source of, or substitute for, warmth (*CP* III,21,3). He several times stated that the (complex) food of plants is elaborated (undergoes pepsis) within them (directly counter to the theory of Aristotle) and that it is translocated to various parts. In this connection he criticizes Empedocles who apparently made a separation between the nutrition of root and aerial parts, and Theophrastus propounds instead the view that the whole plant is an organized unity.[62] It must be emphasized that Theophrastus was relying on observation when implicitly correcting Aristotle on plant nutrition. He saw, and discussed, the dependence of both fruit-ripening and shoot-growth on the weather, and the ripening of fruits after being plucked from the tree, and concluded from this evidence that metabolism of food (pepsis) takes place within the plant (*CP* II,8 ff.).

Leaf-fall and the contrast in behaviour between deciduous and evergreen plants, a particularly striking phenomenon in Mediterranean climates, had already been the subject of investigation by Menestor, who tried to explain the facts by the relative "heat" or "cold" of different plants. The problem is also considered at length in several places by Theophrastus. His treatment is characteristic and remarkable by contrast. He offers a possible explanation—that evergreens are so constituted that they have a continuous internal supply of food—which, though hypothetical, is based on a straghtforward material possibility and not on speculative categories of heat and cold. Even this hypothesis is advanced with caution and the proviso that the problem needs closer investigation, and is accompanied by records of the time of budding in various plants and of the effects of climatic conditions on budding and leaf-fall, from which he correctly concluded that time of leaf-fall depends both on climatic conditions and on the nature of the species.[63]

Theophrastus' scientific attitude appears very sharply illuminated in his thorough discussion of heat and cold in plants (*CP* I,21,2 ff.). This conception was popularized by Menestor and used by him and others to explain the behaviour of plants (growth in wet or dry places, fertility, fruit-bearing, wild and cultivated forms, etc.) by their degree of heat or cold. Theophrastus demonstrates that the supporters of this theory have involved themselves in a web of contradictions because "heat" and "cold" in plants are not perceptible to the senses but simply constructs of the mind. But, he says, the nature of "heat" and "cold" must be sought in objective phenomena (ἐκ τῶν συμβεβηκότων), and he then goes on to suggest actual qualities of plants—the possession of fatty, pungent or fragrant juices, their dryness or combustibility, their hardness, their medicinal effects in man—which might be investigated as real measures of the hypothetical "heat" and "cold". The argument is not carried to completion but the implied conclusion is evident, and Theophrastus though not entirely consistent himself makes little use of the mysterious "heat" and "cold" when dealing with the adaptation of plants to their conditions of life.

The relation of plants to the natural environment was first systematically discussed by Theophrastus who may well be considered the founder of both plant geography and ecology—he not merely listed plants peculiar to particular countries and types of habitat, but shows awareness of plant communities and of the adaptation of specific plants to a definite range of environmental conditions.[64] The philosophical significance of Theophrastus' account of adaptation has been little appreciated. He surveys in detail the effects of climate and soil on plant growth (*CP* II,1–7; and elsewhere), in a way that is modern in approach, and that implies a rational concept of adaptation, open to investigation, and free of the teleology introduced by Aristotle.[65] This was an advance in scientific method and theory that was both specifically Theophrastean and botanical.

In estimating the achievement of Theophrastus in botany, attention has been directed mainly to the emerging theoretical ideas, since these are linked for good or ill to the subsequent progress of the science, but it cannot be too strongly emphasized that these ideas are founded on a superbly organized assemblage of all the factual knowledge of the time, striking in extent and accuracy, and evaluated by his questioning and critical mind. Almost every aspect of modern botany is at least indicated—morphology, anatomy, systematics, physiology, ecology, pharmacognosy, agricultural and applied botany, plant pathology.[66] The inclusion of plant pathology is worthy of note: information is given on the diseases of some economic plants and the methods used to combat them, and the distinction is made between disease due to climate or soil conditions and that resulting from pests.[67]

Theophrastus even appears to anticipate plant biochemistry when he notes that water is a constituent of all parts of plants, even to the dry seeds.[68]

Undoubtedly considerable botanical knowledge had been amassed by the time Theophrastus lectured at the Lyceum, and he made full use of the available sources, in addition to observing and to collecting information himself. His extraordinary merit lay in presenting this knowledge in perspective, in developing a scientific terminology and rational guiding principles, and in his constant appeal to direct observation and patient investigation, to ensure in each case that the facts are correct and that the explanation (λόγος) is consistent with the facts.[69] Unmistakably bearing his intellectual impress, botany became one of the first unified branches of science to be based on comprehensive study and rational theory.

It is true to say that Theophrastus represents the culmination, in the field of botany, of the Ionian scientific tradition, sharing the positive features and the limitations of that tradition. The principal limitation was the absence of systematic experiment, a method of investigation that lay outside Greek thinking, probably partly as a result of the social stigma which attached to manual work because it was the sordid task of slaves and the poorest free-men.[70] It is significant that Aristotle regarded experiment as, in a sense, against nature (παρὰ φύσιν). Presumably Theophrastus would share this view, although his stress on investigation and the probability that he actually observed the course of seed germination, suggest that he was feeling his way to an experimental approach.[71]

In one respect Aristotle and Theophrastus retreated theoretically from the highest speculative level of Ionian thought. They abandoned completely the idea of biological evolution by the survival of better adapted forms, a change of attitude which must reflect changes in social relations since the time of Anaximander and Empedocles. However deep and fluctuating the class conflicts in fourth-century Greece, the main classes were now firmly established, and this relative stabilization of social structure was projected by Aristotle and Theophrastus into biology, where evolution was replaced by the conception of a scale of nature, a hierarchy of natural classes or kingdoms.[72] The conception of living organisms as changing and evolving in time disappeared from men's thinking for many centuries.

Botanists may take legitimate professional pride in the man whom Linnaeus, with complete historical accuracy, called the father of botany. His keen eye captured the essence of plants, both the beauty and the subtle fitness of their forms, as no one before him. Taking from Aristotle the most developed logical tools that existed at the time he sharpened and refined them in his own coolly critical, scientific way, and he stands in the history of science both as a philosopher in his own right and as one of the greatest scientists of all time.[73] To some extent Theophrastus has been overshadowed by or even confused with Aristotle, but careful study of his works shows that in some important and essential ways he went beyond his teacher, and developed the theory and methods of science in a wholly materialist and progressive direction. That this assessment is correct is confirmed by a fragment of a late work by him on metaphysics, in which he explicitly rejects the universal application of Aristotle's final cause to biological phenomena.[74] He argues that phenomena are to be interpreted by relating them to the actual conditions in which they occur—essentially the inductive and experimental procedure of modern biology. In another brief work, *On Fire*, Theophrastus gives closely argued reasons for holding fire to be different in fundamental nature from the other elements (air, water, earth), thus attacking one of the canons of accepted theory. It is evident that he was a deep and original scientific thinker as well as a great botanist.

Notes

1. Recent studies emphasize the intellectual and scientific legacy of Epicurus, the parallel to his exalted ethical teaching which inspired equally so many of the best minds and of the simple unremembered men and women of antiquity. In his teaching he included the most advanced conceptions of Aristotle while continuing the atomist–causal tradition of Leucippus and Democritus and the Sophists, with which Aristotle was not in sympathy.

   Aristotle, although he built on the work of his forerunners, was one of the greatest thinkers of all time, even if (as argued by F. Grayeff's *Aristotle and his School* (1974)) not all the traditional Aristotelean works were actually written by him. The stimulus of his acute mind was certainly behind them.

   By the first century BC Epicurism had become a social movement with considerable mass following among the lower orders, besides attracting intellectuals like Vergil, Horace, Lucretius and others. It was then considered dangerously subversive—not because the Epicureans were revolutionaries, for politically they believed in a quiet life—but because they attacked religion and treated slaves as fellow human beings. The last was the real horror although their opponents concentrated on the religious issue.

2. Of the immense literature, only a few particularly useful works are mentioned below.
   J. Burnet: *Early Greek Philosophy* (1892).
   H. Diels: *Die Fragmente der Vorsokratiker* (1934–54).
   B. Farrington: *Greek Science* (1969); *Science in Antiquity* (1969).
   W. G. Forrest: *The Emergence of Greek Democracy* (1970).
   G. Glotz: *Ancient Greece at Work* (1926).
   W. K. C. Guthrie: *The Greek Philosophers* (1972).
   G. L. Huxley: *The Early Ionians* (1966).
   G. S. Kirk and J. E. Raven: *The Presocratic Philosophers* (1971).
   M. Rostovsteff: *Greece* (1972).
   G. Thomson: *The First Philosophers* (1972).
   A. J. Toynbee: *Hellenism* (1959).
   E. Zeller: *Die Philosophie der Griechen* (1920, 1923).
3. αὐτὸς γὰρ ἐφέλκεται ἄνδρα σίδηρος. *Odyssey* 16.294.
4. Cf. Lucretius (writing in the first century BC): "inque dies magis in montem succedere silvas / cogebant infraque locum concedere cultis, / prata lacus rivos segetes vinetaque laeta / collibus et campis ut haberent, . . ." (*De Rerum Natura* V,1370 ff.) (men compelled the forest to recede every day higher up the mountains and yield the lower slopes to cultivation in order that on plains and uplands they might have meadows, ponds, water-courses, cornfields and happy vineyards . . .).
5. The intellectual revolution took rise in the Ionian and Aegean cities as the result of an exceptional combination of geographical situation and historical events. The whole region was a network of important trade routes at a time when movement by sea was relatively easy compared with the enormous difficulties and dangers of transport by land. The rise of an independent merchant class was facilitated by the geographical isolation of the cities on islands or protected by mountains, which prevented the establishment of a unified political power over a large area and allowed relatively free political development leading to the highest form of ancient society, the democratic city-state. In the old civilizations themselves the emergence of an independent merchant class was held in check by the social structure and constraints of the long-established monarchic or despotic state. Another significant fact was that the Greeks were new-comers, still retaining memories and traditions of barbarian tribal organization, with its primitive energy and spirit of social unity, at a time when they were entering new paths of rapid political and social de-

velopment. With this background, they were profoundly moved and stimulated by contact with the technical achievements of Egypt and Babylonia, which they whole-heartedly admired and began to assimilate. The absence of a distinct and highly organized priesthood in tribal society undoubtedly made it easier for the first Greek philosophers to propound their rational and basically anti-religious theories.

The origin of Greek philosophy and science is not sought in any special quality of the Greeks as a race, for they were themselves as diverse as was the actual population, derived from many elements and movements of peoples. Thales himself was reputed to be a Phoenician, and whether true of him or not, the tradition expresses historical truth about the inhabitants of Ionia.

6. The first three philosophers, Thales, Anaximander and Anaximenes, all flourished in the great trading city of Miletus in Ionia within a single century; Heraclitus was active in Ephesus only fifty miles distant.
7. This point is made by G. Thomson. (See reference in Note 2.)
8. In the following only a brief exposition is given of what were for science the most positive and advanced conclusions reached by the Ionian thinkers, and no account is taken of the detailed position of individual philosophers.
9. F. M. Cornford: *From Religion to Philosophy* (1912).
   See also Kirk and Raven; Thomson (Note 2, above).
10. The problems of formally defining "scientific" is deliberately evaded. Vere scire est per causas scire.
11. This evolutionary view had a long-lasting impact on thought although it was dropped by Aristotle (see below). In the first century BC Diodorus Siculus (1.7.1) describes the formation of the world and of "living creatures generated by heat from slime", a view that derives from Anaximander; whilst Lucretius revived the evolutionary account of Empedocles. It may be noted that Lucretius gives a very complete summary of the highest achievements of ancient science, clothed in moving and imperishable poetry.

    Aristotle's theory of the four elements, consisting of two pairs of basic opposites, is connected with earlier elementary theory of Anaximander, Heraclitus and Empedocles: it took a different form because of changes that had taken place in society.
12. According to Kirk and Raven, φλοιός="bark of a tree", but also "caul". Thus the term is appropriate to both animals and plants.
13. Empedocles was a complex and impressive personality to whom justice cannot be done by the brief reference here. He defended the senses as a source of knowledge, described a simple experiment to demonstrate the materiality of air, and was interested in human physiology and embryology and in the potentiality of drugs. Galen spoke of him as the founder of the Empiric school of medicine. He was probably an adherent of Orphism, and certainly had a less rational side. Thus he held blood to be

the seat of thought, although Alkmaion, whose teaching he must have known, was already clear about the function of the brain. Empedocles also considered that plants had "wisdom and a share of thought", an idea firmly rejected by Aristotle.

Four hundred years later Lucretius could still be inspired by Empedocles' intellectual power: "carmina quin etiam divini pectoris eius / vociferantur et exponunt praeclara reperta, / ut vix humana videatur stirpe creatus." (*De Rerum Natura* I,731–3) (the poems of his exalted mind resound, declaring his glorious discoveries, so that he scarcely seems of mortal stock.)

14. The following fragments (translated by Burnet) are among several in which Empedocles speaks of plants. "When the elements have been mingled in the fashion of a man and come to the light of day, or in the fashion of the race of wild beasts or plants or birds, then men say that these come into being; and when they are separated, they call that, as is the custom, woeful death. ". . . out of water and earth and air and fire mingled together, arose the colours and forms of all those mortal things that have been fitted together by Aphrodite, and so are now come into being, both tall trees and fishes of the sea. . . ."
15. The substance of Empedocles' view is given by Aristotle in *Phys.* B8, 198b29: "Wherever, then, everything turned out as it would if it were happening for a purpose, there the creatures survived, being accidentally compounded in a suitable way; but where this did not happen, the creatures perished and are perishing still, as Empedocles says of his 'man-faced ox-progeny'."
16. This is shown by the summary of his botanical teaching recorded some five centuries later by Aetius (V,26,4).
17. Menestor's works, of which only a few sentences have survived, were evidently known in their entirety to Theophrastus, who regarded him as one of the ancient scientists. He was influenced by Empedocles and Alkmaion; he treated the physiology of plants on the analogy of current ideas derived from hot- and cold-blooded animals and from the medical theory of the maintenance of the correct balance of hot and cold (ἰσονομία).
18. Theophrastus: *CP* I,8,2; II,11.

There are numerous references to Democritus by Aristotle, who is mainly critical of his views, while taking them seriously. It is apparent that Democritus tried to explain biological phenomena according to prevailing physical notions. The speculative nature of these explanations of Democritus (and of Empedocles) is brilliantly and logically criticized by Aristotle (especially in the long, closely argued passage in *Generation of Animals,* 4,1,764a, about the determination of male and female in the animal embryo). Although Aristotle successfully demolishes the theories of Democritus and Empedocles, showing that they do not take into account all the known facts, his own explanations in terms of "final cause" were no better and could be regarded as scientifically less fruitful. Democritus and Empedocles were at least trying to give an explanation in terms of matter and material causes.

Aristotle's other criticism of Democritus is the general philosophical one that he omitted to mention "final cause" and ascribed everything in nature to necessity. Modern science would support Democritus.

It should be noted that the reputation of Democritus was so great that in later times his authority was attached to some dubious and fanciful statements. The botanical information ascribed to him by Pliny is probably spurious, and this is surely true of the rubbish allegedly quoted from him in the *Geoponica*.

19. The origins of rational (empirical) medicine go back to primitive herb lore and primitive surgery. How far Greek medicine drew on Egyptian and Babylonian knowledge, and whether it was connected with a common Indo-Germanic (Aryan) medical tradition from which ancient Indian (Vedic) medicine also descended, are questions still insufficiently elucidated. The combination of observation with the attempt at rational theory raised Greek medicine during this period to a new level from which the beginning of scientific medicine may be dated.

    A primitive non-rational medicine continued to co-exist with the more rational (with a corresponding class distinction between the respective practitioners!). Non-rational medicine was based on ideas of demonology and possession, and practised therapy by exorcism, magical spells and charms, and by simple forms of mental treatment. It was generally associated with religion and priesthood, or with specialized guilds of physicians (e.g. the cult of Asclepius in Greece).

    See E. D. Phillips: *Greek Medicine* (1973).

20. The tract on *Ancient Medicine* in the Hippocratic corpus contains sharp criticism of those who rely on philosophical theory instead of on careful observation and experience. It is clearly directed against Empedocles or at least against those medical men who followed him too dogmatically.

21. Simple "experiments" are described—changing the form of fleshy fruits such as gourd or marrow by growing them in a vessel, or of roots by letting them grow against an obstacle; observation of successive stages in development of the chick within an egg.

22. The Hippocratic medical theory of four humors is related to Empedocles' four elements: the addition of pneuma or breath corresponds to Empedocles' love and strife, the source of movement. The humors (phlegm, black bile, yellow bile, blood) are much more definitely real substances than the universal elements, which are frequently treated as all-pervasive qualities. This materiality of the humors arises from the practical origin of rational medicine.

    The four-element theory was a reflection of tribal structure applied to the world of nature, whence arises the dual aspect of the elements in early thought—as tangible substances and as abstract qualities.

The concept of movement in Greek thought proceeds strikingly in step with social changes. With Anaximander movement is inherent in substance (the basic element). With Empedocles the elements are moved by love and strife, which are both within and outwith the elements. For Aristotle, however, movement originates from a Divine Mover quite outside the universe of men and things. This corresponds to the rise of slavery to a dominant role in the economics of society, a class with no power of self-movement, destined to be ordered about by the divinely ratified will of the slave-owner (see G. Thomson, Note 2, above).

23. Hippon may have been a medical man; he was certainly interested in physiology. He gained the reputation of an atheist and materialist and, probably because of this, was disliked by Aristotle. On the other hand Theophrastus quotes his views on the origin of cultivated plants with great respect.
24. The earliest articles of trade were metals and raw materials, manufactured goods, precious stones, luxury products of various kinds. The economic changes referred to in the text were marked by the appearance on a large scale of primary agricultural products, corn, oil, wine, cattle, horses, as articles of commerce. One other article of trade, human beings, the "man-footed creature" of the Greeks, steadily increased in importance. Slaves were the most profitable commodities of all, although in the long run they proved to be fateful cargoes for the society in which the traffic flourished.
25. "To a careful man who works strenously at agriculture no business gives quicker returns than farming." (Xenophon, *Oeconomicus* XX,22 (Trans. by E. C. Marchant, Loeb Edition).) Aristotle in his *Politics* mentions stock-breeding and agriculture as useful branches of the art of gaining wealth.
26. Cf. Theophrastus (*HP* VIII,6,4) on wheat varieties and soil. Columella about AD 60–65 mentions the improvement of carrots by the Greeks (*De Re Rustica* IX,4,6). There is evidence that the Greeks practised a form of three-crop rotation, but precise information is lacking. The importance of ploughing-in summer fallow before the weed seeds could be formed was well understood (Xenophon, *Oeconomicus* XVI,12–15).
27. Several important introductions from Persia were made, which may have been the direct result of the Persian wars of conquest. Economically most important was probably *Medicago sativa*, the Medic grass or alfalfa, as fodder for horses (referred to by Theophrastus, *HP* VIII,7,1). Other probable introductions about this time were peach, walnut, pistachio, rice, and citron (*Citrus medica*), from the same region.
28. The Lyceum was founded in 335 BC, just three years after the conquest of Greece by Macedonia. Under Plato's influence the Academy had become reactionary in politics and teaching, tied to absurd schemes to preserve, by a mixture of force and fraud, the city-state which had become by this

time an anachronism. Aristotle had left the Academy, probably before Plato's death in 347, having already begun to diverge philosophically (and perhaps politically) from him. Politically Aristotle and his associates looked to a future in which the Greek city-states would become part of a larger unity under the Macedonial monarchy. The function of the Lyceum was to train the leaders, officials and experts of the new era. With its library, museum and botanic garden, and its more up-to-date curriculum, emphasizing the observational sciences and a basically historical approach to all phenomena, the Lyceum soon proved more popular with students than the Academy, although the two continued to co-exist. After the death of Strato (Theophrastus' successor) in 269 science moved to Alexandria and the active life of the Lyceum virtually came to an end. The Academy survived formally for another 800 years until dissolved by Justinian in AD 529.

29. Aristotle was the son of a physician at the royal court of Macedonia which could account for his personal interest in biology. He seems, however, not to have studied zoology systematically until 344 BC when he went to Mytilene in Lesbos (following the failure of a scheme to found an academy in the Troad, under Hermias the local tyrant, due to difficulties with the Persians). Since Lesbos was the home of Theophrastus, the move there may have been his suggestion, and it has been thought that the turn to biological studies may also have come from his interest in this field.

30. The term biology—the science of living things—was not coined until the beginning of the nineteenth century when the word was invented almost simultaneously by J. B. Lamarck (1801) and G. R. Treviranus (1802).

    The term botany, at least in the adjectival form, botanic (botanic knowledge), goes much further back, to mediaeval Latin *botanicus*, derived from Greek βοτάνη (grass or fodder). Curiously enough the word is only twice used by Theophrastus, once to mean weeds, and once to refer to a herb or plant of Gedrosia. His word for plant in general is φυτόν which is semantically if not etymologically the exact equivalent of plant in English. The word βοτάνη was used by Dioscorides to mean herb in general, and this is the likely source of the Latin term adopted by most European language. Pliny, contemporary with Dioscorides, mentions *botanismon* as a term for weeding (runcatio) but does not use the word *botanicus*.

31. Theophrastus was born at Eresos in the island of Lesbos in 373 or 370 BC, and is believed to have gone to Athens as a young man to study at the Academy. He probably accompanied Aristotle to Asia Minor in 347 and may have been with him in Macedonia whilst Aristotle was tutor to the young Alexander. It is certain that he was back in Athens with Aristotle in 335 when the Lyceum was founded, and he became its director in 323 when Aristotle left to return to his homeland to die. He remained head of the Lyceum until his death in 285 BC. In his will he directed that he should

be laid to rest quietly in a corner of his garden, which he bequeathed in trust to a group of friends. It is an interesting point that both he and Aristotle were metics (i.e. immigrants) in Athens, and were never full citizens.

The following recent studies of Theophrastus are of very great value and throw new light on the man and his work.

O. Regenbogen: *Theophrastus*. Sonderabdruck, Pauly-Wissowa Real-encyclopädie, Stuttgart (1950).

G. Senn: *Die Entwicklung der biologischen Forschung in der Antike und ihre grundsätzliche Förderung durch Theophrast von Eresos*. Aaran (1933).

R. Strömberg: *Theophrastea—Studien zur botanischen Begriffsbildung*. Göteborg (1937).

32. G. Senn: Hat Aristotles eine selbstständige Schrift über Pflanzen verfasst? *Philologus* **85**, 113–40 (1930).

    O. Regenbogen: Eine Polemik Theophrasts gegen Aristoteles. *Hermes* **72**, 469–75 (1937).
33. Aristotle's references to plants have been assembled by F. Wimmer and translated into German by E. F. H. Meyer. His works on animals are almost punctuated by the phrase "it is the same with plants".
34. This contradicts Empedocles who thought that plants had feeling and thought.
35. Aristotle speaks metaphorically and certainly does not mean that plants have evolved in this way.
36. The work on plants (*De Plantis*) that is included in Aristotle's minor works is definitely not by him. It was almost certainly written by Nicolaus of Damascus (born 64 BC), court historian of Herod the Great. The version we have is pretty thoroughly garbled and largely incomprehensible, but even in its original state it can only have been an example of the rubbish to which Peripatetic science was later reduced. The matter seems to have been derived from imperfectly understood scraps from Theophrastus and Aristotle but it is a terrible farrago.

    See E. F. H. Meyer: *Nicolai Damasceni de plantis libri duo Aristoteli vulgo adscripti*. Leipzig (1841).
37. The decisive evidence for Theophrastus' authorship of the *Historia Plantarum* and the *Causae Plantarum* is scientific and philosophical and is given in the text, but two additional points can be adduced. The first is a mistake of Aristotle which is corrected by Theophrastus (see Regenbogen, Note 32). Aristotle undoubtedly thought that mistletoe and similar parasites are produced by the tree on which they grow, but Theophrastus (*CP* II,17,5) describes their reproduction by seeds carried by birds, and by emphasizing the peculiarity of their always growing on other plants criticizes Aristotle by inference.

    The second bit of evidence is linguistic. In describing the plumule (embryonic shoot) in seeds Theophrastus consistently uses the morphologically accurate term καυλός (stem), but Aristotle uses the term πτόρθος (sprout, sucker, shoot). This last term occurs—as far as I have been able to check—only once in Theophrastus (*CP* V,1,3) and then it is given as a synonym of the ultimate tips or twigs of branches. There are other instances where Aristotle uses different terminology from Theophrastus.

38. According to Strömberg (see Note 31) Theophrastus actually quotes the dialect words used by the different craftsmen.
39. The *Enquiry into Plants (Historia Plantarum)* will be found in English translation by Arthur Hort in the Loeb Edition, with excellent botanical identifications by Thistleton-Dyer. A short part of the text dealing with aphrodisiac properties of plants was silently omitted by Hort but can be found in J. G. Schneider's 1818–21 text. The *Causes of Plants (Causae Plantarum)* has not yet been fully translated into English, although an edition and translation of Books 1–3 has now appeared in the Loeb Library. Book I of *Causes* was critically edited and translated by R. Dengler and this I have been able to use. For the other books of the *Causae* I had to rely on the Schneider edition and the Latin translation by Theodore Gaza (1483) which it contains.

    It appears from quotations in Plutarch and Pliny that they had access to better texts than that rediscovered in the fifteenth century, but the differences are not substantial.
40. There is no evidence that Alexander took a scientific staff with him on his campaigns as has been suggested (H. Bretzl: *Botanische Forschungen des Alexanderzuges*. Strasburgh (1903)), but some intellectuals apparently accompanied him and sent back reports to Greece. Theophrastus obtained botanical information in this way from Alexander's headquarters. To be part of the entourage of this drunken paranoiac could be a hazardous undertaking, however, as Callisthenes, the unfortunate nephew of Aristotle found, being accused of conspiracy against the great leader and mercilessly done to death.
41. Both the accuracy and the mode of expression of many plant descriptions strongly suggest eye-witness accounts. The descriptions of seed germination and of root systems give the same impression, and it seems likely that systematic observations of many kinds were made in the garden of the Lyceum itself. In relation to seed germination Theophrastus significantly does not introduce the phrase "people say", his usual indication when information is not first-hand. His whole account of seed germination is a highly original contribution. He includes data on the longevity of seeds, factors affecting germination (mentioning the accelerating effect of nitrate), structure and mode of germination. He even mentions the (enzymic) mobilization of food during germination, and recognized the phenomenon of seed dormancy in the soil.
42. The latest internal data is a reference (*HP* V,8,1) to a ship with eleven banks of oars, a type not used before 306 BC. If my argument is correct, we possess the transcript of Theophrastus' lectures in botany as brought up to date about 306 BC or later, that is, towards the closing years of his

career.

43. The physician Diocles of Carystos, who was a contemporary of Theophrastus in Athens, wrote treatises on vegetables and on medical plants, of which only a few fragments are extant (given by M. Wellmann in *Die Fragmente der sikelischen Ärtzte* (1901)). I have compared the fragments from Diocles' herbal (*Rhizotomikon*) with the parallel passages in Theophrastus, and there can be little doubt that Theophrastus quotes directly from Diocles without naming him. There is nothing sinister in this: it was not customary at that time to name authorities as it is today.
    For a discussion of the relation between Diocles and both Aristotle and Theophrastus see W. Jaeger: *Diokles von Karystos* (1938).
44. Varro: *De Re Rustica* I,5,2: "libri [Theophrasti] non tam idonei iis qui agrum colunt, quam scholas philosophorum".
45. In the *Enquiry into Animals (Historia Animalium)* Aristotle divides the parts of animals into those which are simple and uniform (homoiomerous), having parts uniform with themselves, as flesh with flesh, and those which are composite and non-uniform, having parts not uniform with themselves, as the hand does not divide into hands, nor the face into faces. Aristotle's distinction between uniform and non-uniform parts thus had some similarity to our distinction between tissues and organs.
    When Aristotle applied his own terminology to plants he actually used it inconsistently (*Meteor.* 10); Theophrastus used it consistently in Aristotle's own sense.
46. For petiole (or fruit stalk) Theophrastus adopted the new term μίσχος apparently a dialect word, originally meaning a special type of Thessalean hoe (*CP* III,20,8).
47. One of the hallmarks of true science is the recognition that classification is only meaningful if it embraces all the objects of discourse without arbitrary omissions. It was an immense intellectual advance when Aristotle said in speaking of animals, "we will not leave out any of them, be it never so mean" (*Parts of Animals* I,5,645a 10).
48. The word translated as under-shrub (φρύγανον) has the literal meaning of fire-wood or sticks for kindling, whilst herb (πόα) is literally grass. It is impossible to extract from the text clear discriminant definitions of the four classes, nor are the classes always applied consistently to individual plants. Theophrastus was quite aware of this.
49. Compare E. Durkheim and M. Mauss: *Primitive Classification*. English translation (1963). Also Kirk and Raven; Thomson (Note 2, above).
    The reflection of tribal organization in early myth, cosmogony and primitive science is well documented.
50. Theophrastus shows some trace of the Aristotelean view that the tree is the most perfect form of plant, but he clearly interpreted this not in an idealist philosophical sense but as meaning that things are easier to see, more typical, in trees.
    It is interesting that modern botanists have re-emphasized the evolu-

tionary separation of trees and herbs.

51. Almost every page of the *Enquiry* contains examples of precise morphological observation and botanical penetration. To mention just a few: recognition that the spike of cereals and plantains, and the head of Compositae, are inflorescences, not individual flowers; difference between racemose and cymose inflorescences, monopodial and sympodial growth; recognition of nodes, and of phyllotaxy; description of transition from juvenile to adult leaves (heteroblasty) in ivy and other plants; distinction between adaxial and abaxial surface of leaves, and observation of phototropic alignment of leaves, etc.

    In his systematic description of rooting systems of different species Theophrastus gave a type of information that has often been conspicuously neglected even in modern floras. He saw that the absence of leaves was characteristic of the root as a morphological category (*HP* IV,4,4), although he did not use this as part of a formal definition.

52. The traditional inclusion of fungi in the plant kingdom and their study as a part of botany begins with Theophrastus. The many associations of fungi and plants fully justify this treatment, although the weight of modern opinion favours the view that the fungi are an ancient group in their own right, neither plants nor animals.

53. Two striking examples of his botanist's eye are the comparison of the flower structure of poppy and water-lily (*Nymphaea*) (*HP* IV,8,10) and the parallel drawn between the spathulate origin of the flowers of palms and of cereals (*CP* I,20,1).

54. G. Senn (*Theophrasts Differential-Diagnosen für laubwerfende Eichen*. Basle (1928)) has shown that Theophrastus' descriptions of the deciduous oaks of Mount Ida enable his six names to be precisely identified as corresponding to five modern species (two names represent varieties of one species). Of the four Macedonian oaks he mentions, one can be identified with certainty, but the other three only with doubt, owing to the brevity of the descriptions (*HP* III,8,2–7).

    W. Thistleton-Dyer (On some ancient plant names. *Journal of Philology* **33**, 195–207 (1914)) showed that the three kinds of *Arbutus* which Theophrastus describes (*HP* I,9,3) can be unequivocably identified as *Arbutus unedo, A. andrachne* and the hybrid between them.

55. Theophrastus naturally used the ordinary folk-names of plants but sometimes he employed the single popular name to designate the plant which he took as typical, as his starting point. Plants which seemed to be related, but were obviously not the same, were called by the basic name with (usually a single) qualifying adjective or phrase. A similar method was developed by the Chinese; both are simple extensions of popular nomenclature, and the method continued to be used by botanists, although not consistently until Linnaeus established systematic nomenclature.

56. There does not however seem to be any direct evidence that

Theophrastus took plant descriptions from his contemporaries, except, obviously, in the accounts of the flora of countries unvisited by him. The information from Diocles is herbal, not floristic, and the extant fragments of Phanias, a contemporary who wrote on plants and corresponded with Theophrastus, throw no light on the question.

57. For example, the descriptions of Smilax (*HP* III,18,11–12), *Ferula communis* (*HP* VI,2,7–8), the water-lily, *Nymphaea alba* (*HP* IV,10,3), and very many less complete but equally vivid and accurate sketches of particular plants.
58. R. Strömberg (Note 31, above).
59. The fig was of enormous economic importance for food. According to Cato the Elder, the bread ration of slaves was to be reduced by one-fifth when ripe figs were available for them (*De Agri Cultura* LVI). Figs were equally important in Greece. A poem of the fourth century BC (quoted by Athenaeus) gives the diet of an old Greek pauper woman—entirely vegetable except for cicadas—which concludes with "that darling of my heart, a dried fig from a Phrygian fig tree".
60. Characteristically his explanation is a physiological one: the cultivated forms suffer from excess nutriment which causes the seed to degenerate. He supports the theory by referring to the practice of the inhabitants of Thasos who grafted almond trees in order to reduce their rate of growth. This is typical of Theophrastus—speculation, but in terms of real material possibilities, and tested by the facts available to him.
61. The nutrition of green plants by photosynthesis is so complex and so completely different in principle from the nutrition of animals, that it is not surprising that thousands of years of technical progress were required before anyone got even a hint of its real nature.
62. *CP* I,12,5. It is clear that Theophrastus was led to this very perceptive view by observations on bud formation, pruning and grafting.
63. The main factor missing in Theophrastus' list is day-length. Its influence on leaf-fall, flowering and other periodic aspects of plant development was not recognized until this century.
64. "[Even plants generally distributed] must be classed by locality, whether growing in marshes, lakes, rivers or common to many places, distinguishing plants which occur both in wet and dry, and plants which occur only in the wet. . . ." (*HP* IV,10,1). "Trees seek the environment suited to them, and this does not only apply to rare and special trees as described above, but even to common species which spring up everywhere. Some like dry places, others prefer wet or cold or sunny or shady places, and in general some like mountain regions others marshes, as writers have recognized. . . . Natural affinity draws each species to an appropriate and suitable locality when wild plants grow of their own accord." (*CP* II,7,1.)

    Theophrastus described a number of natural plant communities, and also recognized the association of particular weeds with certain crops.

65. One of Aristotle's most significant contributions to biology was his recognition that living organisms and their parts are adapted, often in a remarkable way, to the activities and functions which they carry out (as Anaximander and Empedocles had already vaguely hinted). But Aristotle interpreted the fact of biological adaptation by a social analogy, pointing to the operation of a craftsman, say a builder, who first decides on the plan (the purpose or "final cause") when setting out to build a house, cunningly designed for human living. According to this theory (teleology), the body of an animal develops a structure of limbs and parts suited to its needs because nature has this purpose in view from the start. For Aristotle the "final cause" (for the sake of which something is done) was really the primary cause, although he accepted that what we should call material causes (comprising his formal, material and efficient causes) also take part, but are secondary.

    This view is essentially anti-scientific, since it implies that development takes place in response to something outside natural processes (whether it is called god or divine mind (νοῦς) or nature), and thus stands in the way of any analysis of development and adaption in terms of real existing processes. That Theophrastus came to a carefully considered rejection of this teleological standpoint, and expressed his rejection both theoretically and in his methods of investigation, is of profound significance in the development of biology and a sign of his stature as a scientist and thinker. Inevitably there are passages where Theophrastus is inconsistent and is influenced by the immense authority of Aristotle, but basically he sets himself against explaining biological facts in terms of "final cause" or indeed of any merely speculative causes. Two quotations from the *Causes of Plants* (following Dengler's translation) will show his advanced conception of adaptation in plants: "Early or late growing is clearly not to be explained by large or small size, or heat, moisture, or dryness alone: each plant must in fact show sympathetic relation (συμμετρίαν) to the particular season of the year." (*CP* I,10,5.) "Both wild and domestic plants have many natural and individual (οἰκεῖα) properties directed towards their preservation, endurance, growth, budding and fruit formation." (*CP* I,16,13.)

    Aristotle's teleology was a projection of social theory into biology—its real attraction was that it gave an apparent biological justification for social inequality. By divine ordinance, all are wonderfully fitted for just those social functions that they find themselves born to undertake—especially the lower orders. Aristotle justified slavery precisely on the grounds that some men (not Greeks, of course) were only fitted to be slaves. The idea has served well through the ages to preserve the social status quo. Shakespeare gives an amusing send-up in the cozening of the mutinous citizens by the aristocratic old humbug Menenius Agrippa (*Coriolanus* I,1).

66. The notable absence is genetics, of which some fundamental principles

had been brilliantly outlined by Aristotle. These were assumed to hold for plants but could not be further developed in botany owing to the confusion about sex in plants. Theophrastus got as near plant embryology, however, as was possible without a compound microscope, by looking closely at the internal parts of seeds large enough to be examined.

67. Radishes and cabbages were interplanted with bitter vetch (*Ervum ervilia*) to prevent their being eaten by insects (*CP* III,10,5). Corn sown in fields liable to heavy dews, or in low-lying hollows, or in areas sheltered from wind, was most exposed to attack by rust: these areas should not be sown with grain (*CP* III,24,4).
68. In one sense this statement can be looked on as a purely formal application of the four-element theory, but it is hard to believe that Theophrastus was not also recording the fact that moisture (sap) is always produced when plant materials burn, as he knew from testing the combustibility of various kindling materials.
69. His theory of knowledge emerges from several passages (especially *CP* II,4,8, with its emphasis on sense-perceptual apprehension as the basis of understanding particular phenomena). For him the facts of perception and experience are primary, and theory must be developed in harmony with them, not, he says, an easy process.

    In accordance with this position he always prefers a natural explanation and always adopts a sceptical attitude to popular superstitions and reports of wonders. Thus in dealing with medical plants he makes quiet fun of the rhizotomists' mumbo-jumbo, and when mentioning the story that wheat can give rise to darnel makes clear that he doubts the fact, but that if it be true, then there is a rational explanation that awaits discovery. Even Aristotle's view that leaves serve to protect the fruit is never repeated by Theophrastus.
70. C. Mosse: *The Ancient World at Work* (1969).
71. There is a puzzling sentence in *CP* IV,11,7 where Theophrastus says that what is "against nature" can become "what is according to nature" in course of time. Unfortunately I am not sure what he meant!

    He knew all about the Hippocratic experiments and quotes them twice, and he must have known of the agricultural experiments—a primitive kind of field experimentation—recommended by Xenophon (*Oeconomicus* XX,13). But social attitudes were strong and in any case neither knowledge nor techniques were adequate for an experimental solution of many of the problems. Theophrastus' successor as head of the Lyceum, Strato of Lampsacus, thoroughly understood the experimental method in physics and practised it. Erasistratos, the great Alexandrian physician and physiologist, who had been a student at the Lyceum (either under Theophrastus or Strato) carried out quantitative experiments in physiology, including weighing a living bird (+ excreta) at intervals. There seems little doubt that the scientists at the Lyceum did arrive at some conception and use of experiment.

72. Regenbogen says that Posidonius took up this idea from Theophrastus. It was popular right through the Middle Ages, presenting a biological counterpart to the hierarchy of society.
73. Apart from botany, Theophrastus laid the foundation of mineralogy with his work on *Stones* (extant in part). He also wrote on the behaviour of animals but these works have been lost, as have those on a variety of topics which are listed by Diogenes Laertius.

    In addition to his contributions to scientific method, epistemology and philosophy, which have been discussed, he extended the range of Aristotelean logic by considering hypothetical and disjunctive syllogisms, a development which must be related to the characteristic features of biological processes (see S. Sambursky: *The Physical World of the Greeks* (1963)). At Aristotle's request he wrote a complete history of earlier philosophy, to which, although it is now preserved (except for one fragment) only in the works of others, we nevertheless owe much of our knowledge of the first philosophers.

    He has always been credited with authorship of the *Characters*, a literary work of shrewd observation and attractive acerbity.
74. Theophrastus: *Metaphysics*. Trans. by W. D. Ross and F. H. Fobes (1929).

3

Theophrastus to Galen: Botany in Hellenistic and Roman Times (280 BC to AD 200)

Experience, the most efficient teacher of all things especially in medicine, gradually degenerated into mere words and verbiage. For it was pleasanter to sit diligently listening in lecture-rooms than to go out into the fields and look for different plants at the different seasons of the year.

Pliny, *Natural History* XXVI,11 (*c.* AD 70)

During the centuries when plant science was taking shape in Greece, a parallel evolution was proceeding in China. As far as we know, these developments were independent: the two regions were separated not only by the Indian Ocean and the China Seas, the mountains and deserts of Central Asia, but even more effectively perhaps by the Persian Empire which controlled the overland trade routes.[1] The social changes which stimulated this scientific growth in the two centres were probably basically similar, although later there was wide divergence. The use of iron came somewhat later in China but by the sixth century BC the iron ploughshare had begun to improve tillage and increase the area of cultivation. There was growth of population, communications and trade, the rise of a merchant class, the introduction of coinage. This was the period of classical Chinese philosophy, of new ideas and speculations about the nature of material phenomena, expressed in such concepts as a limited number of basic elements and the conflict of opposing principles (yang–yin antinomy), strikingly similar to the fundamental notions of the Ionian and Greek philosophers, and similarly reflecting the development and change of primitive tribal society.

The ancient and uninterrupted herbal tradition of China has already been mentioned. As in Greece, this became broadened by the inclusion of other kinds of knowledge of plants, so that in China also real botany begins. In the great Chinese dictionary *Erh Ya*, the Literary Expositor, which was compiled about the time of Theophrastus or later, some 334 plants were mentioned, classed as either trees or herbs. The literary and popular name of each plant was given, together with a short descriptive definition. Possibly illustrations were included even in the earliest editions; this had certainly become customary by the fourth century AD. The many technical descriptive terms for plants which appear in the dictionary indicate the building of a systematic botanical terminology. Sometimes the terms show a degree of particularity more primitive than advanced, as when different words are used for the flowers of trees, herbs and cereals, or for the corresponding part in different species. Although there are traces of this practice in Theophrastus, he constantly sought the widest morphological generality, and it appears that the Chinese botanists recognized the same principle and began to develop a descriptive morphology on Theophrastean lines. They also established a systematic method of naming plants fundamentally very close to that of Theophrastus, which served Chinese descriptive botany well for nearly 2000 years and is a witness to their efforts to realize the aim of a rational classification.

In the opinion of Joseph Needham the technical terminology developed by the early Chinese botanists, and fully preserved by the lexicographers, demonstrates that they were thinking about the same theoretical questions as Aristotle and Theophrastus. There was not, however, a Chinese Theophrastus, and ancient Chinese botany never reached the synoptic theoretical level of the Lyceum. Doubtless the cause is to be found in the special features of Chinese historical development. The Chinese merchant class never attained, even temporarily, anything approaching political independence. After the period of the Warring States (650 to 350 BC), which marked the rise of the merchants, the unification of China under a single emperor was finally accomplished with the merchants' aid and support. As recompense the emperor incorporated them as a part of the new ruling class of land-owners and official bureaucrats. They thus became part of a state structure which continued to exist with extraordinary stability for 2000 years, essentially unaffected by dynastic change or foreign invasion.[2]

This stability or, more accurately, the special social conditions giving rise to it, led to a divergence in historical development between China and the Western world which is reflected in a remarkable way in the subsequent history of botany, as in many other forms of cultural activity. In the West the brilliant dawn of botany was quickly followed by decline and prolonged stagnation. If in China the theoretical synthesis was less complete, there was at least no decline from the level reached and no descent into a dark age. If Chinese plant science made no further significant contributions to theory, it nevertheless continued to advance within the circumscribed field of descriptive and medical botany. A short account of these advances in very general terms is therefore in place.[3]

An early characteristic of Chinese civilization was a passion for lexicography and the production of encyclopaedias. Such works, used as textbooks by candidates preparing for examinations for entry into the imperial bureaucracy, contributed to the preservation of Chinese cultural achievements. Botanical works continued to be produced in the form of medical herbals, natural histories and elaborate monographs on particular groups of plants, both economic and ornamental. Nomenclature was stable and scientific, since each plant had a classical literary name, alongside which the synonyms, popular or dialect names, were customarily quoted. A new plant was named by using the classical name of a plant it resembled, combined with a qualifying word: leading to an almost binomial nomenclature analogous to that developed by Theophrastus. Needham has remarked that at least one new and original work on pharmaceutical botany was produced in China each century between AD 100 and 1700, and that a whole group of experts in pharmacology was maintained at the imperial court from very early times. These botanical works contain detailed, well-observed descriptions and accurate illustrations of plants, free from superstition and nonsense; the number of plants described increased with time as observation was extended into new regions or plants were brought in from abroad. These treatises were generally supported, and often initiated, by the imperial government.[4] Herbal knowledge was part of organized medical education throughout the centuries. The emperors appointed professors of pharmacognosy and also established botanical gardens at an early date, with experts in charge.

Two botanical developments almost exclusive to China must be mentioned. The first was the production, between about AD 1350 and 1650, of a series of treatises on emergency food plants, listing wild plants of the countryside that could be used for food or medicine. These were deliberately popular works, with descriptions and pictures specially designed to prevent confusion between similar-looking species. This remarkable initiative had primarily a social purpose, but it led to a sharpening of plant description and was a step towards an indigenous flora. The second development, not exclusive to China but far more frequent and botanically accomplished than anything at the corresponding period in the West, was the writing of elaborate monographs on particular groups of plants.[5]

The striking feature of Chinese botany is the unbroken advance for 2000 years in certain limited areas, leading to a high level of accurate description, superb illustration, and the naming of thousands of plants, together with information on their culture, their economic and medical uses, and often of their geographical and ecological distribution. The social stability that permitted these advances was at the same time a strait-jacket from which Chinese botany was unable to break free, so that it never made the conceptual surge forward or the turn to experimental method which mark the rise of botany in the West when progress there was ultimately resumed. Understanding of the nature of the flower,[6] of sex and fertilization in plants, of anatomy or of nutrition, was not achieved in China, although many acute observations were recorded, which Chinese botany, transformed after scientific contact with European botany during the nineteenth century, is able now to garner.[7] Even in descriptive botany bureaucratic society imposed odd limitations. In spite of their ancient and deep interest in classification Chinese scholars failed to approach a natural classification of plants as a whole, although at lower taxonomic levels they subdivided single groups of plants, genera or even species, with a keen eye for morphological detail, sometimes anticipating modern practice.[8]

The substantial, although sharply circumscribed, achievements of Chinese plant science, of which an unbroken literary record was preserved at all times, unfortunately remained unknown to Europe and, except in Japan,[9] were without direct or indirect influence until absorbed into the world stream of botany during the nineteenth century.

In the West botany took another and very different course. The great synthesis of Theophrastus proved to be a culmination, not a beginning, and was followed by almost 1800 years in which theoretical botany effectually went out of existence and even the meagre additions to empirical knowledge were more than balanced by actual loss of information. The fruitful contact between botany and agriculture was lost, and botany became once more synonymous with the recognition of medicinal plants, only keeping a place in education or general interest as the herbal adjunct of medicine.

The decline of botany after Theophrastus was part of a general decline in all branches of natural science.[10] The special conditions that had fostered Greek rationalism had been destroyed: that growth was followed by actual decline was most probably due to the now preponderant role of slavery in society and the greatly increased reliance on slave labour in production,[11] a social system that retarded technical innovation, discouraged the application of science to agriculture and industry,[12] and acted as a brake on social progress by preventing any permanent union of the two most exploited classes, the slaves and free labourers, that might have alleviated their lot. The intellectual consequences of the mutually degrading relationship between slave-owners and slaves were equally destructive of science. The scientists and philosophers, necessarily associated with the interests of the slave-owning upper class, were cut off from the practical operations of the material world and from the path of scientific observation and experiment by an ingrained contempt for manual labour that was part of their upbringing and education. At the same time the miseries and social stresses of the age gave rise to a host of religious and superstitious trends, some deliberately encouraged and spread by state authority to keep the mass of the people in subjection. Such ideas inevitably became a powerful barrier to the growth of science.[13] It is significant that the only sciences included in the higher educational curriculum were mathematics, astronomy and medicine, and that these were studied primarily as practical arts. Astronomy was further degraded to become an ancillary of the anti-scientific but socially motivated absurdities of astrology.[14]

Figure 3 Figure of *Angelica sylvestris* in the *Cheng Lui Pên Tshao*. A Chinese printed herbal (1249).

The Macedonian conquest of Greece and Persia during the life-time of Theophrastus submerged the old city-states in larger political units, and began the complex process that eventually united much of the Western world under Rome. Throughout this period men's minds were largely diverted into fields other than science and technology.[15] Changes in the technological level of society were slow and retarded, although never, of course, completely halted; in the end the growth of new productive forces became incompatible with the preservation of slavery.[16] By about the fourth century AD slavery was gradually giving place to a variety of basically feudal relations in most of Europe, a change that was hastened by the movements of barbarian peoples into the territories of the former Roman Empire and by the foundation of new kingdoms. While the establishment of feudal society eventually created conditions for some increase in the rate of technical progress and for a rise in productivity, it did not immediately provide any more fruitful a soil for science than the society it replaced. This was especially true in the early centuries of feudalism—the "Dark Age" from about the fifth to the tenth century—when the weakness or lack of centralized political authority over large areas of Europe, added to the general insecurity of life, and kept economic activity at a low level. It was a hierarchic immobile society, most of the producers bound legally to the soil and so exploited by Church and overlord that any incentive to technical improvement was strangled, whilst the intellectuals were as sharply cut off from manual labour and as deeply permeated by anti-scientific ideology as their forerunners in slave society.[17] The history of botany in the West now becomes scarcely more than the record of the slender threads by which some continuity was preserved. While the discussion of medicinal herbs was for Theophrastus only one, and by no means the most important, component of botanical science,[18] in the epoch which followed, it was the herbal component which alone survived to represent botany, the concept of a wider science of plants was unappreciated and eventually forgotten. When Theophrastus was teaching at the Lyceum Greek herbal knowledge had already been gathered together and systematically treated by his contemporary, the celebrated physician Diocles of Carystos, who practised in Athens and was almost certainly known to Theophrastus personally.[19] Among the works of Diocles were two dealing respectively with drug plants and food plants, that is, with

百合味甘平無毒主邪氣腹脹心痛利大小便補中益氣除浮腫臚脹痞滿寒熱通身疼痛及乳難喉痺止涕淚一名重箱一名摩羅一名中逢花一名強瞿生荊州川谷二月八月採根曝乾陶隱居云近道處處有根如胡蒜數十片相累人亦蒸煮食之乃言初是蚯蚓相纏結變作之俗人皆呼為強仇仍即瞿也聲之訛爾亦堪服食唐本注云此藥有二種一種細葉花紅白色一種葉大莖長根麄花白宜入藥用臣禹錫等謹按藥性論云百合使有小毒主百邪鬼魅涕泣不止除心下急滿痛治脚氣熱欬逆吳氏云百合一名

Figure 4 Figure of a lily (*Lilium* sp) from the *Cheng Lui Pên Tshao*. The quality and verisimilitude of Chinese plant depiction in the Middle Ages contrasts with the general decline in European herbals of the period.

medicinal plants in the broad sense, since in Greek medicine diet was considered as a distinct and fundamental branch of therapy. Theophrastus several times quotes Diocles' actual words and undoubtedly regarded him as an authority on pharmacognosy. Only fragments of Diocles' writings have survived in the original form but the evidence of relevant contemporary and later literature shows that his work was accepted as the standard textbook on medicinal plants, and that it was copied, edited, used, and silently appropriated, by other writers, so that much of it has undoubtedly been preserved as the foundation of the herbals of many later authors, including both Pliny and Dioscorides.[20] Indeed herbals were produced by not a few people in the two centuries after Theophrastus, among them the great physician Herophilus of Alexandria.[21] All these writings have been lost, but probably they were mainly based on Diocles, and would be simply copies of one another: an inevitable occurrence when every book had to be copied by hand, and not unknown even in our own days, when more efficient methods of transcription are available. The most notable of the Greek herbalists was Crateuas who flourished in the years between 120 and 60 BC.[22] He was court doctor to that able and energetic rascal, King Mithridates VI of Pontus, long a thorn in the flesh of Rome and of his own reluctant subjects. To Crateuas are ascribed two works that had long-lasting influence on the history of botany. The first was a scientific treatise on botanical pharmacology in which the plants were arranged alphabetically, with a list of synonyms, a description, and an account of its medical use, for each plant. The text of Crateuas' *Rhizotomikon* is lost to us but it undoubtedly incorporated the substance of Diocles' work of the same name. That Crateuas made an original contribution of his own, both in method and content, is supported by his reputation in antiquity and by Pliny's statement that he named a new plant after Mithridates.[23] This work of Crateuas was later the main source of the herbal of Sextius Niger on which Pliny and Dioscorides relied for much of their material, their works in turn becoming the primary source of plant knowledge during most of the Middle Ages.

The other work of Crateuas was evidently intended as a popular supplement to his scientific pharmacology and consisted of a series of painted illustrations of each plant with the name and medical properties below, but without descriptions. Crateuas was thus the pioneer of an enduring and immensely valuable botanical method; Pliny expressly states that he was the originator of botanical illustration among the Greeks.[24] The work obviously met a real need since it was quickly re-issued by others and continued in use until the third or fourth century AD when there is good evidence that descendent copies of some of the original illustrations were combined with the text of Dioscorides,[25] to become the primary source and pattern of all the multitude of herbals that were slavishly copied and re-copied for centuries to come. Thus the content and even the form of botanical writing for well over a thousand years can be directly linked with the herbal of Crateuas, and through him to the herbal knowledge of Diocles and Theophrastus.

The final harvest of Greek pharmacology was gathered and preserved by Dioscorides in his *Materia Medica*, completed about AD 60, and enriched by his personal knowledge and experience. It displaced the *Rhizotomikon* of Crateuas (which no doubt was largely incorporated in it) and became the standard pharmacology of the West until the Renaissance. Of its armoury of about 1000 drugs nearly three-fifths are from plants, and so great was its medical renown and so narrow had the bounds of scientific interest in plants become, that for centuries the work of Dioscorides became synonymous with botany.[26]

Little is known of Dioscorides' career or personality beyond his own statement that he led a soldier's life, and was probably therefore an army doctor; it is also evident from his writings that he had travelled widely and knew the plants of many Mediterranean countries at first hand. He prided himself on his thorough study of previous writers, but even more on his own practical expertise, "knowing most herbs with my own eyes, others by historical relation agreeable to all, and by questioning [and] diligently enquiring of the inhabitants of each sort" (John Goodyer's English translation, 1655). He speaks of Crateuas with very great respect but criticizes Sextius Niger and others for repeating incorrect information derived from hearsay instead of observation, and for mistakes in grouping together medicines of contrary faculties, or for using an alphabetical arrangement (as indeed Crateuas had done) which arbitrarily separates related things "so that they come to be harder to remember".

It was the new, primarily pharmacological arrangement of

Dioscorides' *Materia Medica*, at once logical and practical,[27] which, in addition to its scientific caution and freedom from superstition, probably established its pre-eminence. Another popular and useful feature was the wealth of local plant names provided; the Latin and Greek synonyms were given for each plant, often with the addition of Egyptian, Persian, Syrian, African, Iberian, or Etruscan names where appropriate. Two things set the final seal of success. One was the authoritative approval of Galen, who held up Dioscorides to the world as the supreme guide in pharmacology. The other was the acumen or opportunism of the unknown compiler who (perhaps early in the second century AD) combined the text of Dioscorides, originally lacking illustrations, with a set of painted drawings of all or most of the plants, probably derived from direct copies of the illustrations of Crateuas. This happy combination of the best features of the Greek herbal tradition also marked its culmination. The subsequent herbal transmission during the Middle Ages, was in general a process of decline.

The botanical content of Dioscorides is minimal, although he mentions about a hundred plants that may be additional to the number known to Theophrastus. His descriptions of plants, copied almost without change from Sextius Niger and others, are only hints and would be quite inadequate without illustrations. They are not to be compared with the excellent, almost systematic botanical descriptions characteristic of Theophrastus at his best. Dioscorides follows Theophrastus in the frequent mention of habitat and geographical distribution of species, information very useful in a pharmacopeia intended for use by herb-gatherers in many diverse regions of the Roman Empire. It is surprising that Dioscorides, perhaps because of his roving life, seems to have had no direct acquaintance with Theophrastus' botanical works although they were well known to Dioscorides' contemporary, Pliny.[28]

One of the most remarkable and original contributions of Theophrastus was his attempt discussed earlier, to integrate the traditional practice of agriculture into botany and to establish a causal theory of plant growth (τοὺς τῶν φυτῶν βίους), the first striving towards a study of plant physiology. It is characteristic of the era that followed, that this line was developed no further, although agricultural techniques continued to advance, even if slowly and haltingly, and a new generation of treatises on agriculture was produced mainly in the Latin language.[29] Their authors drew on the earlier Greek agricultural writers as well as on Phoenician sources. The Phoenicians were themselves indebted to the Greek tradition which they enriched by fresh experience gained from conditions in North Africa and Spain.[30] The principal Roman writers on agriculture—Cato the Elder, Varro, Vergil and Columella—represent a continuous tradition spanning the three centuries after Theophrastus.[31] A feature common to them all, in addition to their high standard of technical competence, their common sense and cool practicality, is the treatment of agriculture strictly as an applied science, firmly based on experience but deliberately eschewing general principles. The attitude was expressed by Varro in the remark quoted earlier that the works of Theophrastus, although containing valuable information, were more suitable for philosophers than for practical agriculturalists. Yet certainly Varro, Vergil and Columella were not only well acquainted with Theophrastus but were much more deeply indebted to him than they acknowledge, not merely in relation to tree culture and soil classification (as emphasized by K. D. Whyte), and the principles of manurial application and plant pathology, but above all for the profoundly important conception that each species or variety of plant is specifically affected by the various factors of the environment.[32] The recognition and statement of this principle by Theophrastus was of the greatest possible practical consequence in agriculture, since it means that the requirements of crops and varieties in relation to soil, climate, water, habitat, were not only carefully observed, but could be defined and recorded with some degree of precision. This type of crop–ecological knowledge, together with a systematic analysis of the different methods of plant reproduction, was the permanent legacy of Theophrastean botany to agriculture. It is thoroughly assilimated into the work of Columella,[33] written in the first century AD and retaining its authority throughout the Middle Ages.[34] This treatise is the longest and most systematic account of Roman agriculture and is an example of the Roman applied genius at its best. Written in elegant yet clear and precise Latin, it is notable both for breadth and erudition, and for the balanced evaluation of accepted techniques in the light of the author's own experience and observation. But its very merits emphasize the separation of agriculture from botanical thought. Having incorporated as rules of thumb those botanical concepts that were of practical utility, agriculture made no return contribution to botany.[35]

It may be noted in passing that Columella, like Xenophon earlier, recommends experiment in agriculture. Instead of trying the quality of a soil by kneading, digging or tasting, he says it is better to test it by the yield of crops.[36] But experiment is here limited to simple practicality, the testing of a particular case. It is not a general method of testing theoretical principles: such a method could only be developed and used consistently in a different social and intellectual setting.

The subject matter of two subdivisions of Theophrastus' botany thus became incorporated within medicine and agriculture respectively, being preserved in ossified form as part of the traditional technical practice of these arts. What then became of the impact of botany as a coherent science with its own concepts and field of investigation? The answer is that it was effectively lost, not because the scientific writings of Theophrastus were lost (although this eventually happened), but because Hellenistic and Roman society did not provide the conditions for its survival. The social reasons have been briefly adverted to: they were reinforced by corresponding developments in philosophy, as all the main schools of thought turned away from the problems of natural science.[37] That it was a failure of intellectual interest is evident, for references to and quotations from Theophrastus in Pliny, Columella, Plutarch, Galen and others show that his botanical writings were still known and available late in the second century AD, and Pliny speaks expressly of seeking information in several copies (*in exemplaribus*).[38] Yet apart from the uselcss *De Plantis* of Nicolaus of Damascus the only, very unsatisfactory, presentation of Theophrastean botany that survived into post-classical and mediaeval times is found in the *Natural History* of Pliny in those books (XII–XXVI) which deal with plants.[39] Of this work, written in the years before AD 77), something must now be said.

It is hard to resist the attraction of Pliny, whose enthusiasm preserved for all time so much invaluable information about the ancient world. Shrewd without depth, a learned gossip, intellectually opposed to superstition but unable to resist a tall story, one who could express enlightened humanism—"divinity is when one mortal helps another"—and empty adulation of the regnant emperor in the same sentence, he was filled with insatiable curiosity about the world, but was neither scientist nor philosopher. His treatment of Theophrastus is characteristic both of the man and of his epoch. Throughout the books on plants he draws constantly on Theophrastus, especially on the *Enquiry*:[40] indeed he almost certainly adopted the arrangement of this work as a model for his own, but the logical development of Theophrastus became lost in Pliny's compulsive digressions and obscured by his complete lack of any theoretical understanding, so that all fundamental questions are either confused or ignored.[41] Yet this muddled and emasculated version of Theophrastean botany has one merit for which Pliny should not go unhonoured. He presented botany as embracing all facets of knowledge about plants and not just as the handmaid of medicine or farming; to this extent Pliny maintained the idea of a science of botany in a world where it was in danger of disappearing completely.[42] Pliny obviously had a genuine interest in plants and an enthusiasm that finds frequent, if sometimes odd, expression. Occasionally he seems to write from his own observation, yet such passages often go cheek by jowl with obvious blunders due to careless and uncritical copying of his authorities. He gives much information on agriculture and on the uses and technology of plants which throws light on technical and commercial developments of the time. The number of plants named by Pliny is perhaps twice the number mentioned by Theophrastus, but many names are synonyms and identification is often impossible, since the descriptions are fragmentary or lacking.

However inadequate, Pliny's account of plants remained for centuries as the only reflection of the theoretical synthesis achieved in Greek botany by Theophrastus. In the work-a-day world, however, the influence of Theophrastus continued, powerful though unrecognized, as the accepted foundation of pharmacognosy and agriculture. Most historians of botany have underestimated or ignored the extent, importance and persistence of this influence, especially in agriculture. It is the earliest example of the profound effect of botanical science on the practical affairs and material welfare of mankind.

The slackening of interest in botany in Hellenistic and Roman times is witnessed by the gradual oblivion which buried the text of Theophrastus almost completely after the second century AD. Copying of the manuscripts evidently became very rare or ceased, and only fortunate chance preserved a few forgotten copies, probably in libraries in Byzantium or Alexandria, from which were derived those rediscovered in the library of the Vatican during the revival of learning in the fifteenth century.

The gathering twilight of biology was only briefly illumined by the strangely isolated genius of Galen[43] before the darkness that lasted practically unbroken for more than a thousand years. Galen summed up the main trends and achievements of Greek medicine in a system that maintained its influence throughout the western world until the Renaissance and beyond. He was not only a great physician but also a great biologist who made important advances in the anatomy and physiology of animals and man. He was deeply impressed by the internally regulated unity of the animal organism, physiologically adopted to its way of life, and this concept was perhaps his most important contribution to the development of biological theory. These ideas had no impact on botany, however, and Galen did not consider their extension to plants; in fact, he was content to follow Aristotle in separating plants specifically from animals because the former have no sensations, and to leave it at that. His own interest in plants was purely pharmaceutical and although he lists over 450 herbs, with their medical uses and effects, he gave no botanical details and clearly derived his information directly from Dioscorides. Yet Galen prided himself on being able to recognize and collect his own plant drugs and on knowing where and at what time of the year to find them: all physicians, he says, should acquire this knowledge, so as not to be dependent on apothecaries or rhizomotists, and not to rely on expensive imported drugs when native ones are available in the fields. This was excellent botanical advice at a time when personal acquaintance with plants was already being neglected in favour of reliance on book-learning and professional herb-gatherers.[44] Galen recommended every doctor to learn to recognize and name medicinal plants by seeking practical training from an expert, but the general problem of systematic plant description was outwith his consideration. In the long run his extreme praise of Dioscorides, backed by his immense reputation, may even have strengthened the herbalists' and physicians' temptation to rely on authority and second-hand knowledge, a practice to which Galen himself was so strongly opposed.[45]

Notes to Chapter 3

Notes

1. Silk from China was reaching Western Asia overland as early as 500 BC. The earliest plant introductions to China from the West were the grapevine and alfalfa, both from Iran between 150 and 100 BC.
2. See Wu Ta-k'un: An interpretation of Chinese economic history. *Past and Present* **1**, 1 (1952).

   The author points out two specific features of Chinese society which go far to account for the divergent development in East and West. The first is the early incorporation, following the reform of Shang Yang in 350 BC, of the merchants into the land-owning bureaucracy. Together with the establishment of a government monopoly in iron and other metals, this prevented the formation of an independent merchant class. The accumulation of merchant capital led in these conditions, not to the rise of a capitalist class, but to continuous reinforcement of the land-owning ruling class. The second feature is that the reform of Shang Yang established land as legally alienable private property, with the result that the primary agricultural producer in China was not the slave (although slavery existed), nor the serf tied to the soil as in the West during most of the Middle Ages, but was the free-born peasant proprietor, subject to bitter exploitation through rent and land tax, liable to forced labour and forced tenancy, yet formally free to move and to buy or sell land. The existence of this class was a permanent source of strength and initiative within the restrictive and conservative social structure. It was one influence—the unique situation of the merchants within the official state was probably the other—which saved learning and science in China from the Dark Age which overshadowed Europe.
3. See E. V. Bretschneider: *Botanicon Sinicum* (1882).

   This great pioneer work is still valuable although now supplemented by J. Needham's authoritative account of Chinese botany. Only a bare outline of Chinese botanical development is given here in view of the appearance of Needham's history.
4. Thus in AD1057 the emperor Jen Tsung ordained a new treatment of the existing national pharmacopeia and appointed a committee of two naturalists, a physician, and a scientist–statesman to carry the project through. An imperial order instructed all district governors and magistrates to have drawings made of important drug plants of their regions. More than 1000 drawings were received in the capital, Hangchow, and an illustrated pharmacopeia with descriptions of over 1000 plants, of which about 100 were new was produced (J. Needham).
5. A remarkable fact about the Chinese monographs is that many dealt with plants of aesthetic rather than economic interest such as orchids, chrysanthemums, crab apples, ornamental camellias, paeonies. This contrasts with the state of affairs in the West where the very few monographs produced were always of economic plants (e.g. Gargilius Martialis on the

apple, quince, peach, almond and chestnut). Of course even the ornamental plants were all originally medicinal, the aesthetic attraction came later.

6. Both the description and the depiction of the parts of flowers were much more accurate in China than in the west but the significance of the floral organs was not grasped.
7. In both bamboos and paeonies the Chinese made (sub-generic) divisions on the basis of morphological characters still used by modern botanists.
8. In his Great Pharmacopeia (*Pên Tshao Kang Mu*, published 1596) Li Shih-Chen, one of China's greatest scientists, lists over 1000 plants in groups based on arbitrary characters including habitat, habit, taste, use as food, smell, etc. with no suggestion or recognition of botanical affinity.
9. See Shirai Mitsutaro: A brief history of botany in old Japan, Chapter X, pp. 213–42, in *Scientific Japan: Past and Present* (Ed. Shinjo Shinzo). Kyoto (1926).
10. See, for example, O. Neugebauer: *The Exact Sciences in Antiquity*. Providence, R.I. (1957).
    B. Farringdon: *Greek Science* (1961).
    G. Sarton: *A History of Science*. Cambridge, Mass. (1953–9).
    G. E. R. Lloyd: *Greek Science after Aristotle* (1973).
11. See F. W. Walbank: The causes of Greek decline. *Journal of Hellenic Studies* **64**, 10–20 (1944).
12. Some of the immediate effects of slavery in agriculture were evident to intelligent contemporaries, even if they did not appreciate fully all the social and intellectual consequences. Thus Columella (*De Re Rustica* I,3) ". . . and agriculture, which the best of our ancestors treated with the best attention, we have handed over to the very worst of our slaves as if to the hangman for punishment." Pliny likewise (*Natural History* XVIII,21) "But nowadays those agricultural operations [formerly carried out by senators] are performed by slaves with fettered ankles and by the hands of condemned prisoners with branded faces . . . and then we are astonished that we don't get the same profits from refractory slaves as we used to do from generals."
13. Many writers have noted the rise of mystical, irrational and superstitious trends, both religious and otherwise, in Hellenistic and later classical times. It was against the political use of religion that Lucretius and the Epicureans passionately protested.
14. The Babylonian astronomers had sought to relate great events affecting kings or entire countries to the movements of the stars, but astrology, the pseudo-science which linked the fate of individuals with the stars, was the degenerate offspring of Alexandrian science, strengthened by the authority of this renowned centre of learning, and having its spiritual origin in Plato.

    E. H. F. Meyer, with his invariable acuity, noted the growing reliance on astrological writers during the Hellenistic and late classical period (see his *Geschichte der Botanik* (1854) (1965 reprint I, 295).

Astrology became a persistent anti-scientific trend, especially in medicine, a permanent appeal to the irrational and the supernatural, which remained influential throughout the Middle Ages.

See M. P. Nilsson: *The Rise of Astrology in the Hellenistic Age*. Lund (1943).

15. Revealing of the new attitude is Cicero's judgement of Strato, Theophrastus' successor in the Lyceum: "he abandoned the most essential part of philosophy, which is concerned with morals and conduct, to devote himself to the investigation of nature." (*Academica* I,34.) When Cicero wrote, Rome was already in the thick of the long struggle to unite the Western world under her rule. The problems agitating the upper classes were how to organize masses of men and control their minds; technical and scientific questions seemed less urgent.

16. The principal new invention of the classical era of slave society was the water wheel about the first century BC but, significantly, it did not begin to find widespread application until after AD 500, by which time slave society had largely given place to feudalism. In agriculture some important technical advances were made which may be considered as the progressive side of large-scale slave-worked agriculture. There were developments in three directions: first, the intensive working of the land at every stage of cultivation, including repeated ploughing of the fallow to keep down weeds; second, the introduction of new crops and varieties, especially green fodder crops, and greater emphasis on systematic manuring; and third, many improvements in the design and variety of agricultural implements. (For details see K. D. Whyte, F. M. Heichelheim, loc. cit.)

Although the effects of these advances were constantly undermined by the inherent disadvantages of slave labour (see Note 12, above), they represented real technological progress, the characteristic contribution of Roman agriculture which was carried to most parts of Europe and the Mediterranean regions. It survived all the changes and catastrophes during the break-up of the Roman Empire. As slave economy became unprofitable the land was turned over to small tenants (the *coloni*, former slaves, who became one source of the later feudal peasantry), and it was in the landlords' interest to see that they adopted as much of the best scientific agricultural technique as was possible. In the previous period the level of technique of the existing free peasant proprietors was very low, only the owners of big slave-run estates like Columella were interested in or could afford to practise scientific agriculture. Thus Roman agriculture continued to provide the basic techniques for the peasant-farmers throughout the Middle Ages in the greater parts of Europe.

It should perhaps be emphasized that the disappearance of slavery was a long and complex process, as was the rise of feudalism. Thus, whereas slavery was no longer economically significant, and was morally condemned, in Western Europe by the fourth century, it played some economic role in Byzantium and the Islamic countries until the tenth century. Some historians are so impressed by the variety and complexity of feudal social relations as to deny the existence of feudalism as a meaningful term, but this is surely to question the validity of serious social analysis. Beneath the varied and changing forms the reality of feudalism was the fact that the overwhelming majority of the producers consisted of peasants, bound, whether legally or economically, to the land, and supporting by their toil the immense drain on social production of a military–feudal aristocracy and its partner, the Church.

For a clear account of the period in question, see G. A. J. Hodgett: *A Social and Economic History of Mediaeval Europe* (1972).

17. Throughout the Middle Ages the prevailing theory of knowledge was that of St Augustine who regarded knowledge and the sciences as simply the reflection of the divine mind in human intelligence. Philosophically this idea goes back by way of Plotinus to Plato: it rejects the Ionian and Aristotelean view that knowledge develops from the application of thought to sense-experience. In practice it turned men away from observation and experiment, and encouraged them to rely on illumination by authority, whether divine, as thoughtfully interpreted for them by the Church, or hallowed by tradition, as in the case of some classical writers and philosophers. So in botany men preferred to copy herbals rather than look at herbs.

    For an instructive analysis of the philosophical ideas of the Middle Ages see D. Knowles: *The Evolution of Mediaeval Thought* (1962).
18. C. Singer has suggested (The herbal in antiquity. *Journal of Hellenic Studies* **47**, 1–52 (1927)) that the section on medicinal plants in the *Historia* (IX) is not by Theophrastus but is a later addition, although taken from a genuine Greek herbal of very early date. I see no compelling reason to doubt the traditional ascription of this book to Theophrastus, but even if Singer is right the basic argument is not affected.
19. For the relation between Theophrastus and Diocles see W. Jaeger: *Diokles von Karystos*. Berlin (1963). I have compared the surviving fragments of Diocles with Theophrastus and it is clear that several direct quotations from Diocles are in Book IX of the *Historia Plantarum* which deals with medicinal plants.
20. See M. Wellmann in Pauly-Wissowa: *Real-Encyclopädie der klassischen Altertumswissenschaft* 1131–42 (1905), an article on Dioscorides.
21. This work on plants is lost, but was connected with the flourishing medical school at Alexandria, part of the Museum, founded and financed by the Ptolemaic kings as a centre of learning. Here, in the field of medicine, the biological research of the Lyceum was maintained for some time with success, although eventually the impulse was lost in the general decline of science. In the century after Theophrastus' death Herophilus and Erasistratus made significant advances specially in anatomy and physi-

ology (For detailed accounts see E. D. Phillips, *Greek Medicine* (1973) and G. E. R. Lloyd, *Greek Science after Aristotle* (1973).) This work was directly inspired by the scientific outlook and method of Aristotle and Theophrastus. It is significant that Erasistratus, who was the first to try to apply quantitative experiment in physiology, had been a pupil of Theophrastus at the Lyceum, and his work may fairly be regarded as showing an influence of botany on medicine. Note, for example, his view of nerves as tubes filled with fluid. More important, however, is the general methodology inspired by Theophrastus' plant research.

22. It is disappointing that we know nothing of the personal life of Crateuas to whom Dioscorides pays tribute. He also wrote on metals and on spices, an early indication of the growing importance of the spice trade with the East (on this see J. I. Miller: *The Spice Trade of the Roman Empire* (1969)). A fragment of Crateuas happily preserved in both Pliny (*Natural History* XXI,164) and Dioscorides (*Materia Medica* II,176) shows the scientific quality of his work and his concern for botanical accuracy.
23. Mithridatia (Pliny, *Natural History*, XXV,26), probably *Erythronium dens-canis*, the dog-tooth violet.
24. Pliny points out some of the limitations of botanical illustration, including the errors introduced by copyists (*Natural History* XXV,8).
25. See article on Crateuas (Krateuas) in Pauly-Wissowa: *Realencyclopädie der klassischen Altertumswissenschaft* XI,1644–46, and C. Singer (note 18, above).
26. Thus in AD 540 Cassiodorus, secretary to the emperor Theodoric, wrote "In the first place you have the herbal of Dioscorides (herbarium Dioscoridis) who has discussed the herbs of the field with wonderful propriety and pictured them."
27. There is no trace of botanical classification in Dioscorides that I can detect.
28. E. H. F. Meyer compared the plant descriptions of Dioscorides systematically with the corresponding descriptions of Theophrastus and found no evidence of direct quotation.
29. For a full account see K. D. Whyte: *Roman Farming* (1970).
30. Pliny records (*Natural History* XVIII,22) that when the Romans destroyed Carthage they contemptuously gave away the contents of the libraries to the local petty kings, but the Senate ordered the 28-volume work by Mago on agriculture to be translated into Latin. This translation is not extant but much of it was incorporated by Roman writers into their own works. They all refer to Mago as an acknowledged authority.
31. A detailed study and comparison of these writers would be of extraordinary interest, whether from the point of view of their highly individual and contrasting personalities and styles, or from the changes in agricultural technique and organization over nearly 300 years as reflected in their successive works, but cannot be attempted here. Some valuable information is given by K. D. Whyte (cited above). Cato, Varro

and Columella wrote for the guidance of big land-owners cultivating with large gangs of slaves, but Vergil wrote for the gentleman-smallholder. Cato's work consists of brief notes of guidance for the practical farmer, without art of ornament, clearly revealing his hard arid character, little softened by his insistence on the unfailing value of cabbage as both food and medicine. Both Varro and Columella produced systematic treatises which are for us primary sources of information on the agriculture of their time.

The *Georgics* of Vergil remains unique. A supreme artistic creation, inspired by the ancient scientific and agricultural tradition as expressed by Epicurus and Lucretius, it contrives also to convey a wealth of practical farming instruction. The direct influence of Theophrastus is evident in many places. Vergil's reference to the important practice of seed selection (*Georgics* I,197–9) is noteworthy, since this is not referred to by Theophrastus (as extant, see Note 38, below) although it must have been established from very ancient times and would be well known to him.

32. Varro, *De Re Rustica* I, VI and IX.
    Columella, *De Re Rustica* II,II.
    Very interesting is Varro's definition of agriculture as "not only an art but also a science which instructs us what crops should be sown in each type of soil and what should be done so that the land may continue to give the highest yields" (I,III). This derives directly from Theophrastus.
33. Like many able Romans Columella was a provincial, born in Spain, where the impact of Carthaginian agriculture was probably most directly felt. This stimulus may have contributed to his critical and independent attitude to accepted ideas.
34. Just as Roman agricultural techniques persisted and formed the basis of agriculture in the Western world right through the Middle Ages, so Columella continued to be the main source of scientific agriculture. His work was the basis of many later popular writers including Gargilius Martialis (third century), Palladius (fifth century), Cassianus Bassus (sixth century, the *Geoponica*). A comparison of the magnificent work of Columella with the *Geoponica* shows how far the decline of science went in late classical and early Middle Ages. The latter is a farrago of scraps of ancient techniques mixed up with superstition and rubbish of every kind. All these later works are quite devoid of botanical significance and do not reflect any advances in agriculture either. Even though some changes in agriculture were undoubtedly proceeding, the writers were quite content to copy and re-copy Columella and the earlier georgic works with increasing inaccuracies and omissions.
35. It is worth noting that in almost his only reference to botanical theory (*De Re Rustica* III,X,10–11) Columella quotes Aristotle's teleological view that the function of leaves is to protect the fruits, a theory which Theophrastus certainly did not accept.
36. *De Re Rustica* II,II,19, "(terra) . . . melius proventu frugum approbatur".

37. Cicero, in *De Natura Deorum*, gives an illuminating impression of the main philosophic trends that spanned the centuries from Aristotle and Plato to mediaevalism. His colloquy is, however, an artistic and not a systematic treatment, and is manifestly unfair to the Epicureans whose views were highly obnoxious to him.

Academic, Epicurean and Stoic philosophy were all more concerned with ethical and social problems in the widest sense than with natural science. Knowledge of the natural causes of material phenomena was only considered important in so far as it removed irrational fears that destroyed men's happiness.

The Academy, although maintaining its existence and prestige for a long time, in fact no longer represented a unified philosophy: its teaching degenerated into critical but sterile agnosticism, curiously combined with the elaboration of "neo-Platonic" speculative systems that were later taken up into Christian thought during the Middle Ages.

The Epicureans preserved Greek rationalism and science as part of their teaching, including the main theoretical contributions of Aristotelean and Theophrastean biology (this emerges from Lucretius' *De Rerum Natura*). They stuck to atomic theory which kept them clear of the bog of idealistic speculation into which the four-element theory descended. However their social aim of accommodation with existing society while rebelling gainst it intellectually, stood in the way of trying to advance science further by observation and experiment. They tended to be satisfied if reasonable materialist explanations of nature could be given, and did not consider it possible or necessary in all cases to try to decide between two, equally plausible, explanations. They set a high value on science but were passive in relation to scientific investigation. Furthermore it must be remembered that Epicureanism was generally held to be subversive by the state authorities and in consequence was the least influential trend among intellectuals, who came from the upper classes.

The Stoics were less interested in science. Its chief importance to them was how far it could be used to support religious or quasi-religious ideas about the unifying and guiding power of a divine intelligence ruling the world. In spite of a rational epistemology Stoicism therefore became increasingly infused by superstition: astrology and divination were adopted and made more dangerous by attempts to apply rational procedures to them. In biology the Stoics were especially taken with Aristotle's discovery of adaptation, but the idea was used by them in its most banal and unscientific form as evidence for a divine creator and provider. Thus in plants "the stems both give stability to the parts they sustain and also draw up sap from the ground, by which the parts on the roots are nourished; while the trunks are covered with bark or rind to protect them from heat and cold. Also vines cling to their supports with tendrils as with hands and thus raise themselves erect like animals."

These are examples in which "the rational design of an intelligent being is evident." It is characteristic that Balbus, the Stoic in Cicero's colloquy, speaks of an element that holds the whole world together and then goes on to find that in trees and plants this ruling principle is located in the roots. Thus resurrecting and embellishing for theological purposes a mistaken suggestion of Aristotle which Theophrastus had rejected.

Stoicism was more respectable and powerful than its rival philosophies and in various forms it represented the standpoint of the majority of administrators and intellectual leaders for several centuries, persisting into mediaeval times in various forms (Boethius, *Consolations of Philosophy*, for example).

38. There is evidence that the text of Theophrastus available to Pliny and Plutarch was fuller than the manuscript that has come down to us. Pliny also mentions a work "on flowers" by Theophrastus but this may refer to parts of the *Historia* since this title is not given in the catalogue of Theophrastus' writings listed by Diogenes Laertius.

    Manuscripts of Theophrastus were used by Porphyry, the editor of Plotinus, late in the third century, to support his views on vegetarianism, and manuscripts were also in the hands of Simplicius in Athens and Priscianus in Constantinople as late as the fifth century.
39. Pliny and Dioscorides were writing simultaneously and did not know of each others work. Pliny would certainly have named Dioscorides had he read him.
40. But it is evident (from *NH* XV,10) that Pliny had read (and characteristically misunderstood) the *Causes of Plants*. He also drew on the latter work for much of the information on agriculture in *NH* XVII, XVIII and XIX. For an account of some of Pliny's errors see J. André: Pline l'ancien botaniste, *Revue des Études latines* **33**, 297–318 (1955); for an appreciation of his merits see J. Stannard: Pliny and Roman Botany, *Isis* **56**, 420–5 (1965).
41. Pliny does not discuss any of the questions of principle raised by Theophrastus and does not even try to copy his systematic accounts of particular topics. The question of sex in plants receives only perfunctory and confused mention (*NH* XIII,31). On the structure of plants he ignores Theophrastus' careful analysis and simply offers a crude analogy with the skin, blood, flesh, bones and other parts of animals (*NH* XVI,181). He muddles together fruits and root-vegetables in a way that contrasts with Theophrastus' morphological precision (*NH* XIX,61).
42. Thus Pliny's first eight books on plants deal with plants in general and the following eight books specifically with medicinal plants.
43. Galan was born in Pergamum in Asia Minor in AD 129, an ancient centre of learning which had had close connections with the Lyceum in its heyday. It was a wealthy commercial city and something of a link between East and West. Galen was educated in Pergamum, Athens and Alexandria, and acquired a thorough knowledge of all the philosophic schools of

the time as well as the accumulated knowledge and experience of Greek medicine. The latter part of his life was spent in Rome as physician to the emperor Marcus Aurelius. Both scientifically and philosophically he was an eclectic, and represented the summation of the biology of his time in its strength and its weakness, including the narrowness and isolation into which botany had already fallen.

One botanical observation which he mentions incidentally (*On the Natural Faculties* I,XIV), namely, the uptake of water by wheat-seeds by imbibition, seems to be the first record of this phenomenon, although this property of seeds was evidently well known to farmers who used it to cheat their unsuspecting customers.

44. These tendencies were apparent to Pliny a hundred years earlier. "The reason why more herbs are not familiar is because they are only known to illiterate country people who live among them. . . . The most disgraceful reason for this lack of knowledge is that even those who know refuse to pass on their knowledge, as if they would lose what they impart to others." *NH* XXV,16.
45. Galen is amusingly scathing about writers on herbs who do not know them from personal knowledge but trust blindly to previous writers, who give them fancy names or repeat marvels and superstitions about them. He expressly warns against one Pamphilus, "who most of all is to be avoided, for he never saw, even in dreams, the plants which he undertakes to describe." (XI,792 ff. Kühn edition).

4

The Dark Ages of Botany in Europe (200 to 1483)

Philosophy is the material of the world's wisdom, the rash interpreter of nature and of the dispensation of God. Indeed heresies themselves are instigated by philosophy.

Tertullian: *De Praescriptione Haereticorum* 7 (*c.* AD 200)

Those philosophers whom we rightly hold the best [i.e. Plato and the Neo-Platonists], have said that the intellectual illumination necessary for learning about all things is God Himself, by Whom all things were made.

St Augustine: *De Civitate Dei* VIII,7 (between AD 413 and 426)

Even before the death of Galen in 199 Theophrastus' great synthesis was almost forgotten and the science of botany had degenerated into a drug-list.[1] Throughout the Middle Ages botanical theory was a blank page in knowledge and teaching, following the loss of Theophrastus' botanical works. As I have underlined, this loss was the result, not the cause, of the decline of interest in botany, but the disappearance of what was effectively the only existing textbook inevitably hastened the decline, as at a later period it retarded the rebirth, of scientific enquiry into plants.[2] Some knowledge of plants naturally persisted, since plants were the foundation of medical treatment as well as valuable articles of commerce,[3] while agriculture was the daily toil of nine-tenths of mankind, but botany was reduced to precariously preserved remnants of applied science from the past.[4]

Although barren of significant advance in theory, the centuries under consideration are a fascinating link between ancient botany and the modern science. In spite of some valuable studies there is still much to be discovered concerning the detailed pattern of mediaeval botany.[5] Here we shall only try to define the essential links of botanical transmission during some twelve centuries after Galen, a period that may be arbitrarily but not unfittingly terminated in the year 1483, when the newly recovered and translated botanical books of Theophrastus appeared in print, to reinforce a revival of scientific botany, the signs of which were already apparent.

The general decline of science in Hellenistic and Roman times caused botany to become once more a narrow adjunct of medicine. During the Middle Ages this close and exclusive connection with a single branch of medicine—pharmacology—determined the kind of plant knowledge that was transmitted. Without this link to a practical art botany might indeed have disappeared completely, but the result was restrictive and led to loss of both factual knowledge and systematic concepts. To trace the course of botany some aspects of the history of mediaeval medicine must be briefly touched on.[6]

Medical science as inherited by the early Middle Ages was in substance the Hippocratic rational tradition, culminating in the medical school of Alexandria, and expressed in the copious and dogmatic writings of Galen. The Romans had only primitive folk medicine or temple healing in the first days of the Republic: apart from the priests, who were essentially faith healers, medical men were of low social standing, usually slaves or freed men. As Greek medicine and physicians became established in Italy, the status of doctors rose and Julius Caesar gave citizenship to all immigrant medical practitioners, who were thus enabled to acquire wealth and position by private treatment of the well-to-do. A form of state medical service was later set up throughout the Empire. District physicians—distinct from the regular army doctors who moved with the troops—were appointed, whose primary duty was probably to give medical care to imperial officers and their families. In countries of both the western and eastern (Byzantine) empires, physicians thus became established as a profession with considerable independent standing, which they were able to maintain in consequence of the vitally important services they could render to the wealthier members of society. Doubtless altruistic physicians also treated the poor, but inevitably the latter would have to rely mainly on folk medicine and incantations, and most would live and die without any physicians's help.

The existence of a medical profession implies a system of medical education. In the east many of the ancient medical centres—Cos, Pergamum, Alexandria, Ephesus, Antioch—continued to exist without interruption as repositories of knowledge and as teaching centres, to which others, such as Constantinople and Edessa, were added later. In the west regular medical teaching began at Rome,[7] and as state medicine became organized, a system of medical training with state-paid professors was set up in a number of Italian cities, later extended further afield within the Empire, with medical schools at Carthage, Saragossa, Marseille, Bordeaux, Lyon, and other cities.

Many of these centres, both east and west, had a continuous history through all the troubled events from late classical until well into mediaeval times and the beginning of university medical schools, ancestral to those of our own day. It is certainly true that from the second to the ninth century the content of medical education declined to levels far below Greek medicine at its best.[8] The organization of teaching may sometimes have consisted simply in a youth's attaching himself apprentice-like to an established physician, as many records of father, son and grandson following one another in the profession suggest. Yet it is important to realize that even in the period of greatest intellectual darkness there was always some continuous medical education, and that it was essentially lay education, independent of clerical influence, and in the hands of the profession itself. This must be emphasized in view of the often repeated fallacy that the Church provided the doctors and medical training of the Middle Ages. In fact the Church forbade clerics to train as doctors, while its teaching was a severe hindrance to the progress of scientific medicine, first by its denigration of any empirical studies not directed towards strengthening belief in religion, secondly by its hostility to surgery and its complete ban on dissection of the human cadaver,[9] and thirdly by its explanation of disease as divine punishment for sin or lack of faith. Throughout the period medical men were indeed generally, and often correctly, credited with sceptical, anti-clerical and even heretical tendencies,[10] and they enjoyed, because of their professional services to the upper classes, a toleration that was not extended even to the most exalted in other spheres of life.

The continuity of medical teaching was vital to the survival of botany, although its scope was diminished to studying plants of pharmacological interest only. The relation of Dioscorides' *Materia Medica* to Greek botany and its establishment as the standard pharmacopeia has already been described. Manuscripts of the original Greek text were, from its first appearance, widely and continuously copied in the East and were early provided with illustrations. A famous manuscript of the sixth century[11] throws light both on the state of the best manuscripts at this time and on some features of mediaeval transmission, when Dioscorides was firmly established as a classical authority, to be followed without addition or change. Immense pains were obviously devoted to the production of this treasured manuscript, illustrated by water-colour drawings of nearly three-quarters of the 500–550 plants mentioned. Many of the figures, some almost certainly identical with the originals of Crateuas, are magnificent likenesses, drawn from living plants, making this a key in determining the botanical identity of the plants named by Dioscorides. Already, however, some thirty per cent of the figures have become unrecognizable or fictitious through mistaken or careless copying, and some plants are without illustration.

Apart from the *Naturalis Historia* of Pliny, which continued to be known and quoted, at least in the West, among all who were learned in Latin, the Dioscoridean list of medicinal plants constituted, throughout the Middle Ages and even beyond, the one repository of plant knowledge, kept in circulation by constant copying, because it was the standard work on pharmacology used by the medical profession. Latin versions of Dioscorides, for use in the western empire, appeared very early[12] and in the sixth century a full literal translation in five books was made, specially intended for use by barbarian doctors in Italy.

As Dioscorides was repeatedly copied the manuscripts accumulated errors, and the illustrations in particular degenerated and were more and more replaced by formalized, increasingly fictitious figures. These tendencies were made worse by the assumption, directly contrary to the forgotten plant-geographical facts carefully assembled by Theophrastus, that because the clinically recognizable diseases were universal so should be their antidotes: hence the attempts by physicians, apothecaries and copyists to identify their own local plants with those in Dioscorides, leading to further botanical confusion.

Characteristic of the intellectual regression of the early Middle Ages was the production of excerpts from authorities, which were then used for teaching and reference instead of the originals. Sometime in the fourth century an unknown compiler, using the pseudonym of Apuleius, produced an abbreviated version of Dioscorides containing only 129 plant remedies. Under the name of *Herbarium Apuleii* it proved very popular and many copies were made, with and without illustrations, some in vernacular languages, but naturally all exhibiting the same degenerative tendencies as the full versions.[13]

Until about the middle of the ninth century[14] botany existed in Europe and in Byzantium only in the form of Dioscorides or the potted version of Apuleius. On balance botanical knowledge regressed both quantitatively and qualitatively from what was known to Galen. There is no hint of original observation or thought and no independent botanical writing.[15] The section on plants in the encyclopaedic work of Isidore of Seville, written between 612 and 616, is entirely based on uncritical borrowing from Dioscorides, Pliny, Columella and a few other writers, and contains far less botanical information than his sources. Its only, rather dubious, originality is in the many fantastic etymologies of plant—and other—names. This feature caught the fancy of the learned world of the time and led to Isidore's being frequently quoted as an authority on plants (and many other matters) throughout the Middle Ages.[16]

Although the authority and the teachings of the Church were inimical to rational medicine, this is not to deny or minimize the simultaneous positive role of the Church, exercised through the monastic houses, in two activities which in the long run assisted medical progress, and were of special significance for botany. The care of the sick enjoined on the monastic orders, and the establishment of hospitals and infirmaries staffed and run by the monasteries, provided at least some permanent organization of medical care which was not open to the wealthy alone.[17] The monks and friars were not professional physicians, but some of them knew and used traditional herbal remedies, and a herb garden became in consequence a feature of most monasteries,[18] from which a genuine interest in plants was stimulated, with results that will be mentioned later. The activity of the monks in the copying of manuscripts was of supreme importance for learning during most of the Middle Ages, gradually being taken over by the universities and professional scribes from the twelfth century onwards. This occupation of the monks was of crucial significance for botany: all the manuscripts of Dioscorides, and the illustrations when present, were made and copied in the scriptoria of monasteries, and many must have found a place in monastic libraries.[19] The veneration attaching to Dioscorides, perhaps strengthened by a persistent folk-tradition of the magically beneficent virtues of herbs, probably accounts for the fact that the *Materia Medica* always continued to be transmitted intact, at a time when Galen and Hippocrates came to be represented in the West only by excerpts and isolated topics or by passages incorporated in the writings of the great Greek medical compilers.[20]

In the years when learning was at its lowest ebb in Europe and much of the East, and when even the written records of Greek medicine and science were endangered by fragmentation and loss, there began a renewal of intellectual life in Syria, centred on its capital Edessa. The fascinating history of this renaissance is far from fully documented and is outside our purpose: it seems to have been connected with the special position of this region, situated where the main east–west and north–south trade routes crossed, and astride the ancient Silk Road to China, with the additional good fortune of lying at the limit of Roman power and adjacent to the rival Persian Empire. While formally subject to Rome, the land of Syria thus enjoyed a degree of unusual political independence under local kings. These factors led to great industrial and commercial prosperity, and to the rise of a powerful and cultured class of Syrian merchants whose national resentment at the domination of Rome found expression in supporting the Nestorian heresy and in a passionate interest in Greek science.[21]

A medical school was founded at Edessa in the fourth century, and when this was closed for heresy by the Emperor Zeno in 489 the Nestorian teachers moved to Nisibis, for a few years, and then to Jundēshāpūr in Persia, 500 miles to the south. Here, with the support of the Persian Emperor, a university with medical school and hospital was established. The city became the most important intellectual centre of the time, where many streams of thought came into contact through the medium of the Syriac language.[22] It flourished for three hundred years, until, following the Arab conquest of Persia, Baghdad became the principal centre of learning and the Nestorian scholars were moved there, finding enlightened and generous support from the Abbasid Caliphs.

The importance of the Nestorian Syriac scholars does not lie in any original contribution to science but in their rescue, by translation, of many complete works of Greek science which might otherwise have mouldered into oblivion in the libraries of Byzantium. The collection and translation of Greek manuscripts began in Jundēshāpūr but was most active in Baghdad in the ninth century when many translations into Syriac and Arabic were made. In this way the principal achievements of Greek science came into the possession of the learned world of Islam as complete and accurate versions of the originals.[23]

Most important botanically was the Arabic version of Dioscorides, translated by a pupil of the physician Ḥunayn ibn Iṣḥaq, who himself corrected the text and conscientiously equated the Greek with the vernacular Arabic plant names. As a result Dioscorides became the basis of the Arab pharmacopeia, and the *Materia Medica* was reproduced in beautifully illustrated Arabic manuscripts which came into many libraries. In the prescriptions of Al-Kindī, the Arab philosopher, scientist and physician, and a contemporary of Ḥunayn, about 278 plants were mentioned by their vernacular names, and of these some 240 are found in Dioscorides although Al-Kindī does not quote directly from him.[24] This is an indication of how preponderant was the Greek herbal content in the Arab pharmacopeia: it continued to be the foundation of all subsequent Arab herbals, although drug plants from other sources were added later.[25]

Apart from Greek treatises on agriculture, of which several were translated into Syriac rather earlier, the only other work dealing with plants that was translated into Arabic was the *De Plantis* of Nicolaus of Damascus. This translation was by a less skilful hand than Ḥunayn, possibly his son's. Chance decreed that the assiduous collectors of manuscripts, sent out by the Caliphs and their wealthy grandees, stumbled on this obscure work but not on any of the few remaining copies of Theophrastus. The historical accident by which the muddled nonsense of Nicolaus, and not the science of Theophrastus, reached the Arab world, was singularly unfortunate for the progress of botany as will be seen.

The Arab conquests, from the middle of the seventh century onwards, were followed by a revival of science and philosophy throughout the Islamic dominions, in marked contrast to the intellectual stagnation in Christian Europe.[26] This sprang partly from the commercial prosperity made possible by Arab control of the main trade routes, partly from the enlightened tolerance of the Islamic rulers towards other creeds and from their generous support of scholarship. Even though the religious ban on human dissection was as rigorously applied in Islam as in the Christian world, there was lively progress in medicine, where the heritage of Greek medicine was revivified by Arab ophthalmology and by the translation of Indian medical classics. Progress was most vigorous in pharmacology; many new drugs and formulations were introduced by the Arabs, who systematically observed their effects and determined the appropriate dosage.[27] Persian, Arabian and Indian plant drugs were brought into use; by 1050 Avicenna included about 650 plants in his list of 758 drugs, embracing most of Dioscorides' herbs together with many unknown to the Greek and European pharmacopeia.

The Arab pharmacologists thus carefully preserved, and added to, the list of medicinal plants; they were not botanists, however, and as far as we know added nothing at all to theoretical botany.[28]

From this perforce inadequate outline of botanical transmission into the Arab world, we turn once more to Europe, where, about the end of the tenth century, the first hesitant movements of re-advance were beginning after some eight hundred years of almost complete scientific arrest. The change was associated with more settled conditions of life, accompanied by a significant increase in the rate of technical progress and a rise in trade and industry.[29]

Revival in biology began in fact earlier than AD 1000 with the appearance during the ninth century of an influential medical school at Salerno in central Italy, whose organization foreshadowed that of the later university medical schools. By 985 Salerno was already of established repute and was awarding the title Doctor to its graduates.[30] Although secular in origin it was strengthened by a connection with the neighbouring Benedictine monastery of Cassino, where the best texts of Greek medicine and botany were accessible. Salerno flourished for over three centuries: it was built rather on a return to the best features of Greek medicine as known at the time, than on breaking new ground,[31] but nevertheless became the seat of a true revival of medicine, in the long run not without considerable effect on botany.

An isolated gleam—it is no more—of a new way of looking at plants shines out of a curious contemporary poem, the *Hortulus* of Walafried Strabo, Abbot of Reichenan in Switzerland, describing twenty-nine plants, most of them medicinal, from the garden of the abbey, situated on an island in Lake Constance. What is new for the Middle Ages is not just the delight in plants as plants which infuses the somewhat precious language, but that the writer looked at them for himself instead of quoting some authority, and even expressed an appreciation of the problem of accurate nomenclature.[32] Otherwise the verses are of no scientific value, nor could they have influenced contemporary thought, for they lay forgotten in the library of St Gall for six hundred years. There was indeed no immediate change in botany, which declined yet further in the work known as *Macer Floridus*, probably written by another Abbot, Odo of Meung, some time before 1050. This extraordinary poem in Latin hexameters reduces the pharmacopeia of Dioscorides and Pliny to a list of the medicinal properties of seventy-seven plants, without even the brief plant descriptions found in his authorities. Nor did the Abbess Hildegard of Bingen add anything original in the first volumn of her *Diversarum Naturarum Creaturarum Libri XI*, compiled between 1150 and 1160, and giving the medicinal virtues of about 240 plants but no botanical information.[33]

Two developments connected with the Salerno medical school contributed to the slow stirring of fresh botanical ideas. The first followed the arrival there of one Constantine (Constantanus Africanus) in about 1065, a medical man from Carthage but many years itinerant in India and Persia. On returning to his home town he apparently got into hot water with the authorities and took refuge at the Naples court of the Norman Robert Guiscard. He probably had some brief association with the medical school at Salerno but soon retired to the monastery of Cassino and spent the rest of his life translating Arabic medical texts into Latin. These included Arabic versions of Hippocrates and Galen, and also original works of Islamic physicians which he passed off as his own. Constantine's translations are said to be poor and often incomprehensible,[34] and his significance is that he drew attention to the Arabic–Greek legacy of science a century before translation was taken up on a big scale. His translation of a drug list derived from Isaac Judaeus[35] containing 168 plant drugs, ten of them Oriental or Arabian and previously unknown to the West, was a reminder that plants outside the classical herb store existed and might be useful.

A second development, arising directly from the activity of the Salernitan doctors themselves, was the production of a number of medical treatises, some deliberately popular in style, but all distinguished by a practical, rational and non-religious approach. Among them was a new pharmacological herbal, written about 1150, which came to be known as *Circa Instans* and listed 273 drugs of which 229 were of plant origin.[36] Almost all the plants are drawn from Dioscorides and presumably represent the most generally prescribed classical drugs (a larger selection than in the *Herbarium Apuleii*), together with a smaller number of new drugs, some European and some from the Arabic pharmacopeia. The pharmacology was an advance on Dioscorides but the botany was not. The plants were listed in alphabetical order, devoid of botanical descriptions except an occasional note about habitat or regions of origin. Its importance for European botany comes from the fact that its up-to-date and rational pharmacology caused it to displace the *Herbarium Apuleii* and become the basis of most of the herbals of the later Middle Ages, overshadowing, although never completely driving out, Dioscorides' *Materia Medica* itself. *Circa Instans* was soon provided with figures and such illustrated versions rapidly became the commonest manuscript herbals and formed the source of text and figures for the first printed herbals published in the second half of the fifteenth century.

The renewed conception of botany as a science in its own right found its first expression in Adelard of Bath, the initiator of that revival of mathematics, science and logic in England in the twelfth and thirteenth centuries, the origins of which merit more detailed investigation than they have yet received. Of course there is no new botany in Adelard but it is very significant that the first six chapters of his *Quaestiones Naturales* (written between 1130 and 1140) should be devoted to theoretical problems concerning plants—even though the theory is no more than a re-hash of Hippocratic speculations.[37] An enlarged view of the field of study of botany begins again about this time, no doubt connected with a fairly general rise in the productivity of agriculture, the accumulated result of a complex of technical improvements.[38] The effect of these innovations was strengthened by the profound impact of the re-entry into Europe of Greek science and philosophy, together with the works of Islamic scholars in these areas, as a result of an outburst of translation from Arabic into Latin between 1175 and 1225, when, among other works, complete and accurate versions of Galen, Hippocrates, and the zoology of Aristotle became available.[39] In botany the stimulus was general rather than specific, since the only new works with botanical content to appear were the *Canon* of medicine of Ibn Sina (Avicenna) and the *De Plantis* of Nicolaus. The former immediately became a medical classic and was used for centuries in both East and West. Its botanical results were small, however. Although Book II contains many drug plants new to Europe there are no, or only the most sketchy, descriptions. In so far as the new drugs were used, they can usually only have been known as apothecaries' products.[40] The botanical effect was limited to awakening the conception—an important one for the time—that there could be other plants in the world worthy of attention besides those of Dioscorides and the Scriptures.

The appearance of Nicolaus' *De Plantis* as a representative of ancient botany was disastrous.[41] It was mistakenly ascribed to Aristotle, and its confused obscurity was inevitably invested with his authority. Roger Bacon was moved to deliver a five-week course of lectures on this work at the University of Paris, sometime between 1236 and 1247. Leaving aside the difficulties of mediaeval Latin, the lectures are in a philosophical idiom not readily comprehensible to modern thought. They discuss whether plants possess life, whether plants sleep, breathe, can be transformed into one another, can be mutually grafted, have souls—all questions treated in *De Plantis*. The whole is a scholastic exercise where statements from *De Plantis*, and conflicting passages from various genuine works of Aristotle, are reconciled not by relation to facts or observations, but by juggling with philosophical terms. Since Bacon recognized the role of observation and experiment in science more clearly than most of his contemporaries, his diversion into such sterile paths in botany is evidently attributable to his enthusiasm for what, unluckily, he took to be the wisdom of Aristotle.

Some refreshingly original observations were made by Bacon's somewhat older contemporary Albert the Great in his *De Vegetabilibus*, seven books on plants, forming part of an account of the universe written to educate his Dominican brethren. Albert was possibly attracted to natural science when a young man at the new University of Padua, already the leading medical and scientific centre of Italy. His work on plants was written between 1250 and 1260, perhaps suggested by Bacon's lectures, which he probably read or heard, since their years of teaching in Paris overlapped. What is certain is that Albert also fell a victim to Nicolaus' *De Plantis* which he naturally accepted as Aristotle's and on a level with the latter's zoology, newly translated by Michael Scott.

The first five books of *De Vegetabilibus* are a paraphrase of Nicolaus[42] with commentaries by Albert. He quotes some other authorities whom he considers reliable: principally Avicenna and *Circa Instans*, occasionally Galen and the inevitable Isidore. Albert did not and could not know Theophrastus,[43] and rather surprisingly seems to have known Pliny and Dioscorides only at second hand. His books are much in the style of Bacon's lectures.[44] Facts and fancies from Nicolaus are explained by speculative–deductive concepts of four-element theory or pepsis,[45] derived through Galen from the most outdated aspects of Aristotelean thought, which Theophrastus had already begun to criticize in his day. In addition there are characteristic mediaeval accounts of astrological influences on plants, of magical properties of herbs, and of wonders such as vines growing from acorns. Yet scattered among the misconceived speculations are many acute observations showing that Albert studied plants for himself. He noted morphological and anatomical details not previously remarked on, and observed the range of habitats open to plants and the existence of ecological groupings.

The two last books, which do not depend on Nicolaus, display Albert at his best. Book 7 is on agriculture, based largely on Palladius but with excellent factual accounts of contemporary practice. It is probably the best general work on agriculture since Columella and shows how scientific thinking was stirred by the current technical changes in agriculture. Book 6 is, however, of most botanical interest, being an account of the medical and economic uses of some 270 plants, of which about 250 can be identified to species or genus.[46] The plants are often described with remarkable botanical detail and accuracy, and comparison with Albert's sources shows that many of the descriptions are his own. Details of the structure of several flowers are fuller and more precise than even the best of Theophrastus or Crateuas.[47] The stamens in several plants are accurately described, and Albert considered that these structures are present, in larger or smaller number, in almost all flowers.[48] But he did not develop a general terminology nor approach the conceptual level already reached by Theophrastus in many areas of morphology and structure. In spite of honest and keen-sighted observation Albert could not transcend the intellectual limits of his time or of the authorities he conscientiously followed.

In the preamble to Book 6 Albert stresses his reliance on his personal experience or on the authority of authors whom he believes speak from their own experience.[49] This appeal to observation—a claim to merit in having seen for onself—distinguishes Albert sharply from other encyclopaedists of the period, men like Bartholomew the Englishman, Thomas of Cantimpré or Vincent of Beauvais, to whom it would never havc occurred that their duty went beyond copying faithfully from all the recognized authorities.[50] In this, and in his treatment of plants in a wider context than pharmacology, Albert looks forward to the botany of the Renaissance. But *De Vegetabilibus* remains a pointer to future developments rather than a contribution to them, partly because of its limited circulation in the age before printing, but mainly because its real merits were buried in the obsolete speculations and confusion of *De Plantis* and weakened by Albert's own explicit philosophical standpoint.[51]

In the Islamic world there was a parallel revival of botany during the thirteenth century, significantly in Andalusia, the most prosperous and technically advanced agricultural region of the Caliphate, where Arab and European culture met. Ibn al-Baytār was a physician of Malaga whose interest went beyond pharmacology and who travelled widely around the Mediterranean in search of plants. His treatise on drugs contained about 200 new plants in addition to about 1000 from classical sources. It was a critical summing up of many centuries of Arab pharmacology and had lasting influence in the Arab world but remained unknown and untranslated in Europe.[52]

In the thirteenth century the dawn-glow of modern science may first be seen. Conditions favouring the rise of modern science were *in statu nascendi* within mediaeval society, and although growth was slowed down again by economic recession, and perhaps also by the Black Death in the fourteenth and early fifteenth century, it was not to be halted. A great impetus to natural science was given by deep conflicts in philosophy which agitated the schools. Realism , the prevailing view throughout the early Middle Ages, was now challenged by the more materialist and commonsense standpoint of Nominalism.

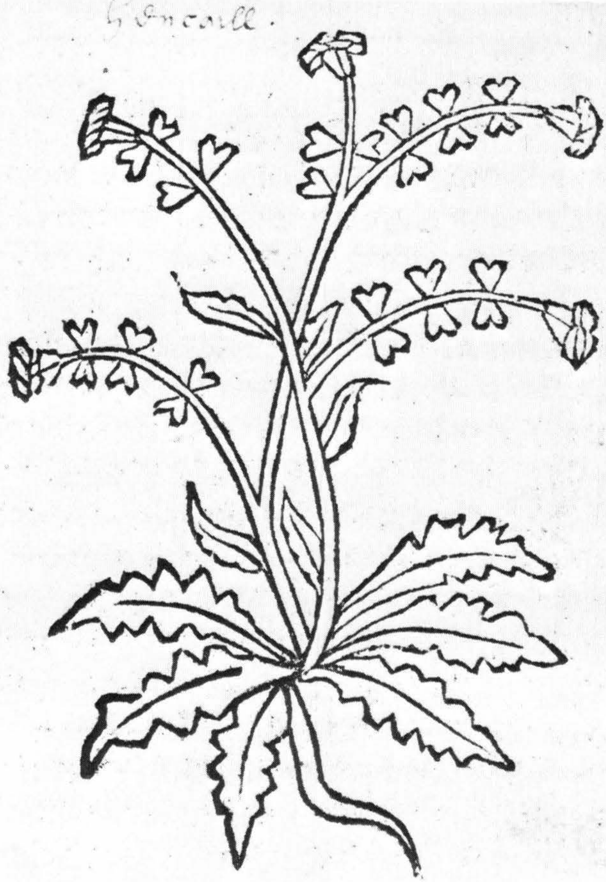
Although the term is now habitually used in a different or even contrary sense, Realism was a form of idealist philosophy, representing an extreme development of the Platonic doctrine of Ideas. According to this view, generic concepts or universals were held to be the primary reality, having an objective existence in the mind of God, of which their exemplification as individual phenomena in the material world is but a shadow. The general is therefore considered as more real than the particular.[53] In botany, the concept "plant" is the true, eternally existing reality, of which actual individual plants are but imperfect examples of subsidiary importance. How scientifically deadening this theory was, especially for biology, is witnessed by Albert the Great himself, a man of acute mind, genuinely excited by plants and convinced of the primacy of observation in science. Yet Albert obviously thought that the theories based on abstract universals which fill most of *De Vegetabilibus*, and which seem to us so boring and pointless, were far more important than his careful descriptions of living plants. He states categorically that theory cannot be deduced from studying specific plants,[54] and offers his account of the latter apologetically as a concession to the curiosity of students but scarcely worthy of philosophers.

Nominalism, the opposing philosophy, considered the individual phenomena revealed by experience to be the primary reality, holding that universals are mental concepts formed by applying logical thought to sense observations. Obviously Nominalism was closer to the view which, with whatever variations of philosophical emphasis, is the basis of modern scientific method. The first nominalist questioning of Realism began before the end of the twelfth century and long continued in the schools and universities as a bugbear to the orthodox, until between 1318 and 1324, the writings of William of Ockham at Oxford established Nominalism as the dominating philosophic trend during the late Middle Ages.[55] Nominalism had a very direct and positive influence on botany, in encouraging the gradual turn towards the study of the specific characteristics of each kind of plant, and away from the fossilized categories of ancient theory.

The universities, which appeared in the twelfth and thirteenth centuries, arose as a form of higher education different in some essential ways from anything previous. Although many grew up in old ecclesiastical teaching centres, and the Church usually contrived to establish some degree of formal control, most universities had, from their often shadowy beginnings, a certain independent and distinctively lay organization corresponding to their relation to the town bourgeoisie, now starting to assert its existence and separate interests. In Italy almost all the universities were municipal foundations, the professors salaried by the city. Indicative of their new social role was the weight given to science, which at first meant medical science.[56] From the beginning medicine was a leading faculty in the universities, bringing pharmacological botany with it as a normal part of a doctor's training. Botany was henceforward a university subject, an important fact for its future development but not leading immediately to any advance. In fact the doctors continued to rely uncritically on faulty versions of the classical herbals for information, and on their apothecaries for the supply of the drugs they prescribed.[57] The compilations of the thirteenth and fourteenth century encyclopaedists, which circulated in the universities, contained, as we have seen, nothing new.

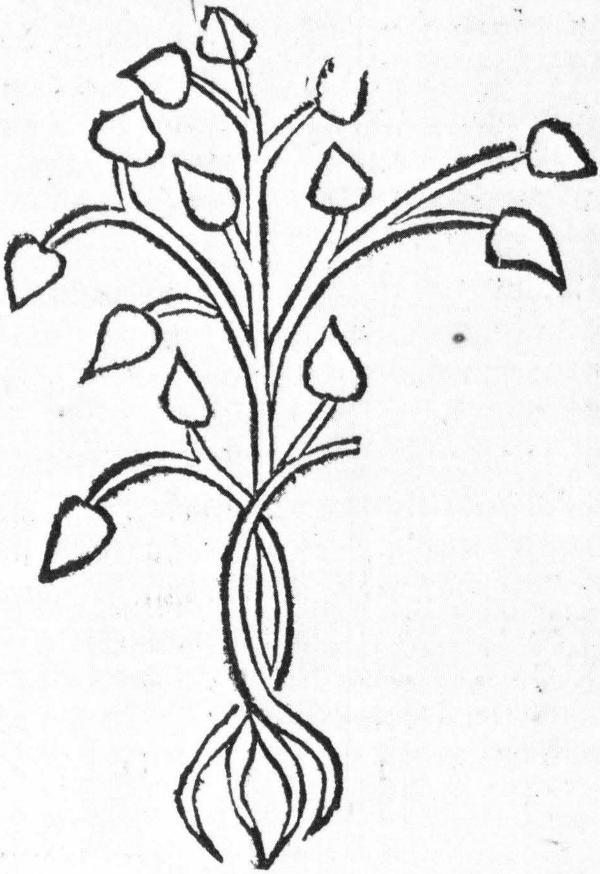
It is to the non-professionals that we must look for indications that a revitalization of botany was on the way—to the monks who copied and illustrated the manuscript herbals, and used herbs from the monastery garden in the infirmary, and some of whom now revealed an awareness of plants beyond the mechanical copying of earlier times. A product of the general intellectual movement that was beginning, their interest must have been specially roused by contact with the unwritten folk medicine that was still alive among country people. The existence of this primitive herbalism of the hen-wife and of the itinerant quacks and rural herb-gatherers, is widely attested. In England, the Anglo-Saxon medical recipes and charms contain the vernacular names of not a few native herbs unknown to the classical herbals.[58] The monks learnt, and no doubt used, the virtues of local herbs—knowledge from which the wealthy town physician was cut off—and realized that the plants they gathered and grew were different from the simples of official medicine. It thus came about that local plants were sporadically added to the classical herbals; sometimes a familiar plant

Figure 5 A plant of shepherds-purse is just recognizable as pictured in a *Herbarius* printed about 1486 in Louvain (now in the Library of the Royal Botanic Garden, Edinburgh).



Bursa pastoris   Teschen cruyt

Bursa pastoris siue sanguinaria e fri. cplexois . hz virtutē stipticādi et sūt due spēs vna hz folia ī modū pere τ dicitur bursa pastoris sz alia dicit̄ cētiodia τ ē herba serpēs super terrā hñs folia ī modū rute τ scz hz circa folia τ dicit̄ etiā ligua passerina Hec herbe mltū iuuāt ad apostēata calida scz ad erisipilā et vz. similiter ad flecmones siue postulas rubicundas



Fraxinus **Eschen**

Fraxinus frigidus et siccus i scdo virtus eius est que cum fuerit recens conglutinat vulnera recentia ꝛ aq̄ i q̄ folia recētia fraxini cū radice eius sint cocta i mo/ dū ēplastri cōfert fractuē ossiū ipa cōglutiando ꝛ con solidādo Itē vinū decoctōis cortic̄ fraxini ꝛ cortici ta maiscī datū i potu ifallibiliter splē3 attenuat Nā res ꝓ bata ē q̄ si detur procello bibere aliquibus diebus et ments with plants.[64] These would be the earliest recorded experiments in plant physiology were there the least evidence that they were ever carried out, but Cusa did not push his ideas to the test of practice (or did not consider the results important enough to record). His brilliant anticipations were thus as fruitless as those of Leonardo da Vinci at a later date.

Botany continued with barely perceptible internal movement during the closing centuries of the Middle Ages, although the forces and events that were factors in the revival of botany in the sixteenth century, were already in train. It will be more convenient, however, to depart from strict chronology and deal with these factors and their relation to botany in the following chapter, and to conclude our survey of mediaeval botany with the event which catalysed the transformation of the science to a new stage. This was the appearance in Latin translation of the long-vanished botanical books of Theophrastus, which the lately introduced Chinese technique of printing now made available to every learned man in Europe.

The rediscovery of Theophrastus was part of the Renaissance and of the enthusiasm for classical learning and science which was at first a passionate revolt against the narrow boundaries of mediaeval thought and later became a critical revaluation of classical thought itself. Libraries were searched for original sources and manuscripts, especially Greek, and Pope Nicholas V instituted a scheme for the translation of those discovered in the Vatican. Here manuscripts of the *Historia Plantarum* and *Causae Plantarum* turned up and were translated by Theodore Gaza, a native of Thessalonica who fled to Italy some time before 1430 when Greece fell to the Turks.[65] He became Professor of Greek at Ferrara and later Professor of Philosophy at Rome. There is no evidence that Gaza was a botanist but his translation was sound and scholarly and a remarkable accomplishment for his day, although he relied fairly heavily on Pliny's rendering of many passages. No history of botany would be complete without remembering this distinguished scholar who made known to the modern world the greatest achievement of ancient botany at a time when it could still be scientifically useful.

was substituted for an unknown mediterranean herb under the old classical name, leading to increased confusion, but in other cases the vernacular name was put in to show a genuine addition.[59] Glosses and comments on the text show that some of the monastic writers were seriously concerned to establish unambiguous naming of medicinal plants, and this is further demonstrated by the many common plants, especially of northern and western Europe, which were given newly coined vernacular names by the monks to prevent confusion with classical plants.[60] In some manuscripts there are original descriptions of native plants that are a step towards descriptive botany: whilst in the illustrations signs of progress curiously intermingle with examples of complete degeneration; beautifully executed realistic drawings of plants from life, instantly recognizable, may be found alongside figures that have become meaningless by bad copying.[61]

The fascination of these pointers to future growth should not lead to exaggeration of their significance. They are isolated phenomena, not records of progress. Nomenclature and plant description were still imprisoned in the needs of pharmacology. Description was not the comparative science of plant form, as Theophrastus had already conceived it, but helpful hints for the herb-gatherer. The laudable aim of building a firm and accurate nomenclature was equally limited by lack of botanical theory: there was even a counter-tendency to name plants according to their reputed pharmacological properties,[62] and so negate rational botanical nomenclature, to which the true approach had also been indicated in principle by Theophrastus. While medicine remained tied to Galenism, and anatomy and physiology were stultified by the ban on dissection, there was no stimulus from this source to investigate plant structure and anatomy. Botanical theory did not exist or was reduced to empty Hippocratic–Galenic speculation carried over from medicine.[63]

One strangely isolated prophet of experimental botany must be mentioned at this point. In 1450 the learned and intelligent Cardinal Nicholas de Cusa proposed a number of experimental investigations using quantitative methods, that is, weighing, including experi-

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Figure 6 The figure representing an ash tree in Louvain *Herbarius* is debased beyond recognition.

Notes

1. This summation of mediaeval botany in Europe is quoted from Charles Singer's *Short History of Medicine* (1928). Yet the connection with practical medicine at least saved botany from the eclipse suffered by zoology, which sank from Aristotle to mythical and moral bestiaries derived from the *Physiologus*.
2. Galen was the last scientific writer for nearly 1300 years who quoted Theophrastus at first hand. Some mediaeval writers knew that Theophrastus wrote about plants but as far as I am aware all references to him are second hand, derived from Pliny, Plutarch or Galen (but see Note 47 on Peter de Crescenti).

   No genuine quotation from Theophrastus appears in the *Geoponica*, a selection of miscellaneous bits and pieces from ancient writers on agriculture, assembled by the Byzantine scholar Cassianus Bassus about 550 and re-edited about 950 by order of the Emperor Constantine VII Porphyrogenitus. An early mention of Theophrastus after the rediscovery of his work is found in *Hortus Sanitatus Major*, printed in 1491 in Mainz.
3. A list of goods subject to special import tax in the Roman Empire in the year 180, contains at least twenty plant products that were important articles of trade, including pepper, ginger, gum arabic, raw cotton, silphium (probably *Ferula tingitana*), the lichen *Roccella fusiformis* (used for dyeing), and valerian root. This list excludes cereals, nuts and food plants. (See H. E. Dirksen: *Abhandlungen der kaiserlichen Akademic zu Berlin* (1843).)
4. This preoccupation with the applied aspects of botany had already been emphasized by Pliny and was strengthened by his great influence. "Principium iure tribuetur homini, cuius causa videtur cuncta alia genuisse natura magna." *NH* 7,1. (The first place is rightly given to man, for whose sake all other things seem to have been produced by great Nature.)
5. Most of the primary sources of mediaeval botany are mentioned in the text. Indispensable for information on all aspects and especially on mediaeval plant nomenclature and synonymy is H. Fischer: *Mittelalterliche Pflanzenkunde*. München (1928).

   Also useful are the following:

   G. Brodin: *Agnus Castus—A Middle English Herbal*. Uppsala (1950).

   J. Camus: Herbiers. *Malpighia* **9**, 283–314 (1895).

   C. M. Haskins: *Studies in the History of Mediaeval Science*. Cambridge, Mass. (1927).

   C. Singer: The herbal in antiquity. *Journal of Hellenic Studies* **47**, 1–52 (1927).

   C. Singer: *From Magic to Science* (1928).

A comparative study of all extant plant lists of the Middle Ages would be invaluable in throwing light on changes in floristic knowledge, but the uncertainties of early plant names, the fragmentation and dispersal of manuscripts, the linguistic and dating problems, and the necessary collation of floristic with pharmacological data, would make it a formidable task: which is why no one seems yet to have made the attempt.

6. For information on mediaeval medicine and pharmacology the relevant sections in the following works have been found useful.
H. P. Bagon: The masters of Salerno and the origins of medical practice. In *Science, Medicine and History* **I**, 203–19 (1953).
A. Castiglione: *A History of Medicine*. New York (1947).
G. G. Coulton: *Mediaeval Panorama* (1940).
B. L. Gordon: *Medicine Throughout Antiquity*. Philadelphia (1949).
D. Guthrie: *A History of Medicine* (1945).
H. E. Sigerist: *On the History of Medicine, Mediaeval Medicine*. New York (1960).
C. Singer: *A Short History of Medicine* (1928).
L. Thorndike: *History of Magic and Experimental Science*, 6 Vols (1934–41).
J. J. Walsh: *Mediaeval Medicine* (1920).
7. The first regular teacher in Rome was Asclepiades (*c.* 40 BC), a Greek from Bithynia in Asia Minor, an Epicurean and atomist. He was an empiric, laying stress on observation, and his therapy was principally dietetic. It is significant that about 80 years after the institution of formal medical teaching in Rome, Cornelius Celsus published the first Latin list of 250 drug plants, closely followed by Scribonius Largius who gave 140 plants and equated the Greek and Latin names. Both pre-dated Pliny, who cites Celsus as an authority but not Scribonius. The medical books of Celsus are a valuable and scholarly source of information on ancient medicine, written in elegant Latin; they were based on Greek sources including the writings of one Aufidius, a Sicilian physician. The Latin plant list of Celsus would therefore be derived directly from the Greek pharmacopeia used in the Greek-speaking medical centres that long survived in Sicily and southern Italy.
8. The content of medical teaching was essentially a corrupted form of Galenism. The full texts of Galen and Hippocrates were lost and excerpts, more or less inaccurate, were used as substitutes, supplemented by the compilations of the Greek medical writers (see Note 20, below).
9. The Church had no particular moral objection to cutting up the living body in warfare, since this form of dissection was not directed to the pursuit of either healing or science.
10. Chaucer's Doctour of Phisik was not noted for his piety—"His studie was but litel on the Bible". Three hundred years later Sir Thomas Browne, himself a doctor, said, "Ubi tres medici, duo athei".
11. The manuscript was made in Constantinople about 512 for Juliana

Anicia, daughter of Olybrius, Emperor of the West in 472. See R. W. T. Gunther: *The Greek Herbal of Dioscorides illustrated by a Byzantine A.D. 512* (1934), which gives the seventeenth century English translation by John Goodyer, with line illustrations of many of the figures.

12. The first Latin translation of Dioscorides was a rather free version, probably by Gargilius Martialis about AD 250. This may be the version referred to by Cassiodorus (see Note 26, Chapter 3). Other translations followed, and in the fifth century a true literal translation in five books was produced for barbarian doctors who did not know Greek. It was used by Italian, Frankish and Salernitan doctors, and was the textual basis of most of the mediaeval manuscripts of Dioscorides.
13. The unknown compiler was variously called Apuleius Barbarus, Apuleius Platonicus or Pseudo-Apuleius. He was not the Apuleius who wrote the well-known story of "The golden ass".

    The popularity of the *Herbarium Apuleii* is shown by the existence of an illustrated Anglo-Saxon translation, of which there is a manuscript in the British Museum. (See A. J. G. Hilbelink: *Herbarium Apuleii*. Amsterdam (1931) for an edition of the text.)
14. The year 850 may not unreasonably be taken to divide the period covered by this chapter into two. From 200–850 technical and scientific progress was minimal, feudalism was in the making but not stabilized, centralized authority was absent over wide areas, and there was general social insecurity. After about 850 more stable, centrally organized and governed, feudal states began to emerge, in which technical and intellectual progress was resumed.
15. The depth to which botany sank in the early Middle Ages can be appreciated from the fact that the sermons of St Basil (329–79) on the six days of creation were for long a textbook of natural history in the schools. The following passage (*Hexaemeron, Hom. V*) shows the ignorance and confusion to which classical science had given place: "People ask why the Scriptures declare that all things growing from the earth give rise to seed, when neither reed, nor grass, nor mint, nor crocus, nor onion, nor rush, nor many others, appear to produce seed. To which I say, many things growing from the earth include the power and virtue of seeds in their lower parts and roots. The reed, for example, at the end of the year puts out from the root a kind of extension which in the future is the origin of the seed. Numerous other plants dispersed about the earth do the same and enclose their progeny in their roots. So nothing is more true than that individual plants contain in themselves either seed or some seminal principle."

    In the West only two writers on plants (before Isidore) require mention. Theodorus Priscianus was a Roman physician who published, towards the end of the fourth century, a list of about 200 medical plants, some of which are not found in either Dioscorides or Pliny. Marcellus of

Bordeaux as a Celt whose medical writings (*c.* 410) were almost entirely cribbed without acknowledgement from Scribonius Largius with the addition of much superstitious nonsense. Their botanical interest lies only in the inclusion of the vernacular Gaulish names of a number of plants.

In Byzantium only fragments from the older georgic writers were preserved, often mingled with superstition. Except for a useful glossary of Arabic plant names, no writings of botanical significance are known. See Margaret H. Thomson: *Textes Grecs Relatifs aux Plantes*. Paris (1955).

16. It may be claimed for Isidore that he did not treat plants solely as objects of pharmacology, but in this he was merely following Pliny and was much inferior to his source. He mentions about 230 plants from classical writings grouped as trees, aromatic herbs, vegetables, scented herbs.

    His etymologies are entirely fanciful: *ulmus* (elm) is so called because it derives advantage from *uliginosis locis* (marshy places), *ficus* (fig) comes from *fecunditas* (fecundity), *laurus* (bay) from *laus* (praise), *juniperus* (juniper) from *pir* (fire), and many similar absurdities. Isidore was probably inspired by Varro, and set a fashion for false etymology of extraordinary persistence, which added its minor share of confusion to botany.
17. In the Middle Ages the Church undertook several functions which later came to be done by the state or by secular bodies. The Emperor Theodoric specifically assigned the care of the sick to the Church.
18. The contents and plan of the herb garden at the monastery of St Gall in Switzerland are on record.

    Alexander Neckham (late in the twelfth century) mentions about thirty herbs found in a herb garden but recommends some exotic plants that would certainly not grow even in southern Europe.
19. The Benedictine rule recommended copying of manuscripts as a suitable monastic occupation. Many classics were thus preserved at a time when actual study of them was not encouraged because of their paganism. There is some evidence of specialization. The monastery of Cassino, a Benedictine foundation, was active in transmitting Latin versions of Dioscorides whereas Bobbio, a Celtic foundation, was the source of the Greek texts.
20. The Greek medical compilers Aëtius, Oribasius, Alexander of Tralles and Paul of Aegina, preserved in their writings much of the history and heritage of Greek medicine that was transmitted through Alexandria. The two last give lists of plant drugs. Alexander of Tralles (525–605) recorded original clinical observations and was the first to define the pharmacological uses of rhubarb and colchicum. His works were known to the doctors of Salerno and of the later Middle Ages.
21. Syrian merchants reached all parts of Europe and North Africa at this period and also financed trade to south–west Arabia, India and Ceylon by way of the Red Sea. In the fifth century St Jerome noted the Syrians carrying on their profitable trade, unfeelingly regardless of the difficulties of the disintegrating Roman Empire.

The Syrians accepted Christianity at an early date and were very active in spreading it in Asia Minor, Egypt and Mesopotamia. They were the first to translate the Old Testament into a vernacular language, and one of the reasons for the intense interest of Syrian scholars in Greek was their desire to study the Greek translation (the Septuagint) that had been produced in Alexandria from a somewhat different original Hebrew text. See A. O. Whipple: The role of the Nestorians as the connecting link between Greek and Arabic medicine. *Annals of Medical History* **8**, 313–23 (1936).

22. Jundēshāpūr welcomed the Neo-Platonists expelled from Athens when Justinian closed the Academy in 529 (thus establishing a philosophical tradition that subsequently powerfully influenced the direction of Islamic thought). It became the meeting place of Greek, Jewish, Persian and Hindu ideas, exchanged through the medium of the Syriac language. The medical school trained physicians for all the Islamic countries.
23. In the ninth century an institute for translation, complete with library, was set up by the Caliph in Bagdhad with Ḥunayn ibn Isḥaq at its head and a large staff of assistant translators. (For details see M. Meyerhof: Science and medicine, in *The legacy of Islam* (1931).) Ḥunayn was a physician and linguist of remarkable ability who wrote an original treatise on ophthalmology, the first systematic work on the subject. He employed the modern method of collating all available manuscripts to establish a critical text from which the translation was made.

    To his labours we are indebted for the fullest collection of the works of Galen, as well as versions of Hippocrates and Oribasius—all of vital importance in the re-awakening of medicine in Europe in the later Middle Ages.
24. M. Levey: *The Medical Formulary or Agrābādhān of Al-Kindī.*

    Levey makes the important point that the existence of Babylonian plant names in *Al-Kindī* is evidence of a continuous *oral* tradition of herbal knowledge, persisting for centuries although all direct written connection was broken.
25. M. Meyerhof: Die Materia Medica des Dioskurides bei den Arabern. *Quellen und Studien zur Geschichte der Naturwissenschaft und der Medizin* **3**, 72–84 (1933).

    Although Avicenna included in his *Canon* many plant drugs additional to those in Dioscorides, two hundred years later the writer known as "Serapion the Younger" only gave a very few non-Dioscoridean herbs in his list of about 360 drugs.
26. To discuss the sources of this intellectual revival in relation to the philosophical and social foundations of Islam would exceed the limits of the most extended note, but the far more tolerant attitude of Islam to other religions and to diverse philosophies, deserves emphasis. It provided a more favourable environment for scholarship and the fostering of learning from all sources, than did the heresy-hunting of Christendom.

27. For an account of Arab pharmacology see E. J. Holmyard: Mediaeval arabian pharmacology. *Proceedings of the Royal Society of Medicine: Section on History of Medicine* **19**, 99–108 (1935).
28. This statement may well require revision when the wealth of unknown Arabic manuscripts has been fully examined.
29. The most significant technical advance was the use of the water-wheel as a means of power. The water-wheel had been invented as early as the first century BC, but conditions for its widespread use only developed when feudal organization was fully established. After about AD 500 the water-wheel came into general use for grinding corn and then in the twelfth century began to be used in fulling mills, for driving hammers and bellows in forges, for sawmills, for pumping and ore-crushing in mining, and for other industrial processes. Windmills spread through Europe during the twelfth century and were used for similar purposes.

    There was a corresponding increase in mining, especially of iron, and in the availability of iron tools for agriculture.

    For details see G. A. J. Hodgett, S. Lilley (loc. cit.)
30. The reasons for the rise of a medical school at Salerno, and its early history, are both obscure. It seems to have been a health resort for the wealthy from quite early times and no doubt physicians would tend to congregate there and the teaching of medicine would follow. Geographically Salerno was well placed to draw on the various schools of medical thought; it was in the part of Italy where former Greek colonies still preserved the Greek medical tradition, and close to Sicily where an Arab medical school was established in Palermo following its conquest by Islam in the first half of the ninth century. The legend that Salerno was founded by four doctors, a Greek, a Jew, a Saracen and a Salernitan, thus contains some truth. See H. P. Bayon: The masters of Salerno and the origins of medical practice. In *Science, Medicine and History* (1953). P. O. Kristeller: The school of Salerno. *Bulletin of the History of Medicine* **17**, 138–94 (1945).
31. The medical teaching at Salerno was based on the classical writers as then known, and was free from astrology and magical formulae. Disease was ascribed to natural causes (the Galenic theory of imbalance of the four humours) and not to the visitation of God. Human dissection was not done but the pig was used instead.
32. Walafried wrote his poem *c.* 840 but it was not found and printed until 1509–10. He expresses doubts whether the ambrosia (probably tansy) in his garden is identical with the plant called so by ancient writers, and comments on the difficulties of knowing correctly the properties and the names of the many species of mint. Characteristically, in a reference to the whorl of stamens in *Rosa*, based on a passage in Pliny, he uses the rare word *crementa* (growths) which has no technical connotation, and which he does not apply to any other flower.

An edition of the *Hortulus*, with an excellent English verse translation by Raef Payne, was published in Pittsburgh in 1966.

33. I cannot find any evidence for Singer's view that Hildegard herself made original observations on plants. The two books on plants (I and III) in her *Diversarum Naturarum Creaturarum Libri* IX, whether hers or merely attributed to her, are entirely derived from Dioscorides, Pliny and other sources. The only original features are the German vernacular plant names side by side with the Latin, and the inclusion of a few north European plants.
34. Constantine seems to have been a rather shady character. He published Ḥunayn's *Ophthalmology* as his own. Chaucer refers to him as "the cursed monk, Dan Constantyne", apparently because of his treatise (or translation?) *De Coitu*.
35. Isaac Judaeus (855–955) was physician to the rulers of Qairawan in Tunisia.
36. The title *Circa Instans* is derived from the opening sentence, "Circa instans negotium de simplicibus medicinis nostrum versatur propositum." (Our task is with the important question of simple drugs.) Its author was probably Joannes Platearius.

    The production of popular, but sound and practical, manuals on medicine became a speciality of Salerno. *Circa Instans* was one of these. It marked a sharp break with the "moral" herbal, a popular degeneration in which a moral or religious significance was attached to each plant, as for example in the section on plants in the *De Universo* of Hraban of Fulda (784–856). Hraban's information was copied from Isidore of Seville with allegorical additions.
37. Adelard (*c.* 1080–1145) was a mathematician and philosopher who probably studied at Chartres and later travelled as far as Syria, Greece, Sicily and Spain (Toledo) in search of knowledge, especially the new learning of the Arabs, receiving maintenance while abroad from Henry I of England. He translated from Arabic the *Elements* of Euclid and the astronomical treatises of al-Khwarismi, and wrote on the astrolabe and on falcons. He was ahead of his time in stressing the need to look first for rational causes of phenomena before invoking the supernatural, and in his contempt for mere authority. Yet in his *Quaestiones Naturales* the answers to the questions posed about plants—why plants grow from unsown soil, why some plants may be warm by nature although all grow from earth which is cold, why plants of opposite natures grow from the same soil, why plants do not grow from water, air or fire, although these are all compound, why the fruit follows the nature of the graft and not the stock—are simply based on ancient Hippocratic notions expressed in the speculative form that Galenism took in the Middle Ages.

    About fifty years later Alexander Neckham of St Albans (1157–1217) included a discussion of plants in his *De Naturis Rerum* and in his poem *De Laudibus Divinae Sapientiae*. He asks the same questions about plants as did Adelard and gives answers similarly derived from Hippocratic and Galenic theories (he had attended lectures on Hippocrates and Galen in Paris, as he himself records). He uses four-element theory to explain why there are no green flowers, unaware that Theophrastus had recognized the existence of green flowers centuries earlier. He mentions over a hundred economic and medicinal plants, naming Dioscorides and *Macer floridus* as authorities. Both Adelard and Neckham wrote before Nicolaus' *De Plantis* was translated.

38. Several technical advances spread gradually, albeit unevenly, through Europe from the eighth century onward. (See Lynn White: *Mediaeval Technology and Social Change* (1962); H. A. Miskinin: *The Economy of Early Renaissance Europe* (1969); Lilley, Hodgett (loc. cit.).) Most important was the replacement of two-field by three-field rotation which increased both soil fertility and the area under crops at any one time. The use of marl and dung for manuring (in themselves ancient practices) became more general, and the proportion of land sown to legumes (mainly peas) was increased. Additional crops such as oats, rye and buckwheat were grown more widely than heretofore, especially in northern Europe. The hinged flail was invented and greatly simplified grain harvesting. The harrow was used for covering sown seed as well as for weeding, and the heavy iron plough attained essentially its modern form. Finally, the introduction (from the East) of iron horseshoes and an improved form of harness enormously increased the efficiency of horsepower and made possible its fuller use in agriculture.

    All these factors together were the potential for considerable increase of agricultural productivity, and the adoption of the new techniques was hastened by the urgent need of the land-owning class to secure more from agriculture at a time when the development of a money economy was raising serious economic problems for them. (See M. H. Dobb: *Studies in the Development of Capitalism* (1946).) At the same time, the potential for higher production was checked by the unproductive nature of servile labour, a conflict which ultimately swept away the feudal social relations which engendered it. The actual movement of agriculture was therefore both complicated and uneven, yet, by and large, there seems no doubt that agricultural production rose, as witnessed by the growth of towns and the doubling of the population in Europe between 1000 and 1300.

    The point is that both technical advance and social tension centred in agriculture during this period and so began to focus attention on long neglected aspects of botany outwith the narrow field of pharmacology.

39. One reason why Arabic learning exerted such a powerful attraction in Christendom at this time was the relatively much greater commercial prosperity of Islam, based on control of the main trade routes. The great centres of translation were Sicily and Toledo. Jewish scholars played an important part in the work of translation.

40. This is exactly how exotic products are described in the herbals. Thus in *Hortus Sanitatis* (1497) behem (probably roots of *Silene inflata* or *Statice limonium*) is simply "radices exsiccata" (dried roots), camphoraca (*Cinnamomum camphora*, a tree) is "herba cuius succus multipliciter utilis in medicina" (a herb whose juice is medicine for many purposes).
41. *De Plantis* was translated from Arabic into Latin by Alfred of Sarashel, known as Alfred the Englishman, in Toledo about the year 1215, and was dedicated to Roger of Hereford. It should be noted that the Greek version published among the minor works of Aristotle (Loeb edition, 1963) is in fact a mediaeval re-translation into Greek made from Alfred's Latin. The English text is thus derived as follows: Nicolaus' original Greek text → Arabic → Latin → Greek → English. The translation in the *English Aristotle*, Oxford (1913) is more direct, coming from the Latin. Roger Bacon criticized Alfred's translation for its errors (J. E. Sandys: *History of Classical Scholarship* (1903)). We do not know how accurate the Arabic translation was. It may be that Nicolaus' book was more sensible in the lost original but what survived was a botanical disaster.
42. Although essentially correct, this statement must be qualified for anyone who wishes to explore *De Vegetabilibus* for themselves. Books I and IV are paraphrases of Nicolaus' two books, and Books II and V are Albert's comments thereon. Book III is a paraphrase of a work of Avicenna dealing with the taste of the juices, fruits and seeds of plants.
43. It is necessary to emphasize this in view of the statement by G. Sarton (in *The Appreciation of Ancient and Mediaeval Science during the Renaissance*. Philadephia (1955)) that "almost the only Christian scholar who read Theophrastus in a creative way . . . was Albert the Great". This is the rare occasion where a great scholar nodded. Apart from the fact that there is no trace of Theophrastus in *De Vegetabilibus*, Albert himself says (II,1,15), "Dicunt autem, Plinium apud Latinos et Theophrastum apud Graecos hanc tenuisse sententiam", which clearly implies that he had read neither Theophrastus nor Pliny. We know also that Albert could not read Greek.
44. Whether there is any significant difference between the botanical speculations of Albert the Dominican and his critic Bacon the Franciscan might be a nice enquiry for a PhD thesis but is not relevant to the history of botanical theory.
45. Pepsis in Greek meant originally softening and, by extension, cooking of food and ripening of fruits. In the Hippocratic corpus, and by Aristotle, pepsis was used as a technical term for the process of digestion and for the "concoction" of physiological "excretions" like bile or semen or even the embryo. Aristotle says "all pepsis works by heat", and concludes that male animals are hotter than female because the latter cannot produce semen (formed from blood by pepsis). Similarly Aristotle thought that the male fig tree (caprifig) helped the female in the formation (pepsis) of

the fruit (by supplying heat). Pepsis became a blanket explanation for various physiological processes and transformations of matter.

46. Albert made particularly clear observations in plant anatomy, recognizing vascular bundles, medullary rays, annual rings, cortical sclerenchyma, and the distinctive nature of the wood of the date palm ("quasi ex asseribus compositum et non ex circularibus tunicis crescens", i.e. as if made up of stakes instead of growing in circular layers). See T. A. Sprague: Plant morphology in Albertus Magnus. *Kew Bulletin* 431–40 (1933).

    A sample of Albert in English is given by E. Grant in *A Source Book in Mediaeval Science*. Cambridge, Mass. (1974).

    Albert divides his plants into trees (about 90 species, including some shrubs) and herbs (about 180 species). He includes about 40 exotic species which he is not likely to have seen himself (unless perhaps at Padua). There is quite a good description of the banana (classed as a tree, *arbor paradisi*, but correctly noted as dying down each season like a cucumber). The best descriptions are of plants he encountered when travelling on foot on official visits to monasteries in Germany and nearby lands.

47. His fullest description is of the flower of borage (*Borago officinalis*) where he noticed the relations of calyx, corona, stamens and style, the constant number of parts in each whorl and the alternation between whorls. He classified the general form of flowers as bird-like (roughly corresponding to bilaterally symmetric or zygomorphic), bell-shaped or pyramidal, star-like (the commonest form), and intermediate between star and bell.

    Albert is less clear than Theophrastus in describing the morphological and functional relation between flower and fruit; he also interpreted the compound leaf as a system of branchlets with small leaves. He repeats the Aristotelean view that the function of leaves is to protect the fruit.

48. "Est tamen non praetereundum hic, quod omnis fere flos, cuiuscunque sit plantae, in medio sui habet granulorum congeriem per parvulos cotyledones fundo floris infixam." (II,2,4). Albert uses *cotyledo* in several morphological senses but never in the modern one. Here it means either the stamens or the filaments, depending on whether *granulorum congeries* means pollen or the whole antlers.

49. It is noteworthy that Albert stresses the importance of observation (*experimentum*) for studying individuals (*in particularibus*) but not for theory (*in universalibus*).

50. The encyclopaedists added nothing to botanical theory or plant description, and are generally inferior to the authorities from whom they took their matter. It was, however, a sign of the times that they attempted to return to Pliny's general treatment of plants, instead of remaining entirely within the limits of pharmacology.

    Bartholomew the Englishman wrote his *De Proprietatibus Rerum* between 1225 and 1240. Among the nineteen books the seventeenth is about plants. Bartholomew wrote too early to quote Albert but he had read Nicolaus' *De Plantis*, which he naturally attributes to Aristotle and from which he includes many passages, both long and short, almost literally transcribed. In one place he calls Nicolaus' book "de vegetabilibus Aristotelis", a fact which misled E. F. H. Meyer into the belief that Bartholomew had read Albert. Bartholomew lists about 120 plants in alphabetical order, each with some account of its medicinal or other uses but with only rare or brief references to botanical features. His information comes mainly from Dioscorides and Pliny, but Isidore is frequently quoted, as well as Avicenna, Isaac Judaeus, and Platearius (i.e. *Circa Instans*). Bartholomew relies entirely on his authorities and there is no trace of originality. His description of the lily has been held as showing original observation and feeling for plants (E. S. Rohde: *The Old English Herbals* (1922)), but in fact the passage is a quote from Isidore who got it from St Ambrose (*Exameron* III,35) who got it from Pliny. Bartholomew's work had a considerable reputation and was translated into English in 1397 and printed as late as 1535.

About the same time as Bartholomew's, another encyclopaedia (*De Natura Rerum*) was produced by Thomas of Cantimpré, a quondam pupil of Albert, after fifteen years study. Like Bartholomew's it was written before Albert's *De Vegetabilibus*. It was popular in the universities and many manuscripts were in circulation. The botanical section gives 116 plants. In 1350 the greater part of Cantimpré's encyclopaedia was translated into German by Konrad von Megenberg, with the aim of opening the doors of knowledge to the laity. Konrad freely extended the original text, whilst never claiming to be doing more than translate for the benefit of the unlearned. In the section on plants he added fifty-seven herbs not mentioned by Cantimpré and included much charmingly naive information, not unmixed with superstition, clearly derived from popular and local tradition. Konrad's work evidently fulfilled a need, for it proved very popular, and with the advent of printing was reprinted several times between 1475 and 1500 under the title *Puch der Natur*, being the earliest printed book containing realistic woodcuts of plants. Thomas of Cantimpré probably provided the model for the *Speculum Naturale*, part of the *Speculum Majus Tripartitum*, an ambitious encyclopaedia of knowledge produced by Vincent of Beauvais about the middle of the thirteenth century, with the support of King Louis IX of France. Books 9 to 14 deal with plants, of which some 425 are mentioned, taken from Dioscorides and Pliny, who are the principal sources of information; the author also quotes from Avicenna, Nicolaus' *De Plantis*, Constantinus Africanus, Rhazes (author of the huge medical work, *Liber Continens*), Isidore, Platearius, Hippocrates, *Macer Floridus* and Palladius, but not Albert. Every type of information about plants is raked in, including their moral symbolism, but it remains an uncritical compilation. It was too expensive to be more than a library curiosity although it was printed once (1473–76).

Finally mention may be made of the *Liber Ruralium Commodorum* completed in 1305 by Petrus de Crescentiis, a retired lawyer with an estate near Bologna. This is primarily about agriculture and closely follows Palladius and Albert. There are two chapters on trees and herbs, dealing with about 185 plants, taken from Albert, from whom long passages are quoted verbatim. In the middle of one of these quotations there is a reference to the opinion of Theophratus concerning the origin of plants in unsown soil. This reference is not in Albert's text, nor in Plutarch or Pliny, so where Petrus de Crescentiis found it is a minor mystery which I have not yet been able to solve.

51. Albert's *De Vegetabilibus* was evidently unknown to Rufinus, writing in northern Italy between 1287 and 1300, for Rufinus was most conscientious in consulting and citing his authorities. (See L. Thorndike: *The Herbal of Rufinus*, Chicago (1946).) E. H. F. Meyer was the first to recognize the originality of Albert, and the account in his *Geschichte der Botanik* is very illuminating, but his enthusiasm led him to some exaggeration of Albert's place in the development of science.
52. Ibn al-Baytār was contemporary with Albert: his work on plants was largely based on an earlier treatise of al-Ghafiqi, also an Andalusian, which according to E. H. F. Meyer contained many careful, almost botanical descriptions. See A. Mieli: *La Science Arabe,* Leiden (1938).
53. It is easy to see, that outside the intellectual arena, the high philosophy of Realism concealed a very down-to-earth political meaning when the Church was coming under fire for the parasitism and dissolute behaviour of the clergy. Realism endowed the Church with a universal, divine existence in which the scandals or sins of individual clergy were submerged. The Albigensian and other heresies centred precisely on this point—and men and women were burnt alive for believing in them.

    In science, Realism elevated the four elements, originally quite material, to universal abstract principles that could be used to explain anything.
54. ". . . de particularibus naturis syllogismus habere non potest." (*De Vegetabilibus* VI,1).
55. One of the earliest to take the Nominalist position was Roscelin (1050–1125) who taught at Soissons, Paris and Rheims and who undoubtedly influenced Adelard philosophically, as the latter's work *De Eodemque Diverso* demonstrates. It was, however, the powerful and original mind of Ockham that established Nominalism as the *via moderna* of the late Middle Ages. Ockham was the philosophical culmination of the English scientific movement that began with Adelard and embraced Grosseteste and Roger Bacon.
56. H. Rashdall: *Univerities of Europe in the Middle Ages*, new Edn (1936).

After Salerno, the earliest university medical faculty was probably Montpellier, already established by 1137, prior to the faculty of law. Medicine and law, but not theology, were established at Bologna by 1150. Early in the thirteenth century the University of Padua was set up with medicine as the leading faculty, closely followed by the University of Naples. Somewhat later, medicine was established at Paris, Oxford and other universities. The study of medicine acquired the reputation of leading to wealth, as shown by the mediaeval jingle quoted by G. G. Coulton: "*Dat Galenus opes, dat Justinianus honores, Sed Genus et Species cogitur ire pedes.*" (Law brings honours and Medicine earns money, But the poor old Arts man must go on shank's pony.)

57. The relation between physician and apothecary was well known to Chaucer: "for ech of hem made oother for to wynne—Hir frendshipe nas nat newe to bigynne." The separation of the functions of physician and apothecary contributed to the decline of botany, for the former no longer knew his drugs as plants and the latter kept his knowledge to himself.
58. See O. Cockayne: *Leechdoms, Wortcunning and Starcraft of Early England* (1864–66).
59. An example is found in a Middle English herbal of the fourteenth century where under the heading Agnus castus (= *Vitex agnus-castus,* a mediterranean central Asian shrub) there is a detailed description of *Hypericum androsaemum* (tutsan), which together with its vernacular name "park leaves" clearly identifies it. W. Turner drew attention to this error in his *New Herbal* (1551).
60. Examples are: Herba St Ruperti (*Geranium robertianum*), Herba St Jacobi (*Senecio jacobaea*), Herba St Joannis (*Hypericum perforatum*), Stramentum St Mariae (*Galium verum,* i.e. lady's bedstraw), Morsus diaboli (*Scabiosa succisa*), Testiculus Bernhardi (root of *Orchis*), *Caput Monachorum* (fruit stalk of dandelion after dispersal of seeds), and many more. See J. Bauhin: *De Plantis a Divis Sanctisve Nomen Habentibus.* Basle (1591).
61. See W. Blunt: *The Art of Botanical Illustration,* and the authoritative account of mediaeval plant illustration in H. Fischer (loc. cit.).
62. For example, several unrelated plants were named Consolida because they were believed to heal bone fractures. Thus consolida major was *Symphytum officinale* (but sometimes *Ajuga reptans* or *Stellaria holostea*), consolida media was *Chrysanthemum leucanthemum*, and consolida minor was *Bellis perennis.*
63. The negative and speculative features of pre-Theophrastean botanical theory were fatally reinforced after the translation of Nicolaus' *De Plantis* became known.
64. In *De Staticis Experimentis* (1450), which clearly reflects his study of Archimedes, Cusa proposed various physical and biological experiments that involved measuring weight, specific weight and time. He suggested that the specific weight and smell of herbs in relation to place of origin

should be used as a test of their quality, in addition to taste, which can be misleading. To determine the relative strength of the sun in different climates, 1000 grains of wheat or barley from the most fertile field in each climate should be weighed. To investigate plant nutrition he proposed taking one hundred-weight of earth and allowing a known weight of herbs and seeds to grow in it until they had increased to one hundred-weight. It would then be found, he said, that the earth had little diminished if it was weighed again; from which one could conclude that herbs had their weight from water, which had been impregnated with a certain amount of earthiness, and had been condensed into a herb by the power of the sun. If the herbs were burnt to ashes one could estimate by difference how much earth was found more than one hundred-weight, and conclude that it was all brought by water.

A full translation is given by A. C. Crombie in *Augustine to Galileo: the History of Science A.D. 400–1650*, p. 265 (1952). See also J. P. Dolan: *Unity and Reform*. Indiana (1962).

Cusa was approaching the conception of controlled and quantitative experimentation in biology. It is of some interest that as a young man he studied canon law at the University of Padua where he would come in contact with the most advanced medical and biological science of the time. His works were not widely circulated in manuscript during his lifetime (he died in 1464) but were printed in 1488 and again in 1502, 1514 and 1565.

65. Theodore (1400–75) made his translation of Theophrastus from a manuscript, now lost, that is not identical with any extant text. Before translating Theophrastus Theodore had translated all the zoological works of Aristotle. Although there were earlier versions by Michael Scot (from Arabic) and William de Moerbeke (from Greek), that of Theodore was much superior and rapidly established itself as the standard Latin translation.

5

Renascence of Botany in Europe: from Herbal to Flora (1483 to 1623)

Now in the matter of knowledge of the works of Nature, I would have thee to study . . . all the several kindes of shrubs and trees, whether in forrests or orchards: all the sorts of herbes and flowers that grow upon the ground . . . .

F. Rabelais: Gargantua's advice to Pantagruel in the 1530s
(Sir Thomas Urquart's translation)

The revival of botany after the torpor of the Middle Ages came in the period of great social and philosophical movement when the rising merchant class of the towns sought to break the power of the feudal aristocracy and the Church, and almost as a by-product of their efforts, established capitalism as the dominant, and ultimately the exclusive, social system in the economically most advanced countries of Europe. The turbulent years of this long and complicated struggle, which found intellectual expression in the Renaissance and the Reformation, also witnessed the first hammering out of the specific methodology of modern science; that uniquely potent combination of systematic observation with critical experiment and rational theorizing, which was to transform man's understanding and control of the material world. Science took modern form in the leading commercial countries in response to the needs and pressures of the developing mode of capitalist production: it became an essential factor in the growth of industry, and this in turn accelerated the further growth of science. The systematic development of science and its practical exploitation, now socially possible for the first time on a large scale, were linked historical events, comparable in significance to the discovery of agriculture, writing or the use of metals, and having even more profound and rapid effects on human society.[1]

By their social origin from the merchants and craftsmen of the towns,[2] and by their direct contact with the workshop during the first stages of investment in industry, the pioneer capitalists acquired an attitude to manual labour and to the so-called mechanical arts very different from the traditional contempt for the *artes sordidae* characteristic of the upper classes throughout classical and mediaeval times.[3] They were excited about practical techniques of manufacture and the means of improving them and learning from them; and were thus led to a wider, passionate curiosity about the world, akin to that of the first Greek philosophers but heightened in quality and aims because of the technical and social advances of the intervening centuries. This humanist curiosity which fired the thinkers of the Renaissance in all branches of knowledge had a particularly important influence on the formation of natural science. In botany it turned men's eyes to living plants in the field and away from the pages of the classics or the herbals.

The modern era, in which science came to exercise so dominant and persistent an influence, began in Italy, in the region of the great commercial cities of the north—Venice, Florence, Genoa, Milan—strategically situated at the centre and cross-roads of all the main trade routes of Europe at the close of the Middle Ages. It has been said that the Middle Ages came to an end in Italy fifty years earlier than anywhere else. Certainly by the beginning of the fifteenth century the merchants and bankers of Italy enjoyed not only unprecedented wealth[4] but had gained very considerable political power and independence, both locally and internationally.[5] Their support of the New Learning established Italy as the acknowledged cultural and scientific leader of Europe, a reputation her universities maintained long after her commerical importance was a thing of the past.

It is not surprising therefore that the revival of botany began in Italy.[6] Before tracing its history, some developments must be mentioned which, already in train in the late Middle Ages, directly stimulated renewed interest in plants and influenced the location and the direction of revived botanical studies. An early sign of the coming change in thought was the re-emergence, in Italy, of widespread interest in Epicurism; not indeed in its full scientific and philosophical content,[7] but in Epicurism as a doctrine which denied the soul's immortality, and therefore by implication supported the new humanism and challenged the privilege and authority of the Church. To Dante Epicurism was a loathed and tragic heresy, but to others it was a powerful influence in forming a scientific outlook. This was especially so in medicine, where it strengthened those who realized that dissection of the human body was essential for progress. Human dissection was introduced as a regular part of medical instruction by Mundino at Bologna in the early years of the fourteenth century, and other universities began to follow suit. The consequent stimulus to medicine established the fame and leadership of the Italian medical schools throughout Europe.[8] New facts were discovered, vital to the understanding of anatomy and physiology, which gradually induced a more critical appraisal of Galen and the ancient authorities. The turn to direct observation and rational criticism affected other branches of medicine, the questioning of dogma spread to pharmacology and thus inevitably to botany.

The works of Dioscorides began to be far more closely studied and critically used than during the centuries when they were regarded as the supreme authority. A new translation into Latin was made by Pietro d'Abano and printed in 1478. In the course of the fifteenth and early sixteenth century a whole series of Italian medical men wrote commentaries on Dioscorides and on Pliny.[9] These works were mostly of very limited botanical value: many were simply concerned with textual problems, but others made some serious attempt to establish which native or known plants corresponded to the plants named, but usually far from adequately described, by Dioscorides, Pliny or the mediaeval herbalists. From this it was a natural step to study native plants, first those traditionally held by physicians, apothecaries and country people to have medicinal virtues, and then plants in general. Evidence of such genuine botanical activity is provided by several manuscript Italian herbals of the late fourteenth or early fifteenth centuries, based partly on vernacular information and personal observation, and approaching in at least one case the outline of a local flora. A new and impressive feature of these herbals is that they are sometimes illustrated by figures of plants drawn from life instead of copied from the conventional sources. One of the most remarkable manuscripts, dated about 1415, contains 443 accurately observed figures of plants, drawn and painted by an accomplished artist, Andrea Amadio by name, of whom otherwise nothing is known.[10]

Botanists thus began the task of enumerating, distinguishing and naming the living plants around them, in order to relate them, if possible, to the plants of the classical pharmacopeia or to the relatively small number of additions made by mediaeval herbalists.[11] In attempting to do this they were soon compelled to recognize the existence of a wealth of plants outside the conventional medical and agricultural stock. The new spirit animating botanists, contrasting sharply with that of the Middle Ages, was clearly expressed by Antonio Musa Brasavola, a physician of Ferrara, in his *Examen Omnium Simplicium Medicamentorum* published in 1536. "Not a hundredth part", he says, "of the herbs existing in the whole world was described by Dioscorides, not a hundredth part by Theophrastus or by Pliny, but we add more every day and the art of medicine advances". This opinion is revealing of the botanical thought of the time—still dominated by the needs of medicine but already moving to the problem of including all plants in a general scheme of recognition and nomenclature, that is, towards systematic descriptive botany. Theophrastus' broader concept of botany, although within the writer's cognizance, was overshadowed by the problem of plant identification and the need to come to grips with the variety of existing plants.

The dawning recognition of this variety—to some extent a rediscovery—was quickened by the voyages of exploration of the fifteenth and sixteenth centuries,[12] becoming a revelation after Columbus, and the greedy hordes who followed, brought evidence of the rich flora of tropical America, a flora as new and exciting as the New World itself, and offering hundreds of strange plants which the classical authors could neither have seen nor heard of. In less than one hundred years more than twenty times as many plants were introduced into Europe as in the preceding two thousand years. Although the earliest voyages were made for the most part by Portuguese mariners, the capital was provided by Italian merchants and bankers, and the profits and products flowed into Italy. It was therefore in Italy that many of the first attempts were made to grow and cultivate the unfamiliar plants from beyond the seas. These experiments in acclimatization, some of which were astonishingly successful and established new crop-plants of permanent value, were encouraged by the intensive development of agriculture in the countryside around the populous cities of Northern Italy.[13] Among the introductions from the New World which came into cultivation during the sixteenth century were maize, sweet potatoes, potatoes, runner beans, French beans, pineapples, sunflowers and Jerusalem artichokes.[14] By 1550 the Italians were gaily eating tomatoes (both yellow and red varieties), calling them love-apples in allusion to their supposed aphrodisiac powers, and appreciating their culinary excellence many years before they ceased to be regarded with suspicion by the rest of Europe. Peppers, the green or red fruits of species of *Capsicum* from South America, were cultivated abundantly in Italy, Castile and Moravia by 1585.[15]

The number of exotic species of plants which came directly to the notice of European botanists was also vastly increased by the cult of the private garden, which became the fashion and pride of Renaissance princes and wealthy families.[16] In the gardens of the house of Medici in Florence, already established in the fifteenth century, experiments in growing potatoes, pineapples and mulberry trees were undertaken. But these activities were less important than the constant importation of foreign plants of every kind for the sake of their beauty of flower or foliage, or some curiosity of form, or simply their novelty. Catalogues of the plants in some of these gardens have been preserved and show that early in the seventeenth century, yuccas, sumachs, passion-flowers, trumpet vines and morning glory (*Ipomaea* spp) were already being grown. The passion-flower was quite a botanical sensation because of the curious flower and the Christian symbolism that could be read into it, and was considered to be a sign from heaven justifying the forcible conversion of the indigenous Americans to Christianity. All the above-mentioned species were from the West, but new plants were also arriving from the East, the rhubarb[17] from Central Asia, aubergines from tropical Asia, *Anchusa azurea* from the Caucasus, *Impatiens balsamina* from the East Indies. The tulip was brought from Persia about 1559 and became so popular in Holland a century later that almost a special horticultural industry flourished for a time, profiting from the fashionable tulipomania.[18]

In some ways it was perhaps the new drug-plants which made the strongest impression on contemporaries, and which were, after gold and silver and spices, the most eagerly sought of colonial products.

Thus Nicholas Monardes, physician of Seville, wrote in his best-seller, translated into English by the Bristol merchant John Frampton in 1569–1571 under the title *Joyfull Newes out of the Newe Founde Worlde*, "Three things they doe bring from our Occidental Indies which at this day be celebrated in all the worlde, and with them . . . doe make the greatest effects that ever was made in medicine . . . to cure infirmities being without remedy incurable . . . [namely] the woodde that is called Guaiacum, the China, the Sarcaparilla".[19] Possibly one reason why news of drug-plants was particularly joyous was that, among exotics, they were the most immediately profitable, coming in dried form straight to an expanding market. The Fuggers of Augsburg are known to have held and jealously preserved the valuable monopoly of guaiacum, which had acquired a reputation, unfortunately ill-founded, as a cure for syphilis.

From this concatenation of events and practical needs and intellectual curiosity was engendered a fresh interest in botany during the first half of the sixteenth century, from which the revival of botany and its development into the science of today may truly be said to begin. That Italy should be the main centre of renewed scientific interest in plants was, in the circumstances, almost inevitable. In addition, the Italian universities, as strongholds of the New Learning and the New Medicine, provided a specially favourable environment whence the impulse spread to other parts of Europe.[20] It was in the Italian universities that two developments furthered the progress of botany to an independent discipline instead of a mere adjunct of medicine. The first was the foundation in several univerities of a special chair for teaching botany, the holder being entitled *lector simplicium* or *professor simplicium*. Although the new chairs were, as the name implied, within the medical faculty, the separate title and specialization was equivalent to the appointment of the first professors of botany. The first chair was instituted in 1533 at Padua, most appropriately by the senate of the Republic of Venice, then dominating the immensely profitable spice trade. The proposal which led the senate to their fortunate and sensible decision had been made by Francesco Bonafede, the professor of medicine at Padua, who was, equally sensibly, invited to fill the new chair. In 1534 Luca Ghini was appointed *lector simplicium*, and four years later *professor simplicium*, at Bologna where he had been teaching in the medical faculty since 1527. Other universities followed suit, with Padua once more pioneering by the foundation in 1561 of a second botanical chair, this time of practical botany (*ostensor simplicium*).[21]

Almost simultaneously with the appointment of the first professor of botany, the first botanical gardens on the modern pattern were set up: gardens linked to universities or other learned institutions, and designed for the double purpose of teaching and the maintenance of a collection of plants for study. Naturally the focus of interest was medicinal plants but the economic and scientific aspects of plants in general began to receive increasing attention. Gardens had been founded in Pisa, Padua and Florence by 1546, and the next twenty years saw their establishment in Ferrara, Sassari, Bologna and many other places in Italy. Later, botanical gardens were founded in many centres of learning in Europe.[22] They became essential organs of research and teaching in botany, and at the present day continue to fulfil this role in almost every country of the world. The garden at Pisa was founded by Cosimo I de Medici at the urging of Luca Ghini, whom he had invited to fill the chair of botany there. Ghini also had a hand in establishing the garden at Florence, whilst Padua, which became world-famous, was founded by the Venetian senate after repeated proposals by Bonafede. It is interesting to see the first professors of botany campaigning for the setting up of botanical gardens, a struggle which many of their successors have had to wage since. Not unnaturally it became the usual practice for the chair of botany to include the duty of superintendent of the botanical garden, another factor tending to make botany independent of medicine.

The rise of botany in the first half of the sixteenth century to become a field of genuine study and of active observation and investigation, owes more to Luca Ghini than to any other individual, and his thirty years of teaching at Bologna and Pisa had far-reaching results. Before discussing his activity, however, a brief reflection on the impact of the rediscovered botanical writings of Theophrastus will be useful as an indication of the prevailing outlook of botanists during this early formative period. His works, now readily available in both Latin and the original Greek, were certainly known and read by botanists; he was frequently referred to and quoted; but the immediate theoretical effect of his work was much less than might have been expected, largely, it seems, because contemporary botanists were overwhelmed by the practical problems presented by the vast accession of new plants, native and exotic, with which they had to come to terms. Hence their overriding prepossession with identifying the plants of the ancients and relating them to living species. Hence Theophrastus was, by first impression, simply the revered author of another list of plants to be compared with the long familiar names in Dioscorides, while his far more significant attempts to give botany a sound conceptual basis were but dimly appreciated.

Somewhat surprisingly this latter aspect of Theophrastus found its earliest reflection not in Italy but in France, in the *De Natura Stirpium* (1536) of Jean Ruel (Ruellius).[23] Most of the three volumes of this work consists of descriptions of about 600 plants taken almost wholly from Theophrastus and Pliny, the only original features being the provision by Ruel of a brief description of his own for any plant not described by his authorities, and the addition of French vernacular names. The first twenty-two chapters of Book I are of greater interest since they take the form of a general treatment of botany, the first since Theophrastus (as E. F. H. Meyer noted) and to some extent modelled on him. Actually it is a curious, essentially uncritical amalgam, in which Ruel certainly reproduces much of Theophrastus but without clear comprehension or recognition of his most important ideas. At the same time he attempted to give a systematic descriptive morphology of plants for which he lists a fairly extensive terminology: this gives a valuable indication of the technical vocabulary of contemporary botanists, pre-dating the glossary of terms published by Fuchs. Ruel did not apply the new terminology consistently and failed to relate it to descriptions taken from ancient writers, which are quoted alongside without discrimination or comment. In this he was no doubt simply reflecting the state of botanical thought at the time: he was a compiler and transmitter, not an original thinker. Although further editions of his book were published in Basle and Venice it had little effect on the course of botany.[24]

A much greater influence was exercised by Luca Ghini, although he left no published record either of his lectures or of his original researches.[25] Yet his attractive personality, his combination of enthusiasm and scientific scholarship, and the example of his constant observation of plants in nature and in the experimental garden, directed learned attention to botany with fresh impulse, defined its immediate course, and turned botanists away from commenting on the classics to critically distinguishing and describing the living plants around them. A whole generation of botanists were his pupils or collaborators, and their adoption of the methods which he taught and practised raised descriptive botany to a new stage.

Two innovations, each at least partly technical, materially furthered the progress of botany, following their adoption at about this time. The first was the method of preserving plants by drying them under moderate pressure between sheets of paper and then mounting them on stiff paper or cards. Specimens could thus be preserved almost indefinitely in a state in which their characteristic features remained recognizable for examination and re-examination: when mounted they could be exchanged by post between botanists and could be conveniently stored for permanent reference. This simple yet almost revolutionary technique was the start of the herbarium,[26] which has been the essential basic tool of descriptive and systematic botany ever since. Whether Ghini was himself the inventor of the herbarium, as Meyer believed, has been questioned; but it is certain that he immediately realized the immense value of the new technique. He built up his own herbarium (unfortunately not preserved) and his letters record the dispatch of mounted dried plants to other botanists. It was to a great extent his influence and example which led to the general collection and use of herbaria.

The second innovation was the use of realistic illustrations of plants drawn (and sometimes painted as well) from living specimens. As noted earlier, some of the Italian manuscript herbals of the fifteenth century show that the value of accurate depiction had begun to be understood. This was partly the by-product in science of the great realistic movement in painting and sculpture of the time.[27] During the late fifteenth century the move towards accurate illustration of plants was temporarily set back as printing came into its own, and printers and publishers, out to make quick money, flooded the market with herbals, almost all hasty copies of poor manuscript herbals, and furnished with crude wood-blocks reproducing, with added inaccuracies, the wretched and debased drawings of the originals.[28] In the early sixteenth century the situation fortunately changed: the technique of wood-engraving was improved and refined, and a number of brilliantly skilled artist–craftsmen arose, whose services were available to publishers. At the same time medical men and botanists became acutely aware of the need for accurate pictures of medicinal plants (in the first place) to replace the useless or misleading fantasies that were being continually reproduced. The need was first supplied by Otto Brunfels and Leonhart Fuchs in Germany.

The pioneer was Brunfels, whose book *Herbarum Vivae Icones*, published in Strasburg in 1530, contained 135 superb wood-engravings of living plants, increased to a total of about 260 in later editions. The popularity of Brunfels's work probably led Fuchs to publish his *De Historia Stirpium* in Tübingen in 1542 (a year before the *annus mirabilis* when Copernicus's *De Revolutionibus Orbium Coelestium* and Vesalius's *De Humanis Corporis Fabrica* appeared). Fuchs accurately figured about 550 plants. These two works have rightly been ascribed importance in the history of botany, and for two reasons. In the first place they established the requisites of botanical illustration—verisimilitude in form and habit, and accuracy of significant detail. In the future there might be variation in artistic quality or scientific adequacy, or in the method of reproduction, but the botanical desiderata were defined.[29] Secondly they provided a corpus of plant species which were identifiable with a considerable degree of certainty by any reasonably careful observer, no matter by what classical or vernacular names they were called by different authors, or in different countries. This group of plant portraits was not a general flora but at least it gave a firm basis on which a general flora could be founded, at a time when the art of botanical description had still to be developed.[30]

Brunfels and Fuchs were apparently the earliest to use the new possibilities for the production of good botanical illustrations; both were fortunate in the exceptionally talented artists and craftsmen whom they were able to employ. Their purpose was eminently practical, however, and they were not alone in trying to raise the standard of plant illustration at about this time. That they had a genuine interest in the plants of their own country is undeniable, but neither made any contributions to botanical theory, Fuchs's list of descriptive terms is far less comprehensive than that of Ruel, and the similarity of some of the explanations leads me to believe that Fuchs was directly indebted to Ruel, or at least that both drew on a technical vocabulary that was already common to amateurs of botany. Sach's use of the phrase "German fathers of botany" with reference to Brunfels, Fuchs and Bock was an unfortunate disservice to their memory and true merits.[31]

The use of illustrations to aid in describing and identifying plants was taken up enthusiastically by the Italian botanists. Ghini himself planned an illustrated work which was not carried out, but he helped and encouraged Mattioli to proceed with his *Commentarii in VI Dioscoridis Libros* which appeared with over 500 mostly excellent figures only a dozen years after Fuchs, and a few years later was reissued with some 1200 figures.[32]

Henceforth herbaria were the indispensable basis for descriptive botany, whilst figures, in which at least reasonable accuracy was aimed at, became a normal aid in communication and in the recognition and recording of plant species.

The almost exclusive prepossession of sixteenth and early seventeenth century botanits with the problems of descriptive botany in a world suddenly teeming with hitherto unseen plants, was strengthened in an interesting way by the ideas of the Reformation which dominated this era. To give equal scientific weight to each and every plant, including the commonest and humblest, was the botanical counterpart to the reformers' insistence on the equality of all men in the scheme of salvation, and reflected the teaching that every individual had a personal relation to God which was not dependent on the Church's mediation. Many of the early botanists were indeed adherents of the reformed religion or were influenced by its teachings.[33] The labour of examining, describing and naming their own indigenous floras, and later the newly disclosed floras beyond the confines of the mediaeval world, became of necessity the primary activity of botanists, and they set about it with an enthusiasm which kindled the interest and enlisted the help of a widespread fraternity of non-professional botanists as well.[34]

Renewed observation of living plants, however valuable, did not immediately lead to much improvement in methods of description, which for a long time scarcely reached the level of the best of Theophrastus or Crateuas. Hieronymus Bock was one of the earliest to give original descriptions of plants instead of relying on what Dioscorides or Pliny had written, but he thought it unnecessary to describe common, well-known plants, and his descriptions of others, in his native German, were short, often naive, and far from systematic; nevertheless he sometimes included such details as stages of growth, number of petals, time of flowering, and type of habitat. The first who deliberately set out to give for each plant a full, detailed and systematic description by which it could be recognized even in the absence of an illustration, was the brilliant young German botanist and pharmacist, Valerius Cordus.[35] He had been trained by his father, Euricius Cordus, who had come in contact with Italian botany when studying medicine at Ferrara in 1521, and who was himself a discriminating botanist and something of a pioneer in trying to remove confusion and correct mistakes in the naming of medicinal plants.[36]

In the years immediately before his tragically early death in 1544, Valerius Cordus wrote an account of about 500 plants, which was published in 1561. To read his description of plants after those of his predecessors and contemporaries is like entering a new world. Each description follows a regular pattern and almost always includes, in this order, the characteristic features of stem and leaves, the flower and time of flowering,[37] the fruit and seeds, the number of loculi in the fruit, the lines of dehiscence, the appearance and the number of rows of seed, the root, whether annual or perennial, taste and smell, and habitat. Cordus thus established in principle the basis of scientific plant description and his transforming influence is evident in most of the leading botanists who followed him. From now on, plant description was gradually improved in power, precision and detail; but the foundation was laid by Valerius Cordus. His limitations were those of his time: first, absence of anything but the most primitive conception of developmental morphology, second, ignorance of the real functions and relations of the floral parts, and third, lack of an adequate descriptive terminology.

Many botanists found full employment for their energies in the empirical tasks of collecting and recording, but the more thoughtful could not fail to be conscious of two closely connected theoretical questions arising from their activities. These questions were, in brief, what characters (*differentiae*) of plants are most suitable to distinguish one kind of plant from another;[38] and in what ways and according to what characters can the numerous kinds of plants be most suitably grouped or classified? The second question could be put in another way: is classification to be simply a convenient arrangement for ready reference and remembering, or should it bring together plants which are naturally related to one another (*affines*)?[39] These fundamental questions had been discussed by Aristotle, and by Theophrastus in relation to plants (see Chapter 2), but had then been forgotten: now the practical problems of the herbarium brought them again to the fore, since the successful development of plant description, terminology and nomenclature largely depended on the answers. The growing accession of new facts made these linked questions more urgent, while providing at the same time the means to resolve them.

It is probable that Ghini, a man of profound general culture, had already begun thinking about diagnostic characters and classification, for both are first referred to in the correspondence of Conrad Gessner who had been in scientific contact with him, and were later considered very fully by Andrea Cesalpino, who had been Ghini's pupil.[40] Theophrastus had gone a considerable way in indicating some significant characters (*differentiae*) that could be used in distinguishing and describing plants, and the rediscovery of his principles had considerable impact on the Renaissance botanists. This influence is clearly to be perceived in the descriptive method of Valerius Cordus, whose acute powers of observation and genial botanical flair led him to use several floral characters that have proved of permanent taxonomic value. Cordus did not apparently analyse his own insight; he was a passionately keen field botanist and too busy for philosophizing. Gessner[41] knew and admired Cordius's work, although he never met him in person, and his attention must have been drawn to the significance of floral characters by their use in Cordus's descriptions, as well as by his own critical observations of plants which he began as a youth and continued all his life. That he had in mind the question of the significance of various possible *differentiae* for defining plants is shown by several passages in his letters to other botanists, in which he stresses that the characters of flower, fruit and seeds are of greater value than leaves for identification and discrimination. In his last years Gessner devoted his entire leisure to producing a series of figures intended to illustrate an account of all plants known to him (a parallel work to his *Historia Animalium*. These beautiful and accurate figures were drawn, painted and engraved from living plants by Gessner himself—an amazing achievement in itself, but even more remarkable scientifically in that Gessner included separate details of flower, fruit and seed for each plant, in some cases evidently observed with the help of a magnifying glass. The inclusion of such details did not generally feature in botanical illustration for another two hundred years or more, and only after considerable advances in morphological understanding. It was a misfortune for descriptive botany that owing to Gessner's early death his work on plants was never published and, with a few exceptions, his figures likewise remained unknown. For many years they were completely lost, until a selection was published after their rediscovery in the eighteenth century, but only now is a facsimile edition of all Gessner's original drawings, with his notes and annotations, in course of appearance. It may nevertheless be doubted whether the botanical world was yet theoretically equipped to make use of Gessner's scientific method of illustration: some examples were in fact published, but the method did not catch on.[42] Botanists could not, however, be unaware of his theoretical ideas, since he conducted a wide correspondence, which was published by J. Bauhin in 1591 and was known to John Ray.

There are indications in Gessner's letters that he was also thinking closely about the relations between different plants and their grouping into lower and higher (more embracing) classes. That his own researches were leading him to a definite conception of genera and species (already foreshadowed by Theophrastus) is clear from the following quotation: "I think that there are practically no plants which do not form some genus that is divisible into two or more species. The ancients described a single *Gentiana* but I have observed ten or more species." He also recommended the experimental test of seeing whether a plant came true to seed in order to determine which characters are truly specific and which are accidents.

The fullest statement of contemporary botanical theory and the most powerful contribution to its further development were given by Andrea Cesalpino[43] in his *De Plantis libri XVI*, published in 1583 after he had taught botany, medicine and philosophy at the University of Pisa for nearly forty years. Cesalpino had been a pupil of Ghini, to whom he paid the tribute of life-long devotion and respectful memory. There is no doubt that he always felt gratitude for the intellectual stimulus he had received from his teacher. His work, however, is very much his own and bears the unmistakable imprint of a highly original mind and of the most discerning powers of observation.

The first book of *De Plantis* consists of fourteen chapters which constitute a statement of the basic principles of botany as Cesalpino understood them. The remaining fifteen books give a descriptive account of about 1500 plants, arranged according to a principled system of classification of which Cesalpino was the originator, and the basis of which is expounded. The whole work is of the greatest scientific and historical significance and deserves close attention. Written in clear but condensed philosophical style, its importance has not always been fully appreciated, in spite of the very high tribute paid to Cesalpino by Ray and Linnaeus.

Figure 7 Andrea Cesalpino (1519–1603). Engraving by F. Ambrosi after G. Longhi, courtesy of the Hunt Institute, Carnegie-Mellon University, Pittsburgh, PA.

DE PLANTIS LIBRI XVI.

ANDREAE CAESALPINI
ARETINI,

Medici clariſsimi, doctiſsimiq; atque Philoſophi celeberrimi, ac ſubtiliſsimi.

AD SERENISSIMUM FRANCISCUM Medicem, Magnum Aetruriæ Duce.

l CH

FLORENTIAE,
Apud Georgium Mareſcottum.
MDLXXXIII.

Cesalpino looks for evidence of homologous physiological processes in plants and animals. He undoubtedly believed in some form of circulation in animals, although there seems no reason to think that he anticipated Harvey in any real sense. From *De Plantis* it appears that Cesalpino thought that, after preparation and concoction in the stomachs of animals, the food passed into the veins, being further altered in the fine veins of the cerebral medulla and the liver, and especially in the heart, which he held to be where most of the conversion of food to internal heat takes place. The fully perfected food is distributed through the arteries to the whole body by the active spirit (*spiritus agens*). The simpler nature of plant food was connected by Cesalpino with the relatively simpler structure of plant organs compared with animal, but the attempt to compare plants with animals raised three problems for him, and it is instructive to see how he viewed them.

The first problem is how plants, especially trees, can grow so much larger than animals although appearing to have so much less internal heat. To this he answers that animals have more heat on account of the operations of sense and motion; they grow less, for the good reason that more food is converted into "spirits" (*spiritus*) and consumed in these operations; this is also why they have wide veins that can contain a great deal of food. Plants, however, which are concerned solely with nutrition, can grow more and form plenty of fruit, with less internal heat. That plants have internal heat is not to be denied merely because it is not sensible to us, since things with less heat than our touch seem cold.

A further question is whether plants have a system of veins like animals since the presence of such ducts is not immediately obvious. Here Cesalpino appeals to observation, showing that he must have been making attempts at dissecting plants and investigating their internal anatomy. That plants do have veins, even though very small, is proved, he says, by plants like the Euphorbias or the fig, from which milky humor flows if they are cut, and by the particularly abundant flow of sap from the vine, although the passages are too small to be seen. Indeed in all stems and roots certain nerve-like elements are apparent, which can be split longitudinally, and these are called nerves in the pine tree, or veins when they become thicker and branch and are most clearly manifest, as in many leaves. Hence food passages corresponding to the veins in animals do exist in plants.

Cesalpino was one of the most learned men of his time, and deeply conversant with Greek philosophy and science, and it is true that he re-stated some of the more speculative Aristotelean generalities about plants, including some which had been quietly disregarded even by Theophrastus because based on false analogy with animals. This was the inevitable negative side of Cesalpino's re-examination of Greek science, and it has, I think, been unnecessarily emphasized by most subsequent commentators.[44] As long as there was a lack of new experimental information ancient modes of thought tended to persist, and Cesalpino certainly illustrates how old and new ideas continued to exist side by side in early Renaissance botany. I shall not, however, dwell on the outmoded aspects of Cesalpino's thought, since these are completely thrown into the shade by the remarkable conceptual advances he made in spheres of botany so important for the future. Moreover, it is essential to recognize that his philosophical manner of thought was always under the direct influence of his own experience as a practical investigator of nature, a fact which emerges very powerfully from almost every page of *De Plantis*; he was personally engaged in collecting, examining, describing and growing plants, without counting his researches in human anatomy and medicine, and it was these activities which led him to views far ahead of his time.

Almost at the beginning of his book Cesalpino introduces a discussion of the nutrition of plants, in itself the sign of a new attitude, the revival of a fundamental problem of plant physiology which had not advanced for centuries. In this discussion he was not primarily concerned with the actual composition of the food of plants. Following Theophrastus he assumes that plants take in through the roots moisture from the earth (*humorem in terra mixtum*) and that this corresponds to the more complex food of animals. He further assumes, again following Theophrastus rather than Aristotle, that the humor is altered or concocted within the plant in order to form the plant body and to give rise to the plant's internal heat (*calor insitus* or *calor innatus*).

Figure 8 Title page of Cesalpino's *De Plantis* (1583). This copy belonged to Dr John Hope, Professor of Botany at Edinburgh 1761–86, whose initials (J.C.H.) in his own handwriting are still visible. On the inside cover he has written: "This rare and long wished for book was given me in a present by Dr. Cullen 29 May (17)80." The donor was probably William Cullen, Professor of Chemistry, and later of Medicine, at Edinburgh 1755–88.

For the reasons given above, Cesalpino is able to explain why plants do not need to have such large veins as do animals, but only have many thin ones. Nor do they require all the food to pass into some kind of common receptacle like the heart in animals in order to generate "spirits". By analogy with animals, however, he considers that alteration of the humor imbibed by the roots is principally done by contact with the *cor medullae* as the humor ascends to the stem. The *cor medullae* or *cor* was Cesalpino's term for the junction of root and shoot, a region to which he assigned special importance as the seat of the vegetable soul, analogous to the heart (*cor*) in animals.

The third problem is how plants are able to draw humor (moisture, water) from the soil. The remarkable thing is that Cesalpino here looks for possible explanations in purely physical terms. First he rejects the notion of an attractive force such as the magnet exerts on iron, for in magnetism, he says, what is larger attracts what is smaller, and therefore the humor in the earth would attract that in plants. Nor can the reason be a vacuum (i.e. in the plant) because earth contains not only humor but also air, and the latter moves more readily to a vacuum than humor, as is evident in cupping-glasses applied to the ground, so the plants would be filled with air rather than with humor. This statement is most interesting since it shows that Cesalpino had done simple experiments on the subject. Cupping-glasses were, of course, still commonly used in medicine; they were applied to the body externally and partially evacuated by suction through a hole which was then plugged. Cesalpino evidently tried them on the soil in which plants were growing and found that they became filled with air. Having rejected these theories, Cesalpino notes that some dry substances, such as linen, sponge, powders, naturally attract moisture, whilst others, like the feathers of some birds or the leaves of the fern Adiantum, are water-repellent. The former substances absorb a great deal of water because they are more compatible with it than with air. Hence he concludes that the parts of plants used by the "nutritive spirit" for taking up food must consist of substances of this [hygroscopic] nature. These parts are not therefore continuous tubes like veins, but are more like nerves consisting of hairy substance, so that their bibulous nature draws humor constantly to the seat of internal heat, as a wick draws oil to the flame. Cesalpino recognized that external heat, and therefore climatic changes due to the seasons, increased the rate of movement of humor in the plant, and suggests that he had some notion of transpiration.

Although the plant physiological ideas of Cesalpino were still partly speculative and included such agencies as the different types of active spirit or soul, they also contain concepts that were to become influential in the succeeding century and were far in advance of contemporary botanical thinking. This is evident in the attempt to find rational homology between the life processes of animals and plants, to explain life processes by physical laws, and to test explanations by careful observation and even by experiment.

In plant morphology Cesalpino made a notable and original step forward when he recognized the principle that plant organs, already defined as individual categories by Theophrastus, do not arise in haphazard fashion but in a regular position with respect to one another as part of an ordered plant body. This is exemplified in his first chapter in the demarcation of stem and root as the two fundamental parts of all higher plants (*plantae perfectiores*), and is enunciated in full clarity in the fourth chapter where he states that there is an orderly arrangement of the buds as there is of the leaves (*germinum ordo spectatur ut foliorum*); buds are not produced from all parts of the stem but only from the leaf axils. He then describes with remarkable precision several types of leaf arrangement, showing that he had observed and understood the phenomenon of phyllotaxy. In concluding this section, he notes that there are some plants in which there are not buds in all leaf axils but only at the top of the stem, which then appears as if it were split in this region: a condition observed in Euphorbia and Linum and, among trees, in Pinus and Abies. These acute observations are the beginning of new concepts of integrated plant morphology that proved of enduring value.

In addition Cesalpino included many other accurately observed details of morphology in different sections of *De Plantis*, some of which will be mentioned later: at this point it is only necessary to add that he gave the fullest account of the structure and germination of seeds since Theophrastus. He noted the occurrence of an embryo plantlet in all seeds and described seeds with two divisions *semina bifida* [dicotyledons: he used the term *divisio* or *foliola* for cotyledon] and compared them with those, like wheat, with only one [moncotyledons]. The emergence of shoot and root at germination is described in vivid detail, and epigeal germination is clearly distinguished from hypogeal. The nutritive function of fleshy cotyledons is assumed: they remain attached to the new plant whilst their milky humor and fat are transmitted as food to the [developing] parts, then the dried residue falls off.

Since Cesalpino, like all botanists of the day, was most occupied with systematic botany, it is not surprising that his greatest contribution was in this field. If his failure to free himself entirely from peripatetic (and mediaeval) speculation is to be remembered, then it must also be said that he used the permanently valuable core of Aristotelean thought more creatively than anyone else of his time. It was his deep knowledge of Aristotle which turned him to the task of establishing a rational classification of plants, when most botanists were unaware of, or indifferent to the need, or like Gessner, were only beginning to think about the problem. Nothing is clearer than that Cesalpino had closely studied Aristotle's fundamental ideas on biological classification, and Theophrastus' discussion of the criteria for classifying plants. In the dedication to Duke Francisco Medici, prefixed to *De Plantis*, Cesalpino thus defined his aim.

> Since science consists in grouping together of like and the distinction of unlike things, and since this amounts to the division into genera and species,[45] that is, into classes based on characters (*differentiae*) which describe the fundamental nature of the things classified, I have tried to do this in my general history of plants, and what progress my limited talents have been able to make in this field, I bring forward for the benefit of all. This rational method of proceeding was indeed indicated by Theophrastus among the ancients, but few have followed him. Among my contemporaries Ruellius attempted it but did not get beyond some general notions which he extracted from Theophrastus.

So Cesalpino expressly acknowledges Theophrastus as the inspiration of his own theoretical views, and shows how profoundly he had entered into some of the most significant thoughts of his mentor.

In the course of the closely argued discussion of the problem of plant classification, which occupies most of the three final chapters of Book I, Cesalpino makes it quite clear that he is seeking a natural classification based on botanical characters:[46] he specifically rejects the pharmaceutical grouping of Dioscorides or the purely artificial, alphabetic arrangement of other authors or all groupings based on *accidentia*, that is, characters such as scent, taste, habitat, utility to man, which are not essentially botanical, or characters such as mere size, which vary with soil, climate and season. He wished to find a natural classification, not only because (to use modern terms) he regarded this as more scientific, but also because it was more practical for classifying large numbers of plants.

It was in defining the botanical characters (*differentiae*) most important for classification that Cesalpino showed his greatest percipience and originality. At the time he flourished he could perhaps hardly escape completely from the snare of the time-honoured division into trees, shrubs, under-shrubs and herbs which he found in Theophrastus, but he took seriously Theophrastus' own criticisms of the division, and after careful discussion of the difficulties decided to unite shrubs with trees and under-shrubs with herbs. Even more significant is that he applied the method of classification at which he finally arrived to both trees and herbs in the same way.

In thinking about the problem of classifying plants Cesalpino undoubtedly related his discussion to certain general philosophical statements taken from Aristotle, but it would be quite wrong to assume that he was therefore simply applying an arbitrary *a priori* scheme which happened to be a lucky hit. The development of his method was the result of detailed comparative observations over many years of the range of form in plants, in which perceptive scientific insight was aided by recognition—missed or disregarded by all his contemporaries—of the importance of some of the morphological relations to which Theophrastus had drawn attention. This was the real source of fundamental advance in botanical theory which he made, yet he was neither deluded nor illogical in linking his final conclusions with Aristotle's view that a plant possesses only the nutritive soul, comprising the two essential aspects (or functions) of growth and reproduction. For Cesalpino saw that while the characters of what he considered the organs of growth and nutrition (root, stem, leaves) could be used to set up broad classes, these classes were arbitrary because they did not yield further useful or meaningful subclasses; whereas classes based on the characters of the organs devoted to reproduction (by which he meant primarily the fructification) readily yielded further meaningful subclasses. Thus observation and experience fitted in with Aristotle's philosophical general principle as interpreted by Cesalpino.[47]

Historically Cesalpino was the first who tried to define the principles on which a comprehensive natural classification of plants could be constructed, and the first to publish a classification which, however imperfectly, reflected real relationships within the plant kingdom. Cesalpino's masterly exposition of the principles of classification may be summarized as follows, using his own words as closely as consistent with an accurate rendering of the meaning: the phrases in square brackets are my own explanatory comments.

Classification must be based, he says, on characters arising from the fundamental nature of plants themselves, that is, on morphological characters of plant organs and parts, not on the properties of plants in relation to man or any other accidental or superficial feature. The morphological characters must be those that are stable, not those that vary with changes of habitat, climate or soil. The characters of all organs and parts of plants can be used for classification, but those of the fruit and the parts involved in fructification [the reproductive parts] are to be used in defining the higher classes, whilst characters from leaves, stems and roots, as well as those from the fructification, can be used in dividing the higher classes into their ultimate species. In defining the characters of plant organs the most important features are the number, position and form of the various parts. Number also appertains to the dissolution of what is continuous [for example, separation of the ripe fruit into several parts by dehiscence] and to what is single [for example, plurilocular fruits which appear to result from the union of several individual seed-vessels]. Texture, colour and other qualitative characters must be compared in corresponding parts. All the forementioned characters were combined by nature in many ways in the construction of the fructification, and from them various higher classes of plants have been established.

In concluding this theoretical discussion Cesalpino states his intention of investigating the classification of plants (*plantarum genera*) using the characters of the fructification as a basis, and dividing first trees and shrubs, and then under-shrubs and herbs, into higher classes (*genera*) and into species. Like Gessner he considered the defining characteristic of a species to be the capacity to reproduce its like,[48] a very important and significant standpoint, providing an objective, experimentally validated basis for the fundamental unit (*ultima species*) of taxonomy.

Before proceeding to the descriptive part of his work, in which he applied his method of classification to the plants he knew, Cesalpino outlined the criteria by which the higher groups of his classification are constituted. His primary division, founded on the presence or absence of seeds as the means of reproduction, was fully consistent with his philosophical outlook, as well as being, according to modern views, fundamentally sound. Seed plants are treated in Books 2 to 15 and seedless plants in Book 16, but it will be convenient to consider them in the reverse order.

The way in which seedless plants are grouped is a tribute to Cesalpino's botanical good sense, when one considers the state of knowledge at the time, and that it took nearly three hundred years before this mixed assemblage could be reduced to rational order. He begins with the ferns and their relatives (*affines*), including *Equisetum, Botrychium* and *Ophioglossum,* all of which are considered to be the most perfect forms because they possess root, stalk [*pediculus* is used to mean the rhachis of ferns, but *caulis* for the stem of *Equisetum*], and leaf.[49] Although lacking flower or true seed they possess something downy on their leaves, which corresponds to seed because it propagates the plant. After the ferns and their allies come groups of less perfect plants which are listed in the order: lichens and hepatics [not distinguished], mosses [including club-mosses (*Lycopodium*) and true mosses], algae [mostly seaweeds but including some coelenterates], and lastly fungi. These groups are termed less perfect because they show less morphological differentiation; algae are said to have root and leaf, or some, leaf only, some fungi have stalk and leaf [pileus], others, such as truffle, only root. Cesalpino accepted the then commonly held view that the less perfect forms (algae and fungi) are produced from decaying matter by spontaneous generation and are unable to produce their like. He lists 18 species of pteridophytes, 19 species of fungi, and 17 species distributed among the other groups. Not surprisingly he mistakenly included a few seed plants: *Orchis, Orobanche* and *Hypocystis* with minute powder-like seeds which could not be seen to germinate in ordinary conditions, some sterile grasses (probably attacked by *Ustilago* and with seeds replaced by fungal spores), and the common duck weed *Lemna* (how many botanists have seen the seed of *Lemna*?). Apart from these anomalies his delimitation and classification of seedless plants was a creditable effort.[50]

The description of seed plants (in which conifers and some other gymnosperms are naturally included) takes up the remaining fourteen books, and the classification is much more fully worked out than that of seedless plants. Since admirable summaries of Cesalpino's scheme have been given by several authors;[51] I shall try here to bring out the more general—and more significant—principles which underlie it, and which have not always been fully recognized.

After the division into trees and herbs Cesalpino distributes seed-bearing plants into several main classes, defined by the relative position of the fruit and the other floral parts [basically, that is, by whether the ovary is superior or inferior], by the number of seeds per fruit, by the number of loculi in the mature fruit, and sometimes by the placentation of seeds in the seed-vessels. It should be noted that although he defined the fruit precisely and accurately as "consisting of the seed and seed-containing parts", he frequently used the term seed when referring to one-seeded indehiscent fruits or parts of fruits (caryopses, achenes, nutlets, cremocarps). The failure to distinguish between one-seeded fruits and true naked seeds was universal among botanists then and for another two centuries. The confusion was not finally and completely dispelled until the fundamental nature of the seed became understood in the nineteenth century, and is permanently enshrined in ordinary non-botanical speech.[52] The major classes are briefly, but quite explicitly, defined by Cesalpino, but the characters used to form subsidiary groupings are not stated in the same way. This has given rise to the totally wrong view (unfortunately shared and given currency by Sachs) that Cesalpino simply created a number of higher classes based, rather artificially, on the fructification alone, and that these classes were not further subdivided. Now in the first place it is evident that Cesalpino had studied Theophrastus thoroughly and critically, and had realized that the relations between the floral parts, which the latter had noted among the possible *differentiae* for classification, were indeed of particular significance: for theoretical reasons, because they are characters linked essentially with the process of development [ontogeny, reproduction], and empirically, because these characters were found by observation to be associated with others in a way that led to natural groupings based on several characters. Cesalpino thus carried forward one of the greatest achievements of ancient botany into the modern science, and his higher classes were very far from being merely artificial groupings.

Nor did he stop at the delimitation of the most widely embracing classes. In view of his own statement of the appropriate techniques for complete classification, it would have been exceedingly unlikely that he himself should proceed in a way directly contrary to his declared intention of discovering *genera et species*, i.e. classificatory groupings at levels from the highest classes to the self-reproducing species. Even a superficial survey of the arrangement of plants within his higher groups is convincing evidence that he was a very perceptive observer and did indeed make use of many morphological characters to aid in the subsidiary grouping of plants. Unluckily he did not state explicitly the characters he used, but there are many incidental statements that are sufficiently revealing.[53] The proof of the pudding is in the eating—it is a fact that Cesalpino's principles led him to put together a remarkable number of natural assemblages, not only of species within a genus (in the modern sense), but even more significantly, of species and genera corresponding to modern families (or sections thereof), and these include Leguminosae, Umbelliferae, Labiatae, Liliaceae, Graminae, Chenopodiaceae, Cruciferae, Rubiaceae, Scrophulariaceae, Euphorbiaceae, Ranunculaceae, Compositae, Valerianaceae, Primulaceae, Caryophyllaceae, Verbenaceae, Cucurbitaceae, Boraginaceae, Rosaceae. It is true that some of these groups (the first five, for example) had been recognized to some extent by other botanists, but only on the basis of general resemblance of form and habit. It is also true that Cesalpino had some odd collections and misfits, but some of these would arise from merely technical reasons. To give but one example, only the use of a better lens than was likely to be available could have shown him that the single "seed" (acorn) of *Quercus* was really the single survivor out of six in a three-chambered ovary (*conceptaculum*). Such inevitable gaps in observation were bound to introduce elements of artificiality, but they cannot detract from the magnitude of the advance he made. When one compares his classification with the almost contemporary arrangement of plants by de L'Obel (Lobelius)[54] based on general habit, or with the curious jumble produced forty years later by G. Bauhin, Cesalpino's superiority is at once apparent.

The chief weakness in the application of his own guiding principles was his failure to make fuller use of the parts of the flower other than the fruit. This was not due to failure to recognize them,[55] but was more probably the result of the lack of knowledge of sexual reproduction in plants. Since the function of stamens and corolla was unknown, Cesalpino no doubt assumed that they were less important and formed only for delight.[56]

The logical relation between the method of description of individual species and the natural system for a general classification at which he aimed, were very perceptively analysed by Cesalpino. He emphasized that the practical advantages of a natural classification included not only the facility of accommodating and remembering large numbers of species, and of incorporating new ones without upsetting the system, but also economy of description, since the defining characters of any higher group do not need to be repeated for each lower subdivision of it. This ultimately became the basic principle of all systematic descriptive floras. He clearly understood that verbal description is essential for morphological analysis, a scientific *sine qua non* for which illustration is no substitute, since "not all characters can be expressed by a figure as they can by language". His own description of species are original, not copied from classical sources, and in many cases accurate, critical and detailed. But frequently they are too brief, and in general are inferior to those of Valerius Cordus in detail and systematic arrangement. In fairness to Cesalpino it must, however, be realized that he was giving a conspectus of plants in their relationships and not a detailed account of species: many chapters which are headed by the name of a particular species, actually describe the range of variation of several species within a genus or family. Although as Professor of Medicine he taught *materia medica*, he only mentions pharmacological properties of plants if previously unknown, or for the purpose of botanical discrimination: otherwise readers who are interested are referred to Dioscorides, Galen and other medical writers.

As the first to put forward the concept of a natural classification of plants, to develop such a classification in detail, and to apply it to all plants known to him, Cesalpino is one of the outstanding figures in the history of botany.[57] He was responsible for the first great advances in botanical theory since Theophrastus, and Meyer was right in regarding him as "unquestionably the greatest botanist of his century".

In the long run Cesalpino had a profound and illuminating influence on the development of botanical thought, yet in his own time and for nearly a century after the publication of *De Plantis* botanists largely

XXIII.

Laurocerasus. Pag. 86.

Arbor hîc exigua pingitur. Flos autem, quorum plures racematim nascuntur, & folium, fructusque dissectus cum nucleo exempto mediocrem magnitudinem præ se ferunt.

Figure 9 Figure of cherry-laurel (*Prunus laurocerasus*) from a drawing of Gessner, included by Joachim Camerarius in his *Hortus Medicus* (1587).

IX.

Barba Capræ. Pag.26.

Vnus Tragus hanc depinxit, & ex hoc poſtea o-
mnes tranſtulerunt. Nos aliquantum emendauimus
& ſemen adiecimus hac nota † inſignitum.

Figure 10 Meadow-sweet (*Filipendula ulmaria*) in *Hortus Medicus* (1587). Camerarius notes that this figure is taken from Bock (Tragus). The addition of details of the fruit by Camerarius shows the influence of Gessner.

failed to appreciate or even to understand him.[58] Some doubtless expected to find a descriptive flora of the kind on which contemporary interest centred, and were simply disappointed. To some extent his mode of presentation may have hindered understanding. He did not expound his system in tabular or easily apprehended form, much is indicated rather than fully stated, and his division into books does not correspond to the divisions of his classification. The work reads like the summary headings of a series of lectures, which would be supplemented by extensive verbal commentary. Yet these cannot have been the main reasons why his work made so little immediate impact—the savants of the day were not put off from quarrying in difficult terrain if they thought there was gold. It seems that most botanists were fully taken up with collecting, describing and naming plants, or with producing local floras, and remained indifferent to the theoretical questions raised by Cesalpino: for organizing the masses of new plants they were content with any convenient artificial grouping or with none at all. On the whole the most popular arrangement was that of Lobelius or something like it, based on undefined similarities of leaf form and general habit, not to be counted as classification except in the most superficial sense. Another factor probably contributing to the neglect of Cesalpino was that the centre of botanical activity had moved—with the centre of trade and industry—to the Netherlands, where capital was being ploughed into intensive agriculture and horticulture to feed the busy towns, and some of the growing wealth was lavished on the cult of the private garden.[59] Three of his leading botanical contemporaries, Dodoneus, Clusius and Lobelius, were all born in the Netherlands and were active there for part of their lives, although each was induced either by religious persecution or by the disturbance of the long war for national independence against Spain, to spend a number of years abroad.[60] All three contributed substantially to the advance of systematic botany, by collecting and describing new species, by good illustration, and by their unstinted mutual cooperation which set a standard of scientific behaviour of inestimable value as a pattern for the future. Their labours and those of many others created the basis for an expansion of floristic knowledge in the course of which the herbal was transformed into, and finally replaced by, the flora. The transition is illustrated in the work of the Netherlands trio. The *Cruydeboek* of Dodoens contains original descriptions of living plants, many of which he collected himself, but it remains a herbal in intention and arrangement; it was translated into several European languages and became a standard medical textbook for many years. Clusius and Lobelius, however, produced essentially floristic work, and the latter's arrangement of plants, the shortcomings of which have been already mentioned, was definitely botanical and not pharmacological. From the middle of the sixteenth century the number of species characterized by reasonably adequate description and illustration rose steadily as new species, both European and exotic, were discovered and listed. Between 500 and 1000 plants are named in herbals at the end of the fifteenth century, representing the legacy of classical and mediaeval knowledge of plants, but in 1613 Jean Bauhin described about 4000 plants in his *Historia Universalis Plantarum* (not published until 1650–51) whilst his brother Gaspard Bauhin included in his *Pinax* (1623) over 6000 plants.[61]

The *Pinax* came to occupy an important place in the development of systematic botany although it was a work of industry rather than originality. Its special significance lay in the inclusion, for every species, of comprehensive references to previous descriptions and figures by other authors; from this information and from his own observations Bauhin established a name for each species and indicated with which names in the literature he considered it synonymous. Bauhin's nomenclature was itself an advance in clarity and convenience, since for most species he employed a binomial, consisting of generic name followed by specific name. Sometimes the generic name is used alone for the best known or earliest recognized species of a genus; sometimes two, or even three, specific epithets qualify the generic name; but binomials form the vast majority of his designations. Bauhlin's use of binary names can hardly fail to have influenced Linnaeus in proposing their universal adoption, but it must be emphasized that Bauhin's specific names were always descriptive and defining: his usage thus differs from Linnean nomenclature although foreshadowing it. Bauhin usually, but not invariably, gives his defining characters for each generic group, but these characters are far from those used to define the corresponding genera today and less precise than those used by Cesalpino. There were certainly more accomplished botanists of his time than Gaspard Bauhin, yet his *Pinax* produced what was needed if systematic botany was to develop—a sufficient foundation of generally recognized and recognizable species, and the beginning of an improved scientific momenclature, at once flexible and stable.

In spite of some similarities the arrangement of plants in the *Pinax* of Gaspard is by no means identical with that in the *Historia Universalis Plantarum* of his elder brother Jean Bauhin, yet in both the main feature is the lack of any comprehensive order. The division into trees, shrubs and herbs, is neither abandoned nor consistently maintained; whole groups based on single morphological character (leaf shape, form of fruit, type of inflorescence) are mixed up with groups based on habit (climbing, spiny), habitat, pharmacology, utility to man, or on no obvious common feature at all. Sometimes the defining character is mentioned, in other cases it can only be inferred. Most notable is the intermixing of seed plants with seedless plants as if the profoundly significant separation of these two classes by Cesalpino had never been made. A few more or less natural assemblages appear amid the chaos (legumes, umbellifers, labiates, bulbous monocotyledons, grasses, fungi), as they do in Lobelius, to whom alone any influence can be traced. There is nothing of Cesalpino's comprehensive classes based on morphological criteria, although the sporadic use of fruit characters may possibly owe something to him.

At a lower and more immediately practical level of classification the situation is, however, very different. The most significant theoretical development in descriptive botany in the late sixteenth and early seventeenth century, accompanying the great increase in number of plants described, was the recognition of groups of related species approximating to modern genera, and more sensitive discrimination of the species within them, a process which led towards the establishment of genus and species as basic units of taxonomy. This development finds expression in a number of authors, but most consistently and effectively in the *Pinax* where plants are arranged as groups of related species within genera, and are systematically named (as explained above) in a way that reflects this classification. This taxonomic advance was the fruit of greatly extended comparative observation of plants, made possible by the greater company of botanists and by the

Figure 11 Etching of a species of *Ranunculus* from Fabio Colonna's *Ekphrasis* (1616).

Ranunculus montanus leptophyllon Asphodeli radice

use of herbaria and improved methods of description and illustration, for communication among them. There can be little doubt that in this connection Cesalpino's analysis of the relation between higher and subordinate classes, his emphasis on self-reproduction as objectively defining the species, and the many examples of his own careful discrimination of species, were influential in developing the new taxonomic concept and the nomenclature in which it was embodied. One of the earliest in whose writings the generic concept was most fully and clearly developed, was Cesalpino's fellow-countryman Fabio Colonna, a man of learning and a botanist of distinction.[62] His account of some 200 rare and lesser known Italian plants (first published in 1606), contains many groups of species, in the majority of cases truly botanically related, each group being listed under a single generic name. Thus to give but one example, Colonna lists under Ranunculus seven species, which he names in this fashion—Ranunculus montanus leptophyllon Asphodeli radice, Ranunculus minimus Apulus, Ranunculus aquaticus umbilicato folio, Ranunculus trichophyllon aquaticus mediolutens, and so on for the rest: his specific epithets are almost always unwieldy descriptive phrases, and he did not approach Bauhin's binomial brevity. Colonna's superb engraved illustrations, drawn by himself, include accurate details of flowers and fruits; they identify his plants without dubiety as species of *Ranunculus* Linn. Rather surprisingly Colonna does not anywhere name Cesalpino, although he could not fail to be familiar with his work, and indeed his own indebtedness is evident in many ways: as for example in the clear statement of principle (Part 2, cap XXVII) that "in plants we must judge affinity not from the leaves, but rather from the flower, the seed-vessel and the seeds".

Gaspard Bauhin's *Pinax* was an important contribution to floristic progress, for it established a more reliable list of known plants, a more convenient standardized method of naming them, and a more complete synonymy linking the new and the older literature, than had hitherto existed. Its publication in 1623 is a fitting formal conclusion to the period under review, since it marks the transition to new stage in plant systematics and also coincides with the beginning of a general extension of the field of botanical enquiry.

Notes to Chapter 5

Notes

1. The background history of the birth of modern science is only touched on here, since there is a vast literature on all its aspects. In my opinion J. D. Bernal's *Science in History* still remains the indispensable classic.
2. Of course this charactrerization of the social background of the early capitalists is only true in general terms—more enterprising members of other social classes joined in as well. The interesting point is that the aristocratic life of idleness became a reproach in their eyes.
3. How persistent were old attitudes is underlined by John Locke almost at the end of the seventeenth century: "and whoever desired to have fair gardens and fruitful fields had more reason to consult the experience of the dull ploughman and unread gardener than the profound philosopher and acute disputant. Let not anyone be offended that I rank the cook and the farmer with the scholar and philosopher".
4. The Medici family of Florence, who made their fortune by banking and investment in the wool and silk industry, lived in a civilized splendour and urbane comfort that even the greatest feudal kings or emperors never knew.
5. The republic of Venice became for a period the greatest naval power of the Mediterranean.
6. The impression given by Julius Sachs in his *History of Botany* that the revival of botany began in Germany and the Netherlands, is erroneous. Equally erroneous is his estimate of the botanical work of Aristotle and Theophrastus, which he regards as almost valueless and without serious empirical basis, and therefore as contributing nothing positive to the re-birth of botany in the sixteenth and seventeenth centuries. Since I shall have other occasions to criticize Sachs, either directly or implicitly, I must correct the balance by paying tribute to the many occasions when he is brilliantly right, and to the vigour and philosophic breadth of his treatment. His *History* will long continue to be a source of stimulus and insight to lovers of botany and scientific truth.

   For details of early Italian botany see W. T. Sprague, *Journal of the Linnean Society* **48**, 545–642.
7. The sixteenth century derived its knowledge of Epicurism from what was reflected in Cicero and Lucretius.
8. Bologna was the first place where dissection of the human body began to be practised again, by Mondino de Luzzi (1275–1326), otherwise Mundinus, who was born and taught there. Mondino did his own dis-secting and his treatise on human anatomy (1316) was in use in medical schools for 200 years. The restoration of anatomy in Bologna and other Italian universities was an important stage in the renascence of medicine. Surgery was raised to a new level by Guy de Chauliac (1300–67) who was a pupil of Mondino at Bologna and also studied at Montpellier, whither

he carried Mondino's influence.

The great medical centres of Italy—Padua, Bologna, Pisa, Ferrara, etc.—were precisely the places where the revival of botanical studies and activity took place in the sixteenth century.

9. Brunfels (1530) refers to a string of such writers, including Hermolaus Barbarus, Nicholaus Leonicenus, Marcellus Vergilius, Pandulphus Collinutius and Joannes Manardus.
10. W. Blunt describes and figures this manuscript, together with two others of about the same date, in *The Art of Botanical Illustration*. All three were produced in northern Italy and contain naturalistic representations of plants.
11. Some twenty to thirty plant drugs were added to the mediaeval pharmacopeia from Arab sources (C. H. La Wall: *Four Thousand Years of Pharmacy* (1927)), but not more than half were botanically known in any real sense (Chapter 4). In addition a small number of European herbs came in from folk medicine. An indication of this number was given by William Turner in 1548 when he listed the names of thirty-seven new-found herbs "not in any olde ancient wryter". These include *Digitalis purpurea, Euphrasia officinalis, Sanicula europea, Hypericum androsaemum, Alliaria officinalis, Polygonum bistorta, Sanguisorba officinalis, Ajuga reptans, Pimpinella saxifraga, Barbarea vulgaris, Capsella bursa-pastoris, Lysimachia nummularia, Plantago coronopus, Filago germanica, Listera ovata.*

    One New-World plant, the tomato (*Lycopersicon esculentum*), is in Turner's list. William Turner (1510–68) is usually counted as the first English botanist. A sturdy, not to say belligerent, Prostestant, he was forced by the Marian persecution to spend some years on the continent. He visited Italy and attended Luca Ghini's lectures in Bologna.
12. During his travels in the thirteenth century (1270–95) Marco Polo had observed a number of plants growing in their native haunts which were then known to Europeans only in the form of commercial products (e.g. rhubarb, cinnamon, turmeric, camphor, coconuts, ginseng). The immediate botanical impact of his travels (known in manuscript after 1298) was slight, and was probably much greater when they were printed in 1477.

    It was the sea voyages of the century and a half after the first expedition of Henry the Navigator of Portugal in 1415 which began to awaken and transform the science of botany. The great expansion of journeying by sea was made possible by the use of the compass, learnt from the Chinese, and by technical improvements in steering and advances in the science of navigation. By 1487 the coasts of Africa and the interior of Abyssinia had been opened, by 1498 India, by 1503 the West Indies and the whole of the American continent, by 1511 Malacca and the East Indies, by 1516 China, and by 1542 Japan. By 1550 the world (except for Australia and New Zealand) was known in outline, and the existence of a world flora had become a fact to be recognized.

13. The feudal manorial system went out earlier in northern Italy than elsewhere in Europe, owing to the influence of the growing commercial cities. Labour services were completely replaced by monetary payments as rent, land was freely bought and sold, farming for the local market became a profitable speculation. Benvenuto Cellini in his memoirs gives an amusing account of his own involvement in such a venture.

    One result of the search for quick profits in agriculture was that the potentialities of new crop plants were tested and Italy became the origin from which the more successful ones spread. Another result was a popular interest in the technique of agriculture which led to the printing and constant reprinting of Latin translations of the classic and mediaeval writers, such as the collection, *Scriptorum rei Rusticae Veterum Latinorum* (Venice, 1470), containing Columella, Varro and Palladius, a translation of the *Geoponica*, or the works of Crescentius. (See G. E. Fussell: *The Classical Tradition in West European Farming* (1972).)
14. The name Jerusalem artichoke (*Helianthus tuberous* from North America) is a corruption of the Italian girasole (sunflower, turning-to-the-sun), an indication of the route by which it reached England.
15. Curiously enough the seed of *Capsicum* appears to have been taken first to the East Indies, whence the plant returned to Europe. Leonhart Fuchs called it the Calicut pepper.
16. Although men and women of the Middle Ages took pleasure in their gardens like men and women before and since, the mediaeval garden was essentially utilitarian in lay-out, contents, and intention.
17. Roots of rhubarb were an important medicinal in Roman times, being brought in dried form from Central Asia—somewhere beyond the Black Sea to the Romans, hence the specific epithet of its modern botanical name, *Rheum rhaponticum*.
18. The detailed history of plant introductions is not the purpose of this book, although the movement of plants about the world by man is one of the most practically important results of botanical study and has had economic and political results on a world scale. Only the reverse effect of plant introductions on the development of botany is considered here.
19. Either Monardes, or his translater, seems to have got in a muddle, since China presumably refers to *Smilax china*, not from the New World, but from China. This was described (China root) by Garcia da Orta in 1563, in his colloquy on the drugs of India, as a remedy for Naples and French disease [syphilis]. "The root is eaten in China cooked with meat as we do with turnips. It is a shrub of 5–6 ft high, root about 1 ft, one thick root and one thin. The leaves are shaped like young orange leaves."

    Sarcaparilla was an American species of *Smilax* (*S. sarsaparilla*) which, like Guaiacum and China, was thought efficacious against syphilis, but was also used against rheumatism and skin diseases.

    Whether syphilis was brought to Italy by sailors from the New World seems undecided, but a virulent form was certainly widely spread by the intense movements of trade in the decades after about 1490, and became an acute medical problem.

The first effective remedy was the introduction of mercury treatment by Paracelsus. This was one of the things that made him so unpopular with the medical and drug establishment.

20. Another reason for the enlarged influence of the Italian universities was that the leading ones were effectively controlled by the municipalities and were relatively free from interference by the Catholic Church. The position was symbolized by the newly acquired importance and status of the Faculties of Civil Law.
21. The duties of the ostensor were originally to demonstrate to students the actual plants in the botanic garden, so that they learnt how to recognize them. The ostensor would deal primarily with the botanical characteristics of plants, whereas the lector would include pharmacological properties. In a sense the ostensor was therefore the true ancestor of the professor of botany, but it is doubtful if the distinction between lector and ostensor really meant much, since the two jobs were so often combined.
22. There is some dispute among Italian authorities on whether Padua or Pisa was the first botanic garden to be established. The point is one of definition and scarcely material, since both were certainly established between 1543 and 1545, and were followed in 1550 by Florence, Sassari, and Ferrara, and in 1567 by Bologna. Some foundation dates of botanic gardens before 1800 are: Leipzig, 1580; Leiden, 1587; Montpellier, 1593; Heidelberg, 1593; Giessen, 1617; Paris, 1620; Jena, 1629; Oxford, 1632; Amsterdam, 1646; Uppsala, 1655; Edinburgh, 1670; Chelsea, 1673; Naples, 1682; St Petersburg, 1714; Philadelphia, 1728; Kew, 1759; Moscow, 1795. This list is illustrative only and very far from complete.
23. Jean Ruel (1474–1537) was physician to Francis I of France and later became a canon of Notre Dame. He was fluent in Greek and Latin, and published a Latin translation of Dioscorides in 1516. Francis I paid the costs of printing the first edition of Ruel's *De Stirpium*, published in Paris in 1536.
24. Many passages in Ruel follow Theophrastus almost literally, but are not identical with Theodore Gaza's Latin version, although I am inclined to think that Ruel had read it.

Of more interest is the fact that he quotes practically in full Theophrastus' section (*HP* 1,13,3) on the position of the fruit with respect to the flower, the significance of which Cesalpino was the first to realize. On the other hand Ruel omits any mention of Theophrastus' observations on the internal structure of seeds. Ruel's longest chapter is on the (imaginary) etymology of plant names, which looks back to a favourite pastime of the Middle Ages. He quotes Varro, Pliny, Galen, Athenaeus, Pompeius, but oddly enough, not Isidore of Seville.

Cesalpino read Ruel but was not impressed by his theoretical grasp and

Ray includes *De Stirpium* in his bibliography to *Historia Plantarum*, but without comment.

25. Luca Ghini (1490–1556) was the son of a notary of Imola but himself qualified in medicine at the University of Bologna. His enthusiasm for plants was evidently awakened at the very beginning of his career and he taught botany (at Bologna and Pisa) all his life. He made many plant-collecting journeys in Italy, accompanied by friends or students, and received plant materials from correspondents in Egypt, Syria, Spain, Sicily and Calabria, and from his own brother who was a lawyer in Crete.

    Ghini's wide culture and selfless nobility of character deeply impressed his contemporaries. Even the awkward and quarrelsome Mattioli admitted that he was entirely without personal envy: Mattioli's commentaries on Dioscorides owed in fact a very great deal to Ghini's unstinted help. The following are some of the contemporary botanists who had either been Ghini's pupils or had had personal contact with him: Cesalpino, Aldrovandi, Gessner, Mattioli, Valerius Cordus, William Turner, John Falconer, Anguillara, Maranta.

    Rondelet visited the universities of northern Italy in 1549–50 just before becoming Professor of Medicine at Montpellier. He certainly made the acquaintance of Aldrovandi and must surely have met Ghini and, in any case, have learnt of his teaching and ideas. Rondelet founded a famous centre of botany at Montpellier, and there taught, among others, Clusius, Lobelius, Pena and Daleschamps.

    J. Bauhin was a pupil of Aldrovandi, whilst his younger brother G. Bauhin studied at Montpellier some twenty years after Rondelet's death.

26. Why the notion of drying plants for botanical purpose should have arisen just at this time is not obvious. It was not due to any sudden increase in the availability or cheapness of paper but may have come from artistic practice, a means of preserving plants as models for drawing or painting —just as realistic botanical illustration was to some extent a reflection of the new naturalistic painting.

    The question is discussed by J. Camus in *Malpighia* **9**, 283–314 (1895).

    The word *herbarius* changed its meaning as the new technique caught on. Throughout the Middle Ages *herbarius* was the Latin word for a written herbal, and it was still used with this meaning by Euricius Cordus in 1534, but soon began to mean a collection of dried plants, apparently changing its gender to neuter at about the same time (other names used were *hortus hiemalis, hortus siccus, exsiccata*).

    The exchange of dried specimens very rapidly became common practice among botanists. Conrad Gessner, writing from Zurich to Dr Kentmann in Dresden, says "if you have any rare plants to be named, it is sufficient to send me the dried flower and leaf". The first written instructions on the method of pressing and drying plants seem to be those given by A. Spigelius in 1603 in his *Isagoges in Rem Herbariam* published in Leiden.

27. The Florentine painters were notable for their depiction of many clearly recognizable species of plants. The supreme botanical artist was probably Dürer; his wonderful painting of a piece of turf must be the first ecological illustration ever made, years ahead of the botanists.
28. An edition of the *Hortus Sanitatis* (Strasburg, 1497) is typical of many. Perhaps forty per cent of the 500 figures have some slight resemblance to the plant supposed to be represented, but with the exception of a very few, all are formalized, crude, and always incorrect in detail even where the general impression shows some likeness. The rest are either wrong or so poor as to be worthless; a few are almost surrealist in their horror. To add to confusion, the printer was evidently short of blocks for all the plants, so the identical block is sometimes used for two, three and even more plants!
29. For details on the development of botanical illustration see W. Blunt (loc. cit. Note 10 above). It must be emphasized that botanical illustration is fundamentally dependent on botanical theory and only secondarily on the technique of drawing or reproduction. Thus, although theoretical pioneers like Gessner and Colonna were including details of flowers and floral parts in their figures in the fifteenth century, this practice did not become general for two hundred years, until the nature and function of the flower was beginning to be understood, and the floral parts had in consequence been analysed and defined.
30. Fuchs's plates in particular played a curious but important part in the development of systematic botany owing to the fact that they were extensively pirated and appeared in very many works during the sixteenth and seventeenth centuries and even later, including Turner's *New Herball* in England and Dodoens's *Cruydeboeck* in the Netherlands. The details are given by W. Blunt (loc. cit. Note 10).
31. A sympathetic and very valuable study of Brunfels, Fuchs, Bock, Euricius and Valerius Cordus, by E. L. Greene, will be found in *Smithsonian Miscellaneous Collections* Vol 54, No. 1870.

    The misleading term "German fathers of botany" was first used by C. Sprengel (*Geschichte der Botanik* 1817) and was taken up by Meyer and Sachs.
32. P. Mattioli (1501–77), a doctor and son of a doctor, who practised in Sienna, Rome, Trentino, Görz, and Prague. His commentaries on Dioscorides became practically a general flora: they were immensely popular in Europe because of their mostly excellent illustrations, and many editions were published in Latin, Italian, German and Czech. Mattioli was overbearing and sometimes careless; C. Gessner's criticisms of him are well-founded in those cases which I have been able to check. Cesalpino thought that he owed more to Ghini than he admitted, but he

and Ghini were undoubtedly far greater botanists than Brunfels and Fuchs.

33. This point is made by E. L. Green. Brunfels, Fuchs, Bock, Turner, Clusius, E. and V. Cordus, Gessner, the Bauhins, were of the new religion; Cesalpino, Aldrovandi, and da Orta were each at some time in bad odour with the Catholic Church on suspicion of heresy. The university of Padua was considered a hotbed of Averroism in the sixteenth century, probably because this doctrine was attractive to medical men (and most botanists were doctors).
34. The network of botanical contacts is reflected, for example, in Gessner's correspondence. It played an important role in the history of botany worthy of a detailed study which cannot be attempted here.
35. Valerius Cordus (1515–44) studied medicine under his father Euricius at the new Protestant university of Marburg, later lectured on pharmaceutics at Leipzig and Wittenberg. His *Dispensatorium*, published in 1546 by the Nuremberg city council, became the standard German pharmacopeia. He died in Italy whilst on a plant-collecting expedition. The singular brilliance of intellect and charm of character of Cordus still shine across the centuries from the tributes of those who knew him. *Historiae stirpium libri IV* and *Stirpium descriptionis liber quintus* were edited after his death by C. Gessner and published in 1563. Gessner states in the introduction that he never met or had personal contact with Valerius Cordus.
36. Euricius Cordus's attempts to correct current nomenclature of medicinal plants are contained in his *Botanologicon* published 1534 in Cologne (Köln) and again in 1551 in Paris. This delightful little work takes the form of a conversation between Euricius and four fellow botanists: it discusses a number of plants and inculcates a critical but commonsense attitude to the problem of removing old errors.
37. In some cases, but not as a general rule, Cordus describes not merely the appearance of the flower as a whole, but also the separate floral parts and their number, distinguishing *calix* (calyx), *foliola* (petals), *stamina* (stamens), *apex* (style). The last term was already being used by Ruel and Fuchs for the head of the stamens (anthers) and later became fairly generally established in this sense.
38. This was also a serious practical question, raised by the inadequate descriptions of plants in Dioscorides, Pliny, and the herbalists. Nor was it by any means obvious what *differentiae* should be used.
39. There is no mystery about the origin of the concept of natural affinity. It had an immediate and perfectly understandable basis in the type of relationship observed between members of the human species who are physically akin. The minutely observed results of breeding in domestic animals (see, for example, Genesis 30) would also be a familiar prototype of multi-relational affinity. Hence Aristotle and Theophrastus and later scientists formed the notion of natural affinity empirically and applied it

to plants and animals, even though they did not in the least envisage different species as physically related by evolutionary descent. It was sufficient to consider natural relationship revealed by affinity as representing the order existing in the mind of God or in the realm of Ideas. The difficulty was that arbitrary, non-natural schemes of classification reflecting various social, utilitarian or otherwise inappropriate categories could also be formed, and these had to be got rid of before scientific analysis could proceed.

40. Although Ghini left no published works some of his comments on particular plants (written for Mattioli's benefit) have fortunately been preserved in manuscript, and were edited by de Toni in 1907 and published by the Imperiale Regio Istituto Veneto. His notes and comments on fifty-six plants are extant and show the care and clarity of his observations; but their great interest is that they reveal that Ghini's primary concern was to distinguish species which had previously been lumped together as a single *genus*, or in modern terms, to define the species within genera. This had a double importance, first as a practical step to natural classification, and second as turning from what the classical authorities wrote to what actually existed in nature. A quotation from Ghini's *placitum* on Horminum [*Salvia*], addressed to Mattioli, will illustrate. "Of horminum I have two species, cultivated and wild (horminum sativum et horminum sylvestre). I am sending you both plants dried and glued to cardboard. It does not matter that Dioscorides mentions only one because in many other cases he does not mention all the species that could be described. I think, my dear sir, that you yourself have observed many more Tithymala [*Euphorbia* species], ranunculi, polygonata, and so on, than are enumerated by Dioscorides. In my own garden I have three species of hastula regia [*Asphodelus*] besides the one described by Dioscorides."
41. Conrad Gessner (1516–65) was born of a poor family in Zurich, where he spent most of his life. His grandfather was a seller of spices and herbs, and he early developed a love of botany from the teaching of his uncle Johannes Frich, a canon, who had a small herb garden. Gessner trained in medicine at Montpellier and Basle. He returned to Zurich and earned a meagre living by medical practice and teaching, but devoted much of his time to natural history, particularly to botany. He visited the principal universities of Italy. For a full account of his life and work see: H. Wellisch: Conrad Gessner. *Journal of the Society for the Bibliography of Natural History* **7**, 151–247; H. Zoller: K. Gessner als Botaniker. *Gesnerus* **22**, 216–27 (1965).
42. After his death Gessner's drawings had a complicated and still obscure history, given in outline by W. Blunt. They passed into the possession of Joachim Camerarius the Younger (1534–98) who published some of them in his *Hortus Medicus* (1588). In fact this book only contains forty-seven plates in all, and four of these do not show flowers, fruit or seeds

separately and are therefore probably not Gessner's, whilst another plate which does show these details is taken from Bock, leaving only forty-one plates drawn by Gessner. After this the drawings disappear until Dr C. J. Trew of Nuremberg purchased them in the eighteenth century and a selection was published in two parts (1751, 1771, Nuremberg) but with plates so reduced in size that detail tends to be lost.

After 1771 the drawings disappeared once more, until in 1929 all Gessner's drawings and notes were discovered in an attic of the library of the University of Erlangen. The drawings and notes are now in process of publication in magnificent facsimile (edited by H. Zoller, M. Steinmann and K. Schmidt: Zurich) revealing at last the loss to botanical illustration caused by Gessner's untimely death. Details of floral structure were also included by Fabio Colonna in his splendid copper engravings in 1592 and 1616, but the practice was not followed by other illustrators.

43. Andrea Cesalpino (1519–1603) was born in Arezzo and after studying medicine under Ghini at Pisa remained there teaching anatomy, botany and philosophy for almost forty years. In 1592 he went to Rome as papal physician. He was a man of powerful intellect, admired and respected by his contemporaries. His philosophical teaching, published as *Quaestiones Peripatetici* (1569), is said to have put him at one time in some danger from the Inquisition, perhaps because he was suspected of Averroism. His anatomical studies led him to reject Galen's view that blood vessels originated from the liver, and he held that blood flowed from the heart through veins and arteries alike; but he seems to have conceived the flow as to and from the heart, and there is no evidence that he really anticipated Harvey. He was interested in mineralogy and wrote on the classification of minerals. Evidence of his extensive personal observation of plants comes from his own statement that for very many years he had explored many localities where different kinds of plants occurred. In addition there is his own herbarium, dated 1563, which is preserved in Florence: this contains 768 plants mounted on 260 sheets, arranged according to his own system, each plant being designated by its Greek, Latin and Italian name, written in Cesalpino's hand.

44. The negative features of *De Plantis* were correctly noted by Sachs, but his lack of sympathy or understanding for Aristotle, and his complete blindness to the extent of Theophrastus' achievements, make his exposition ill-balanced and superficial. On the other hand Sachs had a thorough appreciation of Cesalpino's greatness, and paid him the tribute of serious study, giving an extensive account of the most important advances he made. In my opinion, Sachs's account is none the less not wholly satisfactory for two reasons: his constant failure to realize how far Cesalpino's "deductive" conclusions were linked with a mass of sound empirical observation, and his underestimation of Cesalpino's enormous feeling

for, and progress towards, a natural system, and the way this was supported by the creative assimilation of knowledge inherited from ancient science.

45. The reader must bear in mind that Cesalpino is using genera and species in a general philosophical sense, meaning classes and subordinate classes, or classes and subclasses, not in the specialized modern botanical sense, restricted to lower taxa.

    The gradual restriction of genus and species to serve as terms for lower taxa begins at about this time, but the wider and the more specialized usage continued side by side for a long time.

46. Cesalpino summarized his view in a single sentence which is worth close attention for the light it throws on his philosophical position. "We look for those similarities and differences which make up the essential nature of plants, not for those which are only accidental to them; for things perceived by the senses become comprehended primarily from their essential nature and only secondarily from their accidents." (Cum autem formarum similitudines et dissimilitudines queramus, ex quibus constat plantarum substantia, non autem eorem, quae accidunt ipsis; accidentia enim posterius innotescunt cognita substantia.) (Lib. I, cap. XIII).

    The distinction between *substantia* and *accidentia* comes from Aristotelean thought. Cesalpino's point is that only through their internal causal relations (*substantia*) can we really understand the phenomena revealed by sense perception (*cognita*). Hence his rejection of accidental characters in classification, which immediately follows, is based on practical experience *and* theory, not on either alone; a conclusion which is confirmed by several other passages, as well as by his classification as a whole. At the very end of his discussion of "accidental" characters Cesalpino reveals that he realized that natural classification can sometimes be a guide to the occurrence of such accidentals as medicinal properties or taste (Lib. I, cap. XIV).

47. Nor was this in my opinion merely *post hoc* reasoning. Cesalpino (following Aristotle) was basing himself on a perfectly sensible theory in selecting characters associated with a nodal point (mode of reproduction and its organs) in the cycle of development. He was recognizing, as we do, that among the essential features which (at a certain level) separate broad groups of living organisms, the specific characters of the reproductive process are highly significant. Hence the choice of "fructification" (floral organs) in plants. Some people today are scared of this conclusion, preferring to speak, for example, of the "high information content of the floral organs". But this is mere tautology. The leaf has a "high information content" to anyone who looks carefully, yet systematists accept that the floral organs provide the information on which higher classes (taxa) can be based, whereas leaf characters are most useful in defining the lower taxa, exactly the position adopted by Cesalpino. It is interesting to read Cesalpino's estimate of the "information content" of the

frucification: "And rightly did many classes of plants emerge from the manner of fructification, for in no other parts his nature raised such a multitude of organs and distinguishing characteristics as are to be seen in the developing fruits."

In connection with the soul of plants it is essential to remember that (like Aristotle's) Cesalpino's concept of soul included a purely material aspect corresponding roughly to the metabolic unity or organization of a living body.

48. Aristotle's criterion of species was brought to the fore again by the intensified development of horticulture and experimental gardens.

49. Sachs laid great stress on Cesalpino's statement that because ferns lack flower and seed, therefore they lack true stem (made twice, in Lib. I, cap. XIV and Lib. XVI), regarding it as the origin of a mistaken belief long current, and revived as late as the nineteenth century, that ferns are stemless. However, Cesalpino was only repeating a generally held opinion, since Ruel fifty years earlier states, as an accepted fact, that only plants producing seed (and ferns, he says, do not) have a stem.

The origin of this belief I am not sure of. Perhaps the inference was drawn from Aristotle's association of seed formation with the upper ends of the stems of plants (*Partes Animalium* IV,10,687a). It cannot have come from Theophrastus because when referring to the ferns *adianton* and *trichomanes* he says they have a similar stem, although the description shows that he was actually referring to the rhachis of the leaf (*HP* 7,14,1). Pliny says nothing to imply that ferns have no stems, but uses the terms *ramus, ramulus* or *pediculus* (not *caulis*) to refer to the rhachis: in the case of one fern, *asplenon*, he mentions that it has neither stem, flower, nor seed. I am inclined to think Dioscorides the most likely source of the belief, because in four of the ferns, out of the seven or eight mentioned in his herbal, he expressly notes the absence of stem, and in none does he say it is present.

Jung assumed that ferns are stemless but makes an exception of Filix palustris or Osmunda, presumably *Osmunda regalis* (*Doxoscopiae* Fr. 4, cap. 2). John Ray assumed that all European ferns are stemless, but noted in his *Methodus emendata* that truly cauliferous American and West Indian ferns were then known, and that he himself had seen dried specimens collected by Hans Sloane in Jamaica. This curious story need not be followed further here.

50. Rather oddly, Cesalpino's list of the division of seedless plants in Lib. I is in reverse order to that given in Lib. XVI.

51. Summaries of Cesalpino's scheme are given by Ray (in *Methodus Nova*, 1682), Linnaeus (*Classes Plantarum*, 1738), Sachs (*History of Botany*), Sprengel (*Geschichte der Botanik*), S. H. Vines (in *Makers of British Botany* (Ed. F. W. Oliver) 1913: in an article on Morison and Ray), and C. E. B. Bremekamp (A re-examination of Cesalpino's classification, *Acta Botanica Neerlandica* **I**, 580–93 (1953)). Bremekamp is very illuminating.

52. We speak of the seeds of beet, dandelions, grasses and many others. It would be pedantic to do otherwise, but structurally and botanically they are fruits, because the seed is still enclosed by what was originally the ovary wall.
53. A few of Cesalpino's many remarkable observations may be mentioned to illustrate his keen morphological sense and the kind of criteria he used in classification. For the sake of clarity they will be translated into modern terminology as far as possible.

Cesalpino attached great significance to the region of junction of stem and root, which he called *cor medullae* (heart of the pith) or simply *cor* (heart), because he believed it was the seat of the vegetable soul. But whatever the theory, he made two original discoveries of real importance. First, the phenomenon of polarity in plants and the fact that it is established very early in development, in the embryonal plant in the seed. Second, that the embryo as a whole is oriented in the seed; in other words, he realized the distinction between orthotropous and anatropous ovules (the intermediate campylotropous type he did not notice). Furthermore, he considered the orientation of the ovule (of course, he actually observed orientation in the mature seed in most cases) as an important character to be used in classification; and here modern systematics has amply confirmed him. Difficulties of observation made his own use of this character (he called it the position of the *cor*) sometimes confusing and uncertain. But in one instance he was certainly brilliantly successful, when (Lib. XI) he correctly separated Labiatae from Boraginaceae on the basis of the orientation of the ovule. In an extraordinary passage in Lib. IV he recognizes the phenomenon of the reduction (in some species of a genus) of a many-seeded ovary to one with but a single seed, and in Lib. VI applies this to Fumaria (=*Fumaria* sp), thus correctly interpreting the "seed" of fumitory as an indehiscent fruit, a fact which even Ray did not appreciate a hundred years later. In most other cases of course, Cesalpino assumes achenes, etc. to be naked seeds. Cesalpino did not completely understand the nature of the flower-head in Compositae, although he came very near it, but he divided the Compositae known to him into three groups according to characters of the capitulum: those with only ligulate florets, those with only marginal ligulate florets and the remainder radiate, and those (like Artemisia) in which the florets become dry and persistent—groupings still regarded as probably "natural". He pointed to the similar floral structure of Liliaceae (*lilia*) and Iridaceae *genera iridis*, both having six large perianthe members (foliola) but differing in the inferior ovary of the latter group; and he compared the fruit of *Rosa* and *Rubus*, and *Ficus* and *Morus*, remarking that in each pair the second can be considered the inverse of the first: a truly astonishing insight (Lib. I, cap. X).

Finally his account of the cereals (Lib. IV, cap. 41) draws attention to the constant presence in the seed of the endosperm (*seminis corpulentia*) and the absence of the two seed leaves found in "legumes and many others": a hint of the generalization Ray was to discover a century later. Even more interesting is his description of the special characteristics of the roots, stems, nodes and leaves of cereals, characteristics which he notes are shown by the whole group (*sic frumentorum genus universum se habet*). This statement shows conclusively that Cesalpino used many *differentiae* in classification and did not, as has been so frequently asserted in the literature (by Linnaeus and many since), rely solely on the fructification.

54. Matthias de l'Obel (Lobelius) (1538–1616) was born at Lille and studied under Rondelet at Montpellier, either at the same time as Clusius or within a year or so afterwards. He collected widely in France, Italy, Switzerland, Germany and England, probably partly in the company of Pena. He practised medicine both in the Netherlands and in England, but finally settled in England and ended his days as botanist to James I. It is clear from his preface to *Stirpium Adversaria Nova* (published in London in 1570 under the joint names of Peter Pena and Lobelius) that he was not a little proud of his classification. Unluckily it set the pattern for a century, as most of the illustrated herbals, which began to pour from the presses, followed it.
55. It must be emphasized that Cesalpino, in common with all contemporary botanists, used the term flower in a less comprehensive sense than modern botanists. For him the flower (*flos*) consisted of the calyx and corolla (not separately designated by him, but referred to as *folium*, leaf, if united, or *folia*, leaves, if composed of distinct members), the stamens, and the style (Lib. I, cap. VII). Very surprisingly, he uses the word *stamina* to refer to the style, contrary to what was already becoming common usage among botanists (in one passage, exceptionally, he calls the stamens of the rose *stamina*!). His general term for stamens is *flocci*.

    Thus the flower did not include the ovary (*conceptaculum, vasculum, receptaculum*) or the seeds.

    He notes (loc. cit. above) that the stamens (*flocci*) are very numerous in plants like poppy that have many seeds, "as if each were the product of single seeds", and states that they are the parts whence the flowers exhale (an idea taken up much later by Tournefort). Clearly Cesalpino had no conception of the sexual function of the stamens.

    He notes that in some plants the "flowers" may be reduced to the stamens only, as in the meadow-rue, Thaliethrum.
56. Thus Cesalpino draws attention to "to the wonderful beauty and charm of flowers, which point the way to the delights of creative nature in the developing seeds." (Lib. I, cap. VI).
57. In the dedication of his great book Cesalpino reveals in a couple of sentences his deep comprehension both of the philosophical and the eminently practical reasons for seeking a natural classification. "Dioscorides' ordering [of plants] by medicinal properties, or the alphabetic arrangement used by others, are far from the nature of things. The

best order is according to the community of natures. This is the best and easiest method for remembering, since characters proceeding from nature itself are recognizable and manifest to everyone, and are not deceptive like adventitious conditions which are impermanent. In this way an immense number of plants can be summarized in ordered classes."

58. Adam Zalužanský (1558–1613) of Prague quotes from *De Plantis* in his *Methodi Herbarial Libri Tres* (1592), but did not use or appreciate the principles of classification developed by Cesalpino, whose extensive personal knowledge of plants he clearly did not possess. The most important point made by Zalužanský was that botany must be studied as a science in its own right, dealing with the nature and causal principles common to all plants, and that it must be kept distinct and separate from medicine. In this he reflected the fundamental outlook of *De Plantis*.

    Probably G. Bauhin's comment in a letter to a friend expressed a common reaction. "Cesalpino's book *De Plantis* has been much in my mind; I spent a long time in reading it in order to use it for my classification. He is a learned man but very obscure; I had great difficulty in understanding him, and doubt, whether he would be intelligible to beginners and students." On the other hand Spigelius wrote in 1603: "If anyone has difficulty in determining new names, he should study Cesalpino's books [*sic*] which are now readily available, and from the arrangement therein will be able to deduce as many names as he wishes."

59. One product of this hobby of the new middle classes was the so-called tulipomania, commercial speculation based on the passion for the tulip, which swept the Netherlands in the early seventeenth century. Another product was the Dutch bulb industry.

    The most famous of the Dutch botanists, Clusius, was the founder of tulip culture in the Netherlands and England, since he sent thither bulbs and seeds of tulip which he had received in 1573 from Turkey and had grown in the Imperial Garden in Vienna of which he was Keeper for fourteen years. Clusius also played an important part in spreading the cultivation of the potato in Europe.

60. Rembert Dodoens (Dodonaeus) (1517–85) practised as a physician in Malines for many years. After a brief spell in Vienna as physician to Maximilian II who was tolerant of Protestants, Dodoens ended his life as Professor of Medicine at the new university of Leiden. In classifying plants he sought only an improved pharmacological classification (see preface to *Stirpium Historiae Pemotades Sex* (1583).

    Charles de l'Ecluse (Clusius) (1525–1609) spent three years as a young man under Rondelet at Montpellier. He travelled widely in western Europe collecting plants, adding about 600 new species; he was the first botanist to describe and illustrate more than the conventional handful of fungi. The 105 species of fungi given in his *Rariorum Plantarum Historia* (1601) represent the first substantial contribution to systematic mycology (for details see G. C. Ainsworth: *Introduction to the History of Mycology* (1976)). Clusius translated Dodonaeus's *Cruydebock* into French, and the works of a number of authors, including Garcia, Monardes and Belon, into Latin, in most cases adding information from his own observations.

Clusius was the most brilliant of the Netherlands botanists but was little interested in the general problem of plant classification. In 1593 he was appointed Professor at Leiden where he remained till his death.

61. The brothers Bauhin were the sons of a French physician who quitted France on account of his Protestantism and established himself in Basle, where both his sons were born.

Jean (1541–1613) learnt medicine from his father and then studied under Fuchs at Tübingen. He became acquainted with Gessner and collected plants with him in Switzerland. He visited several foreign universities including Montpellier, Padua and Bologna, where he met Aldrovandi, and collected plants in France and Italy. After practising in Lyon, Geneva and Basle, in 1571 he became physician to the Duke of Würtemberg at Montbelliard near Stuttgart, where he had a botanic garden, and remained till his death.

Gaspard (Caspar) (1560–1624) studied medicine at Basle and Padua. After travelling in France and Germany he returned to Basle where he remained teaching botany and anatomy at the university for the remainder of his life.

62. Fabio Colonna (Columna) (1567/8–1650) came of a noble family and is the exception among botanists of the time in that he was not medically trained. His father was an erudite man who collected and edited the fragments of Ennius, and he himself studied the classics, music, mathematics, optics and the law. As a youth he suffered from epilepsy and it was the desire to find a cure which turned him to the study of herbs. His health apparently improved and he believed at first that the cure was due to the use of the herb valerian, but later he seems to have doubted this, and lays no stress on its virtues. However in the intervals of a professional career in the law—he was a judge in Apulia—he became a discerning botanist. An interesting account of his life is given (in Latin) in the introduction to the 1744 edition of his *Phytobasanos*, a study of some plants in Dioscorides, first published in 1592. His most important work is *Minus Cognitarum Rariorumque Nostro Coelo Orientium Stirpium Ekphrasis* (1606, but in the main edition 1616), which is referred to in the text. Colonna used a lens to look at the floral parts, and was probably the first to do so. He made his own drawings and could do copper engraving as well, but it is most likely that the published plates in *Phytobasanos* and *Ekphrasis* were engraved by a professional after Colonna's drawings.

Colonna was the first to use the Greek word *petalon* (a leaf) in the specialized sense of petal or inner floral leaf (in *Phytobasanos* cap. I and in *Ekphrasis* Part I, cap. 92). In 1628 he edited the plant section of

F. Hernandez's account of the plants, animals and minerals of Mexico which had come into the possession of the Accademia dei Lyncei in Rome. In his notes to this work Colonna proposed the use of the term petal in its modern botanical sense. This suggestion was taken up in 1686 by Ray, and petal thus entered not only botanical nomenclature but even the poetical vocabulary of many languages.

6

A Chart for the Future (1623 to 1694)

Good hope for the further advance of knowledge depends on the inclusion and gathering into natural history of a great many experiments which are of no use in themselves but simply serve to discover causes and axioms, *experimenta lucifera* as I call them, to distinguish them from those I call *fructifera*.

Francis Bacon: *Novum Organum*, Aphorism XCIX (1620)

In the early decades of the seventeenth century we can see the beginning of a qualitative change in the form of scientific activity, which was described by contemporaries as the advent of the "experimental" or the "mechanical philosophy", and has since been referred to as the transition to modern science, or to experimental science, or to the use of scientific method. Perhaps no single phrase is entirely satisfactory to define the change, but this does not alter its reality or importance. Fundamentally it consisted in the recognition that the practical test of experiment in the widest sense, embracing many kinds of purposeful, planned observation ranging from systematic collection of facts to "controlled" experiment, is the touchstone by which theories and hypotheses in science are continually tested, altered and improved, confirmed or rejected.

The philosophical foundation of experimental method was eloquently expounded by Francis Bacon in *Novum Organum*,[1] a work which permanently influenced the course and growth of science by providing the theoretical justification for a method of investigation which was already beginning to be used in practice. There can be little doubt that the immediate model for scientific experiment was found in those capitalist industrial enterprises employing wage labour, which came into being in many parts of Europe, and above all in England, during the final quarter of the sixteenth century.[2] To get the most effective organization of labour and the maximum technical efficiency required methods of quasi-experimental trial and quantitative accounting which were the rough recipe from which the refined methodology of experimental science was developed.[3] Bacon's great achievement which profoundly influenced the seventeenth century scientists and virtuosi, was not only to clarify and define the function of the "experimental method", but also to show that its successful exploitation depended on co-operative organization in scientific research and not simply on isolated experiments, however brilliant.[4]

The tenets of experimental philosophy were given force by the new and exciting methods of seeing the world which technical developments in glass-making and lens-grinding made possible, quite suddenly, round about 1600, when telescopes and microscopes first became widely available, instruments that were to become, as Robert Hooke said, "an enlargement of the dominion of the senses". When Galileo, in *The Starry Messenger* (1610), reported seeing the mountains of the moon, he shook the whole learned world to its depths as perhaps no other scientist has ever done, destroying at a blow the almost sacred edifice of classical astronomy and opening the heavens to "plain observation" by any one with the necessary instrument. After this astonishing revelation of the macrocosm men could hardly fail to start using microscopes to look at the microcosm.[5] The optical and interpretive problems of microscopical observation were, however, more difficult; progress was slower and the results were less dramatic, yet within fifty years the microscope also had become a scientific tool.

Philosophical, technical, industrial and social factors combined to produce an outburst of scientific activity in the second half of the seventeenth century, and botany was affected in common with science as a whole. Its field of enquiry was broadened and it was brought for the first time into contact with other sciences besides medicine, whence experimental and technical methods began to penetrate into botany; thus the way was opened to the formation of new theoretical concepts.

Botanists were slow to be influenced by the "experimental philosophy" since they tended to be immersed in the demanding labour of listing and describing a wealth of plants that must have seemed inexhaustible. Not only was there a constant flow of unknown species from distant parts of the world, but closer study of their own native floras revealed hundreds of common plants to which they had hitherto been blind. Nor can botanists be blamed for their prepossession with floristics for it was in this area that the most pressing practical problems arose. Indeed one of the bitterest medical controversies of the time arose largely from the inadequacy of botanical description and the consequent uncertainty surrounding the species of *Cinchona* which yielded "Peruvian bark" (quinine), probably the most valuable vegetable drug ever discovered. Its effectiveness against malaria (ague, quartan fever) became widely recognized during the seventeenth century but was strongly denied by some physicians, probably in good faith and simply as a result of botanical confusion or the effect of deliberate adulteration.[6] In the early decades of the seventeenth century descriptive botany continued the process of collecting and recording plants but had lost theoretical impetus and direction. This stagnation was ended by extremely important new theoretical developments, particularly in plant morphology, which stemmed from the work of Joachim Jung (Jungius), and which were certainly the reflection, in systematics, of the rising experimental philosophy.

Jung was a man of great versatility and powerful intellect, ranking beside Galileo, Bacon and Descartes, his contemporaries. After studying philosophy, mathematics and astronomy, he qualified in medicine, but spent the last thirty years of his life as Professor of Natural Sciences in the Akademisches Gymnasium in Hamburg, becoming deeply involved in chemistry and botany. He revived the atomic theory of Democritus, supporting it by a discussion of contemporary chemical theory; in addition he wrote a treatise on the place of mathematical reasoning in scientific theory.[7]

In botany, Jung was no mere amateur; his botanical remains show that he had a thorough practical knowledge of plants, pursued far beyond the conventional requirements of a medical course. To this foundation he brought the same urge to generalization as Theophratus and Cesalpino, together with a conviction of the illuminating function of mathematics in science, based on the success of mathematical methods in expressing the laws of astronomy and physics. Jung did not experiment in botany as far as we know, but he was led by philosophy and observation to a systemtic analysis of plant form which had a lasting impact on descriptive botany. Since he was in Padua only fifteen years after Cesalpino's death, he may well have known some of the latter's pupils: certainly Jung had studied Cesalpino, and was the first to appreciate and develop his ideas creatively.

The botanical writings left by Jung were not extensive; they consist of notes made by students from dictated lectures, subsequently corrected and amplified by Jung himself. These were not published during his lifetime but were edited shortly after his death by two former pupils, and printed in the form of two short works entitled *Isagoge Phytoscopica* ("A guide to examining plants") and *De Plantis Doxoscopiae Physicae Minores* ("Brief investigations of plants"). The *Isagoge* was not printed till 1679 but manuscript copies were in circulation earlier, and one was communicated to Ray in 1660: the *Doxoscopiae* were printed in 1662. Together they run to under one hundred and fifty pages but their effect was far-reaching. The *Isagoge* is a brief but remarkable account of the morphology of higher plants.[8] The plant is analysed into a limited number of fundamental organs or parts, which are defined, in essence, by their topological interrelations within the plant body. In addition a comprehensive terminology is proposed for describing, with precision and without redundancy, the range of form of all the plant parts and of the relations between them, as observed in nature. Jung was thus refining and extending the concept of a scientific plant morphology which derived fromTheophrastus and Cesalpino. At the same time his efforts were also part of the process of establishing a technical vocabulary for plant description, which can be traced from Theophrastus, through Pliny, to Fuchs and the sixteenth and seventeeth century botanists, and which had already accumulated a considerable apparatus of botanical terms, some already in general and consistent use, but many ill-defined or otiose and lacking such validation.

It is evident that Jung took Cesalpino as his starting point, and by combining a botanist's eye for detail with the discriminating vision of a mathematician, built a superbly logical structure on the foundation laid by the latter. The formal approach to morphology which he developed was exactly what was needed at the time in order to isolate the regularities of plant form from what might otherwise appear a continuum of bewildering diversity, and hence to frame a descriptive language that was truly analytic and not choked by a profusion of superficial terms. It is striking and somewhat unexpected that mathematics should have played a part in forming the germinal conception of a unified plant morphology, since mathematics, until very recent years, has found little general application in botany.

A plant is defined by Jung in words which include, but are not identical with, those of Aristotle—revealing a subtle change of mental attitude and expressing a more physiological view. "A plant is a living non-sentient body, attached to a particular place or habitat, where it is able to feed, to grow in size, and finally to propagate itself." Propagation is used in Cesalpino's sense to mean reproduction of specific form (*planta gignit sibi specie similem*), and thus includes propagation by vegetative means and by seed. Jung notes that plant growth differs from that of animals in that all parts do not grow simultaneously; some organs are of limited growth, whilst additional new parts may be generated.

The plant body is then considered systematically, starting from Cesalpino's fundamental division into root and shoot, the orderly arrangement of leaves on the stem, and the origin of branches from the leaf-axils. Like Cesalpino he defines the root by its assumed function in attracting food whether growing "in earth, rock, limestone, wood, sand or anything else". He does not give absence of leaves as a defining characteristic of the root except by implication from the definition of the stem: the part extended upwards, symmetrical, simple or branched, bearing leaves, flowers, fruit and such secondary parts as hairs or spines. In another passage he remarks that he knows no stem completely aphyllous: even in Orobanche (broomrape) the stem is clothed with minute leaves. Jung included among plant organs Cesalpino's *cor medullae*, the common limit and meeting place of stem and root. He employs, however, the more neutral term *fundus plantae* [base of the plant], and it is significant that he says nothing more of this imaginary organ, which Cesalpino regarded as the seat of the plant soul.

Apart from the reference to food absorption by the root, Jung does not otherwise use physiological function in defining morphological categories, relying only on spatial and developmental relations.

Rhizomatous stems are not always correctly distinguished from roots, but he notes the origin of roots from the nodes in creeping stems of strawberry and bramble.

The leaf is defined as that which is extended in either height or length, and in breadth, in relation to its point of attachment, in such a way that there is a difference between the internal and external [i.e. adaxial and abaxial] surfaces. Jung was the first who formally recognized this essential foliar character. He remarks that compound leaves may be confused with shoots and branches by the inexperienced or unobservant, but that this asymmetry of adaxial and abaxial surface always enables them to be distinguished, as does their property of falling as a whole in the autumn. It will be remembered that this latter characteristic of a compound leaf had been pointed out by Theophrastus.

The petiole or stalk of the leaf is the part joining it to the stem, and refers strictly only to the part between the stem and leaf-blade, the further extension being called the nerve or *costa* [midrib].

After defining the leaf in this way, Jung characterizes its range of form in detail. Leaves may be simple (as in beech, grasses, lily, etc.), or concave (as in onion or leek), or compound. Compound leaves may be digitate (clover, strawberry, lupin), paripinnate (bean, pea), imparipinnate (rose, ash) or triangulate (celery, paeony). The leaf margin may be entire or dissected, and in the latter case may be further characterized as laciniate, serrate, crenate, dentate. Finally the various types of phyllotaxy, the arrangement of leaves on the stem, are accurately described and designated.

The different forms of stem (terete, angled, striate, with or without nodes) are described, and the important distinction between determinate and indeterminate growth of the shoot is made clear. Coming to the flowering shoot, the types of inflorescence, whether the flowers are solitary, or in clusters of two, three or a few together, or massed in a capitulum, spike, umbel, thyrsus, panicle, corymb, are all described and defined in terms of the site of the flower in relation to the stem.

Jung's treatment of floral morphology is considerably in advance of that of Cesalpino and merits consideration in some detail. It must be remembered that, like Cesalpino, he was not aware of the function of the stamens in reproduction: again, like Cesalpino, he used the word flower (*flos*: plural, *flores*) in a more restricted sese than is usual today, but his analysis of the complete flower and the floral parts is more detailed and accurate than Cesalpino's. I shall use flower in its modern sense, and *flos* in the sense defined by Jung: "the somewhat tender part of the plant, conspicuous by reason of its colour or form or both, which adheres to the rudiment of the fruit". The *flos*, if perfect, possesses petals (*folia*), stamens (*stamina*) and style (*stilus*), and is described as imperfect if it lacks one or other of these parts. Thus poppy and tulip are imperfect *flores* to Jung because they lack a style, although he considers that they possess "a kind of substitute for the style" by which he means the stigmatic surface which is almost sessile on the ovary. When the *flos* consists of stamens only, as in the male catkins of oak or walnut, or the male spike of *Typha*, Jung's terminology, *flores staminei* (staminate flowers), happens to coincide with the modern, but he also uses *flores staminei* to refer to non-petaloid flowers with both stamens and style, as in *Ulmus* or *Sanguisorba*.

In the complete flower Jung distinguished the following parts (modern terminology): calyx, corolla, stamens, style and ovary or fruit. As explained, the corolla, stamens and style, constitute the *flos*. The calyx, called by him *perianthium*[9] or *calyx*, is defined as the part which covers the *flos*, and is therefore thicker and less conspicuous than the *flos* itself. He notes that some flowers (tulip, lily, elder, buckwheat) are without calyx, and that, where present, the calyx may be undivided (*perianthium simplex*) or divided (*perianthium compositum*). Not surprisingly the involucre of Compositae and Dipsaceae is treated as a calyx but he explains clearly that it is common to a whole head of minute flowers, whereas in most plants each flower has its own individual calyx. He further draws attention to the peculiarity of *Scabiosa* (Dipsaceae) in which there is a common *perianthium* to the whole head [the involucre] and in addition each floret has its own *perianthium* [the true calyx] in the form of a notched sack (*utriculus crenatus*). These remarks show that Jung fully understood the nature of the "flower-head" in Compositae and Dipsaceae, and was probably the first to do so. He realized that the capitulum is a collection of many minute but perfect flowers which he called *floscula* [florets], and he was also quite clear about the site of origin and mode of development of the pappus in Compositae, although he did not equate it with the calyx.

Jung did not employ any special designation for the divisions of calyx and corolla. He used *folium* (leaf) both for the whole structure if undivided, and for the individual parts if it were divided: this was the normal botanical usage at the time. However, he explains that in order to avoid homonymy he will speak of *foliatura* when referring to leaves which are not part of the flower (i.e. foliage leaves).

The united gamopetalous corolla is designated simple (*flos simplex*), since it consists of a single *folium*: the *folium* may be entire or deeply lobed, but its simple nature is always manifest because it is shed as a whole. The divided polypetalous corolla is designated as relatively composite (*flos compositus secundum quid*), since it is divided into a number of more or less similar members (*folia*). Thus Jung defines the modern distinction between gamopetaly (sympetaly) and polypetaly, which has since figured with varying degrees of emphasis in most discussions of the classification of flowering plants. His third class of "absolutely composite" flowers (*flos absolute compositus*) contains Compositae, Dipsaceae and their like. He recognized that the number of lobes of the corolla is characteristic for different species, and that flowers with five or six are more frequent than those with three or four. He noted the distinction between regular and zygomorphic flowers, and described many types of flower-form with an appropriate terminology.

Of the interior parts of the *flos*, the stamens are stated to consist of filament (*pediculus*) and head (*capitulus*), but pollen, rather strangely, is not mentioned, although its presence in the anthers was common knowledge by this time, having been well described by Albertus Magnus in the thirteenth century. Jung gives a very precise and detailed account of the range of variation in number, form and position of the stamens, with many references to named species. The style (*stilus*) is defined as the part occupying the centre of the *flos* and attached to the rudiment of the fruit or seed: the range of form of style and stigmatic head is described with examples.

As would be expected, Jung follows Cesalpino in considering the relative position of the petals and stamens with respect to the fruit to be a significant morphological character; this is equivalent to the modern distinction between the superior and inferior ovary. The fruit is defined as the part adhering to and following the flower, which separates spontaneously from the plant, and when nourished by earth or other suitable food, forms the beginning of a new plant. The fruit is either a seed or a vessel containing the seed, and no distinction is made between the naked seed and an indehiscent single-seeded fruit. Several alternative terms are used for the seed-vessel—*conceptaculum, vasculum, folliculus, caapsula, theca, involucrum*—but they are not differentiated or given specialized meanings. Jung's description of the structure of the seed is less thorough than that of Cesalpino: he mentions that some seeds are divided into two parts like hemispheres between which the rudiment of the plant is often plainly seen, and he briefly notes the position of the *cor.*

The new rigour which Jung brought into morphology is shown by his reference to the brightly coloured, almost petal-like, leaves which occur at the apex of the stem in some plants, as in some species of *Salvia.* To these Jung gives a special name, *cymae*, remarking that although they appear to be flowers they are in fact not so, because they correspond in form and position to leaves, and do not adhere to a fruit.

The foregoing account of Jung's treatment of morphology, as transmitted through the *Isagoge*, will I hope convey something of the powerful impulse this work gave to the development of systematic botany. Jung's criteria and categories of morphological analysis became—following their adoption by Ray and later by Linnaeus—a fundamental part of botanical theory, and also formed the foundation for a systematic descriptive terminology, which by its elegant rationality became a pattern and guide that was seized on in practice. Many of Jung's terms entered botanical language permanently, but their evident fittingness was the consequence of his unifying conception of morphological relationship. Some of the terms he used were already current and others he created for the purpose; his real contribution, however, was to give order and precision to terminology by linking it to principled definitions, which were exemplified by constant reference to named plants.

Whilst Jung's decisive influence was in morphology, the five "fragments" on various unrelated topics published as the *Doxoscopiae,* show both his detailed knowledge of plants and his broad theoretical views. In spite of the many points of interest, mention will only be made of those on which he expresses opinions that were ahead of his time and probably influenced the later development of botanical thought.

In the first fragment Jung discusses whether there is a real basis for the division of plants into trees, shrubs, under-shrubs and herbs. He brings forward many cases of intergrading, and is at pains to show that all attempted definitions of these categories break down in practice. Furthermore he shows that even the division between trees and herbs breaks down, quoting among others the example of the mallow, given by Theophrastus (*HP* 1,3,2) as a herb which can become tree-like. Thus Jung was the first (after Theophrastus himself!) to make a scientific case for abandoning the time-honoured classification of plants by habit. He also expressly rejects the class of vegetables, *olera,* adopted by Nicolaus Damascenus[10] and subsequently picked up by Albertus Magnus.

In rejecting the tree–herb dichotomy as a valid major division of plants (and Jung makes clear that he is speaking of major taxonomic ranking, "*de summis plantae speciebus*"), he was opposing, or at any rate abandoning, Cesalpino's half-way proposal to retain the division into trees and herbs whilst distributing shrubs and under-shrubs between them. At lower levels of classification ("*de inferioribus speciebus*") Jung closely follows Cesalpino, emphasizing that the essential criterion for classification must be the form of the plant, above all the form and relative position of floral parts and fruit, adding that he himself nevertheless always pays great attention to the leaves since they can be found at any age of the plant and are very conspicuous parts. Accidental characters (*differentiae*) such as colour, odour, medicinal powers, habitat, are useless.

In the fourth fragment is included a long discussion of spontaneous generation, a question that was once more beginning to engage scientific attention. There is a summary of all Theophrastus' statements on this topic, including his recognition of the inconspicuous seed of some plants, and the dispersal of seed to a distance by wind, rivers, and birds. Jung concludes that the weight of evidence is against spontaneous generation of plants.

This fragment also contains Jung's comment on the orientation of the *cor medullae* [the micropyle] of the seed in relation to the fruit, a character stressed by Cesalpino and to which reference was made earlier. Jung points out that where there is a single seed per flower this orientation can usually be determined, but where there are many seeds, particularly if embedded in flesh or pulp, it is uncertain and unobservable: in such cases it is merely a piece of Peripatetic theorizing. This epitomizes Jung's independent and incisive judgement.

Finally, in the fifth fragment the interesting physiological suggestion is made that the roots may have pores which in different plants are permeable or impermeable to the same material, thus enabling plants to select their appropriate food as animals do—an indication of the new kind of explanation of the activities of living things which was now being looked for.

It is perhaps not surprising that in botany the "experimental philosophy" expressed itself in the first place, through the impact of Jung, in the theoretical renewal of already existing patterns of investigation. The application of experimental methods to the investigation of plants came more slowly than in the physical sciences, probably because living things were at once both too close and familiar, and too complex; nor could their behaviour be represented by any simple mathematical formula as Galileo had shown to be possible for mechanical processes. Pioneer experimental work in biology began in medicine, still the centre of biological thought and teaching, with the researches of Sanctorius at Padua, published in the famous *Ars de Statica Medicina* (1614). He studied human metabolism quantitatively by repeated weighing of a man (usually himself) suspended in a cage from the arm of a balance, thereby establishing an experimental technique of far greater importance than the actual results he obtained. Much more influential in turning biologists to the experimental path was William Harvey's brilliant proof of the cirulation of the blood (*De Motu Cordis,* 1628).[11]

In relation to plants Bacon himself suggested some general lines of research, directed to making them more useful to man, and he actually made some investigations into seed germination, use of manure, ripening of fruit, which were published posthumously in *Sylva Sylvarum* in 1627. He saw the possibility that methods might be found to make plants grow earlier or later, and that their qualities might be improved by grafting or culture. The ideas of Bacon were widely quoted and evidently inspired some rather naive experimenting by gardeners and horticulturalists. These first attempts at the experimental study of plants were made chiefly in Germany, the Netherlands and England, where horticulture was vigorously expanding, but inevitably the experiments tended to remain within the restricted field of practical trial and error and were far from being *experimenta lucifera.* The immediate results contributed much to real advances in horticultural technique as the handbooks of the period show, but comparatively little to botany, beyond strengthening reliance on the test of practice for deciding questions of theory. These simple experiments did, however, demonstrate that certain ideas, some traditional, some the products of exuberant renaissance fancy, were untrue, misapplied or ineffective, and some long-persisting errors were finally laid to rest.[12]

The earliest experiments concerned with fundamental general principles of plant behaviour were done, as it happened, for non-botanical reasons as an offshoot of attempts to clarify chemical theory, then emerging from alchemy in a state of excited confusion about the existence and nature of the elements of which matter was conceived to be composed—a question which had become highly controversial as a result of the irruption into medicine of the ideas and mineral drugs of Paracelsus, and of the bitter conflict between traditional Galenists and the Paracelsians which ensued. The Aristotelean elements of air, water, earth and fire, were now being challenged as the ultimate constituents of the cosmos by other elements, of which sulphur, mercury and salt proposed by Paracelsus were the most widely favoured.[13] Experimentation began, some of it naturally rather uncertain in method and intention, but with the general aim of determining if elementary substances existed and what they were. So it came about that the first controlled experiment on plant nutrition was carried out some time in the 1640s by J. B. van Helmont,[14] an original-minded physician and chemist, in order to throw light on the chemical nature of water. Van Helmont actually did the experiment which Nicolaus of Cusa had suggested two hundred years before. He planted a willow tree weighing 5 lb in 200 lb of dry earth in a perforated container made of tinned iron. The tree was watered at intervals and allowed to grow for five years: at the end the tree, together with fallen leaves shed during four autumns, weighed 169 lb 3 oz. The earth, when re-dried at the end, had lost but 2 oz; hence 164 lb of the substance of the tree appeared "to have sprung from the water". Independently, but for the same reasons, Robert Boyle did similar but more careful experiments a little later, growing squash and cucumber plants to fruiting in soil, and rooted cuttings of mint, balm, marjoram and pennyroyal in water only, and demonstrating big increases in weight although the plants were "cherished only by water". Boyle distilled one of his well grown plants and found that several volatile substances came off leaving a coal-like residue of "salt and earth".[15] Both Van Helmont and Boyle concluded that water has been transmuted into the various substances of the plant body and could not therefore be a simple element. These experiments were not unnoticed by botanists: horticulturalists soon showed that a great variety of plants could be rooted in water and grown for long periods, sometimes flowering and fruiting, with nothing but water added. By his own account John Ray carried out some experiments along these lines as we shall see later. The conclusion seemed obvious—water, absorbed principally through the roots, could provide all the food that plants require.

With present knowledge it is easy to see the theoretical and practical limitations of these experiments which made them irrelevant to the conclusions they were used to support, but historically their significance was very great. They marked the beginning of experimental plant physiology, entailing the even more significant consequence of bringing the age-old techniques of plant cultivation into the field of scientific investigation. The state of knowledge in other sciences, especially chemistry and physics, limited possible progress in plant physiology, but at least experiment now began to replace the speculative interpretations which, like a parody of the already out-dated medical "humors"[16] had reigned so long in botany. The laws of behaviour of plants began to be looked for in consonance with the laws of behaviour of the matter composing them, and by the same methods as were employed in the material sciences.

This was a revolutionary advance in botanical thought and method, and required many years and much controversy before being fully and universally accepted, but which from the beginning brought valuable gains in knowledge. The philosophical spur clearly came—at a time when Bacon's proposals were being translated into practice—from such thinkers as Joachim Jung, Descartes, and Pierre Gassendi, who exercised a profound influence on scientists around the middle of the seventeenth century. Their influence has been much studied and no detailed analysis need be attempted here, but two aspects, particularly important for the course of botancial research, are worth noting. Descartes's treatment of a living organism as a piece of mechanism, however assailable philosophically, jolted botanists into a totally new way of exploring how plants work, and proved in the event a much more fruitful and stimulating guide than Bacon's far-sighted generalities. The impulse from Cartesianism was strengthened by a second revival of interest in Epicurus, originating in Gassendi's critical studies of his life and teaching. Unlike the revival in the fifteenth century which had stressed the anti-religious element in Epicurus' teaching, this was focused on its scientific content. Interest was thus renewed in the atomism of Democritus, which had been preserved and carried forward by Epicurus and his followers. Arising from his study of Epicurus, Gassendi developed his own atomic hypothesis,[17] which materially helped in the rationalization of chemical theory and so ultimately in the growth of plant physiology.

The most immediate extension of botanical investigation was, however, in plant anatomy, where the microscope revealed an undiscovered world and in less than thirty years created a new branch of botany. As already noted, the microscope took longer than the telescope to become an effective instrument. First used by Italian scientists, its potentialities were brought to the notice of the learned world in 1665 with the publication of Robert Hooke's *Micrographia* containing illustrations of microscopic observations of randomly chosen objects of animal, vegetable and mineral origin.[18] It was an advertisement for microscopy, not a systematic study of any particular group of things, yet the botanical figures alone show how acute and thoughtful a scientist Hooke was, and two of them became the starting point from which other investigators went further. He saw "pores" in cork, realized that they were closed, bladder-like structures which he called "cells", and showed that similar structures occur in many plants: in the pith of several trees, in stalks of carrot, fennel, burdock, teazle, ferns, reeds, and in leaves of mosses. In fern, moss, and two kinds of mould fungus, he seems to have seen spores. He calculated their size and guessed that they represented "seed" minute enough to be dispersed by air, and concluded therefore that moss and moulds are true plants and do not just arise from corruption—thus putting the weight of his scientific authority against the ancient doctrine of equivocal or spontaneous generation.

The foundation of plant anatomy was laid by two professional physicians, Nehemiah Grew in England and Marcello Malpighi in Italy. They were both exceptionally able investigators who exploited the now popular "magnifying glasses" to take a new look at plants.[19] Both were impelled to this study by sound scientific reasons: Grew, who put it with characteristic piety, "because both plants and animals came out of the same Hand", and Malpighi because, as he carefully explains, he had first studied animals and insects, and took up the study of plant anatomy in the hope that he could return to animals with more understanding after studying simpler forms of life.

Their earliest work on plants was done independently and without mutual knowledge. Grew presented his work in manuscript to the Royal Society in May 1671 and in printed form, entitled *The Anatomy of Plants Begun,* in December of the same year. By coincidence, Malpighi's first work, *Anatome Plantarum Idea,* which had been published at Bologna in November 1671, was presented to the Royal Society in December at the same meeting. Thereafter both men continued to work and publish independently, although no longer in ignorance of each other's activity. There is no suggestion of rivalry between them or of anything but sincere mutual respect in pursuing parallel lines of research.[20] Nor is there any ground for the accusation that Grew failed to acknowledge adequately Malpighi's contributions. He expressly acknowledged Malpighi's recognition of spirally thickened vessels in the wood, where Malpighi undoubtedly had priority. For the rest, each may well have learnt something from the other during some fifteen years research on the same problems, but comparison of the dates of publication of their work and of its detailed content provides conclusive evidence that they worked independently and that any mutual indebtedness never took the form of unacknowledged borrowing.[21] What is most significant is the wide and fundamental agreement between these two observers in an unexplored field, a tribute to their remarkable technical and critical ability. It may be said that both penetrated as deeply into plant structure as the optical limitations of their microscopes would allow, and that they were not in any essential way at variance in the interpretation of their numerous and often complementary observations. Furthermore, both illustrated their work with many labelled figures—accurate, detailed and beautiful—establishing henceforth a high standard of critical excellence for researchers in this field.

Malpighi certainly saw more clearly than Grew in some areas of detail, but Grew developed a more complete and integrated view of plant structure. The measure of the advance they jointly made is that for nearly a century and a half plant anatomy remained where they left it; no one questioned their observations and no one added to them, except Leeuwenhoek, whose unsystematic glimpses of plant structure, reported to the Royal Society between 1678 and his death in 1723, produced no significant advances.[22]

In assessing their achievement it seems best to consider their work as a whole, and for this purpose Grew's *Anatomy of Plants*, published in 1682 three years after the appearance of the second and final volume of Malpighi's *Anatome Plantarum*, may not unfairly be taken as the fullest statement. Although it was essentially a republication of all Grew's own researches as revised by him in the light of his matured opinions, he wrote in full knowledge of Malpighi's work, and with the avowed intention of producing a complete account of plant anatomy—in effect, the first textbook of the subject. Malpighi's *Anatome* was not intended to be more than a straightforward account of his own researches: as such, it is a remarkable exposition, which has not only the interest of an independent view of most of Grew's observations, but also describes several features which Grew either missed or failed to record.

It is not practicable to summarize the mass of new information which Grew and Malpighi discovered: I shall try instead to identify the main conceptual advances which resulted, and shall limit the account of new facts to what seems requisite for this purpose. For clarity I shall use modern terminology, since Grew and Malpighi, writing in English and Latin respectively, often used different terms to refer to the same thing. The very wide scope of their observations needs to be correctly appreciated. Modern botanists tend to restrict the term anatomy to the realm of microscopic phenomena; but Grew and Malpighi used it in a wider sense, and combined a comparative study of the external morphology of plants with an examination of their internal and microscopic structure. They used the naked eye, the hand lens and the compound microscope to look at different levels of structure, and this combination of techniques and viewpoints enlarged the comprehension of plant morphology in two ways. It led in the first place to a clearer understanding of the nature of the principal organs and tissues of the plant, and of the formal relations between them. This was a carrying forward of the morphological analysis begun by Theophrastus, and continued by Cesalpino and Jung. But Grew and Malpighi also investigated how organs and tissues are formed during growth, and this was an essentially new kind of enquiry, leading to the conception of the plant body as a co-ordinated developing sructure, and marking the beginning of efforts to link structure and development, which were to become an increasingly important part of botanical investigation in the future.

In his opening words Grew announced his scheme of describing the structure of a plant during the complete cycle of development from seed to seed, this being the "method of nature herself in her continued series of vegetations". Grew was right in seeing this as the way in which plant morphology was to be securely established and related to the underlying principles of anatomical structure, and both he and Malpighi were consistent in following this method. The general outcome of their multitude of detailed observations was to show that the morphological categories and organs of higher plants could not only be defined by their characteristic mutual relations within the plant body (as Jung had recognized), but also by their structure, including internal anatomy, and by their mode of origin and development. Thus root and stem need no longer be questionably distinguished by function, the root absorbing food, the stem bearing the seed, nor by position in earth or air respectively. A true morphological distinction could be derived from the fact that roots do not bear leaves, that branch-roots arise from the inner tissue only (endogenously), and that the woody tissue lies centrally in the young root (a fact only clearly revealed by the miscroscope). Stems on the other hand bear leaves, produce buds in whose formation all the stem tissues take part (exogenously),[23] while the woody tissue is not central but either in a ring or in scattered bundles towards the exterior. In addition Malpighi observed that roots, unlike stems, terminate in a rootcap, a point ignored by Grew. In origin, root and stem arise opposite to one another in the embryo of the developing seed. Thus root and stem (shoot) are morphologically distinct, yet closely connected as integrated parts of the whole plant body, a fact demonstrated by their association in the embryo, by the continuity of the "lignous" (i.e. vascular) tissue between them, and by their co-ordinated growth.

This single example illustrates how the painstaking comparative observations of Grew and Malpighi began to create a new factual basis for the further development of plant morphology.

Bilateral asymmetry had been recognized as characteristic of leaves by Theophrastus (*HP* 1,10,2) and used in formal definition by Jung, but Grew and Malpighi were able to relate the phenomenon to a definite asymmetry of anatomical structures. Furthermore by cutting sections of buds and examining them microscopically, they saw how leaves originate as outgrowths from the stem close to the growing apex, arising in a precise temporal and spatial order. They also observed that the vascular bundles of each leaf are connected with those of the stem through leaf-trace bundles, which in each particular species are definite in number and follow a characteristic course.

Some of the most important observations of Grew and Malpighi were those on the origin and nature of buds; and here microscopy yielded an insight that could not have been gained otherwise. Malpighi's contribution to bud anatomy was particularly impressive: he studied buds of more than twenty different species in section, including oak, fennel and beet. The indefinite but closely co-ordinated growth of plants was seen to depend on the origin of buds at certain positions only, either terminally or in leaf axils. The internal structure of buds revealed that, whether growing or temporarily dormant, each bud is in fact the growing point of a shoot (as Malpighi noted, "like an undeveloped plant in miniature"), with the anatomical structure of a shoot, having connection below to the vascular system of the parent shoot, and with the new rudimentary leaves arising around the shoot apex, and therefore at the centre, with successively older leaves surrounding them. The bud-scales present on the exterior of many winter buds could now be correctly interpreted as specialized leaves, with the same mode of origin and fundamental morphology as foliage leaves.

Both Malpighi and Grew were not surprisingly fascinated by the resemblance of the bud to a condensed and tiny shoot. Grew describes how the youngest leaves cluster round the stem tip with the "central and minutest . . . five hundred times smaller than the outer", and notes how the youngest and most delicate leaves are protected by the older leaves and bud-scales, as well as by the frequent presence of hairs among them. He describes in some detail the varied, beautiful and complex folding (vernation) of the unexpanded leaves in the bud, and was the first to observe this phenomenon, which has recently re-aroused interest as a character in plant classification. With considerable insight, Grew remarked on the co-ordination of growth and organ formation in the bud, i.e. at the growing point. He conceived growth in a physiological way as a movement of sap into the growing point, proceeding with a "motion most even and gradual so as not to cause the least breach of its parts", whilst the growth of branch and leaves takes place by "accretion of new, and partly the extention of its already existent parts".

This investigation of the structure of buds and their growth was particularly illuminating for the further progress of morphology; the recognition of the developmental aspect gave a more objective and widely applicable method of analysing plant form. The first fruits appeared in the work of Grew and Malpighi themselves. They were able to expose the true morphological nature of a range of plant organs (bulbs, bulbils, thorns, spines, tendrils, rhizomes, etc.), and show the rational order behind the picturesque variety of traditional description. It may be noted that Grew did not always trouble to make his terminology fully consistent; he continued to refer to rhizomes as roots although quite aware that they are truly stems.

In their survey of plant form Grew and Malpighi examined the flower in many different species and published figures displaying the floral parts with great accuracy and detail. The use of a lens enabled them to see clearly and easily the structure of many small flowers which botanists had heretofore tended to neglect. It was not that the floral parts could not have been seen with the naked eye, at least in all but the very smallest flowers, but that botanists had not generally looked closely at small or inconspicuous flowers, partly from simple human laziness in face of difficulty, but even more because, the function of the seed alone being known, there seemed to be no compelling reason to analyse the other floral structures more carefully. Grew and Malpighi were in a sense merely trying out their new microscopic technique on flowers, but in so doing they did much to reveal the regularities of floral structure and to bring certain less "typical" flowers into relation with the rest.

They first made apparent to all, by means of well executed illustrations, that the "flower" of Compositae is a condensed capitulum of numerous florets, each floret being a small complete individual flower—a point on which Cesalpino seems to have been not entirely clear but which was already well understood by Jung. Malpighi recognized in each floret the five anthers united into a conical tube round the style, a characteristic of this family. Grew described the same structure, calling it the "sheath", but without realizing that it represented the connate anthers. Malpighi cleverly compared the "flower" of the fig, "missed by the botanist", with that of the Compositae.

Besides many bisexual flowers with brightly coloured corollas, such as rose, lily, paeony, almond, speedwell and campion, other less conspicuous flowers were examined. Among the last, many features were noted and adequately figured for the first time, including the complete structure of the graminaceous flower as seen in wheat, oats and maize, and the complex flower (cyathium) of *Euphorbia*. In the male flowers of maize Malpighi observed the lodicules: he also accurately pictured the orchid flower with pollinia, the staminate flower of poplar with five stamens, and the female flower of the oak with trilocular ovary and two pendent ovules in each loculus. It may be recalled that in the oak Cesalpino had only seen the single seed which comes to maturity. The many descriptions and figures of flowers produced independently by Grew and Malpighi were a significant step forward in botanical illustration; accurate representation of the form of living plants was extended to include the systematic display of the floral organs.

The most important theoretical result of their observations was to strengthen the growing conception of a basic generalized morphology of the floral parts corresponding to that of the rest of the plant body. The facts of the regular occurrence and arrangement of certain characteristic floral organs, made easier to see by "magnifying glasses", became common knowledge. Most significant was the recognition of the almost universal presence of the stamen, and of its structure, having a sac at the tip (the anther) which opened to liberate a mass of dust or globules (the pollen). Grew particularly emphasizes the regularity in the number of stamens in many species, and the fact that the number of stamens and petals is so often the same. The constant presence of the stamen as a morphological unit contributed to strengthen the thought, undoubtedly beginning to arise in more than one mind about this time, that here was the organ in plants corresponding to the male generative organ in animals, producing pollen, which must therefore correspond to the spermatic fluid. This question will be discussed later, but it is worth noting that Grew came to accept the probability that the stamen is the male organ of the plant; he stated this supposition hesitantly in his work on the anatomy of flowers in 1676 and more definitely in the final edition of his *Anatomy* in 1682. Malpighi, strangely enough, seems never to have entertained the idea, although he made elaborate analogy between the animal uterus and the plant ovary, to which he also gave the name uterus.

The researches on floral anatomy also helped in the long process of reaching a fixed and uniform set of terms for the various organs and structures. In this it must be said that Malpighi played the more useful part, since he adopted the vocabulary that was coming into use by continental botanists and was derived from Latin, whereas the English terms invented by Grew (e.g. empalement for calyx, attire for stamen, semets for anther, etc.)[24] were a confusing diversion.

Grew and Malpighi also studied the development, structure and germination of seeds, a field of experimental observation stimulated by the contemporary boom in horticulture, and in which Ray had to some extent anticipated them in 1674. Later, Ray referred to their work in connection with his use of the number of cotyledons in classification. Several passages from their writings show that these studies helped to illuminate their morphological ideas, but the great significance of this work in the history of botany is that it marks the beginning of plant embryology. The most extended observations were those of Malpighi, who examined microscopically sections of the developing seeds of apple, pear, flax, pea, various other legumes, wheat and hazel, and clearly saw the growth of the very young embryo within the embryo sac and its gradual increase in size to fill most of the seed at maturity. In the hazel he evidently saw the multiple embryo sacs which occur in this species (*Corylus avellana*). However Malpighi seems to have confused himself by attempting to see structures present in the animal uterus and not all his figures are free from errors of observation due to this cause. Grew appears to have confined his attention to the almond, but he was not led astray by analogies with animals, and he illustrates surprisingly well the early stages of growth of the embryo within the embryo sac, showing the suspensor (which he calls the "navle string") with the embryonic bud at the tip from which two cotyledonary lobes arise as it enlarges. Both Grew and Malpighi realized that the mature embryo in the seed was morphologically a rudimentary plant. They described and named the parts of the seed, including the double testa, and showed experimentally that the micropyle is a true opening in the testa; their studies of germination confirmed Ray's observations without adding anything of substance.

The contribution to basic morphology made by Grew and Malpighi was thus very fruitful: it was enriched by the use of microscopy but was not necessarily dependent on the new technique. In their investigations into internal anatomy, for which microscopy was absolutely essential, they were the undisputed discoverers of a totally new field. In many ways what they found was too novel to be easily grafted on to the stock of existing knowledge. Moreover their brilliant expertise led them so close to the limits of their instruments and techniques, that less accomplished investigators could make no further progress, and were probably unable to see, much less interpret, what they had described.[25] Hence their contempoaries and successors failed to a large extent to comprehend their discoveries in detail, or to follow them up, in spite of the excited interest they aroused. Nevertheless the revelation of the new dimension of internal anatomy had a profound effect on botanical thought, demonstrating that besides and beneath the outer form, plants have an equally characteristic, ordered, inner structure, that is, with only a limited and regularly repeated range of variation, the common anatomical basis of them all. Grew had no doubt of the importance of this conception, deriving directly from his own and Malpighi's microscopic researches.

> All the parts of a vegetable, the root, branch, leaf, flower and seed, are still made up of two substantially different bodies. And as every part hath two, so the whole vegetable taken together is a composition of two only, and no more: all properly woody parts, strings and fibres, are one body: all simple barques, piths, parenchymas and pulp, and as to their substantial nature, pills [peels] and skins likewise, are all but one body: the several parts of a vegetable all differing from each other only by the various proportions and mixtures, and variated pores and structures of these two bodies. What from these two general observations might reasonably be inferred, I shall not now mention.[26]

When Grew speaks of two bodies from which all plants are constituted he is referring to the broad division of plant tissues into fibro-vascular tissue (including supporting tissue) and parenchymatous tissue, a division which both he and Malpighi independently recognized and described. Elsewhere Grew says that in all plants there are only two essentially distinct organical parts—pithy and lignous [i.e. parenchymatous and fibro-vascular].

This important generalization was based on an even more fundamental observation, namely that the two tissue types are distinguished by the character of the majority of the units composing them, "lignous parts" are built mainly of elongated structural units, described as "fibres", "tubes", "vessels", whilst the "pithy parts" are built of more or less spherical "bladders". Although Grew made no explicit statement, there seems no doubt that he recognized, or came very close to recognizing, the universal cellular structure of plants. The evidence of this is worth considering in some detail.

Although Hooke had been the first to see "cells" in plants and to call them by this name, it was Grew and Malpighi who showed that cells make up the normal structure of the parenchyma in all plant organs in every one of the hundreds of species they examined. The term parenchyma to denote the ground tissue of plants consisting of relatively thin-walled more or less isodiametric cells was coined by Grew and has been used ever since.[27] Both Grew and Malpighi looked very carefully into the nature of the cells, designated "little cells or bladders" by the former and "utriculi" or "sacculi" by the latter, and concluded that each cell when young was filled with sap (but might become empty when older, as in bark or pith), and that there were no open pores in the walls, so that the sap must pass from cell to cell through the walls and (in Grew's words) "be strained a hundred times over" in passing "from bladder to bladder". They both showed that a coloured liquid (probably they used ink or dye) did not penetrate the cells from outside, and Malpighi even recognized the intercellular air-spaces that he observed using this method. That parenchyma is a structure formed of cells was obviously quite clearly understood. In order to avoid any misconception it must be emphasized that this was definitely not an anticipation of later "cell theory". Grew and Malpighi had no conception of the cell as a persistent living unit, or of cell division. They certainly did not see new cells arising by division in the conical tips of the buds which Malpighi in particular sectioned and drew with such remarkable skill. Yet Grew assumed that cells are formed in some way at the shoot tips, remarking that "as bladders are still generated they are at the same time also filled with sap", which was a pretty clear-sighted view.

Did Grew and Malpighi realize that cellular structure was also the basis of the "lignous parts"? In the case of Malpighi it is not easy to

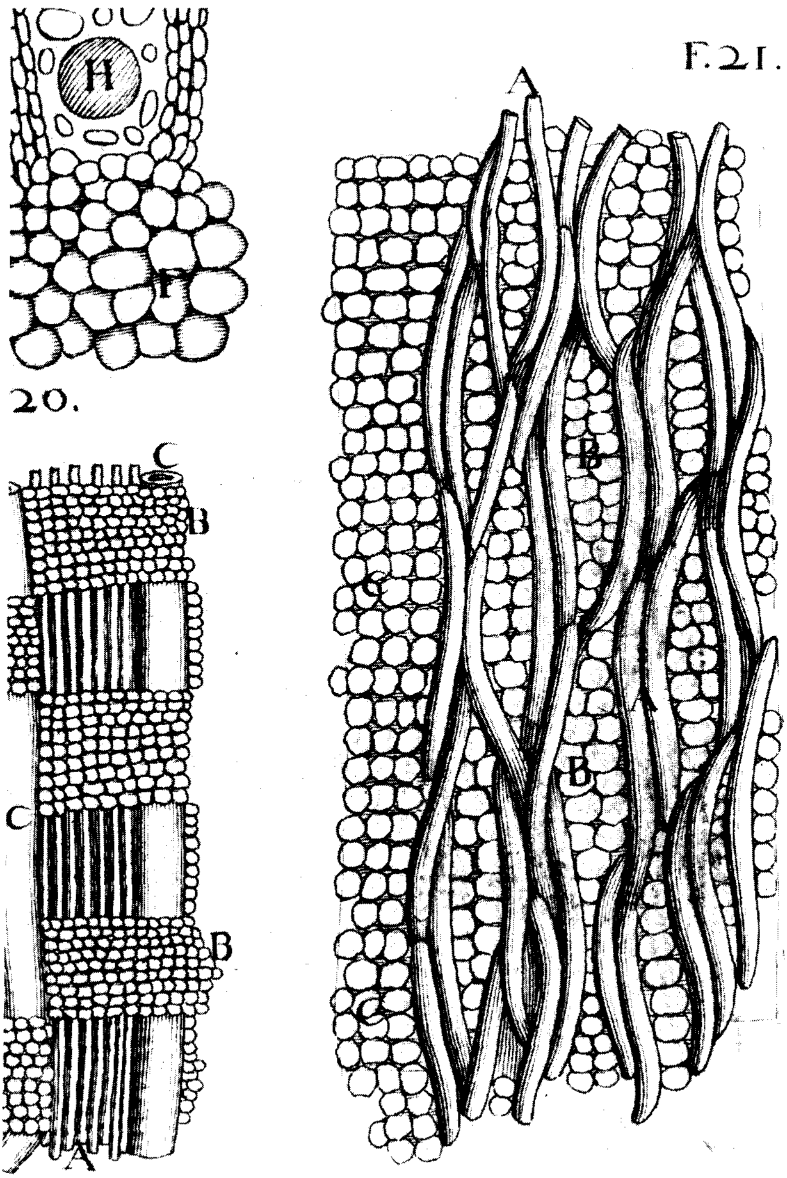
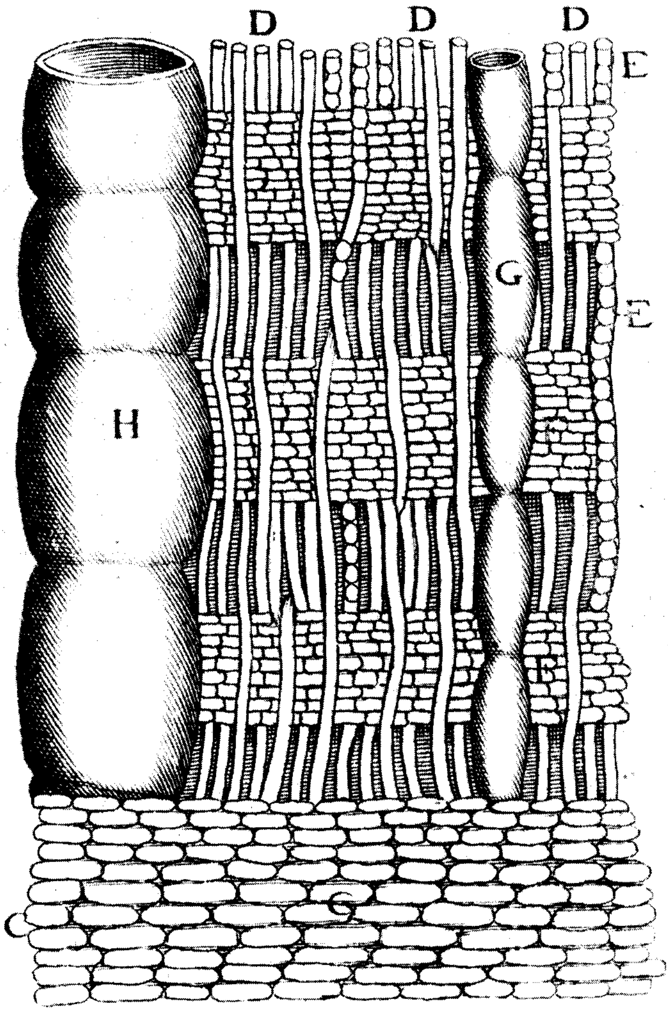


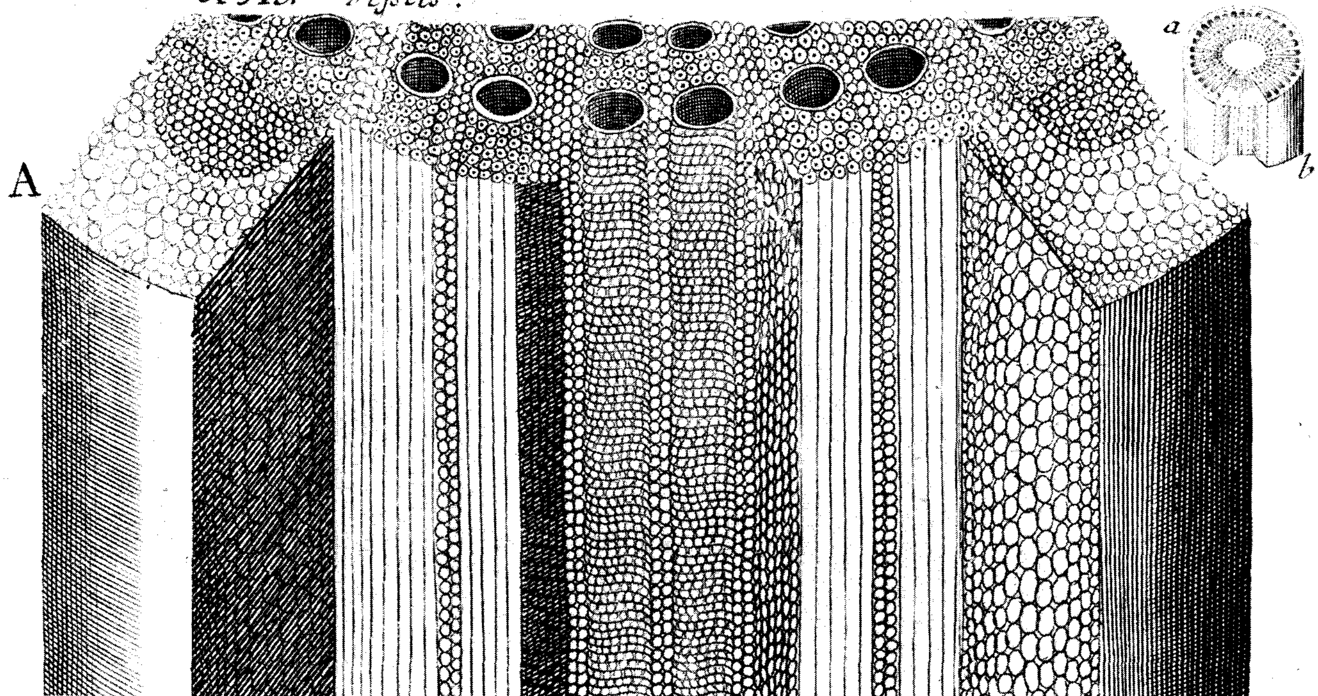
Figure 12 Cells and tissues of the xylem of oak



depicted by Malpighi in *Anatome Plantarum* (1679).

AB Piece Cut out of (ab) and Magnify'd to Shew y^e Lymphæducts & Aer-Vessels.

a.b. Part of a Vine Branch Cut transversly



answer: he was most impressed with the fact, as it seemed to him, that the lignous parts are bundles of continuous tubes, and he even thought that he had observed peristalsis. He called the xylem vessels tracheae, a name which has stuck, because he thought them equivalent to the respiratory tubes of insects. But Grew came very near to the notion of the unitary cell-structure of all tissues. In the first place he saw quite clearly that parenchyma is present in the vascular tissue, especially in the medullary rays running through the wood, which he was the first to describe and understand. He also perceived the close association and interpenetration of the parenchyma with the wood and bark so that the whole body of a tree is "truly continuous by means of the parenchyma". Grew showed by very simple experiments that some of the large xylem vessels are continuous tubes of great length (like Malpighi he not unnaturally thought they functioned as "air-vessels"), but his figures show that he recognized that some long fibrous elements of the wood are nevertheless closed at each end, and he emphasizes that each "pore" in the wood is the "concave of a fibre" and not simply space between. Finally he makes the percipient suggestion that the long cavity of a vessel probably arises from a vertical row of parenchyma cells by dissolution of the transverse walls between them. Possibly he actually saw this happening but was cautious in saying so. This seems to be the first inkling of the process of cell differentiation in plants:[28] if Grew was really convinced of his own suggestion then he can without doubt be credited with recognizing the universal cellular structure of plants. He considered, correctly as we now know, that the cell walls constitute a continuous fabric which encloses each sap bladder and concavity. The wall he held to consist of interwoven fibres, and he therefore compared the structure of the whole network of walls to that of lace. Grew believed that he had visual evidence for this theory: in certain parenchymatous tissues (the pith of thistle and bulrush) and in the wood of flax and of fir, he could see the tiny parallel fibres making up the wall. What he actually saw (as is plain from his own figures in Tables 38 and 39), were the successive layers in secondarily thickened walls, and his interpretation of these as constituent

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Figure 13 Structure of vine stem depicted by Grew in *Anatomy of Plants* (1682).

fibrils was a very reasonable one. In fact his idea of cell-wall structure is curiously like the modern concept of crystalline micro-fibrils, and he even developed a speculative theory that the regular structure of the wall arose by crystallization of the "saline principle of vegetables".[29]

The many anatomical observations made by Grew and Malpighi still excite astonished admiration by their completeness, accuracy, and grasp of reality—almost all eventually became part of the enduring foundation of plant anatomy. Their parallel efforts revealed much of the range of cell form, and of the position, arrangement and composition of the principal tissues, as well as the existence of many specialized structures such as stomata, glandular hairs, spiral and other types of thickening of vessels and tracheids, lenticels, resin canals, and probably phloem.[30] They distinguished the two main types of arrangement of the vascular bundles in stems, either as rings surrounding the pith or scattered. The former arrangement is characteristic of dicotyledons, the latter of monocotyledons, but neither of them noticed the association or commented on it, although Malpighi noted that scattered bundles occurred in date-palm and maize, and also in the rhachis of a fern (bracken). The most important general result of their microscopic studies was to demonstrate the existence of a limited number of basically similar anatomical structures in all higher plants, arranged in certain recognizable and regularly occurring ways: from which it followed that consideration of internal anatomy could be important and useful in comparative morphology.

One problem to which Grew and Malpighi gave particular attention was the growth in thickness (secondary growth) of the stem, a process whose nature had hitherto been little investigated or understood, in spite of the immense store of practical know-how about timber handed down for thousands of years. They described the structure of the annual rings and the differences between spring and autumn wood for the first time, and investigated the mechanism of growth in thickness of stems and roots. Grew reached the essentially correct conclusion that yearly growth takes place, from spring to autumn,[31] in the thin layer between wood and bark, and that this layer (for which he coined the term cambium,, still in use) added wood internally and bark externally. The cambium was seen by Grew as a shining region, soft and slippery, where the wood and bark were easily separable because, as he thought, there was a great accumulation of sap in this region, the sap moving thence into the wood and bark, where it formed additional layers. This was the theory behind his use of the word cambium, late Latin for a place of commercial exchange, but adopted since the fourteenth century to designate one of the four alimentary humors which, according to Arabic medical theory, nourished the bodily organs.[32] Physiologically Grew's theory was close to the mark, even if expressed in a naive way. Unfortunately in this case his microscope was not quite good enough, and he failed to see that the cambium consists of cells essentially similar to those of parenchyma in general.

This attempted physiological exlanation of cambial growth illustrates the way botanical research was enlarging its horizons, influenced by developments in the physical sciences and by the prevailing "mechanical philosophy" and, more directly, by the revelation of the complex internal structure of plants and the urge to relate structure to vital function, as Harvey had done for the heart and circulation in animals. Neither Malpighi nor Grew was primarily an experimentalist; however, they saw the importance of experiment in analysing plant behaviour and both did some simple but revealing experiments. How they established the existence of intercellular spaces and the continuity of xylem vessels and the relative impermeability of cells to external liquids has already been mentioned. Grew also investigated geotropism and, by germinating seeds in moist air, showed that the root grows downwards even when not in contact with the earth, so disproving the very ancient assumption that the root by its nature sought the earth, and the stem by its nature sought the air. Grew may probably be credited with the first biochemical investigation of plants: given the state of chemistry his experiments could not come to much, but he extracted various kinds of "saline" from plants, and got crystals from the extracts, and he also found that the green pigment of leaves could be dissolved by olive oil and that the extract showed what is now called fluorescence. Malpighi found a reduction in growth and fruiting when he cut the leaves from growing plants, and concluded from this that leaves have some nutritive function, the first slender experimental evidence for this key conception. He also obtained some indication that the nutritive sap can move both up and down, by making cuts in the veins and the bark, thereby initiating an experimental procedure which subsequently became standard technique for research on translocation of nutrients in plants.

Taken as a whole, the work of Grew and Malpighi represented much more than the beginning of plant anatomy. It marked the entry of experimental investigation into botany, and with it, the bringing of many diverse and little-considered aspects of plants into relation with one another, and the opening of new fields of research. Grew had a clear perception of the perspectives that lay before botanists, and in the introductory chapter of his *Anatomy* entitled *An Idea of a Philosophical History of Plants* he put forward what was in effect the first comprehensive programme of botanical research, a remarkable and far-seeing document, even though some of the suggestions outran the bounds of immediate possibility. Every area of botany was embraced in a survey of what should be looked into and included classification (the adjustment of the order and kindred of plants), physiology (making trial of the growth of plants in all kinds of simple soils), anatomy (comparing all parts at all seasons, and, for different kinds, noting change of dimensions and qualities), experiments on the chemistry of plants. A proposal under the last heading gives a vivid picture of the strength and the weakness of Grew's approach. Since all plants consist of two, essentially distinct, organic parts, the pithy and the lignous, he says, then if plants can be found which give these unmixed with each other "in some good measure if not perfectly", then they could be put to chemical test to find "what principles and proportion of principle concur to specify their substantial forms".

More important for the future direction of botany than any actual experimental results or detailed suggestions for research was the twofold principle which Grew held should inspire research and which he enunciated with vigorous clarity. In the first place he accepted reliance on experimental investigation of causal relations as the basis of gaining complete knowledge of plants, holding it axiomatic that "one property, agreeing to diverse vegetables, should have one cause". Secondly, he largely abandoned the common assumption that plants and their various parts were created simply for man's use or delight, stressing that plant structure is determined primarily by the plants' own functional needs. Although some of the "outward elegancies of plants" might be for man's delight, the "inward ones, which are as precise and various as the outward", must be for the benefit of the plants themselves. This viewpoint is implicit throughout his account of plant anatomy and is plainly expressed in many passages, notably in the discussions of the connection between anatomical structure and the mechanical properties of stems and roots, and of the movement of sap between different organs and tissues. So Aristotle's concept of functional adaptation was revived and applied to plants, but now in the form of a theory based solely on the inner nature of plants, open to experimental enquiry, and freed to a large extent from religious, speculative or fanciful interpretations with which it had become encumbered. This development in botanical theory was an essential condition for the subsequent growth of plant physiology. Although owing much to parallel theoretical development in animal physiology, it was also immeasurably strengthened by the finding that plant anatomy is as regularly and precisely ordered as that of man or animals.

The new ideas and forces shaping science were remarkably reflected in the life and work of John Ray,[33] who influenced both the theory and the practice of botany more decisively than any other single person in the latter half of the seventeenth century. The springs of his scientific activity have been fully and sympathetically explored by C. E. Raven in relation both to the social and intellectual upheavals through which he lived, and to his own character and personal fortunes. It was very much a sign of the times that he was neither a physician, nor medically trained, and did not come to study plants from the background of pharmacology, but through a more general but passionate interest in natural phenomena which seized many of the best minds of the age. Ray became linked by association and friendship during his student days in Cambridge, with some of those able and enthusiastic men who were later among the founders of the Royal Society. Descartes's *Discours sur la Méthode* (1637) appeared in Latin translation in 1644, the year Ray entered the university, and had an electrifying effect on a whole generation of "natural philosophers", already excited by Harvey's experimental proof of the circulation of the blood and by other advances that were shaking the fabric of traditional medicine. In the countryside the social and agrarian conflicts from which the English revolution sprang were raising a burning interest in problems of agriculture and fertility, and the "improvers" were looking to the more advanced methods of the Netherlands for scientific guidance.[34] These were some of the currents that helped to turn Ray's keen and sensitive mind away from the usual exclusively classical studies, in which he excelled, to life-long preoccupation with natural history, and with botany in particular.

It was equally a sign of the times that Ray, the son of a village blacksmith, came from a class that only in the period of his own life was coming to play an active and independent role in society, a class that had hitherto only very exceptionally contributed to the ranks of scholars and scientists: indeed Ray himself owed the opportunity to study at Cambridge to the kindly interest and help of the local vicar. Raven has pointed out how Ray's family and class origin gave him an interest in mechanical arts which he kept all his life, and which helped to form his careful and laborious habits of work. When in later life Ray moved as a respected equal among the intellects and virtuosi of his day, he never lost the calm consciousness that most of them were his social superiors. To this feeling may be attributed not only the outward reserve that protected an inner warmth and humanity of which his closest friends speak with unmistakable affection, but also what seems in retrospect his chief scientific weakness, a sometimes excessive caution in drawing the final conclusions to which his own evidence and opinion impelled him.

One thing above all it is right to stress—how completely Ray was, morally and intellectually, a man of the Commonwealth, a product of those years when science first effectively acquired a social status in England, thanks to the encouragement and administrative intervention of the great Lord Protector himself. Although Ray never expressed himself politically, and held firmly aside from partisan struggles of any kind, he proved in 1662 that he was more deeply and sincerely attached to the highest ideals of Puritanism than many who had been louder in voicing their beliefs. Rather than subscribe to the Act of Uniformity, a compromise with royal authority he might have made without reproach, he submitted to the deprivation of his Fellowship at Cambridge, thereby abandoning any hope of career or worldly advancement, and quietly turned to the pursuit of science, and such modest and precarious livelihood as might go with it, for the rest of his life.[35] This moral decision freed Ray from the time-consuming routine of a conscientious college teacher and administrator, and had the most fortunate consequences for botany.

The sequence of Ray's botanical researches and writings—his most lasting contribution to science, although he also made valuable studies on the natural history of animals—shows how closely his theoretical ideas were linked to the progress of his practical and experimental observations. When first attracted to botany he not unnaturally looked for guidance among the learned of his own university, but soon found that there was at that time no instruction in the subject at Cambridge and no one capable of providing it. With the determination ingrained in his nature he set to work to study the relevant botanical literature for himself, and started to look at the common plants around, both wild and cultivated. The first result of his botanical observations, made over a period of eight or nine years in the leisure hours of a busy academic life, was an account of the local Cambridge flora, *Catalogus Stirpium circa Cantabrigiam Nascentium*, published anonymously in 1660, although the name of the author could have been no secret. It was modestly offered as a guide to the study of native plants in the hope that some—and the author was principally addressing his fellow university men—would be encouraged to revive a neglected subject as a hobby, and that by making similar surveys elsewhere the materials for a British flora ("a complete *Phytologia Britannica*") might be assembled. These hopes were largely fulfilled as a result of the book's real merits.

Already in this initial work Ray showed the qualities which raised descriptive botany to a new level. He combined systematic collecting from all types of habitat and many localities, with the most careful, detailed comparison between each species found and similar species already recorded in the literature. For every species not previously described he gave a description in standard form, which included habit, morphological characteristics, time of flowering, whether annual or perennial, and medical properties, if any. Such full and systematic description was not yet the rule in floristic literature (and unfortunately Ray did not supply descriptions for species already described, often inadequately, by others). Ray considered that a botanist should know as many plants as possible in the field, avoiding exclusive reliance on dried specimens, and this gave his book freshness and popular appeal; but the reliable identification of plants, based on accurate observation and thorough collation with the literature, was its great attraction. The book aroused new interest in botany as Ray hoped, and "many were prompted to these studies and to mind the plants they met with in their walks in the fields". It may well have contributed to the eventual establishment of botanical teaching at Cambridge University,[36] but the greatest effect of the *Catalogus* was on the development of Ray himself.

During its preparation he had come to realize that a complete and reliable account of British plants was still lacking, and he had already embarked on the long arduous researches which ultimately resulted in the publication of what was, in effect, the first British flora. He made journeys to many parts of Britain to collect plants, and being cut off, as he said, from the resources of a botanic garden, managed to set up at Cambridge a small plot of ground as an experimental garden. Later, after losing his Fellowship, he extended his travels to Europe and acquired first-hand knowledge of many plants of the Netherlands, Germany, Austria, Italy, Malta, Switzerland and France, which enabled him to compile at least the beginning of an authoritative European flora. For fifty years of his life, indeed, Ray never ceased to occupy himself with systematic botany. Floristically it was an exciting time; as Ray said, botanists fully trained in the European flora were now travelling to America, Africa, the East Indies, China and Japan, and were sending back specimens and descriptions of an incredible number of new species. As far as he could, Ray incorporated the thousands of new plants in successive volumes of his *Historia Plantarum* (1682, 1688, 1704), the earliest steps towards the conception and compilation of a world flora.

When Ray published his first work on the plants of Cambridgeshire, his approach was, in the best sense, empirical and factual. He was still almost entirely immersed in problems of precise identification, naming, synonymy and description; and he made advances that were of inestimable value for his own future work and for the progress of descriptive botany. Although his bibliography included almost every work on plants from classical times onwards, he does not conceal that it was taken almost entirely from Gaspard Bauhin, and the text makes it quite evident that he had himself, at that time, only studied deeply those authors, Jean and Gaspard Bauhin, John Parkinson, John Gerard, and the late sixteenth century botanists, whose work was directly relevant to the British flora. The plants in the Cambridge Catalogue are listed alphabetically as a matter of convenience, and no kind of scientific classification is attempted. The only indication that Ray was beginning to think seriously about classification is a reference

Figure 14 John Ray (1623–1705). Engraving by W. Elder after W Faithrone, courtesy of the Hunt Institute, Carnegie-Mellon University, Pittsburgh, PA.

in the concluding sentence to the possibility of classifying plants in several alternative ways, and a list, printed without comment as an appendix, of what Ray calls "the more usual classes or divisions of plants". These divisions (as Raven very acutely noticed) turn out to be almost identical with the groups used by J. Bauhin in *Historia Universalis Plantarum*, from which Ray evidently took them.

The period of sustained study of plants in many countries which occupied the years immediately after the appearance of the Cambridge Catalogue, brought Ray, who united an intensely practical bent with his philosophical cast of mind, to a thorough consideration of the basic problems of plant classification,[37] and at the same time led him to realize the importance and interconnections of many other fields of investigation within the compass of botanical knowledge. No doubt this extension of his interest owed something also to personal contacts with continental botanists during his travels, particularly in such long-famous centres of botany as Leiden, Padua, Bologna, Pisa and Montpellier. The development of his theoretical awareness, apparent in *Methodus Nova* (1682) and the first volume of *Historia Plantarum* (1686), also reflects greater awareness of the thought of earlier botanical writers. The bibliography prefixed to *Historia Plantarum* is almost the same as that of the Cambridge Catalogue of twenty-five years earlier, but there is no doubt that Ray had by now critically studied and thoroughly assimilated the work of his predecessors. Nothing is clearer than the impress on his thought of the great theoreticians of the past: of Theophrastus, whom he was able to read in the original Greek, of Cesalpino, to whom he pays an admiring and respectful tribute,[38] and of Jung, whose descriptive terminology he cites with approval and largely adopts.

The direction of Ray's scientific work was also influenced in an important way by the Royal Society, of which he was elected a Fellow in 1667.[39] As a matter of policy the Council urged Fellows to undertake experimental researches, and requests for experiments and information on plants were addressed to Ray. By the nature of his interest, and by reason of his retired life and modest means, Ray's experimenting was necessarily restricted,[40] but he tried to accede to these requests, and the experiments which he undertook in response—on the movement of sap in trees and on the structure and germination of seeds—were very important in the formation of his theoretical views as will be seen. It should be added that the Royal Society encouraged Ray to proceed with his botanical and zoological labours and gave help in publishing the results, although they could not, or would not, provide money for plates for the *Historia Plantarum*.

It is now time to examine Ray's botanical work and thought in detail. His most original contribution was, understandably, to the development of plant classification, and was the fruit of his own many years of observation and reflection. His three great works, *Methodus Nova* (1682), the first volume of *Historia Plantarum* (1686) and *Methodus Emendata* (1703), most completely sum up both the way his ideas grew and ripened, and the final result—the transformation of Cesalpino's brilliant vision into the first outline of a system of plant classification based on natural affinity.

In arriving at this, Ray started, like Cesalpino, from a consideration of the essential characters (*differentiae* or *notae characteristicae*) on which classification should be based, and like Cesalpino he rejected the use of such accidental characters (*accidentiae*) as habitat, size, time of flowering, medicinal powers, utility to man, or mere variations in colour, taste or smell. Accidental characters separate manifestly cognate species (*cognatas species*) and combine those which are unrelated (*alienas*). One might as well, says Ray in his letter to the Royal Society on specific differences in plants, "admit blackmore and European to be two species of men". It is worth noting that Ray's deciding reasons for rejecting accidental characters are derived from horticultural observations and experiment. Changing conditions or place of cultivation affects the size of plants, the amount of fruit they bear, even the degree of "doubling" of flowers. Different varieties may arise from the same root or from different seeds of the same plant, but they cannot be propagated true from seed but only by vegetative offsets or cuttings. Essential characters on which a method of classification can be based, should be taken from the principal parts of plants, that is, from the flower,[41] calyx, seed and seed-vessel. The reason why these parts are selected is because for any one species they are stable and constant in form and are reproduced from seed; furthermore they are readily observed, have many conspicuous features of position, form and number, and are associated with other characters common to a particular group (*genus*). The final clause shows Ray's grasp of the basis for determining natural affinity. The importance of the characters of flower and fruit was being increasingly recognized in descriptive botany, but Ray's carefully argued statement of principle went much deeper, making clear the inadequacy of reliance only on one or two characters, however fundamental they appeared to be. In connection with some remarks on the value of floral characteristics in the *Dissertatio* (1696), Ray at the same time denies that flower and fruit can be uniquely essential parts [i.e. essential to all plants] since some plants lack them altogether. In *Methodus Emendata*, at the very end of his life, Ray remarked,

> I do not fear to put in the same class plants which have many similar parts and characters and which agree in their total habit and construction, even though they differ in the form or number of petals of the flower, in whether the seed is naked or enclosed in a seed-vessel, in the number of divisions of the ovary, or any other particular individual character.

These statements of Ray sufficiently indicate his deep understanding of the principles of natural classification.

Ray made valuable contributions to classification at every level. His early advances in the definition and description of species have already been mentioned; and these led to clearer notions of the relations between species and genus, although it was Tournefort[42] who, by his system of brief definitions of genera, did most, at this period, to establish the genus as a universally recognized taxonomic category. Indeed, in *Methodus Emendata*, Ray paid special tribute to Tournefort for his merits in this respect, and to a large extent accepted his generic concepts.

Some groupings of plants at family level had been arrived at by Cesalpino: many of the carefully defined lower groupings in Ray's classification (e.g. Tetrapetalae, Stellatae, Asperifoliae, Compositae) are familial in character and Ray not infrequently used the name family for them. The proposal to establish the family as a distinct taxonomic grouping was, however, first made by Pierre Magnol[43] in 1689 in his *Prodromus Historiae Plantarum in quo Familiae Plantarum per Tabulas Disponuntur*. Ray had met Magnol at Montpellier in 1664 and had been impressed by the intelligent young man of twenty-six and by his knowledge of plants. In the preface of the *Prodromus* Magnol says his thoughts were turned to possible families of plants by observing grades of affinity in animals; at the same time he enthusiastically acclaims the "new method" of Dr Ray, which he holds to be the most natural and philosophical, because related plants are united in the same table. Magnol defined a series of plant families which he designated Malvaceae, Ranunculaceae, Papaveraceae, Papilionaceae, and the like. They were not, of course, equivalent to the eponymous modern families but many represented fairly natural groupings and pointed the way to the formation of a new and very useful taxonomic category. His concept of the family is of great interest: it cannot, he says, be based on the characters of the fructification only, but must include affinities derived from other parts, root, stem, flower, seeds, and also from the totality of their relations [*compositio*], something which is sensed but not expressible in words. Obviously Magnol had been stimulated by Ray's methods of classification in general; equally there is evidence that some of Ray's later modifications to his own scheme, which appear in *Methodus Emendata*, were made in the light of Magnol's suggestions.

It was in the discrimination of the highest, most fundamental, natural divisions of the plant kingdom (the *summa genera* of the *supremum genus Planta*) that Ray showed the greatest originality and insight. The recognition and delimitation of these higher (or more fundamental) divisions, whilst of less importance for the immediate aim of systematically describing all the existing species of plants, was of supreme importance for understanding the real "inner nature" of plants: it represented in botany the same kind of deepening of comprehension as the discovery of a "natural law" in the physical science. This was the significance of Ray's discovery that seed-plants fall into two broad natural divisions when classed according to their possession of two seed-leaves (cotyledons)[44] or of only one. This division into *Dicotyledones* and *Monocotyledones* (dicotyledons and monocotyledons) was soon to be generally accepted and to become a basic feature of the classification of flowering plants.[45]

Ray's attention was drawn to the cotyledon as a plant organ by his own experiments on seed germination done in 1674, from which he was able to give the first completely clear and full account of the comparative structure of dicotyledonous and monocotyledonous seeds, including a correct understanding of the nature of the endosperm (in seeds where it is present), and an analysis of the principal modes of germination. This work was reported to the Royal Society several months before Malpighi's series of similar observations on seeds. It is characteristic of Ray that he never failed, in later publications, to refer to Malpighi's work, and even used, with due ackowledgement, some of his published figures. Ray's greatness lay in perceiving, fully in the spirit of his own taxonomic principles, that the number of cotyledons (in isolation an apparently accidental character), was linked with a complex of associated characters so that it became an essential character, signifying a true congeneric grouping. There is a long passage in Ray's preface to his *Stirpium Europearum . . . Sylloge* (1694) in which he makes this point in detail, showing how important he felt it to be. His emphasis comes from the fact, stated by Ray himself, that botanists tended to favour his earlier (1682) three-fold division of herbs into those with no flowers or only apetaloid staminate ones, those with perfect flowers and naked seeds, and those with perfect flowers and seeds enclosed in a seed-vessel: a division which he now rightly saw as artificial, and which he thought should be replaced by the more fundamental division into dicotyledons and monocotyledons.

Nothing can detract from Ray's achievement in perceiving the taxonomic significance of dicotyledony and monocotyledony, and that it formed, in his own words, the basis of a broad division of plants (*generalis plantarum distinctio*), but it is germane to recall that Theophrastus had described the two types of seed with some accuracy; and there can hardly be any doubt that Ray's decision to look more closely at the structure of seeds was prompted, or at least strengthened, by his close study of Theophrastus. In fact he gives a remarkable hint that this was so. When describing dicotyledony and its significance (*Historia Plantarum* Lib. I, cap. XV), he added after the Latin term *bifolia* the Greek equivalent διλόβῳ, as if in a moment of recall.[46] Only very rarely does Ray quote Greek directly in this fashion, and when he does, the special reason for it is never far to seek. Thus through Ray, as earlier through Cesalpino, the greatest scientific generalizations of ancient botany, preserved and recovered by a fortunate chance, entered and enriched the renascent modern science.

The separation of dicotyledons and monocotyledons was by no means the only fundamental classificatory division used or suggested by Ray, that proved fruitful in the long progress towards more natural systems. He pointed to the distinction between Angiospermae (Enangiospermae) and Gymnospermae, that is, between plants with enclosed seeds and plants with naked seeds, as a division of substance, and paid tribute to Theophrastus for first putting it forward. This distinction was later to become recognized as a fundamental one; unfortunately Ray's use of it was a temporary blind alley because he shared the universal confusion of the time between naked seeds and some types of one-seeded fruits. His recognition of a major distinction between plants with flowers (Floriferae) and those without flowers (Flore destitutae) was an important step forward. Particularly significant is the fact that Ray substituted these terms for the terms "perfect" and "imperfect" which he had originally used for flowering and flowerless, on the grounds that even lower plants (*infimi ordinis plantae*) are perfect in their own way: a penetrating scientific and physiological acceptance of all plants as equally meriting investigation. He carried this principle into practice by distinguishing the ferns as a class more clearly than any previous botanist. This class, the *Capillares*, is defined as plants possessing true leaves, but having no flowers, and with only very minute, powdery seeds, borne on the leaves. The recognition of the last characteristic was mainly the result of microscopic observation of spores by both scientists and amateurs.[47] However, in the third (posthumous) part of Morison's *Plantarum Historia Oxoniensis Universalis* (1699) there is recorded an experiment, apparently carried out by Morison himself, but possibly by Bobart, in which he scattered the powder (spores) from mature leaves of hartstongue fern on moist, shady ground and lightly dug it in with his fingers. In the following year there appeared "many plants with delicate leaves, at first subrotund, showing that the labour had not been in vain, nor hope deceived". Other people may well have made similar trials. By the end of the seventeenth century it was thus fairly generally believed that the "seed" (spores) of ferns, and possibly of mosses also, was a means of reproduction, although it was long before the life cycle was fully known. Within ferns Ray distinguished three groups: those ferns with seed on specialized leaves, those with seed on the reverse surface of ordinary leaves, and those with seed on the margin of ordinary leaves. These characters have frequently been used since in classifying ferns.

Fungi had been grouped together from Theophrastus onwards, but Ray made a serious attempt to define anew their features as a class.

> Fungi have almost nothing in common with more perfect plants, neither green colour, nor texture, nor the possession of flower or seed as far as

known, one or two forms only excepted [Ray meant the birdsnest fungi (Nidulariae) in which he took the peridiola for possible seeds], nor any leaf in the strict sense. They are ephemeral, except those on trees.

Ray also made the first attempt to classify fungi according to the morphology of the sporophore, rather than their esculent properties, and this was in itself a considerable advance.

It is evident from this bare summary that Ray broke new ground in many ways, and made very real steps to what can justly be considered as the first natural system of plant classification in more than intention.[48] All the more surprising, therefore, is his retention of the old division into trees and herbs, in face of his own demonstration that both trees and herbs fall naturally into dicotyledons and monocotyledons, and the obvious consequence that their artificial separation half-spoiled the great advance he had made. The illogicality of keeping trees and herbs separate had already been shown (leaving aside Theophrastus, whom Ray knew better than anyone) by Jung, by Ray's correspondent Rivinus,[49] and by his friend Magnol who remarked how absurdly the species within the Papilionaceae would be torn apart if the separation of trees and herbs were applied to them. Even more astonishing is that Ray, on two occasions, said that the division was neither accurate nor philosophical, and then justified his continued retention of it on the grounds that it had been known and widely accepted for a long time and that he did not know a more convenient one! This curious failure to accept his own conviction seems to be the negative side of the scientific probity and punctilious regard for the contributions of others for which he gained universal respect.

Before leaving this aspect of Ray's activity brief mention must be made of six illuminating rules which he laid down to be observed in classification. They are summarized below and give an admirable example of his combination of sound principle and practical common sense. There should be the minimum innovation and changing of commonly accepted names. The distinguishing characteristics of both the higher and lower classes must be clear and distinct and capable of precise definition (excluding, for example, vague distinctions based merely on size). Characters should be obvious and readily observed (not such as necessitate carrying round a microscope to see them). Widely recognized classes (e.g. Umbelliferae, Papilionatae) should not be split. Cognate and congeneric plants should not be separated, nor dissimilar and alien plants associated. Defining characters of a class should be kept to the minimum needed for certain determinations.

The problems of plant description and classification are intimately connected with morphology as Jung was keenly aware. Ray had the good fortune to see Jung's work in manuscript as early as 1660 and made use of the published version, with full acknowledgement, in the first volume of *Historia Plantarum*. He accepted Jung's morphological system and terminology almost in its entirety, making some modifications and extensions in the light of his own researches and those of others, including Malpighi and Grew. Ray's greatest contribution to morphology was to give general currency to Jung's refined terminology and to the principles on which it was based, but he also extended the morphological analysis of the flower and seed, making good use of the observations of Grew and Malpighi. He gave a wider but more precise definition of the flower, which approaches closer to modern usage. The perfect flower consists, according to Ray, of calyx (also called perianthium), petals (delicate and fugaceous parts, conspicuously coloured), stamens and style; only the seeds and seed-vessel were not formally included as parts of the flower. Petal had been suggested by Fabio Colonna as a name for the corolla and its divisions, to replace the commonly used *folium* which applied equally to foliage leaves. Ray accepted Colonna's proposal in *Historia Plantarum*, and since the term "petal" fulfilled a definite need, it rapidly came into general use.[50] It is worth noting that in conformity with his characterization of the petal as a fugaceous part, Ray limited its use to parts that are shed before fruit formation; therefore the brightly coloured perianth segments of some species of *Polygonum* were not petals by his definition, since they persist in the fruit.

The word pollen was first used by Ray to denote the globules liberated from the anthers ("apices"), and subsequently the term was accepted by Linnaeus and became universal. Cotyledon was adopted by Ray as the regular designation of seed-leaf (*folium seminale*), and he thus established it in botanical terminology.

The circumstances which impelled Ray to do some simple physiological experiments were mentioned earlier. This pioneer work on the movement of sap in plant did not lead to any very definite results in spite of much care and thought on Ray's part, evident in his account presented to the Royal Society in 1669. The effect was nevertheless lasting, for Ray from this time began to treat physiology as an integral part of botany, which had not been done since Theophrastus' remarkable attempt in the *Causae* two thousand years before.

In the first book of *Historia Plantarum* Ray collected almost all the factual information on plant physiology that then existed, and fifteen years later he brought it up to date in his *Wisdom of God* with reports of additional facts and experiments. Taken as a whole, his account of physiology shows a notable breadth and mastery in assembling what was known, and a constant effort to interpret physiological facts rationally according to "mechanical principles" and the "Law of Motion"—these are Ray's words in the *Wisdom*— yet without concealing the difficulties or the absence of firm knowledge. At the very beginning, when contrasting the growth of plants with that of animals, Ray subjoins a definition of growth as "an increase of substance", a simple additional statement that is none the less a landmark, a sign of the birth of physiological understanding. The discovery of the Sensitive Plant (*Mimosa pudica*), with its curious abrupt movement when touched, had raised the question of whether a plant can be really without feeling (*non sentiens*) as the standard Aristotelean definition states.[51] Ray admits that it is hard to explain the behaviour of *Mimosa* by mechanical reasons, but then proceeds to suggest that possibly contact causes a loss of turgor and consequent collapse of the leaves—thus correctly recognizing one factor that is involved in plant movement. He adds that the "sleep" movement of clover leaves, and the closing of many flowers at night or when it is cold, may be due to the same cause, but is not completely satisfied that this is the true explanation. Ray described the essential nature of transpiration in plants (and animals) as a state of constant water flux, and explained that leaves retain their consistency and extension because of their water content.

On the central problem of nutrition the following summary from *Historia Plantarum* (Vol. 1, 1686), mainly in Ray's own words, will best give an idea of Ray's treatment of this topic and of the state of contemporary knowledge.

> Nutrition refers to the distribution into all parts of the plant of the food that has been taken up and altered, and to its transformation into their substance to replenish what is continually consumed by the power of internal or external heat, and evaporates. Plant nutrition differs from animal in that

> animals digest food taken through the mouth in the stomach, break it up and weaken the union of its parts so that they separate more or less spontaneously from one another. Pure and impure, suitable and unsuitable food, can be separated without difficulty; the suitable food can pass through the pores or orifices of the mesenteric vessels (which correspond to the roots of plants) whilst the unsuitable (excrementary) is driven through the parts and channels destined for that function. Plants however do not prepare nutritive sap for they have no apparatus of parts to carry out this function, but what sap they find in the earth is extracted and assimilated by the roots.
>
> Whether plants select in some way the food taken, so that they only imbibe what is suitable for their nutrition, rejecting what is not, or whether they admit indiscriminately whatever is available, is undecided. Some people report selective attraction, which I regard, however, as not proven, in the first place because I can hardly admit as likely the existence in nature of attraction in the strict sense. It may be however that the pores of the roots are so structured that the particles suitable for the nutrition of the plant are admitted, whilst those that are foreign and unsuitable are excluded, in the same way that liver separates bile and the kidneys, passing urine, separate it from the blood held within. That this is not the explanation [in plants] is proved by many experiments. That ordinary water easily enters the cavities of the fibres and readily permeates them I showed above. In spring, especially in frosty weather, the liquid flowing from an incision cannot be distinguished by taste from water. I therefore think it more probable that all plants take in whatever sap they find in the earth, that it is mixed in the vessels with the proper juices of each one, is digested and assimilated, and what is superfluous and unsuited for nutrition is rejected and evaporated. . . . That plants can be fed by water alone and can grow, has been shown by our own experiments and by those of others. Sharrock[52] has shown that cuttings of many plants will grow when immersed in glass phials filled with water. Water is therefore not a simple and pure element but contains many heterogeneous elements, especially saline, in itself.

Later, in the *Wisdom of God*, Ray referred to Malpighi's experiments[53] in which he had shown that trees die if defoliated, that the grapes will not mature on a defoliated vine, and that by ringing the bark of a tree (an experiment that Thomas Brotherton had also done) "the part above increases, but not that beneath". These observations gave the first experimental evidence that leaves are in some way connected with nutrition, and Ray immediately perceived their extraordinary significance, concluding that the "principal use [of leaves] is to concoct sap for nourishment of the fruit and whole plant, not only that which ascends from the root but what they take in from without, from dew, moist air, rain."

The problem of the ascent of sap was closely examined by Ray as it had been by Grew and Malpighi, whom he mentions. He admitted that he could not give a mechanical explanation, since rise by capillarity or under atmospheric pressure were both inadequate to account for the rise of sap to the top of tall trees. On the other hand he thought there was no evidence for the presence of valves in the vessels, or for the occurrence of true circulation as in animals.

Ray undoubtedly assumed that plants respire, as is clear from the discussion in *Historia Plantarum* about water plants, in which he concludes that sufficient air enters through water for the vegetation of plants and the respiration of fishes. In the *Wisdom* he says that plants have a kind of respiration, but his only evidence is drawn from the "air-vessels" in all parts of plants discovered by Malpighi. A study of the records of the Royal Society shows that a number of experiments were either done or planned, to see whether plants, like animals, succumbed if deprived of air by being placed in a vacuum. The exiguous records suggest that, as we now know was only to be expected, the results were neither striking nor clear when green plants were tested. Ray would certainly be aware of the lack of clear-cut evidence from these experiments. Unfortunately a treatise which he wrote on respiration has not been preserved, but in one of his letters he speaks of his interest in the "primary use of respiration".[54]

The foregoing account shows that Ray can well be regarded as the founder of plant physiology, even though his original contributions were modest. He gave a basis of facts and principles from which later workers could advance. One of his great merits was that he drew stimulus and guidance from animal physiology, and looked for similarities between animals and plants, without being led astray by ill-considered analogies as some of his fellow scientists were.

By the time he wrote the first volume of *Historia Plantarum* Ray had gained an encyclopaedic knowledge of the literature of botany and horticulture, from ancient times to the work of his contemporaries, including the latest acquisitions from microscopy. His clear mind and balanced judgement enabled him to select the well-attested facts from this mass of material and to present them in rational perspective. The first book of the *Historia* is in fact a survey of the whole field of botany in thirty concise chapters. Not only are classification, morphology and physiology dealt with, but every other branch of botany as well:

anatomy (summarized from Grew and Malpighi), methods of propagation, grafting, age and duration of plants, medicinal properties,[55] relation between plants and habitat (an approach to ecology), methods of collecting, drying and preserving plants, chemistry of plants (a section written by Ray's friend Dr Tancred Robinson), and finally plant disease (including some account of plant galls and malformations based on Malpighi). The whole constitutes the first textbook of modern botany, and provided a logical framework within which it was to develop. By his comprehensive treatment and unfailing awareness of the need for a consistent theoretical outlook, specific yet consonant with that of related sciences, Ray accomplished for the new empirical botany what Theophrastus had done for ancient botany, and welded it into a unified science. It is this achievement that puts Ray above all his contemporaries and justifies Albrecht von Haller's judgement that he was the consummate botanist of his age. Grew's programme for botanical research, published under the title of *Idea of a Phytological History* as an introduction to the *Anatomy of Plants*, and Ray's *Historia Plantarum* constitute the foundation and chart for the modern science of botany.

This is not the place to discuss Ray's scientific activity outside the field of botany, except to record that he was truly a biologist of genius who made almost equally original and valuable contributions to zoology. In addition, he had a remarkable knowledge of every branch of science, and in the *Wisdom of God* was able to give an illuminating survey of the state of each, raising many searching and fruitful questions, and making an eloquent appeal for the greater study of science. His scientific distinction and breadth of knowledge were united with a deep interest in philosophy and an unusually explicit commitment to a definite philosophical position, which must be briefly examined since it was not without lasting consequence for the progress of botany and, indeed, of science in general.

His position is stated very clearly in the *Wisdom of God* (1691) which expresses his mature outlook on science, philosophy and religion. His religious feelings, deeply and sincerely held, led him to reject the Aristotelean hypothesis that the world is co-eternal with God, and likewise the Epicurean view that the world was made by casual concurrence and cohesion of atoms. Interestingly, Ray particularly attacks Epicurus' hypothesis of the declination of atoms and does so from materialist physical theory—since all atoms are alike they must either all decline or all not, or do they cast lots? Lastly he refutes Cartesianism and the idea of a divine start of the world mechanism which is then left to itself. Having, as it were, secured his religious ground, Ray states categorically his acceptance of the atomic theory (we saw earlier how he treated experiment and explanation in physiology from the standpoint of "mechanical principles and Matter moved"). He considers that atoms are "indivisible, not absolutely but by any natural force", and that the number of [elementary] principles is limited, but that possibly the immediate component particles of bodies of plants and animals may be themselves compounded. This last statement is certainly based on the views of Gassendi. I believe that Gassendi is also echoed by Ray in a very brief but extremely interesting philosophical passage in the *Dissertatio* (1696), in which he rejects the Platonic (or Realist) conception of universals,[56] and goes on to emphasize that sense impressions are the only direct source of knowledge of the essential nature of things.

Alongside the mechanical materialism of atomic theory, Ray accepted from the Cambridge neo-Platonists[57] the probable operation in living things of "some intelligent plastick Nature" which guided and controlled those processes in the "whole oeconomy of plants" which it was hard to conceive could be carried out "by matter however moved by any laws or rules imaginable". In practice this dualism was no bar to experiment and precise observation, although it gave too easy a refuge where materialist explanations appeared to be lacking; what was more important at the time—although Ray himself, in his straightforward piety certainly did not have this in mind—it allowed the scientist a clear field of practical and theoretical operation in which he could be independent of religious ideology and relatively safe from direct interference from the clergy. This account does less than justice to the depth and seriousness of Ray's thinking on the relation between science and philosophy. However the point is that dualist theories of this type came to exercise an abiding influence on scientists, especially on biologists, and sometimes had very tangible effects on the course of investigation.

The understandable popularity of Ray's book, constantly reprinted during the eighteenth century, made many minds receptive to this pragmatic dualism, which became the dominant, if often unacknowledged, philosophy of both botany and zoology.

One fundamental problem of plants—whether they possess sex or sexual reproduction—had remained unsolved and largely neglected since Aristotle and Theophrastus had given it serious attention. Even the sixteenth century revival of botany brought no immediate revival of interest in this particular question, and botanists who mentioned it at all were generally content to repeat what Theophrastus had said and to leave it at that. During the seventeenth century interest in the problem returned, fostered by the immense increase in horticulture and the growing of new varieties of plants, and by the more thorough study of floral anatomy. It seems likely that the almost universal presence of stamens and pollen in flowers began to lead more than one botanist or observant gardener to suspect that stamens and pollen correspond to the male organ and semen in animals. The first publication of the suggestion that this was the case was apparently in 1682 in Grew's *Anatomy of Plants.* According to Grew's account Sir Thomas Millington, a distinguished physician, told him at a meeting of the Royal Society that "he conceived the attire [stamens] doth serve, as the male, for the generation of seed". To which Grew replied "that I was of the same opinion, and gave him some reasons for it, and answered some objections which might oppose them".

Some of Grew's reasons were rather obscure and need not concern us, but one was the analogy between hermaphrodite plants and snails. Hermaphroditism had recently been established in snails by J. J. Harder of Basle, and this argument from zoology had a big effect on botanists. In 1686, in *Historia Plantarum*, Ray quoted Grew's opinion about the male function of the stamen with obvious approval; he mentions in support his own observations on two sexes in willows, and the similar situation in many other plants (date-palm, hop, nettle, spinach, dog's mercury and others), but concludes that "this opinion concerning the use of pollen still requires confirmation". When he wrote his catalogue of European plants eight years later Ray gave a number of reasons why stamens are considered not superfluous but necessary and useful parts: their universal presence even when coloured petals are absent, the fact that in plants with distinct sexes the catkins or staminate flowers always precede the fruit in spring, or at least come out at first budding and shed their pollen, the fact that the apices [anthers] dehisce and shed their pollen at maturity, and that in the date-palm and other similar plants the female does not bear fruit unless the male is close by and is more fertile if aspersed with pollen. He concludes with the definite statement, "in our opinion the pollen is equivalent to the sperm of animals".

When he wrote this Ray did not know that experimental confirmation of the male fertilizing role of pollen had just been provided by Rudolf Jacob Camerer (Camerarius) working in the Botanic Garden at Tübingen of which he was the Director. The announcement was made in the form of a letter to his colleague, Dr Valentinus of Giessen, and was printed in the Transactions of the Tübingen Academy in 1694. Few epoch-making papers can have had a smaller circulation than this famous *De sexu plantarum epistola*: at the time of his death in 1705 Ray was certainly not aware of it.

It is curious that the experimental proof of sex in plants should have come from central Germany and not from England, the home of experimental science. But Camerarius came from a long line of doctors and pharmacists experienced in the practical art of cultivation of herb gardens.[58] Much of Camerarius's letter is taken up with a detailed rehearsal of all the circumstantial evidence, from the earliest observations to the most recent, for the existence of sex in plants. He cites Grew and Ray as the only authors, with the exception of J. C. Sturm,[59] who definitely support his own view that sex in plants, so often rejected by botanists, is very probable, and he points out that the hermaphroditism of snails, recently established, makes it probable that plants also may well be hermaphrodite. He further shows that many of the statements of the older writers can be interpreted as consistent with sexual reproduction in plants. The principal theoretical arguments depend, however, on his own very able comparative examination of detailed floral structure in a variety of flowers.

He observes that stamens are present in the vast majority of flowers, usually in a definite number and invariably in a position close to the style. The anthers always split open, usually by two apertures, when mature, so that the stigmas become powdered with pollen.[60] Camerarius used *stilus* to embrace both style and stigma, but he plainly recognized the stigmatic surface as an inseparable and essential part. If the pollen is the male element, then most flowers are evidently hermaphrodite, and these structural arrangements seem exactly calculated to ensure fertilization of the seeds by the pollen. Naturally

Camerarius assumed that hermaphrodite flowers fertilize themselves. He does, however, raise the question of whether they can be fertilized by pollen of neighbouring flowers, but did not try to test this. Petals, although so frequently present and so closely associated in position and number with the stamens, are not necessary for the production of seed, because in some flowers, such as vine or wheat, they are absent; only stamens are present, but the plants produce fertile seed. On the other hand, gardeners are well aware of the tendency of some flowers to "doubling"; an increase in the number of petals often accompanied by the disappearance of the stamens. When the stamens are absent, however, no seed is usually set. Such observations and reasoning make a *prima facie* case for sexual fertilization in plants, with the pollen as the male element.

The evidence is strengthened by the microscopic investigations which Camerarius undertook, making due reference to earlier work of Grew and Malpighi and in particular to the latter's elegant illustrations. In the first place he confirmed that the pollen consists of globular grains, of different forms in different species, sometimes with a rough or spiny outer surface; but the most important results followed from observing the development of the seeds in a "large flower of the Papilionaceae", presumably pea or bean. At first he could see in the seeds [ovules] only vesicles filled with clear liquid: these would be the embryo sacs, which Malpighi and Grew had also seen. After the pollen and petals had fallen and the pod begun to swell, he observed the appearance, in the middle of the cavity of the vesicles, of a green point or small free-swimming globule, not previously visible. At first this showed no organization or structure, but later he observed two leaflets arise, a gradual reduction of the liquid, and finally the formation of a complete embryo with cotyledons, plumule and radicle. Camerarius recalls that in animals signs of the embryo only appear after fertilization, thus implying, although this is not explicitly stated, that he regarded his observations as proving that in plants the embryo was only formed after pollen had reached the stigma.

From this study of hermaphrodite flowers Camerarius was led to the first clear understanding of the much smaller number of species in which the stamens and the ovaries are produced in separate ("male" and "female") flowers, either both on the same plant (monoecious), or on separate and distinct individual plants (dioecious). The staminate catkins of such trees as hazel, oak, willow, had puzzled botanists since Theophrastus or earlier, but once they were accepted as bearing the male organs or elements, everything fell into place, and Camerarius was able to show that flowers fell into one of three classes, hermaphrodite, monoecius and dioecious (the two latter terms were not used by Camerarius who simply called them plants of the second and third class). In hermaphrodite flowers he assumed that fertilization is ensured by the close proximity of anthers and stigma, and the fact that the pollen is extruded or falls out of the anthers; that insects could be involved does not seem to have occurred to him. He appreciated, however, that pollen must be transferred by some other means when a plant has separate male and female flowers, and had no hestitation in assuming wind to be the agency, pointing out very acutely the vast amounts of pollen usually produced by species of this type, and the fact that their stigmas are usually fully exposed above the flowers, as in maize.

It was with this well-assembled evidence in his mind that Camerarius took the decisive step, the appeal to experiment, which marks the great advance in his work and gives it such historic importance.

The experiments arose directly from the theory he had formed and from his consequent realization that plants with separate staminate and pistillate flowers were the ideal objects for testing it. He carried out investigations over a period of several years and some of the results were reported in communications to the Tübingen Academy before their inclusion in his final summing up in *De Sexu Plantarum*. The first observations were made on *Morus* (mulberry) and *Mercurialis* (dog's mercury), which are dioecious. A mulberry tree with female flowers, growing with no male tree anywhere near, produced berries but not a single embryo appeared to have developed in them. Plants of *Mercurialis* were grown and all plants with male flowers were removed; the female flowers were found to produce seeds but not one of the seeds was fertile when sown. Another dioecious plant, *Spinacia* (spinach), was tested in a similar way by removing all male plants. The previous results were confirmed, very few fruits were formed, and in these the seeds were sterile.

Camerarius next experimented with two monoecious plants. In *Ricinus* (castor oil) he removed the globose staminate flower buds before they opened and carefully prevented the appearance of any

Figure 15 Rudolf Jacob Camerer (Camerarius) 1665–1721. Engraving by J. C. Dehne in the collection of the Linnean Society of London, print at the Hunt Institute, Carnegie-Mellon University, Pittsburgh, PA.

more; the result was that he never obtained a perfect three-cornered seed [fruit] from the uninjured pistillate flowers, and saw the empty seed-cases hang down and eventually wither. Similarly when the staminate heads of a maize plant (*Zea*) were cut off in good time before they opened, the two ears which came after were completely without any seeds, and only a large number of empty seed-coats remained.

These experiments Camerarius rightly believed to give convincing support to his view that flowering plants form seed as a result of a sexual process equivalent to that in animals. His discussion of the experiments is distinguished by the complete honesty with which he admits that some results failed fully to confirm his expectations. Thus in the experiment with maize there was a third ear which contained eleven seeds with embryos, although the greater number proved to be sterile. This could have resulted from chance pollination by wind, although Camerarius emphasizes that the staminate flowers had been carefully removed and that there were no other flowering maize plants anywhere near. More serious difficulty arose from an experiment with hemp (*Cannabis*), in which all the staminate plants (hemp is dioecious) were removed from a field sowing, but the pistillate plants nevertheless produced quite a few fertile seeds, "at which", says Camerarius humorously, "I must admit I was quite upset". He considered the possibility that other plants such as *Ricinus* or *Humulus* (hop) might have fertilized the hemp, and therefore collected the seeds and sowed them the following year in an isolated plot. Only hemp plants were produced, with equal numbers of staminate and pistillate plants, eliminating the possibility of hybrid fertilization as Camerarius evidently recognized although he does not actually say so. He removed all the staminate plants before they flowered, but the result was as in the previous year: a fair amount of seed was produced, mostly sterile, but some seeds were fertile, mainly those produced early and close to the stem. Camerarius makes no attempt to explain the results away: he merely indicates his intention of investigating the question further in the future, and quotes a dictum he attributes to Robert Boyle: "Experiments must be carried out with care and repeated, once successful ones must not be relied on".

Unfortunately Camerarius either never found time to pursue the problem of hemp or never published his results, perhaps hindered, as Sachs suggested, by the disturbances of war. But he discovered the solution in principle a year or two later when he showed that in several normally dioecious and monoecious plants, for example, nettle, spinach, maize, occasional male or hermaphrodite flowers appear exceptionally on the pistillate plants. In retrospect, Camerarius's reports of his apparent failures make his experiments more convincing, but of course this argument could have no weight with his contemporaries.

There was a second difficulty in accepting the "sexual theory" for plants—the apparent existence of plants with "anthers" but without flowers or seed, for example, *Lycopodium* (club mosses) and *Equisetum* (horsetails). The sporophores of these plants produce microsporangia which split open like anthers and liberate masses of spores consisting of globules, blown about by the wind, and exactly resembling pollen. Camerarius discusses this problem frankly, and suggests that such plants be temporarily excluded from consideration since they are "imperfect" forms without distinct flowers and seeds, whose origin and reproduction is therefore still obscure. He makes clear that the situation in these plants should not affect the proofs that have been offered of the existence of sexual fertilization in flowering plants.

In conclusion Camerarius asserts very modestly and soberly his claim to have given practically overwhelming evidence for sexual reproduction in plants, particularly stressing his satisfaction that a fundamental unity of reproduction in animals and plants has been demonstrated and is being increasingly recognized. He is very careful not to claim too much: what has been demonstrated is that pollen falling on the stigma acts as the male fertilizing agent, not how it acts. In this connection he refers to the differing views about fertilization in animals, whether the embryo arises from the female or from the male sperm, questions we are not called on to settle; but if such matters are not clear in animals, where sexuality is plainly admitted, then one cannot demand complete clarity in plants. What is needed is a microscopic investigation to determine what pollen grains contain, how far they penetrate into the female apparatus, if they reach the seed uninjured, and what emerges when they burst.

Thus Camerarius was led to give much closer attention to the style (and stigma) and to bring to light the universality of this floral structure, in the same way that the universality of the stamen had come to be seen. Particularly interesting in this connection is his recognition that the style is present and functions in relation both to seeds in a seed-vessel and to the so-called "naked" seed; apart from Cesalpino, Camerarius must be the first to recognize, at least by implication, that the "naked" seed is really enclosed in a seed-vessel in all flowering plants.

The charming and discursive style of Camerarius's letter graces a splendidly lucid and powerful piece of scientific writing, which settled in principle one of the age-long central problems of botany and formed the starting point of many new developments. It epitomizes both the fruitful link with ancient botany, so characteristic of the work of the great botanists of the sixteenth and seventeenth centuries, and the impact of the new experimental philosophy from which modern botany grew, and is thus as well fitted to close the period we have been discussing as to open the one that followed.

Notes

1. The fundamental characteristic of scientific method is the creative interaction between hypothesis and the practical test of hypothesis. A genuine scientific theory is predictive and therefore susceptible of experimental test. The test, which may be an experiment in the strict sense, or may take the form of more observations or of observations by other methods, affects the status of the original hypothesis by tending to confirm or disprove it, or by showing the need to modify it. Bacon understood very well how scientific theory develops from this interplay between hypothesis and practical investigation, and it was the great lesson which he wished to impress on his age.

   Some present-day philosophers of science have entirely failed to understand the dialectic of the experimental method. From such misunderstanding comes the often repeated yet absurd statement that experiment can only disprove, never prove, a theory. Of course no experiment can prove or disprove anything *absolutely* and for all time; what it does is to modify theory, both positively and negatively, continuously moulding theory, although not necessarily by steady or uninterrupted progress, into a fuller and more adequate representation of the ever-unattainable "absolute" truth.
2. The period of Bacon's lifetime was marked by a big increase in capital investment in English industry, especially in mining, metallurgy, textiles, brewing, sugar-refining, and the manufacture of soap, alum, glass and salt. The Bacon family was among the new investors, having acquired their fortune out of Henry VIII's plundering of the monasteries. (See B. Farrington: *Francis Bacon: Philosopher of Industrial Science* (1949).)

3. The feature which distinguished these capitalist undertakings was a new form of the division of labour, essentially quite different from that in older societies or in the guild workshop of the Middle Ages. This new organization of labour gave rise to new methods of bookkeeping (double entry) and statistical recording, both originating first in the commercial cities of northern Italy. The protocol of the scientific experiment was to some extent a reflection of these methods of accounting.
4. The type of experiment which Bacon advocated, and which became the method for science, differed from the isolated experiments of the ancients, or the trial-and-error improvement of crafts, or the labours of the alchemists, not only in the greater use of quantitative measurement and mathematical techniques, and in more critical control of conditions, but also in generality of application and in its conscious design as a tool to test hypothesis in order to arrive at general theories. Above all, Bacon emphasized the social character of experiment and of science, a doctrine which would have been inconceivable in previous forms of society.

   The great outburst of science in England after about 1650, while based on the industrial developments already mentioned, also owed much of its impetus and character to Bacon and his *Novum Organum*. The group of brilliant men who founded the Royal Society were profoundly imbued with Bacon's ideas and were actively concerned to carry out his scientific method and programme.
5. The name microscope (*microscopium*) was first suggested apparently by J. Faber of Bamberg, physician to Pope Urban VII, in 1625. It should be noted that during the seventeenth century the word was used to cover both simple lens and the compound microscope of the time.
6. See A. W. Haggis: Fundamental errors in the early history of cinchona. *Bulletin of the History of Medicine* **10**, 417 (1941).

   In Ray's *Historia Plantarum* the description of Quinquina (Cortex peruviana, Jesuit's bark) corresponds to a species of *Myroxylon*, not to *Cinchona*.
7. Joachim Jung (1587–1657) was born in Lübeck and studied at the universities of Rostock and Giessen. He was appointed professor of mathematics at Giessen at the age of twenty-two and delivered his inaugural lecture on "The splendour, excellence and utility of mathematics". Under Galileo's influence he became interested in astronomy and made observations on sunspots, but then turned to medicine from which began a life-long interest in natural science. He founded in Germany the Societas Ereunatica, dedicated to scientific research. He wrote on logic and the place of mathematics in science, and these works were known to Robert Boyle.
8. The restriction of his morphological principles to *higher* plants is explicitly stated by Jung.
9. Thus Jung's use of *perianthium* is more logical than the modern use of

perianth for the floral leaves collectively, which is etymologically nonsense.

10. It is interesting that Jung expresses doubt whether *De Plantis*, now known to be by Nicolaus, is correctly ascribed (as it was then) to Aristotle.
11. The rudimentary state of chemical knowledge prevented Sanctorius from drawing any conclusions of permanent value from his results, but the effect of the bold simplicity and quantitative precision of his methods was enormous, as is shown by the frequent references to him by later writers (by Ray, for example, in *Historia Plantarum*).

    Harvey was already convinced of the circulation of the blood, and speaking of it in his lectures in 1615, but he devoted twelve years to its experimental demonstration. The strength of his proof came from the combination of the new observational anatomy of Vesalius and the Italian medical schools and of Harvey himself, with logical experimentation and simple but decisive quantitative analysis of the phenomena involved. This work stimulated a great upsurge of research in human and animal physiology, and the awakening of the first serious interest in plant physiology since Theophrastus.

    Harvey's work on the development of the ovum and embryo in animals, *Exercitationes de Generatione Animalium* (1651), must have influenced Malpighi, followed by Grew, to make the first-ever studies of plant embryology.
12. The work of Peter Lauremberg of Rostock, published as a book, entitled *Horticultura*, at Frankfurt am Main in 1654, is typical of the experience and ideas that began to flow into botany from horticulture. Lauremberg still relies heavily on classical sources and recommendations, and uses the terms of mediaeval four-element theory, but when he comes to discuss the different theories of the location of the plant soul (*anima*)—thought by some to be the medulla, by others the cortex, and by Cesalpino "most fittingly" to be the *cor*—he comes right down to earth, saying that all must be rejected, because "horticulturalists knew" that plants could live and reproduce themselves from very small pieces cut from the roots [i.e. rhizomes, stolons, etc.] as well as from branches, stems, seeds, and even leaves (as in the case of the Indian fig). Therefore the soul or vital force (*vigor vitalis*) is not in one part more than other, but diffused through the whole plant body.

    Lauremberg describes his own experiment, lasting three years, in which two hundred vine cuttings were grown in close association with two varieties of cabbage in order to test an ancient belief, mentioned by Pliny, that vine and cabbage adversely affect each other. He found, however, that both species flourished and there was no evidence of mutual inhibition (but of course he knew nothing of control experiments and statistical treatment).

In other experiments he found, contrary to tradition, that rue and fig did not benefit from interplanting.

There were many gardener's notions about how seeds were best oriented when sown; the wrong way was said to give dwarf or unthrifty plants. Again, Lauremberg made his own observations with seeds of pea, cucurbita, walnut, almond, date and others, finding that the stem grew upwards and the root downwards irrespective of the original orientation, and that the alleged effects of malplacement were "empty superstition".

It is an interesting sign of the times, that Lauremberg published an account of garden plants, bound together with his *Horticultura*, and that these are almost all ornamentals, and include 146 varieties of tulip and twenty-two varieties of crocus.

The technical and practical aspects of horticulture are dealt with very fully by Lauremberg, but important as they were in relation to the general growth of interest in botany, they need not be detailed here.

13. This is an over-simplification of a very complex situation. To the original four elements taken from Greek (and possibly also Chinese) sources, the alchemists had added sulphur and mercury (and sometimes arsenic) from Islamic sources, and Paracelsus added salt. He himself employed all seven elements in his writings but not always consistently. It has to be remembered that the alchemists (and philosophers generally) understood the elements in a dual sense, both as material substances and as qualities or principles characteristic of the elemental substances. Furthermore the elements were conceived as capable of being transformed into one another in the right conditions. See J. Reade: *Prelude to Chemistry* (1936) for an introduction to this field.

Such ideas were fundamentally different from the conception of the chemical element which began to take shape in the seventeenth century, most clearly in the writings of Gassendi and Robert Boyle. This conception was much more closely related to Democritean–Epicurean theories of matter, which is one reason why the rediscovery of these theories was such an important event.

14. J. B. van Helmont (1577–1644) was one of the greatest chemists before Lavoisier: he used gravimetric methods and showed for a number of chemical reactions that there was no change in total weight during the reaction. He studied gases extensively and invented the word "gas" for this state of matter, thus registering a conceptual advance of the highest significance.

His works were published by his son in 1648 and appeared in English translation in 1662. Robert Boyle refers to him as "an author more considerable for his experiments than many learned men are pleased to think him".

Evidence has recently been brought that both van Helmont and Cusa may have got the idea of the famous experiment on plant nutrition from a "thought-experiment" put forward in a third-century Greek manuscript incorporated in the eighth book of the pseudo-Clementine *Recognitiones*! See H. M. Howe: A root of van Helmont's tree. *Isis* **56**, 408–19 (1965) for this curious detective story.

15. Boyle described his experiments in *The Sceptical Chymiste* (1661), including a careful account of van Helmont's experiment, with which he had evidently only become acquainted after his own were concluded. Boyle's essential conclusion is worth recording in his own words: "I may deduce from what I have tried concerning the growth of vegetables, nourished with water . . . that salt, spirit, earth, and even oyl (. . . of all bodies most opposite to water) may be produced out of water."

16. More rational conceptions of the nature of disease were expressed by Hieronymus Fracastorius in *De Contagione* (1546) and in the writings of Paracelsus (1493–1541). The latter tried to bring the chemistry of his day into relation with human physiology and medicine; however mistaken his ideas and impossible his behaviour, he had an immensely stimulating effect on his contemporaries and roused the fury of the medical establishment of his day. See W. Pagel: *Paracelsus*. Basle (1958).

    If Paracelsus had any direct influence on botany it was unfortunately negative, since he popularized the doctrine of signatures with its emphasis on fortuitous resemblances between the parts of plants and the human body.

17. The influence of Pierre Gassendi (1592–1655) on the development of science was recognized by his contemporaries, but has, in my opinion, been generally underestimated sincc. It is perfectly true that in spite of his keen and subtle intelligence and his command of the knowledge of his times, he was not profoundly original either in science or philosophy, and that his philosophical standing is weakened for posterity by a sincere but scarcely consistent religious orthodoxy, which promptcd Karl Marx's comment that he tried to clothe matcrialism in a nun's habit. Yet the fact remains that his re-statement of atomism in terms of elemental atoms, capable of forming certain precise structural combinations, or molecules, which are the building stones of things (*corpuscula composita subtilissima, moleculasve tenuissimas, quae sint quasi semina rerum*), and which moreover are not inert but endowed with self-motion, was exactly fitted to provide a basis for the new chemistry and physiology which scientists were trying to develop. He not only introduced the term molecule but gave it definition and concreteness; it is a specific combination and arrangement of particular atoms (*certarum atomorum in certam figuram conformatio et coincidentia*), not a mere agglomeration.

    His view of the world as consisting of matter in motion (*Syntagma Philosophicum* Op 1, 335b) was combined with a clear perception of the active role of observation in cognition, and in the progress to deeper objective knowledge of the material world.

Gassendi's complete works were published in 1658. There is no doubt that Boyle was powerfully influenced by his views; he refers to both Gassendi and Descartes at the beginning of his *Tentamina quaedam Physiologica* (1661), in a passage which John Locke transcribed into his notebook in 1667. Gassendi's re-appraisal of Epicurus (1647–49) was in itself a major contribution to the progress of science and philosophy.

18. The first microscopes were made in Italy and the most active early investigators with the microscope were members of the Accademia dei Lyncei in Rome, founded by Federigo Cesi, Duke of Aquasparta, himself a microscopist, who was probably the first to discover the spores of ferns. (Cesi produced an immense but uncompleted set of *Phytosophicae Tabulae*, intended to be a systematic summary of botany: it is a nightmare of muddled and outdated erudition, quite useless.) Other early microscopists were J. B. Porta, A. Kircher and P. Borel.
19. Malpighi and Grew were both born in 1628, and both studied medicine and were qualified doctors. For biographical details see W. Carruthers: On the life and work of Nehemiah Grew. *Journal of the Royal Microscopical Society* 129–141 (1902); and the monumental study by H. B. Adelmann: *Marcello Malpighi and the Evolution of Embryology*. New York (1966). Malpighi made fundamental contributions to human and comparative animal anatomy and embryology, as well as to botany, whereas Grew's interests were more closely restricted to plants. Grew was probably the first person ever to hold a purely botanical appointment, when in 1672 he was made Curator of the Anatomy of Plants to the Royal Society at a salary of £50 a year to be raised by subscription from "willing members".
20. In a letter to Malpighi in 1672, Grew wrote "I have myself benefited from your writings, and am truly proud to have so benefited"; he then goes on to mention Malpighi's observation of "spiral tracheae" as a case in point. In the same letter he informs Malpighi that he is just sending his anatomical observations on roots to the printers and will send the same to him for perusal.
21. The suggestion that Grew plagiarized Malpighi was apparently made by Schleiden in 1845 (J. Sachs, *History of Botany*) and was firmly rebutted by Sachs. The evidence that they worked independently and at the same time with acknowledged mutual indebtedness is overwhelming. It is based on a study of the actual time sequence of their research reports, on a detailed comparison between what each observed (or did not observe), on differences in nomenclature, on Grew's scientific punctiliousness (his generous reference to Hooke's work, for example), and finally on a reference in the *Philosophical Transactions of the Royal Society* in 1675, to "a very happy concurrence of these two eminently learned persons" in relation to the appearance of Grew's *Anatomy of Trunks*.
22. Leeuwenhoek's discovery of micro-organisms, infusoria, rotifers, and of spermatozoa, had far more impact on biology than his botanical observations, which did not go beyond those of Grew and Malpighi, although

he saw some new things, such as crystalline inclusions in cells, pitted vessels in secondary wood, and possibly nuclei, without linking them to existing knowledge by interpreting them.

23. In Grew's words, the bud "carries along with it some portion of every part in the trunk or stalk, whereof it is a compendium".
24. Grew's term for the filament, chives, revived the use of an old word going back at least to the fifteenth century.
25. No one who has conducted a class in plant anatomy will ever underestimate the powers of human misapprehension.
26. In this, as in most quotations from Grew and other writers of the time, I have omitted the capital letters which were such a characteristic typographical embellishment in the seventeenth and eighteenth century; these are distracting to modern eyes and tend to conceal the good sense being expressed. I have not changed the spelling.
27. The derivation from the Greek, meaning "poured in beside", reflects Grew's earliest conception that the softer tissues were somehow poured in among the harder ones, from which he moved a long way towards the recognition of a basic cellular structure.
28. Grew compared differentiation of plant cells to the change of the larva of an insect into the chrysalis. In a handwritten note in his own copy of the first edition of *Anatomy of Plants* he wrote "Air-vessels out of Parenchyma, transformed, as Caterpillars to Flys".
29. This theory was connected in Grew's mind with evidence of the effect of manurial treatment on plants. The "saline principle" is said by him to be a generic name under which various species are comprehended, and its importance for plants is "argued from the frequent experiment of good husbandmen that most bodies which abound with salt are the greatest nourishers of plants".
30. The "lymphaeducts" almost certainly represent the phloem in some of Grew's figures.
31. In this instance Malpighi was less clear; he thought that each year's new cylinder of wood already existed in a compressed form in the bark.
32. Cambium was first used to designate the alimentary humor by Arnold de Villa Nova at Montpellier in the fourteenth century.
33. The most complete study of the life and work of John Ray (1623–1705) is to be found in C. E. Raven: *John Ray* (1942).
34. See, for example, Sir R. Weston: *Discours of Husbandry used in Brabant and Flanders* (1650).

    The Royal Society established a special committee in 1665, the Georgical Committee, to collect data on different types of soil, manuring practices, rotations, etc. with a view to improving methods of agriculture. The first recommendation of the committee was the planting of potatoes. In the event the committee never did very much beyond collecting information, but the fact that such a committee was set up at all is indicative of the wakening concern for scientific agriculture, to which botanists began to respond. (See R. Lennard: English agriculture under Charles II: the evidence of the Royal Society "Enquiries". *Economic History Review* **4**, 23–45 (1932).)

35. Ray became a member of the household of his aristocratic friend Francis Willughby, probably undertaking the nominal duty of chaplain, in fact supported by Willughby, and after the latter's death, by an annuity left to him. Willughby was a man of ability and generous character, passionately interested in natural history, whose work on fishes Ray edited (generously enhanced by his own work) after his death.
36. The first Chair of Botany at Cambridge was not founded till 1724. Oxford founded a Chair of Botany in 1669 but left it in abeyance for forty years after the death in 1683 of Robert Morison, the first holder—so honours seem to be even.
37. Ray's turn to the problem of classification may have been precipitated by a curious episode of which full details are given by Raven. In 1667 Ray drew up, at the request of his friend John Wilkins, a tabular classification of plants to go in the latter's *Essay towards a Real Character and Artificial Language*, published by the Royal Society in 1668. This classification was purely artificial and was drawn up in bifurcating form and in accordance with certain requirements specified by Wilkins. In 1669 Ray was deeply hurt when Robert Morison brutally attacked his classification, totally disregarding the context in which it had been fashioned, and implying that Ray was a botanical ignoramus. This episode led to permanent bad feeling between the two men, although Ray was never led into open controversy.

    Morison made great claims for himself as a pioneer in plant classification, and his monograph on the Umbelliferae had some merit.

    His general scheme of classification was not published until after his death, when it appeared as edited by J. Bobart. In spite of his claims to originality, the merits in Morison's scheme derive almost entirely from his unacknowledged borrowings from Cesalpino. S. H. Vines's account of Morison and his method of classification is more than fair to him (see *Makers of British Botany*, Ed. F. W. Oliver (1913)).
38. The following is a translation of the relevant passage (from the preface to *Methodus Plantarum Nova* (1682)).

    The method of classification adopted here is not by habitat or by utility for food, medicine, pleasure or technical arts, but from the similitude and likeness of the principal parts, root, flower, calyx, seed, seed-vessel [conceptaculum]. This method was used with extraordinary sagacity by that most careful observer of plants, Andrea Cesalpino, who was the first, as far as I know, to classify plants according to the number of seeds and seed-vessels produced by each flower, and according to the position of the *corculum seminale*, that is, the point where germination begins.

39. John Wilkins and John Locke were elected Fellows at the same meeting.
40. It does not appear that Ray ever possessed a microscope or even a lens. In his later years of retirement at Black Notley he carried out many simple, but valuable and important, experiments on the life-histories and feeding habits of insects.
41. It is odd that in this quotation from *Historia Plantarum* the calyx seems to be separated from the flower, since Ray's definition of the flower comprises calyx, petals, stamens and style. Perhaps he was unconsciously recalling Jung's terminology in which the calyx was excluded.
42. J. P. de Tournefort (1656–1708) was Professor of Botary at the Jardin des Plantes from 1688, and was in charge of a scientific expedition to Asia Minor and parts of Europe. In *Institutiones Rei Herbariae* (1700) he defined 698 genera (with illustrations) principally on the basis of characters of the corolla and the fructification.

    Many of his genera continued to be recognized although re-defined and re-named by Linnaeus.

    He introduced the term pistil (*pistillum*) to designate the central organs of the flower comprising (when present) ovary, style(s) and stigma(s) *Pistillum appello partem eam, quae floris centrum inter stamina occupare solet*].

    In his *Éléments de Botanique* (1694) he criticized Ray for using more characters than were essential in defining genera and species. Ray replied to these criticisms in the *Dissertatio de Methodis* (1696) (to which I have referred in the text). The *Dissertatio* was a statement and defence of the principles of natural classification against such artificial "essentialist" classifications as those of Bachmann, Tournefort and others.
43. Pierre Magnol (1638–1715) was Professor of Medicine and later director of the botanic garden at Montpellier.

    In the preface of the *Prodromus* Magnol notes that Bauhin's *Pinax*, although a most painstaking work, fails to group species in wider classes, and often mixes them up. He says he found Morison's tables of plants helpful, but that all the best features of his classification were, in fact, borrowed from Cesalpino and Colonna; he then acclaims Ray's classification as the best (specifically mentioning his use of the seed-leaves as a differentia), but notes that some of his groups may contain plants having nothing in common but the defining character of the group. Magnol says he is planning a larger work in which all plants will be classed in known families, with figures, synonyms, and brief descriptions; but this was never carried out. Magnol's last work, *Novus Character Plantarum*, published posthumously in 1720, was retrograde, attempting to base classification on features of the calyx alone.

    Magnol was a friend and correspondent of John Locke, who visited Montpellier Physic Garden in January 1676, recording in his diary that he picked "blew violets, full blown and very sweet".
44. Ray in his earliest writings referred to the cotyledons as seed-leaves (*folia*

seminalia). The word cotyledon was first used in relation to seeds by Malpighi in 1679 (it had been used in zoology since Aristotle to refer to the uterine placenta). Ray first used the word as an alternative to seed-leaf in *Historia Plantarum* (1686) but in 1703, in *Methodus Emendata*, he defined the cotyledons formally as follows: they supply food (to the new plant) just as the uterine placenta or cotyledons in animals. In some plants there is only one, but in the majority there are two (called seed-leaves). Hence the division of plants into Monocotyledones and Dicotyledones.

Ray discussed the structure of seeds and the number of seed-leaves in the preface to *Methodus Nova* (1682) but did not use the information in his classification. In *Historia Plantarum* (1686) he divided herbs (but not trees) according to the number of cotyledons (*Herbae bifoliae* or *unifoliae*). In his final classification in *Methodus Emendata* (1703) he divided both trees and herbs (separately) into Dicotyledones and Monocotyledones.

45. It is to be noted that Ray did not separate the gymnosperms (Coniferales) from flowering plants. In his earlier classification in *Historia Plantarum* he put *Pinus* with the monocotyledons, but in his final classification in *Methodus Emendata* the Coniferales are (more correctly) included with dicotyledons.
46. Curiously enough his memory was not quite accurate, for Theophrastus did not actually apply διλόβῳ to the seed, instead he said that (dicotyledonous) seeds are διμερῆ or δίθυρα (i.e. made of two parts or two doors).
47. Thus on March 30, 1680, Locke recorded that Mr Cole of Bristol "showed me the seedes of fern and Lunaria which are either of them above an hundred times lesse than small sand."

    Ray noted in *Historia Plantarum* that before the invention of the microscope ferns had been thought to be sterile even by some great botanists.
48. Ray's ideas on classification progressed throughout his active life and his real accomplishment must therefore be studied in *Methodus Plantarum Emendata et Aucta* (1703) (referred to in the text as *Methodus Emendata*). This is summarized by S. H. Vines in *Makers of British Botany*. A point of great interest is that in dealing with trees, Ray essentially adopted the classification of Cesalpino, adding, of course, his own division according to the number of cotyledons.
49. A. Q. Bachmann (Rivinus) (1652–1725) was from 1691 Professor of Botany, Medicine and Chemistry at Leipzig. His method of classification of plants was very artificial, relying on whether the corolla is regular or irregular and and paying little attention to the other floral organs.
50. Colonna had used *petalum* (Greek πέταλον, a leaf) on one occasion in his *Phytobasanos* (1592) (Cap. 1) and on one occasion in his *Ekphrasis* (1616) to signify the coloured corolla. However, in the notes which he contributed in 1628 to F. Hernandez's plants of Mexico, *Nova Plantarum Animalium et Mineralium Mexicanorum Historia*, not published till 1651, Colonna

suggested that *petalum* would be a useful technical term for the floral leaves (*floris foliola*).

51. The Sensitive Plant not unnaturally excited much curiosity when first brought to Europe. Samuel Pepys recorded in 1660 that he "met with Mr Lynes the surgeon who promised me some seeds of the sensitive plant".
52. R. Sharrock: *History of the Propagation and Improvement of Vegetables* (1672).

    In May 1658 he found that cuttings of some twenty to thirty different plants grew and rooted in water alone and increased in weight. Some species continued their growth from year to year, but there were also some which failed to grow in these conditions and rotted away.

    Sharrock mentions many horticultural and agricultural experiments he did, including a whole series on the alleged effects of treatments claimed to speed up the germination of seeds; but any acceleration was inconsiderable, and he found the only sure method was in hotbeds made with horse manure and fine mould above. He tried grafting many different kinds of roses and showed that, contrary to the statements of Kircher, the colour of the flowers of the scion is not influenced by the nature of the stock.
53. Ray also refers to, and had clearly read, Edmé Mariotte's essay, *De la végétation* (1679). This work treated vegetable physiology fully from the new standpoint of Ray, Grew and Malpighi. Mariotte attempted a chemical investigation of plants, drawing the conclusion that the variety of different substances he found in plant bodies must have been produced by the transformation within the plant of the water taken in by the roots, and could not have been present, already formed, in the earth. Apart from this, Mariotte does not appear to have done any experiments, but he tries to give a rational and material explanation of a number of observations on plants.
54. We get an indication of what Ray thought about respiration from a letter from a Dr Connor (Ray's *Correspondence* I, p. 309) who had read Ray's treatise. According to Connor, Ray's view was "that [in animals] air passes from bronchia and lungs into the substance of the blood, where like a kind of food (*pabuli instar*) it foments and maintains the vital flame as air does a candle, and that nitre has nothing to do with this effect". Apparently Dr Connor differed from Ray in how respiration actually rarefies and vivifies the blood.
55. Ray emphatically rejected the doctrine of signatures, the idea propounded by Paracelsus that each plant bore a divinely inscribed sign of its medicinal use or power, and he also rejected the explanation of the medicinal powers of plants in terms of the degrees of internal heat, cold, wetness or dryness, which they allegedly possessed. Of the latter doctrine he remarks that it seems more ingenious than useful, and that

those who delight in such matters must go to the medical writers (*Historia Plantarum* I, cap. 24).

56. *De variis Plantarum Methodis Dissertatio brevis* (1696). There can be no doubt that Ray had read Locke when he wrote the *Dissertatio*.
57. The neo-Platonist influence on Ray came from Ralph Cudworth's *True Intellectual System of the Universe* (1678). He employed the term "plastick Nature" and thought of it as a kind of intermediary or agency between God and the material world. Among the problems that Ray found difficult to explain "mechanically" he mentions the regular production of five petals (neither more nor less) in a particular species of flower. It must be admitted that the mechanism of these morphogenetic processes still remains extremely obscure.
58. R. J. Camerarius (1665–1721) studied medicine at Tübingen where his father was Professor of Medicine. He travelled for a year in Germany, Holland, England (where he made the acquaintance of Robert Boyle), France and Italy. On returning to Tübingen in 1687 he took his doctorate and became extraordinary Professor of Medicine and Director of the Botanic Garden.

    In 1695 he succeeded his father as ordinary Professor of Medicine and spent the remainder of his life in Tübingen.
59. J. C. Sturm was Professor of Mathematics and Physics in Altsdorf. I have not been able to find out what he wrote about plants.
60. Camerarius generally used the term *pollen* (less frequently *pulvis* or *farina*), which he probably took from Ray. His work led to the general adoption of the term even before Linnaeus finally established it.

7

Camerarius to Linnaeus: the Recognition of Sex in Plants and the Exploration of the World Flora (1694 to 1753)

Botany is that branch of natural science which enables us, most happily and with the least trouble, to know plants and to remember them.

H. Boerhaave (quoted by Linnaeus)[1]

After the rising flood of scientific activity in the middle of the seventeenth century, its closing years brought a certain slackening, not only in England where growth had been most rapid, but in other European countries as well.[2] This pause was connected with the period of necessary consolidation of the growing economic forces which prepared the way for, and were finally released by, the industrial revolution; at the same time there was in many countries a political reaction in favour of the old order, which also tended to put the brake on science. In England the bourgeoisie and their allies had won complete military and political predominance during the Civil War, but after the Restoration the more conservative sections made a compromise with their former opponents at the expense of the radicals within their own ranks. This compromise forced John Ray out of his university post, and although in this case the result happened to turn out well for science, the general effect was to re-entrench in the English universities men of the established religion and conservative outlook, and to make these institutions for more than a century indifferent or hostile to science, even when they harboured a few individuals whose genius or enthusiasm could not be suppressed or discouraged. The same reaction kept Oxford for forty years without a professor of botany, and in 1700 tried to prevent its undergraduates from reading the subversive doctrines of John Locke.

In France the bourgeois classes had not yet defeated the landed aristocracy but had attained such wealth and influence that they could no longer be excluded from high government offices in the largest and most powerful nation in Europe. After the revocation of the Edict of Nantes in 1685 there was, however, a partly successful struggle by the aristocrats to force men of bourgeois origin out of leading positions under the crown, a policy that was accompanied by anti-scientific and anti-intellectual pressures, and which contributed to the peculiar fury with which the French Revolution was eventually fought out. Against this background of political reaction can also be understood the attraction of some retrogressive biological theories such as preformationism, and a tendency in some circles to regard science merely as fashionable curiosity, the occasion for surprising or amusing display, whether in the form of a conservatory of rare flowers or the sparks from an electrical machine.

In the physical sciences the triumphant progress of the seventeenth century reached its climax with the publication of Newton's *Principia* in 1687 (the year after Ray's *Historia Plantarum*). Although the style and methods of this great work prevented it from being read or understood except by a relatively narrow circle of experts, the effects on the whole scientific world were profound. The apparent completeness and finality with which Newton was able to state the laws of physics and mechanics affected all contemporary thought. It was not merely that he solved for the time the main practical problems in these fields, and provided a set of laws and concepts that any intelligent person could understand and use—although this in itself would have been sufficiently impressive. By uniting the mechanics of celestial and terrestrial bodies in a single system of uniform law, Newton seemed to have established that all the phenomena of the material world are governed by inherent and ascertainable material laws. He thus appeared to his contemporaries and successors as the man above all who had enthroned the "mechanical philosophy" in science: this conclusion from his work had very considerable influence on subsequent developments in botany (and in biology) as will be seen. In particular Newton's conception of a dynamic universe, initially deriving its movement from God, but thereafter moving according to strict internal law without divine intervention to sustain it, was admirably fitted to include and rationalize the study of the world of living things. It was a point of view closely allied to that of Ray.

The direction of botanical research was more directly influenced by Newton's last publication, the *Opticks* (1704). More accessible to biologists than the *Principia*, it gave an account of the properties of light as determined "by reason and experiment". The clarity of this work and the author's immense prestige made it a persuasive stimulus to the experimental study of the effects of light on plants, a topic that was to become of vital significance. In the physical sciences the very magnitude of Newton's accomplishment seems to have slowed further progress for a time, giving the impression that nothing important remained to be done. The only new developments were in areas untouched by him. Research in electricity grew slowly as the eighteenth century advanced, until its progress became linked with that of chemistry after 1760.

The impetus to growth was more actively sustained in the biological than in the physical sciences, largely because of the colonial expansion then in progress, initiating a second phase of world exploration in which animal and plant resources were investigated far more completely and systematically than in the earlier voyages of discovery. In botany it is arguable whether there is any decline at all. It is certainly true that for some fifty years botanical theory showed little advance, failing to rise beyond the level of understanding reached by Ray, Malpighi, Grew and Camerarius, but poverty of ideas was at least compensated by the rapidly increasing knowledge of the variety of form in the plant kingdom, a basis of raw fact which had to be established before some of the fundamental questions of botany could even be stated, much less solved.[3] Interest in botany was not only roused by the stream of new plants from abroad, but also by a further upsurge of horticulture and gardening, ministering to the appetites and the fashionable tastes of both the new middle class and gentry, and a refurbished aristocracy. For these reasons botany was, throughout the eighteenth century, a leading and officially encouraged science[4] in most European countries, as a glance at the proceedings of various national academies of science sufficiently shows. Expeditions for scientific research, often supported or financed by national governments, became a regular thing, and botanical exploration and the search for new plants were invariably among the most important objectives. The accumulation of floristic knowledge thus naturally continued to dominate botanical enquiry during the period.

It was John Locke, the contemporary of Ray and Newton, who more than any other single person provided the philosophic basis of science during the eighteenth century. Although less original than Descartes, Gassendi and Hobbes, to all of whom he was indebted, his simple yet convincing demonstration that men's ideas are not innate but are derived from "sensation", that is, from human experience; his assertion that knowledge has to be improved by "experience" and by "rational and regular experiments"; and his analysis of the nature of rational probability and of the positive contribution it can make to the growth of knowledge;[5] all these propositions of enlightened common sense caused the *Essay concerning Human Understanding* to become the guide and justification for observational and experimental science. The *Essay* appeared first in 1690 and was reprinted four times within ten years; it was translated into both Latin and French and thus carried the influence of Locke's ideas throughout Europe. Its impact was strengthened rather than weakened by the fact that Locke himself believed, like Kant later, that there are limits to the scientific apprehension of reality: bolder minds merely disregarded Locke's reservations, while others accepted them as leaving a domain for religion or speculation. Locke's influence in freeing the way for cautious but untrammelled practical enquiry was made more widely effective by the spirit of toleration, and of calm devotion to truth, which infused his own life as well as his teaching.

In biology the assembling of many comparative observations was probably a more immediately fruitful and necessary task than experiment, and this situation was accurately reflected in the faintly passive nuance of Locke's dictum that "perception is the inlet of knowledge". Before turning to epistemology he had had a thorough training in medicine and science at Oxford, and experience of practical research during collaboration with Robert Boyle in what must have been the earliest study of the chemistry of blood. In the context of this history it is a matter of particular note that Locke was also an enthusiastic and competent botanist,[6] since several strands of his thought in the *Essay* were of peculiar relevance to the direction of contemporary botany and its subsequent development.

When Locke wrote that "the way to improve our knowledge . . . is to get and fix in our minds, clear, distinct, and complete ideas, as far as they are to be had, and annex to them proper and constant names", he could hardly have stated more clearly and distinctly what botanists should be, and to some extent were, trying to do: to describe plants with diagnostic completeness, and to establish a stable and generally accepted system of nomenclature.[7] When, furthermore, he asserted that a genus was a mental grouping of specific things in some way related, he was not merely removing a source of rather outworn philosophical hog-shearing,[8] but was stating an urgent botanical job, namely, the need to supplement and give firm foundation to the "intuitive" recognition of genera of plants which botanists naturally make use of, by making a precise comparative examination of the essential characteristics of each constituent species. In considering the various possible types of relation between things or species, Locke included as one special class those relations dependent on "the circumstances of their origin or beginning, and not afterwards to be altered", calling them *natural relations*, the archetype being, of course, human kinship. His generalization of genetic relationship (in its widest sense) and his recognition of its unique significance was an important step in the general development of scientific theory: in particular, it contributed to raising more sharply and clearly the problem of a natural classification of animals and plants, although I do not believe there is any evidence that in so doing Locke had any evolutionary ideas in mind.

In a brief, remarkable passage[9] Locke attempted to define the identity of a plant, distinguishing the plant body equally from an unchanging mass of matter and from a piece of mechanism. He saw the plant as a coherent body, having internal self-motion, and consisting of parts united in a specific organization that is fitted to its common vital activity. While pointing out those features, such as the powers of growth, repair, and formation of new organs, in which a plant or animal body differs from a piece of mechanism such as a watch, he also emphasizes some true similarities, and hence the presumption that a living body functions, in large measure, according to "mechanical" laws.[10] This analysis pregnantly foreshadowed concepts in process of formation and destined to play a significant part in the development of plant and animal physiology. For a century or more after the publication of the *Essay* its arguments influenced the thinking and activity of scientists, and were most potent in illuminating the special problems of biology.

In the period we are now considering, almost coincident with the first half of the eighteenth century, the theoretical directions and problems of botany were perhaps most clearly expressed, and its practical progress most effectively assisted by a man usually remembered for his achievements in another field. This was Herman Boerhaave,[11] better known as the founder of scientific medicine and the pioneer of a materialist interpretation of human physiology, whose teachings dominated medical science for more than a hundred years. Boerhaave firmly held the conviction that medicine must be linked with, and make full use of, all relevant branches of natural science. After his appointment in 1709 to the chair of medicine and botany at Leiden, this conviction, reinforced by the fact that superintendence of the botanic garden was part of his duties, led him to a more serious study of botany than he had yet undertaken,[12] and his great scientific ability soon made him master of contemporary botanical knowledge and its basic problems. His enthusiasm for botany lasted all his life and inspired many generations of students. He devoted much energy to increasing the stock of plants in the Leiden Botanic Garden, adding more than 2000 species in the first ten years: he also created an arboretum. This was the golden age of Dutch commercial and colonial expansion, and Boerhaave made use of many agents, including men in the service of the Dutch East and West Indies Companies, to send him seeds and plants from overseas, which he would regularly distribute to other botanists with unfailing generosity.

It was also the golden age of the University of Leiden, founded during the darkest days of the struggle for national independence and now enjoying the fruits of success in that struggle. For over a century Leiden was the intellectual centre of Europe, owing much of its fame to the university's policy of toleration of "Jewish and all religions including Romish", as John Ray noted. Many brilliant men, excluded by religious bigotry from higher education at home, sought the intellectual freedom of Leiden. The international repute of the medical school drew many students thither, and not a few gained from Boerhaave a lasting interest in botany. On returning to their own countries some were encouraged to found botanic gardens or to revive existing ones, and they continued to receive help, and new specimens from their old teacher. Since the accurate observation of living specimens of a wide range of plants was the primary botanical need of the time, Boerhaave's practical contribution to the development of botany was a major one.

His influence on botanical theory was also considerable, even though his writings on the subject consisted of little more than two editions of the catalogue of plants in the Leiden garden, supplemented by a few prefaces which he wrote for the works of others. Yet his broad scientific outlook enabled Boerhaave to analyse contemporary botanical problems with clearer understanding than many more outstanding botanists; and his years of teaching, his friendly intercourse with many botanists, and his international authority, made his influence wide and effective. His attitude to the main botanical questions thus provides a mirror and commentary to the time.

Although, on the surface, botany in the early eighteenth century seemed a continuous progression from what had gone before, the discovery of sex in plants caused fundamental changes in emphasis and outlook, and raised completely new questions and areas to explore. The most significant conclusion that followed from the recognition of the sexual function of the flower was that both plant and animal kingdoms showed the same law of generation, as Boerhaave was one of the earliest to point out.[13] The apparent difference between reproduction in plants and animals had been a puzzle since ancient times, and it was now suddenly resolved in a way that extended the reign of rational order in the world of living things, just as Newton had extended it for the world of mechanics. An important consequence was that the nature of sexual fertilization, and whether it was the same in essence in plants and animals, and what was its relation to embryonic development, now became subjects of lively enquiry, both experimental and speculative. The beginning of a *rapprochement* between botany and zoology at this level, was the first step towards their still distant union in a single science of biology.

For botany there were immediate practical consequences. Once the primacy of the floral parts was understood, their detailed form and arrangement were studied much more intensely, at a time when an astounding variety of flowers from all over the world was available to be looked at. These studies led to the rapid development of floral morphology and of a corresponding terminology, fitted to answer the needs of taxonomic research and description. Floral structure in relation to plant classification was brought to the fore, whilst the emphasis on floral parts turned a few botanists to the problem of those plants which have no flowers, and thus investigations began into groups of plants (later called cryptogams by Linnaeus)[14] which had hitherto been largely neglected.

The understanding of the function of pollen in the fertilization of higher plants marked the beginning of true plant breeding, as distinct from empirical or unconscious forms of selection that had been used from the earliest times. Attempts to produce plant hybrids by artificial pollination began to be made sporadically by gardeners quite early in the eighteenth century, before any systematic experiments were undertaken by botanists.[15] From the practical arts of plant and animal breeding came ultimately the science of genetics.

Boerhaave appears to have recognized and accepted the existence of sex in plants soon after Camerarius's experimental researches became known; he was teaching the doctrine to his students by 1718 or earlier, and his great repute must have helped to secure its general acceptance. The careful and thorough descriptions of floral structure in his catalogue of Leiden plants, and his emphasis on the significance of these parts for classification, reflect his full agreement with the views of Camerarius, Grew and Ray.

The existence of sexual generation in flowering plants and of the male fertilizing function of pollen, were accepted fairly soon by the vast majority of botanists, although for a time there was a dissenting minority which included some notable figures. The great botanist Tournefort at his death in 1708 was still convinced that the stamens were purely excretory organs, a suggestion put forward by Malpighi: and Pontedera denied the sexual role of stamens in 1720. There were indeed isolated opponents of sex in plants long after it had become part of botany. They included the Edinburgh professor, C. Alston, a former pupil of Boerhaave who had not been convinced by his teacher, and J. Siegesbeck of St Petersburg, to whom sex in flowers was not only scientifically unconvincing but morally revolting as well. There were even oddities like F. J. Schelvers, professor of botany at Jena, who as late as 1820 was confiding to an interested Goethe his philosophic doubts about the dogma of sexuality in plants. By 1720, however, Patrick Blair in his *Botanick Essays* was treating sex in flowering plants as something which almost all botanists accepted as proven.

It is an interesting fact that most botanists, including Boerhaave himself, regarded the rational parallel between sexulity in animals and plants as the strongest argument for the sexual functions of stamens and pistil. Sexuality seemed to explain so perfectly the structure and arrangement of the floral organs, that this in itself carried conviction, and Camerarius's experimental proof seemed almost unnecessary confirmation of what was already established by reason.[16] Camerarius himself had, as we saw, strengthened his experimental proof by a detailed account of the structure of hermaphrodite flowers, whch he related to their presumed sexual function. All this makes it probable that when cautious men like Grew and Ray expressed their belief in the male fertilizing role of pollen, they had some unwritten horticultural evidence to back them up.[17] Some gardeners may have already formed a guess at the function of pollen based on their own observations, perhaps on experiments of a sort. Jacob Bobart, for example, had found in 1680 that seeds from a flower of *Lychnis* in which no anthers were present, were infertile when sown.[18] It is difficult otherwise to see why Camerarius's careful experiments were so much taken for granted, for they certainly became widely known, even though published in the obscure transactions of a small, German learned society.

There was no immediate rush by others to test Camerarius's conclusions by further experiments, but again there are indications that some horticulturalists may have tried experiments on pollination without bothering to record what seemed to be undisputed. A few people did, however, publish experiments which provided some independent confirmation of Camerarius's conclusions. The first was Richard Bradley in 1717, who removed the stamens from the flowers of twelve tulips and found that they failed to set seed, whereas 400 non-castrated flowers did so.[19] This modest experiment was important because it was the first in which hermaphrodite flowers were used, and provided experimental proof for what Camerarius had only established by analogy for this, the commonest type of flower. In 1751 Philip Miller did some similar experiments with tulips, with the same results, but was observant enough to notice that bees sometimes carried pollen to the stigmas of castrated flowers—the first intimation of the role of insects in pollination. Others who gave experimental evidence for sex in plants returned to using dioecious or monoecious plants as Camerarius had done; Logan (1739) in North America used maize; Gleditsch (1751) in Berlin claimed to have done experiments for many years with dioecious plants, but only describes in detail his experiment with the palm *Chaemerops humilis*, probably because the results were rather dramatic. The single specimen in the Berlin Garden was a female, eighty years old, which flowered each year but never produced seed. In 1749 male flowers were received from a tree in Leipzig. Owing to delays on the journey the pollen on arrival was completely dry and had fallen from the anthers, being collected in paper. Only one branch of the female tree still bore flowers, the rest having fallen. The pollen was applied to this one bunch of flowers which proceeded to set seed, and in the following spring the speed was sown and germinated successfully. Gleditsch makes the interesting statement that whilst the existence of sex in plants had been for a long time a matter of debate among naturalists, it was now established on the firm foundation of reason and experience. Very few now had any doubts and these were confined to those ignorant of the experiments or of the structure of flowers. His own experiments were only done in order to attain entire conviction.

Thus by mid-century sexual generation in flowering plants had been accepted by all but a very few. The conviction of the majority was founded, as Gleditsch put it, both on reason, that is, on general biological probability, and on experience; and experience included not only the relatively small number of decisive experiments, but also the everyday experience of practical men cultivating their gardens.

Sebastien Vaillant, who had studied under Tournefort and held an appointment as botanist at the Jardin du Roi in Paris was one who was early convinced of the correctness of Camerarius's doctrine of the sexual function of flowers.[20] At the opening of the garden at a new site in 1717 he used the occasion to give an address entitled *Discours sur la structure des fleurs* which created something of a sensation, particularly among the students. Vaillant gave an exposition of the sexual function of flowers which was rendered vivid and a little shocking by his use of vernacular terminology in comparing the stamens to the penis and testicles of animals, and by humorous references to the innocent sexual pleasures of flowers. In spite of this, it was a serious discussion and presentation of the new theory, and played a considerable part in securing its general acceptance. In addition the work emphasized the need for a terminology of the floral parts which should correspond to the new understanding of their functions and be generally accepted by botanists. Vaillant's discussion was an important step towards such a terminology, and the adoption of the terms stamen, filament, ovary, ovule, and placentation, in their modern sense, was due to him. At the suggestion of William Sherard,[21] and with the help of Boerhaave, the French text of Vaillant's lecture, together with a Latin translation, was published at Leiden in 1718. Thus Boerhaave and Vaillant between them did much to create an understanding of the primary function of the flower and floral organs in sexual reproduction.

When Camerarius published his evidence for sexual reproduction in plants, he concentrated on the essential fact that its occurrence could be experimentally proved or at least made very probable; deliberately and wisely leaving the details of fertilization for future investigation. The latter problem was much discussed by botanists following on Camerarius's work. There was at the time a corresponding interest in the process of fertilization in animals, aroused by Leeuwenhoek's discovery of the spermatozoon, as well as by the contemporary theory of preformation.[22] In plants there was a special problem: how could the pollen, manifestly the male element, reach the ovules and effect fertilization, when the ovules were completely enclosed in an ovary and the stigmatic surface, on which the pollen could easily be seen to be deposited, was separated from them by a style which was often of considerable length and apparently solid.

The question was first considered by Samuel Morland, just eight years after the appearance of Camerarius's *Epistola.* He failed to produce any evidence from observation or experiment, but accepted the preformationist view that the embryo is brought to the ovule in the pollen, and he therefore concluded that the pollen grains must pass down the style, and are probably driven through by rain or wind. However, several observers were able to show that in many, possibly in all plants, the style is completely blocked by tissue so that no pollen grains could possibly penetrate to the ovules. Vaillant argued very neatly from *Papaver orientalis* in which the pollen is deep purple, that since the colour can be seen staining the stigmatic tubules, whilst the placentae and ovules remain white, and since many pollen grains would be needed to impregnate that many ovules, therefore it is evident that the pollen does not penetrate as such or the purple colour would appear in the ovary. Hence what must penetrate to the ovules is a "volatile spirit" derived from the pollen, and this is the effective agent of fertilization. Patrick Blair adopted Vaillant's suggestion and assumed that the pollen supplies a "Prolificke Virtue" or "Vivificke Effluvia", brought to the ovules by the "ordinary circulation of the juice of the plant and the dilatation of the tubules which convey it".[23] Bradley thought that the fertilizing principle was conveyed by some kind of attraction or "magneticke virtue".

These views are sufficiently representative of a state of knowledge that persisted for a long time. It was indeed over a century before pollen tubes were observed and the method of fertilization understood. Apart from the difficulty of seeing the real state of affairs with the microscopes and methods in use, observation was probably blinded by two concepts derived from other fields of science. One was the assumption that fertilization in plants must be wholly analogous to that in animals. The other was the hypothesis of subtle fluids and of influences acting at a distance, which reflected the great theoretical impact of Newton, but unfortunately happened to be inappropriate to biological systems.[24]

The situation was more or less stabilized by the perfectly correct but, as it happened, misleading observations on pollen grains made by the English Jesuit J. T. Needham in 1745.[25] He found that when pollen grains are placed in water for microscopic examination, large numbers of them burst to give a mass of tiny globules. Burst grains and globules were also seen on the stigmas of flowers examined in water. He therefore assumed that the globules were the fertilizing substance, and that they were able to penetrate and pass through the style. This provided a reasonable materialist explanation which appeared to agree with what was observed, and it satisfied the majority of botanists for a very long time. It is the account of fertilization given currency by Linnaeus,[26] although he opted for a seminal effluvium, rather than visible globules, as the effective agent.

The mantle of order which the doctrine of sexuality threw over the cohorts of seed plants, made more striking the nakedness of those long-recognized, but little understood, groups which did not fit into the scheme. In spite of the attraction of the overwhelming numbers of flowering plants, a few botanists now began to look more closely at the so-called lower plants or cryptogams, whose intimate structure and modes of reproduction were still unknown. Although this line of investigation was ultimately to provide the key to an understanding of the fundamental relationships among the diverse groups of the plant kingdom as a whole, the pioneer observations, admirable as they often were in isolation, could not be brought together into any comprehensive view. The sexual theory which illuminated the flowering plants gave rise to confusion and false analogy when the attempt was made to apply it to non-flowering plants. In addition there were deficiencies in anatomical knowledge and microscopical technique which could not yet be overcome and which made progress halting and difficult. Interest in non-flowering plants was most lively among French botanists of the Jardin du Roi and the Académie des Sciences. The eighteenth century upsurge of French botany forms part of the subject matter of the following chapter since its full flowering came in the second half of the century, but the signs were already present in the breadth of research carried out by the generation which followed Magnol and Tournefort. A few examples will indicate the fresh ground that was broken in the study of lower plants.

The microscopic spores of ferns and mosses were well known objects by the end of the seventeenth century and were generally assumed to function as reproductive "seed": the word *semen* was used to cover both these microscopic bodies and the true seeds of flowering plants and conifers. The first experimental evidence that the spores of ferns are reproductive bodies was published in R. Morison's *Historia Plantarum* (Part 3) in 1699, where there is an account of how the powder [spores] from the underside of leaves of harts-tongue fern was sprinkled on moist shady soil. In the following year numerous young fern plantlets appeared on the ground where the sowing had been made.[27] This straightforward demonstration appears to have been soon forgotten, or overshadowed, in the confusion caused by later attempts to equate the spores with pollen and to find in ferns an equivalent for the pistil. Bernard de Jussieu made some excellent observations (1739, 1740) on heterosporic ferns, which are only mentioned at this point as they will be referred to in more detail later.

In 1711 Réaumer gave an account, in the *Mémoires de l'Académie des Sciences*, of the marine alga *Fucus*, which was a model of accurate observation and description. The salient features were noted with remarkable objectivity. He saw and figured the two types of external openings in the thallus: the non-sexual cryptostromata, which he interpreted as staminate flowers, and the conceptacles containing the sexual organs, which he thought were female flowers. With a lens he was able to see the oogonia and antheridia within the conceptacles, but he interpreted them as the seeds, correctly noting that each conceptacle had an opening externally through which they could escape. This paper illustrates the brilliant observations made by some of the early cryptogamic botanists, as well as the fundamental difficulties which it was no reproach to them that they were unable to conquer. Marsigli in Italy was making studies of many seaweeds at about the same time (*Physique de la Mer* Part 4, 1725); he was a much less accomplished observer but studied a wider range of forms. In 1713 J. Marchant gave an excellent description of the liverwort *Marchantia* (named by him after his father Nicole who had been a royal botanist at Paris before him). He called the antheridiophores and archegoniophores flowers, and assumed that the spores are seeds because small plants grow up around the parent plant and on nearby walls and paths. He surmised that many tiny plants on walls and trees arise in this way and that "if well examined one will discover among them an affinity of many different genera of plants . . . showing the immense fecundity of nature and the great extent of botany": a prophetic vision of the rise of cryptogamic botany. Marchant was the first to describe the elaters and their peculiar movements in the sporangium.[28]

Two significant beginnings were made in the study of fungi. In 1728 Antoine de Jussieu argued the need to set up a special class of plants to contain the fungi and lichens, pointing out certain characteristics suggesting that these organisms are closely related.[29] More will be said later of Jussieu's paper in which he used total affinity as a guide to classification, a principle the French botanists were soon to take the lead in establishing. Micheli, in 1729, published an account of the structure and reproduction of fungi, and an attempt at classifying them, which may be said to mark the emergence of mycology as a definite field of study.[30]

The first monographic study of mosses was published by Dillenius in 1741.[31] He made many accurate observations on their morphology and began critical delimitation of species, making use of several characters that proved of permanent taxonomic value, but his view that the sporogonia represented male flowers, while not implausible at the time, could only be a blind alley.

These early researches on cryptogams opened an important new field of botanical enquiry, but exploration could not for a long time get beyond random foraging. The results had little effect on general ideas and were sometimes made the basis for unprofitable speculation. Progress was retarded by optical problems in microscopy and by the failure of researchers to improve or even to master the techniques of Grew and Malpighi: in higher plants too, anatomical investigation remained at a standstill.

In spite of the call to physiological research raised by Grew, Malpighi and Ray, plant physiology had attracted almost no attention from botanists in general. The only exception was in England where the experimental tradition, founded by the Royal Society, was strongest, and where, in social conditions relatively more settled than in the rest of Europe, a few men of property and leisure began to perceive how science might be the means of raising the yield of their estates, farms and gardens.[32] Some not very well planned or informative experiments on plants were carried out by Woodward, Beale and other Fellows of the Royal Society as the eighteenth century opened. Woodward used the method of water culture, pioneered by Sharrock; he measured the large amount of water lost through transpiration in mint plants in proportion to their weight, but was unable to exploit the technique further.[33] Not till the experiments of Stephen Hales was plant physiology raised to a new level. His work was so great an advance that it stands alone in its time and deserves close attention.

Hales went to Cambridge in 1696, the year that Newton left for London to become Warden of the Mint and a government servant. Ostensibly studying divinity, Hales was deeply interested in experimental science from early in his student days, and was fortunate to coincide with a number of able scientists grouped round Richard Bentley, who encouraged and supported them at a time when science

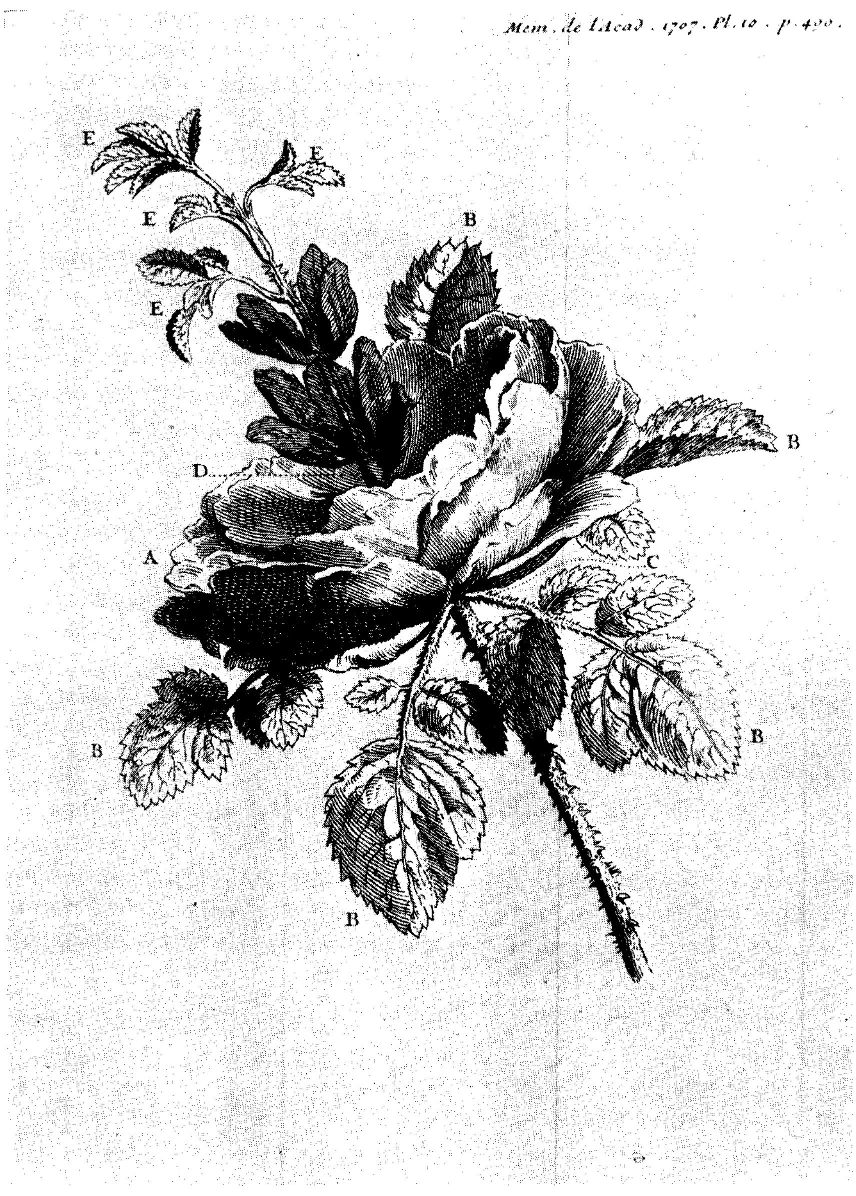

Figure 16 "Rose monstrueuse" described by N. Marchant in the *Mémoires de l'Académie Royale* (1707). A reflection of newly growing interest in the developmental aspects of plants.

was at a low ebb in the university.[34] Botany was among Hales's interests from the beginning; he used Ray's *Flora of Cambridge* in his rambles, and must have read Ray's outline of botany in the *Historia Plantarum*. Hales was well grounded in all branches of contemporary science, in mechanics, chemistry, hydrostatics and pneumatics, and in botany and natural history. This breadth of knowledge, and the inspiration of Newton's experimental philosophy which was still a powerful influence, helped him to create a new outlook and methodology in physiology.

His tenure of a college Fellowship allowed him to serve a long apprenticeship in science. After leaving Cambridge he was appointed to the Perpetual Curacy of Teddington and he spent the rest of his placid life in the conscientious performance of his clerical duties, whilst devoting an amazingly industrious leisure to the pursuit of science, refusing offers of preferment in order to do so. For the first nine years he concerned himself with blood circulation and blood pressure in animals, experiments which brought him to the notice of the Royal Society of which he became a Fellow in 1718. At about this time he began his long series of experiments on plants, which were published in 1727 under the title of *Vegetable Staticks*.

The title itself reveals what Hales saw, correctly, as his special contribution, the method which truly began a new stage in physiological experimentation. The word statics, with its reminiscent allusion to Archimedes, had become synonymous with precise measurement, and in his introduction Hales emphasizes this as the key to his method and the point in which he claims to have advanced beyond his predecessors. After a generous tribute to Grew and Malpighi as experimentalists, he none the less opines that "had they fortuned to have fallen into this statical way of enquiry", they would have made greater progress in understanding "the several quantities of nourishment, which plants imbibe and perspire". Hales then defined the essence of the statical way in the clearest possible terms. "Since the all-wise Creator observed exact proportions of number, weight and measure, in the make of all things" . . . so the "way to insight into nature . . . must in all reason be to number weigh and measure". In applying these concepts in his own experiments on plants, he employed and adapted techniques for the measurement of mass, area, volume, pressure, specific gravity, temperature, which were already the hallmark of the physical sciences. The new prescription for precise quantitative experiment in physiology was the most valuable legacy of Newtonian experimental philosophy to biology.

In stressing the role of experiment, Hales had very much in view the practical benefits for men that would flow from the improvement of agriculture and gardening, fully in the spirit of the age. He also saw, however, that "the most rational ground for success in this laudable pursuit must arise from greater insight into the nature of plants", that is, from research in plant physiology, as Grew had foreseen. In a sentence which plainly echoes Locke, he concluded that nature can only be analysed by "numerous and regular series of experiments".

Throughout his experiments Hales scrupulously adhered to his own stated method and principles. As far as possible he made all his observations quantitative, and developed for the purpose novel and ingenious procedures, which have been used by generations of plant physiologists since. His experiments were numerous, for he took care to repeat them with different species of plants and different life forms (herbs, trees, climbers); and they were regular, for he planned them logically to answer precise questions, tested each conclusion before going further, included controls at every stage, and recorded in minute detail what he did and what were the results. His consistent use of control experiments and checks on techniques is itself a measure of the great advance made by Hales in the methodology of biological experimentation. His experiments are classical in the proper sense of that much abused word: they set an authoritative standard for conducting and reporting experiments in plant and animal physiology by which all subsequent work had perforce to be judged.

His practical outlook moved Hales to attack those questions that were most exercising scientists at the time: the mechanics of blood circulation and its relation to muscular activity, the nature of respiration and of combustion, the behaviour of elastic fluids (i.e. gases) and their fixation in living bodies, shown by the release of gases from plant and animal tissues by heat or fermentation. These were the key problems of animal physiology and of chemistry, and were already in Hales's mind when the "bleeding" from a cut vine stem in his own garden started him, almost by accident, on a sustained investigation of parallel phenomena in plants. This research occupied him for nearly nine years and was concerned with three groups of problems. The most extensive series of experiments centred on the movement and possible circulation of "sap" in plants, on which Ray and Willughby had made preliminary and inconclusive observations fifty years earlier.

A summary of Hales's principal results is enough to show how completely he transformed the state of knowledge of the water economy of plants by critical quantitative experiments. In the first place he established the constant uptake of water by plants and its loss by transpiration ("perspiration"), as a fundamental physiological process, not by qualitative observations of wilting, but by actual measurement of water loss by weighing, and of water uptake by the movement of water in a siphon tube, using a variety of plants, including sunflower, cabbage, mint, vine, apple and lemon.[35] He determined rates of water movement through plants continuously over definite periods of time and in various conditions of the environment. He showed that transpiration occurs almost entirely through the leaves by comparing leafy and defoliated shoots, and by expressing the rate of water loss on the basis of unit leaf area, was able to make meaningful comparison of transpiration rates between different species. In this way he established that transpiration in twelve species of evergreens was lower than in non-evergreens. He showed that transpiration depends on temperature, being "activated by warmth" and reduced by cold; and that it is repressed during the hours of darknes, by rain, and by immersing the leaves in water. He collected some of the water transpired from leaves by allowing it to condense on glass and showed that its specific gravity was equal to that of pure water: it was perfectly clear, but if kept, stank sooner than pure water. He showed that there is a reserve of water in the soil, and calculated that a sunflower plant could survive for twenty-one days, without watering, in four cubic feet of soil. He further made calculations from his measurements of transpiration and soil water, which proved that the annual rainfall at Teddington is sufficient for all the needs of vegetation.

Undoubtedly Hales's most brilliant theoretical achievement was to point out and clearly distinguish between three factors of water movement in plants—which he designated "imbibition", "root pressure" and "leaf suction"—and to make quantitative measurements of root suction, root pressure and leaf suction by means of a mercury manometer. The values he obtained, from one-quarter to half an atmosphere, are now known to be low but are remarkably good in view of the extreme experimental difficulties of such direct measurements: the important and amazing fact is that such measurements were undertaken at all. He observed that root pressure is seasonal and not always detectable, and concluded from this and other evidence, that in raising water (sap) through a plant or a tree the "imbibing power" of the leaves is the main force, "not pulsion nor trusion"—a very accurate and penetrating conclusion.

By a series of experiments with shoots, which involved ringing, incision, inter-grafting, inverting, etc., Hales demonstrated that the main flow of sap is upwards in the wood, but that the flow can also move sideways round an incision and can sometimes be reversed in individual branches. He also found some evidence suggesting to him that there is a movement of sap in the bark, but he concludes a fairly lengthy discussion by saying that there is no sufficient ground to assume the existence of a true circulation in plants. By this work Hales did another great service to plant physiology by effectively putting an end to attempts to find in plants a type of circulation analogous to that of the blood in animals.

So Hales revealed the basic facts in one important area of plant physiology, and at the same time gave a very practical demonstration of a powerful experimental method, a general technique for investigating all aspects of the functioning of living organisms, which had scarcely yet been applied to plants. The demonstration was all the more impressive because Hales did not philosophize about the limits of experimental investigation, but simply went ahead on the assumption that the known laws of matter operated in the bodies of plants and animals, and could be explored by the same methods that proved rewarding in non-living systems. Furthermore Hales combined this practical method of proceeding with a simple piety which regarded scientific discovery as a revelation of the wisdom and beauty of divine creation.

The connection between the growth of plants and the passage of water through them caused Hales to look more closely at growth, and to him this meant seeing how it could be measured. He recognized that increase in weight or mass is the essential basis of growth and that it is accompanied by varying degrees of extension in length, area and volume of the different organs. He devised the method of recording growth of a plant by drawing equidistant marks or equal areas on the surface, so that rate and degree of extension could be measured by the relative displacement of the marks. Change in area of leaves he measured by tracing their outline at intervals on square-ruled paper and counting the squares.[36] These almost absurdly simple techniques were quite novel in botany, and they opened a period when vague notions of plant growth began to be replaced, however slowly, by scientific analysis based on quantitative data.

Besides studying water relations and growth, Hales made some investigations which may be considered an early approach towards biochemistry. The experiments on plants were, for Hales, only part of a comprehensive

> attempt to analyse air by a great variety of chymio-statical experiments, which show in how great a proportion air is wrought into the composition of animal, vegetable and mineral substances, and how it readily resumes its former elastic state when in dissolution of those substances it is disengaged from them.

This was a bold programme and in its declared aim was doomed to failure, no less by the existing state of chemistry, than by Hales's exclusively physical approach, which led him to neglect the qualitative properties of the different kinds of elastic fluid ("air", gas) which he encountered, and which he therefore failed to distinguish. It was Priestley's careful attention to the specific differences between the different kinds of "air", which, forty years later, began the break-through towards true chemical discrimination. Unlike the experiments on water movement in plants, the "chymio-statical" experiments could only amass a rather chaotic set of observations which neither Hales nor later students of his work could interpret: nevertheless they were not without effect on the course of science. Halcs's observations aroused great interest among chemists and stimulated further researches (by Priestley, for example), whilst his technical methods for handling and isolating gases, in particular the use of the pneumatic trough,[37] were widely adopted and played a significant part in developing the new chemistry. Lavoisier studied Hales's work attentively and was led by his observations to the important conclusion that effervescence in fermentation and certain chemical reactions was caused by the release of "fixed air" (carbon dioxide).

Only the experiments involving plants need be briefly mentioned. Hales was impressed by Malpighi's opinion that the tracheae (vessels) in plants transmit air, although rather strangely he makes no mention of Grew's discovery of stomata. He found that air could be drawn through all parts of a plant by an air-pump, indicating that it could enter roots, stems and leaves. Earlier he had noticed bubbles in the sap exuding from cut ends of vine shoots and thought that this air must have entered the plant through the roots. From such observations Hales concluded that there must be a circulation of air throughout the plant.

In chemical experiments he showed repeatedly that all parts of a plant when heated to high temperature give off "fixed air", in which a sparrow died instantly.[38] That large amounts of elastic air are fixed in a non-elastic state in the plant (and animal) body, profoundly impressed Hales and led him to suspect that plants were "probably drawing through their leaves some part of their nourishment from the air". Since at that time water, with the "saline" that might be dissolved in it, and "air", were the only substances known to enter plants, Hales's suggestion was a reasonable and far-seeing inference from known facts. The inclusion of "air" as a plant nutrient was quite a new idea, which sprang directly from recent advances in physics and chemistry, specifically, from the acceptance of "air" as a material substance with weight or mass like any other, and from the fact that "air" could be liberated from plant substance by heat and other treatments, as first shown by Boyle and subsequently by Hales.

Immediately after putting forward the view that "air" provides part of the food of plants, Hales cautiously speculates on the part played by light: "May not light also, by freely entering the expanded surfaces of leaves, contribute to the ennobling of the principles of vegetables?" In support he quotes Newton: "Are not gross bodies and light convertible into one another? and may not bodies receive much of their activity from the particles of light, which enter their composition?" In making his extraordinary surmise, I think that Hales was probably also influenced by his knowledge of plants' complete dependence on light which his long experimenting and growing plants in his own garden had taught him. However vague, this was the first hint of the nature of photosynthetic nutrition, founded on Hales's synthesis of his own unrivalled experience. The suggestion alerted later workers to the possibility of associated effects of light and air on plants, and helped to prepare the way for the discovery of photosynthesis.

Within a year of the publication of *Vegetable Staticks* Boerhaave was including an account of Hales's researches in his lectures and recommending the book to his students,[39] and by 1770 it was circulating throughout Europe in Dutch, French, German and Italian editions containing his experiments on animals as well. In the long run *Vegetable Staticks* had a profound effect in establishing exact quantitative methods and systematic experimental procedure in plant physiology, and in combining the techniques of physics and chemistry with others specifically adapted to living organisms. Conditions were not ripe, however, for the appearance of bands of eager followers and Hales's work remained for some time as a splendid but isolated achievement.

In all the more advanced countries of Europe there was, during the period we are considering, a certain expansion of agriculture connected with the growth of industry and towns. In consequence, academies of science and private individuals began to take the first hesitant steps towards a science of agriculture. Most of their efforts, like those of the Royal Society two generations earlier, were still at the level of technical improvements in cultivation, rotations, manuring, and the like, but sometimes more fundamental questions were broached. In 1738 the Royal Academy of Bordeaux offered a prize for an essay on the cause of differences in fertility between different soils. The offer stimulated Dr J. A. Külbel, a physician who had been a pupil of G. E. Stahl, founder of the theory of phlogiston, to a piece of research work which must qualify as one of the earliest serious contributions to soil science but which also had some importance in the development of ideas about plant nutrition, and therefore in the development of botany. This work was published at Dresden in 1740 in Latin, and at Bordeaux a year later in French.[40] Külbel started from the common observation that rain, sun and air do not fully account for fertility: there is also a certain quality of the soil. Furthermore a plant has only exceedingly fine pores in the root and can only take up from the soil "earthy parts" which are in solution in a sufficient volume of water. He therefore made repeated boiling-water extracts of soil, which were filtered and then combined. If the extraction was repeated several times there finally remained a sandy residue from which nothing further could be extracted.

The soil extract was brownish in colour and when evaporated to dryness left, in addition to "neutral salt", a brownish residue consisting of a "fatty and subtle earth" (*terra unguinosa subtilis*), for which the term humus came to be used by later writers (although not by Külbel). He therefore thought that plant nutriment consists of one part salt with about five or six parts of the unctuous earth. The most significant finding, however, was that the amount of humus was greater, and its brown colour more intense, the more fertile the soil, clearly indicating to Külbel its importance as a plant nutrient.

Külbel relates his experiments to common farming practice in which humus (I use the word that became accepted) can be replaced in sterile soil by adding farmyard manure, mud from the bottom of lakes and ponds, ashes, chalk, and other similar materials. Of these, farmyard manure is certainly the best, for it yields a brown liquid impregnated with humus and saline parts. Mud is also extremely efficaceous in improving the fertility of soils, but chalk and ashes mainly add salt, not humus. Roots of stubble or of weeds during fallow also replenish the humus (oily fertile earth).

Finally Külbel points out that van Helmont's famous experiment can be differently interpreted. Water is not the sole plant nutrient, for it always contains (as evaporation shows) minute amounts of light subtle earth, which can nevertheless supply enough nutrients, because very large quantities of water are absorbed and evaporated by the plant.

This work of Külbel was actually a considerable advance in the conception of plant nutrition via the roots, although the inclusion of humus as a nutrient, reasonable enough on the experimental evidence available, was destined to be a source of confusion and acute controversy for a very long time indeed. The nutritional importance of humus became widely accepted, no doubt because the weight of evidence from manurial practice seemed so convincing. In *Philosophia Botanica* Linnaeus states that "subtle humus is the primary food of plants, as Külbel observed, hence most plants like humus, a fact confirmed by the experience of horticulturalists". In addition to humus, Linnaeus names water and air as plant nutrients, giving Hales as the authority.

The extension of botany into more diverse fields, however important for the future, was in the first half of the eighteenth century still only a minor adjunct to the floristic studies which fully occupied most botanists. The number of known species grew continually as the European flora was more thoroughly explored, whilst plants poured in from the rest of the world as the fruits of trade, exploration and colonization.[41] The stove or heated greenhouses, which began to be commonly used after 1700[42] now made it possible to study many exotic plants as living specimens, with all the attendant advantages. The vast additions to the world flora raised more sharply the problems of nomenclature and classification which had already been given fundamental consideration by Ray.

Theoretical and practical questions were curiously interwoven. Nomenclature had been much advanced by Tournefort when he defined and named nearly 700 genera at the very beginning of the century.[43] He was a splendid systematic botanist whose combination of accurate observation and keen intuition led him to form many good "natural" genera, even though he used only a small number of floral characteristics for their formal definition. The practical merits of his system were so clear that his generic names and circumscriptions were soon widely adopted, since they offered stability in the inevitable confusion when many botanists were naming new plants, with no universally accepted system of nomenclature to guide or restrain them.

The naming of species was an even more troublesome problem. As botanists strove for more detailed and accurate descriptions in order to separate species within a genus, the specific diagnostic features were summarized in a phrase or sentence, which then served as the specific name. This was a reversal of the trend towards binary names that had been evident during the seventeenth century. It was a result of increased botanical knowledge and more perceptive diagnosis, and to this extent was an important advance, but the practical consequence was that specific names became more unwieldy and inconvenient as they became more informative and diagnostic. The involved specific epithets were particularly unhandy when synonymy was looked for between species described by different botanists. These difficulties hindered progress and caused increasing disquiet among botanists, although few appreciated that they arose from more fundamental and still unresolved problems concerning the determination of taxonomic relationship.

This last question also lay at the root of classification, and we saw how thoroughly it had been analysed by Cesalpino and by Ray, and how far they had advanced towards the conception of a natural classification founded primarily on affinity of the floral parts, without, however, excluding other characters from consideration when determining relationship. In his *Methodus Plantarum Emendata et Aucta*, published in 1703, Ray had bequeathed to the new century what was at least the attempted prototype of a natural classification (although he did not use the term), conformable to his own principles for establishing natural affinity by using many diagnostic characters or differentiae, principles he had enunciated most fully in the *Dissertatio* of 1694.

Early in the eighteenth century, under the influence of Locke's criticism of essentialist classification,[44] biologists began to apply the term natural rather broadly to various methods of classification which all had in common the principle of using a relatively large number of morphological characters and character-complexes to determine relationship. Experience confirmed that this method of classification tended to unite together species which intuitively appeared to be fundamentally related, whilst their affinity was proved, or at least strengthened, by the observation that such groups of species had more characters in common than those actually used to form them: in essence, this was an experimental test. Precisely which characteristics, and how many, should be utilized in building a natural classification were questions that remained to be clarified.

Meanwhile there were may botanists less impressed by argument about the most natural classification than by the need for some convenient way of ordering their masses of herbarium specimens. They sought the solution in artificial systems of classification, simpler and less demanding than Ray's, because based on the minimum number of easily observed characters that would divide plants into distinct groups of reasonable size. These two approaches to classification developed side by side during the period under review. Ray's *Methodus Emendata* (1704) aiming at a natural system, and the artificial system of Tournefort, expounded in his *Institutiones rei Herbariae* (1700), were the leading examples of the two systems. Tournefort divided flowering plants into twenty-two classes based primarily on the general form of the corolla, with subclasses depending on the superior or inferior position of the ovary. Other floral parts played a subordinate role, and Ray's fundamental division into mono- and dicotyledons was passed over. Tournefort's system became popular and was widely used, especially in France where it held the dominant position for over half a century. The reasons for its strong appeal were its simplicity and ease in use, the undoubted excellence of Tournefort's flora and illustrations, and above all the fact that Tournefort settled in practice the circumscription and names of so many plant genera. The conception of genus and species was now established in main outline, although Linnaeus was to make important clarifications in practice. From this time forward classification of plants acquired a new dimension, in which the wider grouping of the basic units (genera) into families, orders, classes and divisions, assumed increasing significance.[45]

Other artificial systems of classification were put forward, almost simultaneously with that of Tournefort, by Hermann in Holland and by Bachmann (Rivinus) in Germany. The former used mainly characteristics of the fruit as a basis for his system, whilst Rivinus classified by the form and number of the petals in combination with three types of fruit. These authors were followed by many others, each producing his own ephemeral system,[46] but Tournefort's won the widest following and acclaim before it was finally eclipsed by Linnaeus's Sexual System. As pointed out earlier, Ray's theoretical defence of the natural system in his last works was, in part, a reply to the artificial systems of Tournefort, Hermann and Rivinus, which Ray considered to be fundamentally fallacious.

The position of Boerhaave in relation to these basic theoretical questions of the time shows a scientific acumen and balance which do much to explain his far-reaching influence. We saw how his understanding of the significance of Camerarius's discovery had sharpened his view of floral morphology and its importance for classification. In this connection it was Linnaeus, never one to give unmerited praise, who said that Boerhaave was the first botanist to use all parts of both flower and fruit in the delimitation of genera.

Although Boerhaave wrote little and briefly, there are sufficient indications scattered in his works to show his advanced thought on current problems, especially in relation to the basis of natural affinity. In a reference to different systems of plant classification he shows his belief in the superiority of a natural system by emphasizing that Ray's method is the best, because, although more difficult, it gives a deeper knowledge of plants: he draws attention to the great importance of Ray's division of flowering plants into monocotyledons and dicotyledons, and recommends Ray's use, not only of the parts of the flower and fruit, but also of "any parts whatever which show vital, manifest, stable and strong affinity". He makes the suggestion, very far ahead of his time, that both anatomical structure and physiological function could be used for purposes of classification. These statements show how fully Boerhaave had grasped the concept of multi-relational affinity as the basis of natural classification. His own method of classification combined features from both Ray and Tournefort, retaining the more natural divisions of both, and rejecting Ray's separation of trees and herbs. Boerhaave's botanical lectures, as far as we possess them, confirm his deep knowledge of contemporary theoretical developments in botany and the extent of his personal contribution to them.

The first phase of the great floristic exploration of the world found its culminating botanical expression in the work of Linnaeus, who was deeply and consciously motivated by the practical and theoretical problems connected with the new knowledge. By the sheer magnitude of his achievement, by its timeliness, assurance and influence, even by its limitations, Linnaeus played a most important part in the development of botany, and it is therefore appropriate to consider the man and his work in some detail.

Carl Linnaeus,[47] son of a pastor of the Lutheran church, was born and grew up in a backward, rural province of Sweden, a country which had only begun to expand economically in the previous century on account of its iron and copper. A series of wasteful and futile wars, aiming unsuccessfully to make Sweden a great power, led to a temporary decline, but by the time of Linnaeus's boyhood attempts were being made to develop manufacturing industry and expand overseas trade, and in 1731 a Swedish East India Company was formed.

Linnaeus was intended for the church, but he early acquired a passionate interest in botany from his father, who saw to it that pleasure and discipline strengthened each other by insisting that the correct name of every plant must be learnt and remembered. The impression made by his father's teaching never left Linnaeus, and it was reinforced by his own temperamental love of order. At the Gymnasium he studied classics, Hebrew, theology and what passed for Aristotelean philosophy, but he reserved his energy and enthusiasm for botany, and was fortunate in finding sympathy and encouragement from some of his teachers. Dr Johan Rothman, the state provincial doctor, who combined this office with teaching logic and physics at the Gymnasium, had a doubly decisive influence on Linnaeus. When deficiencies in scholarship were held to preclude Linnaeus from a clerical career, it was Rothman who, realizing his ability, persuaded him to embark on the study of medicine. Intellectually Rothman's influence proved even more far-reaching, for he made Linnaeus acquainted with the forefront of contemporary botany by introducing him to Tournefort's classification and to the doctrine of sex in plants, as expounded by Vaillant in his famous lecture eight years earlier. Apparently Linnaeus did not actually read Vaillant until two or three years later, but Rothman's account made a very great impression on him. He accepted the existence of sex in plants without hesitation; he found the idea, by his own account, exciting and fascinating, and was thereby impelled to pay very close attention to the details of floral structure.[48] He examined every flower that he could lay hands on, and claimed to have studied over 7000 species during the next ten years—a survey that must have been invaluable in developing his ideas in classification and his feeling for systematic affinity.

Linnaeus continued these intense botanical studies throughout his medical training at Lund and Uppsala. At Uppsala his outstanding ability was recognized and he was asked to give demonstrations and lectures in botany. These attracted large audiences, but internal rivalries prevented his gaining a permanent appointment.

A botanical expedition to Lapland did much to broaden his scientific outlook and to establish his reputation. Then at the age of twenty-three while still at Uppsala he began work on the manuscript which became the *Fundamenta Botanica* and which dealt with what seemed to him to be the basic problems in systematic botany. At this time he abandoned Tournefort's system of classification because it seemed to him inadequate, and he began to replace it by what later became his "sexual system", founded primarily on the number, form and position of the stamens.

In 1735 Linnaeus made the momentous decision to visit Holland. The excuse was to take his doctorate in medicine there.[49] The real reason was, without doubt, to seek personal contact with Boerhaave and the group of brilliant men who at that time had made Holland the centre of European botany. The story of this wonderful visit has often been told and need not be repeated.[50] Suffice it to say that it determined the success of Linnaeus's career as decisively as he must have hoped. Once they met, Boerhaave recognized the brilliant botanical gifts of the young Swede and with unexampled generosity opened all doors to him. Through Boerhaave he was fixed up with an agreeable job as house-physician and scientific advisor to George Clifford, the wealthy owner of a private botanical garden, and was enabled to meet every botanist in Holland. During his sojourn in Holland he made a brief visit to England, where Boerhaave's introduction secured him a cordial reception by Sir Hans Sloane and other English botanists.[51] But by far the most valuable help Linnaeus received from Boerhaave was in encouraging and facilitating publication of the manuscripts that he had brought with him from Sweden. These included the *Systema Naturae*, the *Fundamenta Botanica*, the *Genera Plantarum*, and others, constituting his theoretical work; and the flora of Lapland, the proof of his talent as a sound original investigator. All these works were published in the three years spent in Holland between 1735 and 1738, and they brought Linnaeus an international reputation. But it was through Boerhaave's sympathetic interest that they were given to the world at the right time and in the right place to make them most effective. This was the old man's last and perhaps most lasting service to botany, and to do Linnaeus justice he did not fail in gratitude to the man whom he spoke of affectionately as his great teacher.

In 1738 Linnaeus left Holland in spite of attractive offers to keep him there. He spent a few weeks in Paris, where he was made welcome by the three brothers de Jussieu, and then returned to Sweden, already famous abroad, although not yet at home. He had to spend three years in medical practice in Stockholm before being appointed in 1741 to one of the chairs of medicine at Uppsala, where he remained for the rest of his life, devoting most of his phenomenal energy to botanical research and teaching, the care of the university garden, and the assembling of his private herbarium.[52]

In this sketch of Linnaeus's life only those aspects and events have been mentioned which had an unmistakable influence on his development and therefore help to throw light on what he himself called his botanical philosophy. One all-important fact should always be kept in mind in judging his work and its influence: Linnaeus was a systematic botanist of genius, whose factual knowledge of plants was unrivalled in his day, and who was also gifted with an intuitive perception of their form and affinities unique in its power and penetration.

Linnaeus's theoretical ideas were most fully expressed in *Philosophia Botanica*, published in 1751 simultaneously in Stockholm and Amsterdam, a book which was repeatedly re-issued and carried his influence throughout Europe. This work will be used as the principal source on which discussion of his thought will be based. It is, however, necessary to emphasize that the *Philosophia* is a re-issue, with supplementary explanations, of *Fundamenta Botanica*, which Linnaeus had begun writing in Uppsala as early as 1730 and had published in 1735 within two months of his arrival in Holland. The *Fundamenta* was cast in the form of aphorisms, numbered from 1 to 365,[53] and these reappear in the *Philosophia*, unchanged in number and, with very few exceptions, essentially unchanged in form and wording, but with extensive additions in smaller print. The other works published by Linnaeus between 1735 and 1738 were (except for *Flora Lapponica*) either elaborations or applications of principles laid down in the *Fundamenta*.[54] The *Philosophia* can therefore be taken as a statement of the mature views of Linnaeus, and was the vehicle by which they were disseminated;[55] it is a matter of great interest that he had already given his doctrines their final shape in the *Fundamenta* and scarcely changed them in substance or even in expression in the remaining forty years of his life.

In spite of its title, the *Philosophia* presents a strangely narrow and one-sided conception of botany, almost archaic compared with the modern spirit of Ray or Grew. The many developments of the previous one-hundred and fifty years are scarcely reflected by Linnaeus. Almost the sole reference to physiology is the jejune summary of the "food of plants" quoted previously, whilst the great advances in anatomy are reduced to the statement that plants consist of three kinds of vessels: those containing and conveying latex, flask-like utriculi which hold sap in their cavities, and tracheae which draw in air. Malpighi and Grew are classified by Linnaeus, along with gardeners and doctors, as amateurs (*botanophili*) who investigate matters concerned with plants which do not properly belong to botanical science! Indeed Linnaeus always considered systematic botany to be the only true science of plants.[56] For him it had the excitement of a youthful enthusiasm added to the sustained attraction, for his intensely practical mind, of being at that time the one branch of botany having immediate or potential economic value. This limitation of outlook was also the source of his peculiar strength. His ingrained passion for logical order and his practical bent made him most keenly aware of the burning problems of contemporary systematics, and these form the central theme of the *Philosophia*, and in one way or another lie at the root of all Linnaeus's work.

It must be observed at the outset that Linnaeus never gave a fully reasoned statement of his theoretical principles, as had been done by Theophrastus, Cesalpino, Jung and Ray; and although he had studied his predecessors closely, and could give a very shrewd account of them, he never tried to explore the connections between his thought and theirs except in a naive and blunderbuss fashion. Instead, he chose to express his views in dogmatic aphorisms, which helped to secure their adoption in practice, but tended to conceal their origin and the assumptions behind them.

According to Linnaeus, botany is based on the double foundation of classification and nomenclature (*dispositio et denominatio*), and the foundation of nomenclature is classification. The method of classification is therefore the primary question, and for Linnaeus this resolves itself into asking, what are the essential characters (*differentiae essentiales, notae characteristicae*), the particular parts or organs of plants, on which classification should be based. He proceeds to give the answer at once without discussion: the classification of plants must be based on the fructification. Earlier authors thought that the fructification was insufficient because only a few of its parts were known to them, but he (Linnaeus) has introduced more than sufficient parts. He defines the fructification as comprising the flower and fruit together, consisting in all of seven parts, four of the flower (calyx, corolla, stamen, pistil) and three of the fruit (pericarpium [ovary], receptacle, seed). Taking all the parts of the fructification according to their number, form proportion and situation, provides many characters for classification.

Now in the first place it is to be noted how closely this point of view is akin to, and indeed derives from, that of Cesalpino, a fact which Linnaeus does not directly state but on the other hand does not conceal, since he lists Cesalpino as the first true systematist and remarks on his use of the characters of fruit, receptacle and seed, whilst in the *Classes Plantarum* he gave a detailed and laudatory account of

Cesalpino's classification.[57] Furthermore Linnaeus manifestly regarded the fructification as an extension, by the addition of new knowledge, of the characters used by Cesalpino, for he speaks of the "discovery" of the fructification by recent authors. As pointed out earlier, Cesalpino's choice of the fruit as the most important character-complex for classification was founded both on empirical observational grounds and also on the not unreasonable, but nevertheless *a priori*, essentialist view that the fruit must be the most important part because of its reproductive function. It is astonishing to find that Linnaeus's reasons for making the fructification the basis of classification are even more essentialist than Cesalpino's. The latter stressed the association of fruit characters with other features (including those of habit) in defining even the higher taxonomic groups, and Ray adopted the same view, whilst rejecting the "essence" of a plant as unknowable except through its characteristics and properties. But for Linnaeus the essence of the plant is in the fructification, because "the fructification is a temporary part dedicated to generation, marking the end of the old plant and the beginning of the new". Other characters than those of the fructification are completely excluded by him from the definition of all taxa except the species.

This essentialist idealist stand is constantly present in Linnaeus's thought, yet it would be incorrect to see it as completely dominant. It was in practice linked with a powerful empiricism founded on keen observation and an amazing knowledge of plants. From the practical side of his nature came his almost instinctive grasp of plant affinities and morphology. Linnaeus was far too good a botanist not to utilize many characters at every taxonomic level, and this gave rise to contradictions between his theory and his results, as well as within his theory. Thus having laid down (*Philosophia*, 164) that the main taxonomic groups (*dispositio primaria*) must be formed from the fructification alone, he remarks (*Philosophia*, 168) that habit needs to be taken into consideration in secret (*occulte*), in order to avoid forming fictitious genera [i.e. taxa]. He then proceeds to define habit as a certain conformity of related and congeneric plants, and analyses the vegetative features of plants at considerable length, supplying a descriptive terminology applying to all parts of the plant body: cotyledons, roots, mode of branching, leaf form, phyllotaxy, vernation and types of inflorescence. Linnaeus adds the significant gloss that habit, both in animals and plants, often provides an intuitive revelation of natural groups.

The contradiction between down-to-earth empiricism and his idealist frame of thought frequently recurs with Linnaeus, but practical sense and botanical insight usually win the day. In the long run his essentialist theory of classification could, and did, have restrictive consequences, but in the day-to-day work of floristics experience amply confirmed the high taxonomic value of the fructification; and Linnaeus's strong emphasis on this character-complex, and the admirable terminology which he adopted to describe the component structures and their relationships and range of form, resulted in great advances in descriptive and taxonomic botany. One effect of the concentration on floral characters was to give the final blow to the age-old separation of trees and herbs that had proved so strangely persistent.

The ascription of supreme taxonomic importance to the fructification was especially relevant to the delimitation of genera, which Linnaeus held to be the foundation of classification. We have already traced the evolution of the concept of the genus as the lowest taxonomic group (taxon) above that of the self-reproducing species. There were clearly good empirical reasons for the important place of genera in classification, quite apart from a basis in common descent which few were yet seriously thinking of, but it is characteristic of Linnaeus that his reason was religious and based on the doctrine of special divine creation. "We count as many species as there were diverse forms created in the beginning", he wrote in the *Philosophia* (157), a view which in this extremely naive form was already old-fashioned among scientists, even though they did not for the most part question divine creation in principle. Linnaeus immediately adds an alternative statement of the same doctrine, repeated verbatim from his *Classes Plantarum* of 1738:

> There are as many species as the Divine Being brought forth diverse forms from the beginning, and these forms have given many more according to the appointed laws of generation, like always producing like. Therefore there are as many species as there are diverse forms, i.e. structure, at the present day.

He then summarizes the modes of reproduction and the generative cycle in plants, and concludes that the occurrence of new species in plants is disproved by the repeated observations of their continuous generation and propagation, and by their cotyledons [by the last rather curious statement Linnaeus seems to be stressing the equivalence of the seed with the animal foetus]. This dual appeal to religious dogma and to the facts of experience is characteristic of the dichotomy in Linnaeus's thought. He was stressing the almost universal abandonment by contemporary biologists of the ancient notion of spontaneous generation, "long exploded by experiments" as he notes (*Philosophia*, 135), and asserting that the constancy of species is proved by observation.

Linnaeus's belief in the constancy of species had indeed been shaken by two observations which he refers to at this point in the *Philosophia*. The first was J. Marchant's discovery of two aberrant forms of *Mercurialis* in 1719, probably the first scientific record of an undoubted mutation in plants (and to which reference will be made again in Chapter 8), and the second was his own finding of peloric forms of *Linaria* in 1744.[58] However, the failure of these forms to reproduce themselves regularly by seed restored his conviction that they could only have the status of varieties, and varieties he always recognized as the product of cultural conditions.

Since Linnaeus held species to be created and constant, he held that genera are also, for genera consist of groups of species which agree in the construction of their fructification. He singles out genera and species as being always the work of nature: they are *natural*, by which he means that they exist in nature and were therefore created by God. Every genus, he says, is natural, and created as such in the beginning; genera and species are confirmed by revelation, discovery and observation (*Philosophia*, 159). The statement is revealing: he claims, with justification, that his genera are based on observation and analysis, and he sets the seal of divine approval on his own method of defining them! It is interesting that when, later in life, influenced by reports of plant hybrids, Linnaeus somewhat modified his views on the constancy of species, he continued firmly to hold that genera were created as such by the Almighty, although subsequently blended by nature to give the species existing at the present time.[59]

The higher taxonomic groupings, which Linnaeus designated as classes and orders, were always regarded by him as the joint product of nature and art, that is, as man-made groupings of the genera and species found in the world. It was to the genus alone that Linnaeus gave divine validation, as a result of his almost passionate perception that stability in the definition and naming of genera was an absolute prerequisite for removing confusion from systematic botany and creating the basis for advance in the future.

The practical application of Linnaeus's concept of the genus was given by him in the *Genera Plantarum* (1735), and it was undoubtedly a very great success. Tournefort, as we saw, had defined some 700, mainly natural, genera. He employed a limited number of floral characteristics to form primary genera, and created from these a number of secondary genera by dividing them according to certain vegetative characters. Linnaeus based himself on the work of Tournefort, to whose merits he paid high tribute, but applied to Tournefort's genera his own method of delimitation and definition according to the characters of the fructification alone. This method, aided as it was by Linnaeus's intuitive or *sub rosa* use of other morphological features, produced a high proportion of natural and well defined genera. Linnaeus could find no reason to reject many of Tournefort's genera, but he could claim with reason to have defined them better, more completely and systematically, and at the same time more concisely.[60] In other cases, however, his use of the fructification as the sole criterion for defining the genus, led him to combine or abolish many of Tournefort's secondary genera in a rather ruthless fashion; and some of these draconian judgements have been since reversed. Nevertheless the soundness of the Linnean generic reform could not be denied, despite some contemporary opposition roused by the self-confident and high-handed way it was carried out. The *Genera Plantarum* quickly became accepted as the basis for the definition of existing and the naming of new genera. It provided the stability which Linnaeus aimed to establish, and was welcomed with something like relief by the majority of botanists.[61]

Although the genus and its correct delimitation came first and foremost in his taxonomic thought, Linnaeus was also intensely interested in the classification of the plant kingdom as a whole. The genera were naturally the building stones of any more embracing classification, since good genera (i.e. those constituted according to Linnean criteria) grouped together related species within them. Linnaeus expounded his ideas on general classification most fully in *Classes Plantarum*, a brilliant survey of all the different systems of classification that had been proposed from Cesalpino onwards. In the prefatory section he begins by stressing the absolute necessity of having some system of classification (*methodus syystematica*), as the only way by which the botanist, faced with the vast multitude of plants, can readily arrive at a particular species and its name. Thus the primary function of classification was for Linnaeus the practical one of making storage and retrieval of information as convenient as possible.

Systems of classification are of two kinds, he says, artificial and natural. The latter preserves natural classes, that is, those containing only such plants as are related among themselves (*affines*), agreeing in appearance and nature. In artificial systems, however, the classes may contain totally diverse plants which only agree in a single character selected by the author of the system. Artificial systems are the easiest [to construct], because the author imposes his rules on the plant, whereas in natural systems he has to investigate with the greatest pains what are the special characters imposed by nature on some plants, but not on others. Artificial systems are only a substitute and cannot fail to give place to the natural system if it is discovered.

In spite of this apparent recognition of the superiority of natural classification, the earliest system proposed by Linnaeus, and the one he stuck to in practice all his life, was an artificial one according to his own definition. He devised his system as early as 1731 to replace Tournefort's, following an extended study of floral structure to which his eyes had been opened by the exciting realization of its function in sexual reproduction. This background explains why Linnaeus called it the "Sexual System", otherwise a not very appropriate designation, as many commentators have pointed out.

The Sexual System was worked out long before Linnaeus came into personal contact with the Dutch botanists, and he used it to classify plants found on his expedition to Lapland in 1732. He took the method to Holland with him as part of the manuscript of the *Systema Naturae*, a work which immediately impressed Boerhaave and Gronovius. The latter financed the publication of the *Systema Naturae* which thus became Linnaeus's first printed work and brought his Sexual System before the botanical community, among whom it won rapid acclaim.[62]

The basis of this system is explained by Linnaeus in the *Philosophia* (68) in these words: "I elaborated the Sexual System according to the number, relative proportions, and position of the stamens, together with the pistils". There are in fact twenty classes based on the stamens, three classes for plants in which stamens and pistils are in separate flowers, while one class (No. 24) contains the Cryptogamia or plants without true flowers (ferns, mosses, algae, fungi). The main classes are subdivided into orders according to the number of pistils. It is odd to find Linnaeus including the fig, *Ficus*, with the Cryptogamia in the first appearance of the System, but in all later editions from 1737 onwards he placed it correctly with the flowering plants in the class Polygamia.

Linnaeus was justly proud of his Sexual System and its undoubted success. For nearly one hundred years it was widely used and proved itself perhaps the best and most successful artificial system ever devised. In basing it on stamens and pistils Linnaeus selected parts easy to observe and which, even in isolation, often yielded complexes of considerable taxonomic value. He was particularly impressed by the fact that several classes of the System turned out to be natural groupings or to contain natural groupings as suborders.[63] The Sexual System proved a useful tool in the organization of floristic knowledge; as a practical measure it filled the gap at a time when the principles of natural classification had still to be settled by argument and experience, while the regularities and exceptions revealed in applying it helped to reveal more natural relationships. The simplicity of the System made it especially popular in the late eighteenth and early nineteenth century[64] with the many amateur botanists whose diligence and enthusiasm contributed much to the advance of floral knowledge.

Given Linnaeus's strong practical bent, it is not surprising that he turned first to working out an effective, although artificial, system of classification. It seems likely that Linnaeus's interest in a natural classification was only seriously aroused after he came into personal contact with Boerhaave, van Royen[65] and other Dutch botanists, among whom the influence of Ray was strong, and who were already discussing the question. In the *Systema* and the *Fundamenta*, which were essentially completed before his journey to Holland and published within a month or two of his arrival, Linnaeus makes little more than passing reference to the natural system, accompanied by the promise that he will give examples later. Not till three years later in *Classes Plantarum* did he give the more principled definition of natural classification, which was quoted above, and followed it by a list of over 700 genera grouped in sixty-five "natural orders".

This list of natural orders, each consisting of a number of genera which he considered to be related, was termed by Linnaeus "fragments of a natural system" (*Methodi naturalis Fragmenta*). The *Fragmenta* represented Linnaeus's practical contribution to the development of a natural classification of plants, and as such had an important influence, of which more will be said later. Linnaeus accepted the desirability of a natural classification; it is and will remain the final aim of botany (*Philosophia*, 206) he says, and in *Genera Plantarum* he notes that it reveals the nature of plants, whilst an artificial system is only useful for identification. He was, however, deeply impressed by the difficulty of attaining a natural system because so many plants were still unknown, but declared that he would strive towards the desired aim throughout his life. Successive editions of the *Fragmenta* show that he took the task seriously, but the actual changes he made seem to have little significance, and the arrangement in the *Philosophia* can stand for all.[66]

It is not necessary to look at the *Fragmenta* in detail. The important point is that Linnaeus's skilled use of the floral characters and his botanical flair in calling other features of form and habit to his aid, resulted in his uniting many genera which are still considered closely related, and so in arriving at a high proportion of natural orders (or sections thereof) whose "naturalness" has stood the test of time.[67] This was an impressive and original achievement and Linnaeus viewed it with evident satisfaction, remarking that any other attempt at founding a natural method must be tested against his natural orders, and only if it preserved them would it be worthy to be called natural. His self-confidence was solidly founded in a profound and detailed knowledge of plants, that allowed him to escape from the limitations of his own theoretical outlook. In practice Linnaeus manifestly made use of multiple affinity to establish natural relationships, as is demonstrated by the natural orders proposed in the *Fragmenta*. Yet his own statements show that he never unreservedly accepted or even fully understood the role of multiple affinity in determining natural relationships, and that his concept of natural classification always contained restrictive and contradictory elements.

The conflict between empiricism and essentialist thinking in Linnaeus is indeed nowhere more sharply expressed than in relation to the concept of natural classification—the central biological question of the

75. FUNGOS (77. 67) DILLENIUS (37) ſecundum Pileolos, MICHELIUS (37) ſecundum fructificationes diſpeſcuit.

DILLENII diviſio ſecundum Pileos, unde

Lamelloſi,
Poroſi,
Echinati.

76. LITHOPHYTA olim relicta *Plutoni*, MARSILIUS *Floræ* imperio ſubjecit, at PEYSONELLUS eadem *Faunæ* Regno reſtituit.

Amæn. acad. 80. ratio *Peyſonelli* 1727. B. *Juſſiæi* 1771.

77. METHODI NATURALIS Fragmenta ſtudioſe inquirenda ſunt.

Primum & ultimum hoc in Botanicis deſideratum eſt.

Natura non facit ſaltus.

Plantæ omnes utrinque affinitatem monſtrant, uti Territorium in Mappa geographica.

Fragmenta, quæ ego propoſui, hæc ſunt:

1. PIPERITÆ.
Arum
Dracontium
Calla
Acorus
Saururus
Pothos
Piper
Phytolacca.

2. PALMÆ.
Corypha
Boraſſus
Cocus
Chamærops
Phœnix
Cycas

3. SCITAMINA.
Muſa
Thalia
Alpinia
Coſtus
Canna
Maranta
Amomum
Curcuma
Kæmpferia.

4. ORCHIDEÆ.
Orchis
Satyrium
Serapias
Herminium
Neottia
Ophrys
Cypripedium
Epidendrum
Limodorum
Arethuſa.

5. ENSATÆ.
Iris
Gladiolus
Antholyza
Ixia

Siſyrin-

Figure 17 Page from Linnaeus's *Philosophia Botanica* (1751) where he introduces his Fragments of a natural method (of classifications). From a reprint published in Vienna in 1780.

eighteenth century—because its solution was the stimulus and to some extent the pre-condition for the emergence (or re-emergence) of the concept of organic evolution.

The limitations imposed by Linnaeus's theoretical views are not immediately obvious to a reader of the *Philosophia* or *Classes Plantarum*: they are obscured by the terse aphoristic style and by the repeated references to the natural classification as the prime desideratum in botany. In his oft-quoted statement, "all plants show many-sided affinity, like territories on a geographical map", Linnaeus even appeared to recognize multi-relational affinity. Yet many other statements, some of which I have already quoted, show without any doubt that Linnaeus in fact refers only to many-sided affinity of the fructification and its parts. For him the fructification was the essence of the plant, its essential character, and therefore only characters of the fructification are primary and properly to be used in classification above the level of species. Hence natural classification is based on multiple affinities of the fructification, a conception far removed from that of relationship determined by multiple affinity based on many characters, advocated by Ray and by those who accepted his views. The practical result may not have been much affected, because of the high taxonomic value of the fructification and the concealed use of other characters, but in principle the Linnean view obstructed the approach to a natural system in a number of ways.

By restricting the number of characters that could be used, and at the same time diverting attention from others, classification at all levels becomes more arbitrary; and the bringing of non-flowering and crytogamic plants into natural classification is made especially difficult. Even among flowering plants exclusive emphasis on the fructification restricted classification to the putting of genera in orders or families, neglecting fundamental divisions at higher levels. This weakness is exemplified in the *Fragmenta*, where Linnaeus deliberately did not try to arrange the orders in classes, because, he says, this will be easy when all existing orders have been established.[68] He does not even use Ray's great division into monocotyledons and dicotyledons, although he was, of course, well aware of its significance, and with one exception his orders are consistent with it.[69]

The arrangement of the principal orders in the Sexual System and in the *Fragmenta* shows one curiously revealing feature. In both the admittedly artificial system and his attempted natural system Linnaeus placed the lower (non-flowering) plants last, deliberately rejecting what he calls the "mathematical method" of Ray, Boerhaave and others [he might have added Cesalpino], who start from the simplest and ascend to the more complex (*a simplicibus ad composita*). Natural instinct teaches us, says Linnaeus, to know first those things nearest to us, and the smallest things last; to proceed, for example, from man through quadrupeds, birds, fishes, insects, to mites, or from the higher plants to the smallest mosses (*Philosophia*, 153). This statement looks back to a mediaeval conception of the world which was logically incompatible with any idea of evolutionary advance from lower to higher forms of life.[70] The ascending order on the other hand, which Linnaeus characteristically rejected, while not, of course, an example of evolutionary thinking on the part of either Ray or Boerhaave, at least made possible the conception of a world that changed and progressed with time, instead of blocking such a view in principle.

There is no doubt that by his generic reform and by the preliminary grouping of genera into natural orders in the *Fragmenta*, Linnaeus made a fundamental practical advance towards a natural classification of plants; unfortunately his theoretical ideas were a very real obstacle to its further development.

Of the two foundations of botany according to Linnaeus the second, after classification, was nomenclature. In almost the words of Locke he says that without names there can be no permanent knowledge: where there is a single genus, there must be a single name. Acutely aware of the confused state of contemporary botanical nomenclature, which Dillenius in 1737 likened to an Augean stable, Linnaeus had already begun the task of putting it to rights in the *Fundamenta* and *Critica Botanica*. He realized that clarity and stability of nomenclature could only begin when classification—by which he meant the delimitation and diagnosis of genera as the essential basic units—had been firmly settled. This Linnaeus effectively did by his generic reform, creating well-defined stable genera to which stable names could be applied. For the formation of generic names he laid down precise rules which we need not go into.[71] He has often been criticized, in his own day and since, for his arbitrary dogmatism and cavalier treatment of names coined by other botanists. Yet there was much practical common sense in his forceful creation of a set of rules for naming genera;

some of the rules are still accepted today though others have been relaxed or abandoned. Something needed to be done to cut through the confusion, and Linnaeus did it with a determination that soon won general adherence. The principle that there should be some uniform and generally agreed system of creating new generic names was important for taxonomy, and it was Linnaeus who established it.

The great innovation, for which Linnaeus will always be remembered and acclaimed, was his adoption and popularization of the binomial (or binary) system of designation of species. It is interesting to see how this idea arose in practice from his attempts to make more accurate and memorable diagnoses of individual species. The method of plant nomenclature commonly used in the seventeenth century has been already described, but may be briefly recapitulated. The first known or best known species of a genus was often called by a single name, roughly equivalent to the name of the genus without qualification: other species were then called by the genus name, followed by an adjective or qualifying phrase to distinguish them. Linnaeus at first used this method as he found it, but sought to make the qualifying name always genuinely diagnostic, that is, expressive of those specific features which distinguish one species from every other in the genus (hence he called this the "specific" name, *nomen specificum*).[72] Unfortunately the attempt to make the *nomen specificum* absolutely precise led to two difficulties. First, the specific epithet tended to become longer and longer, developing into a chain of qualifying phrases, in which form it could not be remembered or indexed. Secondly, as new species were discovered it often became necessary to change the *nomen specificum* in order to keep it specific, and this destroyed all the stability of nomenclature which Linnaeus (and botanists in general) regarded as the prime desideratum. Linnaeus solved the problem by a simple but brilliant inspiration—he gave each species a trivial name (*nomen triviale*) consisting of one single word, normally a Latin adjective, but any other single word would do, since the function of the trivial name was only to identify unequivocally a particular species, not to describe it (as the forename Carl identifies a particular Linnaeus but does not describe him).

To Linnaeus the trivial name was simply a handy reference to the specific name which truly defined the species, but the device proved so convenient that binary nomenclature (generic name plus trivial name) was soon universally adopted for both plants and animals and has been used ever since; the specific name (phrase), to which Linnaeus attached so much importance, was absorbed in the descriptive diagnosis. So complete was the victory of the trivial name that today it is universally referred to as the *specific* name of the species, a change of usage which Linnaeus would not have understood or approved. Although Linnaeus had begun to use trivial names earlier, it was the appearance in 1753 of his *Species Plantarum*, in which every species was given a trivial name, that led to the general adoption of binary nomenclature and made its use practically universal by the time of Linnaeus's death in 1778.

Linnean nomenclature gave taxonomy a tool of inestimable and lasting value, but its overwhelming success did not result merely from its convenience, practical sense and stability, important as these qualities were. Its real strength came from Linnaeus's taxonomic genius, which provided a firm foundation of many systematically described and, for the most part, natural genera, and of thousands of species linked to specimens in Linnaeus's own herbarium.

The descriptive terminology of the *Philosophia* was in itself an important contribution to the advance of botany. Here Linnaeus owed an acknowledged debt to Jung, whose method of defining descriptive terms by dual reference to the morphological interrelations of organs and parts, and to specific examples, he adopted. Linnaeus established many terms in their modern usage and increased the technical vocabulary to cover many more structures and properties. He created methodical terminology, both precise and flexible, for the scientific description of flowering plants. Later it acquired additional significance as a model for developing a terminology applicable to other groups of plants and to other levels of morphology, microscopic, cellular and, ultimately, subcellular.

Whatever his limitations, it is impossible to disagree with the opinion of his contemporaries that Linnaeus was the master of the botany of his time, and that his influence on the development of botanical science was powerful and lasting. In a period when for both economic and scientific reasons systematics was the dominant area of botany, he created the technical means for its rapid expansion, while his personal contribution to floristic knowledge, and to the recognition of natural taxa, greatly advanced its progress, and that of those other areas of botany on which systematics necessarily impinges. His work demonstrated the success of his improved methods of description, diagnosis and nomenclature, and made detailed systematic observation the guide and criterion in taxonomy.[73]

In all these fundamentally practical aspects, exemplifying the empirical–mechanistic trend in eighteenth century science, the work of Linnaeus is creatively linked with the next phase of botanical progress. In his theoretical ideas, on the contrary, Linnaeus was a man of the past who never escaped from the restricting circle of idealist–essentialist thought in which his early high-school training had confined him. This was the background to the contradictory statements in the *Philosophia,* to his narrow view of botany, his blindness to the advances in plant physiology and anatomy, his unquestioning acceptance of special creation. Linnaeus had little understanding of experiment: when he mentions Camerarius's experimental evidence for sex in plants, he appears to attach equal or superior importance to the fact that the anther is the "essence" of the flower.[74] In taxonomy his practical sense led him to discover natural taxa despite his own firmly held theory. He quotes without comment such ancient notions as that the earth is the belly of plants, and from Cesalpino's theory of the medulla develops a more complete theory of his own with much less logical justification.[75] Unlike many of his contemporaries Linnaeus seems to have been scarcely troubled by the existence of fossils or the growing evidence for a vast extension of geological time; he was, it seems, quite unaware of the new perspectives opening in science.

In relation to botanical theory Linnaeus stands at the end of an epoch. For this reason, the publication of the *Species Plantarum* in 1753 is an appropriate formal ending to the developments chronicled in this chapter. In this profoundly influential work the practical achievements of Linnaeus were incorporated, and with it modern systematic botany begins. Yet at the time of its appearance new ideas were already arising in biology that were quite incompatible with the static "system of nature" which had satisfied Linnaeus.

Notes

1. But Linnaeus characteristically only quoted part of Boerhaave's definition of botany. The latter also included the statement that "botany is the branch of natural history which teaches the structure, properties and use of plants"; and he taught plant physiology in his lectures. See the 1727 (Rome) edition of Boerhaave's *Historia Plantarum quae in Horto Academico Lugduni-Batavoram crescunt*, from which Linnaeus was quoting.
2. An exception was Russia where science started late because of the delay in establishing a national state owing to wars and invasions. There was an expansion of science following the foundation of the St Petersburg Academy by Peter the Great in 1725, which brought together a number of brilliant scientists, including Lomonosov, Bolotov and others, but they were hampered by disturbed political conditions and a backward economy.
3. Thus progress in classification, comparative morphology, and plant life-cycles was very much dependent on more accurate knowledge of the complete range of form among existing plants.
4. Naturally official backing was often miserly, but at least botany was viewed as a possible source of public or private profit. There was therefore some national support forthcoming in many countries for botanical expeditions, museums, gardens, and professorships.
5. See the *Essay* Book IV, Chapter XV. The importance of probability in biology was recognized by Theophrastus (Simplicius: *Physics* 325,24).
6. Locke's dried herbarium is preserved at Oxford. He visited the botanic gardens at Leiden and Montpellier and was friendly with Pierre Magnol.
7. Scientific nomenclature, not only in biology but in general, owes much to Locke's Doctrine of Signs, the use of "words as the great instruments of knowledge". The stipulative definition of technical terms was particularly important in the progress of botany and zoology.
8. Locke's own term for logic-chopping.
9. *Essay* Book II, Chapter XXVII, para. 4.
10. Like Ray, Locke suggests a physical cause for the movements of the Sensitive Plant (*Mimosa*), but his theory is less plausible than Ray's.
11. H. Boerhaave (1668–1738) was especially notable for his attempt to apply to human physiology the principles of physics and chemistry as then known. His own text book on the *Elements of Chemistry* was translated into French and English, and was for long the standard work on pre-Lavoisier chemistry.
12. According to his own account, Boerhaave had botanized in the polders and dunes as a student, using as a guide the local flora of Paul Hermann, then Professor of Botany at Leiden, but had not bothered to attend Hermann's lectures.

13. "Thus generation by male and female is a law common to animals and plants." From Boerhaave's preface to Marsigli's *Physique de la Mer*. In the same preface credit is given to Malpighi, Grew, Leeuwenhoek, Morland, Robart [Bobart?] and Vaillant, for "assigning to the respective parts of the flower their particular office in the generation of plants". This is a rather odd collection of names: Camerarius is not mentioned, whilst Malpighi thought stamens were organs of secretion.
14. Cryptogamia (cryptogams, or plants with "hidden marriages") was the name given by Linnaeus in his *Systema Naturae* to most nonflowering plants, such as ferns, mosses, algae, fungi, etc. in which "the nuptials are celebrated in secret", i.e. the sexual process was not then known as it was in the flowering plants and conifers.
15. R. Bradley mentions in 1717 that a Mr Fairchild of Hoxton crossed sweet william and carnation and got intermediate forms in the progeny.
16. Linnaeus, in *Philosophia Botanica* (1751), places the same weight on the structure of the flower as on castration (i.e. experiment), as proof of sexual reproduction in flowering plants.
17. Experience with the cultivation of the dioecious shrub *Carica papaya* (pawpaw), introduced from tropical America, and described by Clusius in 1607, may well have caused renewed attention and thought to be given to the similar and long known case of the date palm, in which fertilization of the female flowers by pollen from the male trees was an ancient technique. This likely suggestion was made by Conrad Zirkle in an article on Nehemiah Grew.
18. The date 1680 is given by Patrick Blair, but G. C. Gorham (1830), in a note to Thomas Martyn's *Memoir of John Martyn FRS*, gives the date as "about 1700" on the authority of W. Sherard. In any case the indication is that experiments were being done by practical men.
19. R. Bradley: *New Improvements of Planting and Gardening both Philosophical and Practical* (1717). Bradley was a good observer and had a real interest in experimental investigation of plants. In his last years he was Professor of Botany at Cambridge, where his activity or alleged inactivity earned him a bad reputation, which may not have been entirely deserved. (See H. Hamshaw Thomas: The rise of natural science in Cambridge. *Cambridge Revue,* 434–6 (1937).)
20. S. Vaillant (1669–1722) came of farming stock and was of lower class than his colleagues and superiors at the Jardin Royale des Herbes Medicales (Jardin du Roi), which perhaps partly explains the evident ill-feeling between him and Antoine de Jussieu, the professor. Vaillant made his way by sheer ability and drive. He appears to have picked up some medical training in hospital at Pontoise, and to have practised surgery in the army and then in Paris. He attended botanical courses under Tournefort and was put in charge of the practical running of the garden, becoming demonstrator of plants. He built the first greenhouse in France, to grow exotics, in 1714, and a second larger one in 1717. His flora of the Paris

region, *Botanicon Parisiense,* was edited after his death by Boerhaave and Sherard.

21. W. Sherard (1659–1728) had studied three years under Tournefort and then at Leiden with Hermann, and was a friend of Boerhaave and J. Bobart. An enthusiastic botanist and a man of some means, he collected plants in Cornwall, Jersey, the Alps, Italy and Greece, and corresponded with most of the botanists of his time, being known for the unselfish help he vouchsafed to all who called on him. In his will he endowed the Sherardian Chair of Botany at Oxford.
22. The theory of preformation (also called evolution in the eighteenth century) denied the epigenetic development of the embryo in animals and plants. The new embryonic organism was assumed to begin as a minute replica of the adult, which increased in size but did not show serial changes or a gradual increase in complexity with time. Aristotle had shown that observation was against such a view, but it was put forward in the seventeenth century by Swammerdam with a certain genuine scientific basis in his observations of larval and pupal development in insects, and again in the eighteenth century by Bonnet, who supported the idea by his discovery of parthenogenesis in aphids. The theory had been proved incorrect by Harvey, and obviously led to such absurd consequences as an infinite series of preformed embryos, one within the other, within the female ovary, but it became popular for a time in the first half of the eighteenth century. Philosophically the theory went back to Platonic idealism and also had some affinity to Leibnitz's monads. It did not evoke much interest among botanists, probably because of Grew's clear account of the epigenetic development of the embryo in fertilized ovules of the almond.
23. Blair was writing in 1720 when a circulation of the sap in plants was still looked for, by analogy with animals. After Hales rejected it in 1727 the idea was generally abandoned. Thus Linnaeus noted as an accepted fact "there is no circulation in plants" (*Philosophia Botanica*, 133 (1751)).
24. For an interesting discussion of this question see P. C. Ritterbush: *Overtures to Biology: the Speculations of Eighteenth Century Naturalists* (1962). In the previous century van Helmont had been led astray by the belief that magnetism affected wound healing.
25. J. T. Needham: *An Account of Some New Microscopical Discoveries*, London (1745). French translations were published in Leiden 1747 and Paris 1750, so the book had wide influence. Bursting pollen grains had been seen and reported by Bernard de Jussieu in 1739.
26. *Philosophia Botanica*, 145: "The pollen ruptures and emits a seminal effluvium which is absorbed by the humour of the stigma."
27. Part III of Morison's work was issued by Jacob Bobart after his death, so it is not certain whether Morison or Bobart did the experiment. Linnaeus (*Philosophia Botanica*, 138) ascribes it to Bobart.
28. Elaters are specialized cells with spiral thickenings on the walls; they per-

form hygroscopic movements and probably assist in dispersing the spores.

29. Antoine de Jussieu: De la nécessité d'établir dans la méthode nouvelle des plantes, une classe particulière pour les Fungus, à laquelle doivent se rapporter . . . les Lichen. *Mémoires de l'Académie Royale des Sciences* 377–83 (1728).
    The reference to the "new method" indicates that de Jussieu has natural classification in mind.
30. See G. C. Ainsworth: *Introduction to the History of Mycology* (1976).
    Micheli brought forward experimental observations to show that fungi actually are reproduced from their "seed", as was generally surmised.
31. J. J. Dillen (Dillenius), born in Germany in 1687, was brought to England by Sherard to assist in a projected revision of the *Pinax*. He was appointed Professor of Botany at Oxford, where he died in 1747.
32. This reflected the preponderance of tenant farmers in England, and the absence of a true peasantry.
33. Woodward's investigations were reported in the *Transactions of the Royal Society*.
34. Hales was lucky to be at Cambridge when Richard Bentley, Master of Trinity, was actively encouraging experimental science in that college, providing laboratory space there for demonstrations in hydrostatics, pneumatics and chemistry, conducted by Roger Cotes, William Whiston and John Francis Vigani. Hales took part in these experiments and acquired the technical training which he used so effectively later.
35. In Hales's experiments he took the precautions which have now become "routine" but which were then not so obvious, such as allowing for water loss from the surface of the pot and the soil. His estimates of transpiration compare well with modern results.
36. He also devised an expansion lever to magnify and demonstrate growth.
37. The collection of gases by displacement of water from an inverted jar in a pneumatic trough, was the vital technique in the progress to modern chemistry. Hales was probably not the sole discoverer but his experiments popularized and made the technique widely known. The use of mercury instead of water was introduced by Cavendish and was the key to the discovery by Priestley of a series of gases soluble in water (HCl, NH_3, H_2S, NO_2, SO_2).
38. Apart from causing death in a sparrow, no other property of "fixed air" was noted by Hales. It was this failure to investigate other properties, physical and chemical, that prevented his making any progress in the analysis of air. Progress began when Joseph Black, and later Priestley and others, started looking at the qualities of the various kinds of air. "Fixed air" became gradually associated with various specific properties which ultimately proved it to be carbon dioxide.
39. Following the appearance of *Vegetable Staticks*, Boerhaave added to his

definition of a plant that it is "corpus hygro-organicum", a hydraulic body.

40. Johann Adam Külbel was physician to the king of Poland at the fortress of Koenigstein. The details given of his experiments convince me that he must have carried them out himself.
41. Although plants came from all over the world, the greatest influx was from North America and South Africa during the period 1680–1770.
42. The earliest use of the glasshouse in Europe was probably 1619 in Heidelberg for growing orange trees. Glasshouses soon appeared in Holland and other countries, one being built in England at Chelsea Apothecaries' Garden in 1684. The first glasshouses had opaque roofs and were heated by hot embers, later by furnaces with flues in the floor or walls, and were principally designed as orangeries. The glass roof was introduced early in the eighteenth century and greatly increased the efficiency and versatility of the glasshouse, the use of which now became widespread.
43. Tournefort's work *Élements de Botanique* was published in French in 1694, and in a fuller Latin version, *Institutiones rei Herbariae*, in 1700, which made it internationally available to all botanists. The *Institutiones* defined 698 genera with illustrations. In it Tournefort introduced the term pistil to signify the ovary and its parts. "Pistillum appello partem eam, quae floris centrum intra stamina occupare solet."
44. Locke makes particular use of biological examples when showing the fallacy of classifying by "essence" instead of "discoverable qualities". See the *Essay* Book III, Chapter III, and elsewhere. Theophrastus made the same point as Locke in his discussion of classification in *Historia Plantarum*.
45. Thus the development of natural classification, based on multiple affinity, became an important impulse to the discovery of new facts and new fundamental relations. It forced attention on both deeper and finer divisions between plants, hitherto unnoticed or unconsidered, which were seen to be significant; from this came investigations of other great divisions of plants besides the flowering plants, the distinction between angiosperms and gymnosperms, knowledge of different reproductive cycles, etc.
46. In *Classes Plantarum* (1738) Linnaeus listed and summarized all the systems for posterity.
47. The secondary literature on Linnaeus is immense and I have therefore tried as far as possible to use his own writings to assess his theoretical ideas.

    The most illuminating modern study is F. A. Stafleu's *Linnaeus and the Linneans* (Utrecht, 1971). No one can be unaffected by this authoritative and penetrating work to which I am deeply indebted.

    I have also gained enlightenment and information from J. L. Larson:

Reason and Experience (1971) and from the works (too numerous to list) of W. T. Stearn.

48. "The singular structure and remarkable office of the stamens and pistil enticed my mind to enquire what Nature had concealed in them. They commended themselves by the function they perform." (Linnaeus).
49. This could be done in a few days at the University of Harderwijk by presenting and defending a dissertation. It should be emphasized that this was a serious examination and could only be taken by suitably pre-qualified aspirants, as Linnaeus was. There is no evidence that the Harderwijk doctorate was inferior—merely that the final degree could be taken there in a very short time after proper study elsewhere.
50. See F. Bryk: *Linnaeus in Ausland*. Stockholm (1919).
51. These included Philip Miller, T. Martyn, J. J. Dillenius, W. Sherard, Peter Collinson.
52. The fate of Linnaeus's herbarium was extraordinary. The full story is told in B. D. Jackson's biography of Linnaeus, and elsewhere. Briefly, it was bought by J. E. Smith from Linnaeus's widow, at the suggestion of Sir Joseph Banks, and brought to England in 1784, finally coming into the custody of the Linnean Society of London in 1828. Regrettable as was the loss to Sweden of this historic collection, its accessibility to systematic botanists was maintained, and it continues to the present day to be of vital service to taxonomy.
53. It is curious to recall that an ancient Chinese herbal and an Anglo-Saxon herbal both had 365 entries.
54. As explained in the text, the 365 aphorisms of *Philosophia Botanica* (1751) correspond closely to the 365 aphorisms of *Fundamenta Botanica* (1736). Of the aphorisms of the *Fundamenta* and *Philosophia*, 1–4 are equivalent to the botanical part of *Systema Naturae* (1735), 5–52 are equivalent to *Bibliotheca Botanica* (1736), 210–324 are equivalent to *Critica Botanica* (1737). Finally, *Classes Plantarum* (1738) is an expansion of *Fundamenta* (and *Philosophia*) 53–77.
55. Thus Goethe wrote, "Linné's *Philosophia Botanica* was my daily study, and so I continually advanced in systematic knowledge, as I tried as far as possible to assimilate what would give me a more general view of this vast kingdom."

    The attraction of the *Philosophia* can still be appreciated today. The succinct, didactic, but by no means colourless style gives the reader the feeling of being presented with the elements of the subject in a singularly perspicuous and complete form.
56. Linnaeus thus defines a botanist (*Philosophia*, 151): All plants are learnt in a year, at first sight, without a teacher, without pictures or descriptions, and are firmly in the memory. He who has learnt how to do this is a botanist, no one else is.
57. "Cesalpino established the first true and solid foundations of botany on the basis of the fructification, and was the first who, with supreme

practical knowledge (*experientia summa*) divided plants into classes according to the elements of the fructification".

"He may be considered the first who, without difficulty, observed many of the natural classes recognized today."

58. Peloric (Greek "monstrous") is a term used to denote the abnormal, radially symmetric flowers which are sometimes produced instead of the normal zygomorphic (bilaterally symmetric) flowers.
59. The theory is stated by Linnaeus in the appendix of the 1764 edition of *Genera Plantarum*. It is illogical and obscure, and offers no explanation of how the blending was supposed to take place. Probably Linnaeus never encountered a genuine, undoubted plant hybrid, and apparently never became acquainted with Koelreuter's production of true plant hybrids 1761–66.
60. Linnaeus was quite clear what was the essential thing he had done. "I examined all these [i.e. the existing] genera according to the rules of the art; I reformed their diagnostic descriptions (*reformavi characteres*) and established them as if new." *Philosophia*, 209.
61. The fifth edition of *Genera Plantarum* (Stockholm, 1754) was revised by Linnaeus in conformity with the *Species Plantarum* of 1753. The latter work was subsequently laid down in the International Code of Botanical Nomenclature (operative today) as the formal starting point of valid plant nomenclature. Thus the principle of Linnaeus's generic reform has been crowned with the approval of posterity.
62. One thing that did a lot to popularize the Sexual System was a beautifully executed set of illustrations of the principal classes, drawn by the young German artist G. D. Ehret, who later became one of the greatest of the great flower painters. His tabella, as Ehret called it, was produced with Linnaeus's help and the title acknowledged its source in the *Systema Naturae*. Ehret sold it at two Dutch gulden a copy and says that almost every botanist in Holland bought one. Perhaps Linnaeus bought one too; he certainly used it—without acknowledgement to Ehret who was plainly rather hurt—to illustrate the System in some issues of *Systema Naturae* and *Genera Plantarum*. Ehret's plate was indeed widely copied and appears in other botanical publications of the period, not by Linnaeus.
63. Of the Sexual System Linnaeus himself said, "I would not call it a natural method, nor any other method either", implying that his System has natural features all the same. The reason for this he considers to be, that "in these [the stamens and pistils], which appear, as it were, of no account, is concealed the essence of the flower itself". The quotations are from *Classes Plantarum*.
64. This great and practical interest in botany was not the hobby of ladies and gentlemen and country parsons only, but roused the enthusiasm of increasing numbers of artisans and working men. The turn to natural history, and botany in particular, was no doubt partly a reflection of the Romantic revulsion against the horrors of industrialization, but for many

it must have been a much more direct form of protest and escape from the grimness of life.

This whole subject deserves more comprehensive historical study. See, for example, D. E. Allen: *The Naturalist in Britain: a Social History* (1976). But the phenomenon occurred in other industrial countries.

65. Adrien van Royen (1704–79) was a pupil of Boerhaave and succeeded him as Professor of Botany and Medicine at Leiden. Van Royen's interest in a natural classification is evident from his *Prodromus Florae Leydensis* (1740). In the introduction he pays high tribute to Cesalpino for determining the affinity of plants, not from leaves, but from flower, seed-vessel and seed, and using the method in practice to distribute all plants into their main classes according to the structure of the fructification; no method, he says, can be more beautifully and easily reduced to a natural system. Van Royen arranged his plants in a natural system of his own, which (like Boerhaave's) owes a great deal to Ray. He divides plants into monocotyledons (containing three classes) and dicotyledons (containing seventeen classes); the twenty classes are mainly natural and the characteristics of each class are defined (this was not done by Ray for his higher taxa).

    Van Royen gives a key to the twenty classes of his system, in the construction of which he was helped by Linnaeus (in 1738).

66. The *Fragmenta* were published in 1738, 1751 and 1764. The number of genera included rises from 746 to 1170 to 1344, showing that Linnaeus added newly discovered genera as time went on. The natural orders in 1738 (sixty-five in all) were numbered but not named, but in 1751 and 1764 each natural order was named (e.g. Piperitae, Palmae, Gramina, Coniferales, Compositi, Umbellatae, Senticosae, Inundatae, Papilionaceae, Filices, Musci, Algae, Fungi, etc.), there being sixty-seven in 1751, reduced to fifty-eight in 1764. About 120 genera were placed in a separate group because Linnaeus could not decide on their natural affinities.

    In the first edition of the *Fragmenta* one order included sponges, madrepores and corals, but this was omitted in the later editions after Bernard de Jussieu had shown in 1741 that these are really animals. The heterosporic ferns *Pilularia* and *Marsilea* are not included in Filices in 1738 nor in 1751, but appear with the ferns in 1764; they had been assigned to the ferns in 1739 by Bernard de Jussieu.

67. Both Ray and Magnol had of course already grouped genera into a certain number of natural orders or families, but Linnaeus was able to define many more families because more genera were known and his taxonomic net was finer.

68. The idea that it is necessary to wait until all plants are known shows how Linnaeus's basic essentialism always prevented him from fully appreciating the meaning of a natural classification founded on multiple affinity. Even Aristotle pointed out that the strength of a classification based on

many characters is that newly found forms can be interpolated without upsetting the whole system.

69. The exception is the placing of *Piper* and *Phytolacca* in a group of monocotyledonous genera. In the case of *Piper* this may be regarded as an example of his keen eye for affinity, since the Piperales have been thought by some botanists to link monocotyledons and dicotyledons. Apart from this, all his groups of flowering plant genera are either monocotyledonous or dicotyledonous. Most of the monocotyledonous orders come together at the beginning of the *Fragmenta*, but one dicotyledonous order is put among them for no obvious reason, and a division into monocotyledons and dicotyledons is neither indicated nor stressed. Yet in *Philosophia*, 114, Linnaeus says that the primary and most natural division of plants is according to the cotyledons.
70. See F. Moed: Carl von Linné und die Konstanz der Arten. *Zeitschrift für Geschichte der Naturwissenschaften, Technik und Medizin* **1**, 1–3 (1966).
71. The rules, which are not without their amusing side, are given in *Philosophia*, 210–50.
72. "The legitimate *nomen specificum* distinguishes a plant from every one of its related species (*ab omnibus congeneribus*)." *Philosophia*, 257.

    The very great importance attached by Linnaeus to the specific name is shown by his claim in *Critica Botanica* (1737) that he has supplied new *nomina specifica* in every case.
73. The concluding words of the *Philosophia Botanica* express the sum of Linnaeus's practical wisdom. "In natural history the principles of truth must be confirmed by observation."
74. One consequence of this curious attitude and of the popularity of his Sexual System, was that for a time Linnaeus acquired a false reputation as having proved the existence of sex in plants. Apart from a few chance confirmatory observations, described by him in his prize essay to the St Petersburg Academy in 1759, Linnaeus did no experiments and his sole contribution was to popularize an idea that was already scientifically established by others.
75. It must be remembered that Cesalpino assumed the medulla to be the seat of the soul or life of the plant on the basis of an analogy with animals. In animals it was the inmost soft tissues (*viscus*) which were the seat of life, because their removal caused death, whereas the outer parts could be injured or removed without necessarily causing death. Since the seed was the reproductive part of the plant, he thought it arose from the medulla, whilst the other parts of the flower came from the outer tissues of the stem. Linnaeus adopted the theory in a more elaborate form, holding that the calyx arises from the outer cortex, and the corolla from the inner cortex or bast; both stamens and pistil arise from the innermost, medullary tissues. In other statements of the theory, however, he makes the stamens arise from the wood and the pistil alone from the medulla (see *Philosophia Botanica*, 86, 88, 79).

Cesalpino was quite aware that, in many mature plants, the medulla broke down, or could be removed, without injury to the plant. He assumed that either enough was left clinging to the inner part of the cortex or wood to maintain vitality, or alternatively that it was enough that medulla was always present in young stems. He discusses the relation between grafting and the position of the medulla in stock and scion, but his views are, of course, only hypothetical and I am not sure that I can follow them completely.

8

Enlightenment and Revolution in Botany (1753 to 1809)

If the universe bears a greater likeness to animal bodies and to vegetables, than to the works of human art, it is more probable that its cause resembles the cause of the former than that of the latter, and its origin ought rather to be ascribed to generation or vegetation than to reason or design.

David Hume: *Dialogues Concerning Natural Religion* (1751, printed 1779)

Nature, by his [the Creator's] prescribed laws, changes, destroys, unfolds, renews, creates.

Georges Leclerq, Comte de Buffon: *Sur la Nature* (1753)

During the seventeenth century the greatest theoretical advances in science had been in astronomy and physics. In biology very important additions to existing knowledge were made but caused no fundamental change in outlook. Harvey's proof of the circulation of the blood, and Borelli's researches into animal movement, extended the sway of physical laws into the realm of animal and vegetable physiology; Camerarius's experimental demonstration of sex in plants solved one of the oldest problems of biology, and was at the same time a demonstration of the essential unity of behaviour of plants and animals; but the effect of these vital advances was rather to strengthen principles that were already widely accepted, than to destroy the static picture of the living world presented by philosophy and religion. The real break with the past in biology was not sudden, but it began unmistakably during the eigthteenth century with the dawning recognition of the possibility, and then of the probability, that living organisms had not reproduced themselves unchanged since some moment of divine creation, but had undergone a development in time, in which simpler organisms gave rise to more complex ones, fitted for many habitats and ways of life.

It is convenient to use the term evolution for this new biological concept, even though the word was only given its modern sense by Charles Darwin,[1] and the first ideas of evolution were vague and tentative. Simply to speculate that present-day creatures differ from those that lived in the past in consequence of a process of natural transformation during descent, was itself a profound disturbance of established thought. That evolutionary theories arose at this time in biology, as in other unrelated branches of knowledge,[2] was closely connected with the intellectual stirring of the Enlightenment, that movement of thought and opinion which dominated the eighteenth century. We shall not dwell on the many facets of this brilliant and fascinating stage in the growth of modern thought,[3] but note only its most general and lasting achievement: the apprehension of the world as history, as a process in time, in which all things are subject to change and development according to immanent laws. This meant breaking away from the static conception of the world as an agglomeration of unchanging or, at most, cyclical phenomena, which had dominated men's minds throughout the Middle Ages and beyond.[4] Instead, the thinkers of the Enlightenment began to investigate all fields of experience from the viewpoint of historical or evolutionary change.[5] The first consistent ideas of biological evolution arose in France, where the Enlightenment found its clearest and most conscious expression.

In biology the birth of evolutionary theories was hastened by two developments in science itself. The first was the beginning of systematic studies in geology,[6] stimulated by the increased scale of mining in many parts of Europe. A few isolated works were published in the sixteenth century, but the number grew considerably in the late seventeenth century, especially after the pioneer work (1669) of Nicolaus Steno in Italy,[7] and by the middle of the eighteenth century there was already an extensive literature. The question of the true nature of fossils (or "formed stones" as they were at first called) quickly proved to be the key to a rational theory of geology, a theory which necessarily involved abandoning a static creational view of the past history of plants and animals.

Fossil organic remains were known to the Ionian philosophers, and later to Theophrastus and to the mediaeval Arabian scientists. The occurrence of fossil sea-shells high up in mountain ranges excited their wonder, but none hesitated to accept that such fossils were the remains of once living organisms and that therefore the sea must at some time have covered what was now dry land. Although this interpretation was enshrined in the Latin classics,[8] it was either ignored or remained without impact until Steno, followed by John Ray and many others, by more extensive investigations had rediscovered fossils, established their frequent and widespread occurrence, and begun to make their significance disturbingly apparent. If fossils were indeed the remains of actual living organisms—as seemed incontrovertible in spite of some ingenious attempts to maintain the contrary[9]—then two conclusions followed, both at variance with current thinking. The finding of fossils clearly different from present-day species, implied that some created species had perished, contrary to both philosophy and scripture; whilst the deposition of fossils in strata by natural terrestrial processes manifestly required the lapse of immensely longer periods of time than were consistent with accepted religious chronology. Both these difficulties were frankly stated by Ray,[10] and as Raven has pointed out, it says much for his scientific vision and integrity that Ray never retreated from his conviction, based on a cool and thorough study of the facts known to him, that fossils are the genuine remains of living organisms of earlier times. Ray rejected with little hesitation the theory that fossils are relics of a great disturbance of the earth and a rising of the sea caused by the biblical Deluge; he thought their distribution quite inconsistent with such an explanation. After studying specimens of fossils plants, supplied by his friend Lhwyd, Ray, in his preface to the second edition of his *Synopsis stirpium Britannicarum* (1696), went so far as to add a section on palaeobotany, the first intimation of what was to become a supremely important and rewarding branch of botany. Both Steno and Ray had glimpses of the revolutionary conclusions to be drawn from the facts, but the full consequences were only appreciated later as the weight of evidence steadily increased.

A second scientific development most relevant to the rise of evolutionary theories, was the wider study of comparative morphology. In plants, as noted earlier, this was mainly limited to floral morphology, whereas in animals it took the form of a detailed investigation of the anatomy, particularly of the skeletal anatomy, of many groups; in both kingdoms, however, the observations embraced far more species than had ever before been examined. The results focused attention more sharply on the many family-like groups that could be picked out within what seemed to be a continuum of common morphology. The more frequent use of the word family by botanists and zoologists to designate such groups, shows how they were already beginning to see families as if they were groups of organisms related by common descent, even before they consciously thought of them in this light or began to appreciate the theoretical consequences of such a view. Comparative morphology, and attempts to build more natural systems of classification, reacted on one another, suggesting to some investigators at least, that the relationship between similar species could be, and probably was phylogenetic.

The first scientist to publish an overt evolutionary hypothesis to explain the variety of present and past living organisms, was Buffon.[11] The suggestion was made in the form of a speculative aside in the third (1753) volume of his great *Histoire Naturelle* (1749–67), and the link between speculation and the new facts of geology and comparative morphology is plain. Most of his first volume is indeed devoted to establishing a theory of the evolution of the earth, invoking only the operation of natural and still-continuing processes. Buffon used the evidence of climatic changes in the past, and of associated changes in the nature and distribution of fossil animals, to approach a modern conception of the duration of geological time.[12] The brilliant description of a changing physical world is supported by a mass of factual observations: it thus forms an essential and ever-present background to the survey of the world of living organisms which follows.

The hint of an evolutionary history of living things occurs in Buffon's account of horses and asses, where they are shown to be so close in morphology and anatomy that it is difficult not to think of them as related members of single family.[13] But, says Buffon, if one accepts this, then one must also accept that there are other small families, among both animals and plants as a whole, "projected by nature and produced by time", some families containing only two individual species, others with several, and among plants even families of twenty, thirty or more species. Buffon refers rather obliquely to two possible philosophic views of the family. It may be, like the animal kingdom as a whole, conceived and created by God alone out of nothing: this implies that the family is merely a convenient mental grouping, uniting species that are only actually related by their simultanous divine creation and the preconceived logic of God. Buffon does not say this explicitly, probably because he was already under pressure from the Jesuits and was writing with caution. On another view, the family represents a true aspect of things as they exist: this implies that families are formed by nature, and consist in fact of phylogenetically related species. This proposition is stated clearly by Buffon although in the conditional mood.

> If these families really exist, they can only have been formed by crossing, successive variation, and degeneration of the original species; and if one admits that there are families among plants and among animals, that the ass is of the family of the horse and differs only in having degenerated, then one can equally well say that the ape is of the family of man, that it is a degenerate man, or that man and ape have had a common origin like the horse and the ass, that each family, whether of animals or plants, came from a single stock, even that all animals came from a single animal, which in the passage of time has produced, by perfecting itself and by degenerating, all other races of animals.[14]

Buffon was one of the quickest minds of his time, expert in many branches of science, and a practical researcher as well, but he could only indicate the probability of evolution using evidence that lay to hand, and did not attempt to explain, except in most general terms, how species could change. For one thing, the apparent stability of species at the present day was a scientific difficulty of which Buffon was very sensible, and for another, he was not a man to push theory to a confrontation with the ecclesiastical establishment. In any case, his guiding principle in natural history was to collect all possible facts without prejudgement, and let them speak for themselves. As a result of these conflicting considerations his attitude to the evolution of species by transformation was equivocal, and sometimes contradictory, to the end of his life. The immense popularity and influence of the *Histoire Naturelle* was, however, enough to make his tentative suggestion of biological evolution widely known. In France the idea became familiar in scientific and intellectual circles, and by the 1760s men like Diderot and D'Alembert assumed as a matter of course that animals and plants had changed in the course of ages and would continue to change in the future.[15]

A more complete and consistent conception of evolution had already been outlined by Offray de La Mettrie in his *Système d'Epicure*, published in 1750, and which Buffon may therefore have seen while engaged on the *Histoire*.[16] The short essay of La Mettrie is the earliest statement of evolution with an unmistakable modern ring. After recalling the ancient evolutionary view of the world going back through Epicurus to Empedocles and Anaximander, he put forward his own version, which, however sketchy, has features that break very sharply with the past and make it the foundation of a new theory of the development of life on earth. In the first place La Mettrie sees the processes of nature as going on blindly and unconsciously in accord with the internal laws of movement of matter only, without divine intervention at any stage. "Simple matter"—earth, mud, moisture, endowed with a minimum amount of movement—changes and develops by existing physical laws, and gives rise in course of time to an infinite number of combinations of matter, from one of which a perfect [i.e. a functioning] animal can arise. From such a perfect animal the generations of today have been perfected. Another remarkable feature of La Mettrie's formulation is that purpose or teleology finds no place at all in his scheme. He says graphically that nature had no more idea of making an eye to see with than has water of acting as a mirror for a shepherdess. Given the existing laws of movement it was impossible for the material elements, in their agitation and mutual combinations, not to have formed eyes, bodily organs, etc. including the organs of thought and thought itself. Finally, La Mettrie's account implies that the perfecting of organisms involves a form of natural selection. The less perfect animals arose earlier than the more perfect; the cradle of life was possibly the sea, which originally covered the entire world (the last idea is probably derived from De Maillet's *Telliamed* and was also put forward by Buffon). This is the least developed part of La Mettrie's sketch and goes little beyond the primitive notion of selection arrived at by Empedocles, but it envisages the essential role of selection in the mechanism of evolutionary change.

La Mettrie's incisive statement, so consonant with some of the basic tenets of modern thought, had a lasting effect in raising evolution to the level of the possible, making it a conceivable explanation of the development of living matter, in the second half of the eighteenth century:[17] it was the philosophical parallel to Buffon's scientific intuition. The ancient materialist tradition preserved by Epicurus and Lucretius was thus, for the third time, recalled and revitalized to become a formative influence in the growth of modern science. In the Renaissance, the teaching of Epicurus had been evoked against religious ideology and influence; in the seventeenth century, in support of atomism and order in the physical world; and now in the century of biology, it was once more invoked to re-establish the concept of evolution, which Aristotle had effectively banished from thought for two thousand years.[18]

The penetration of evolutionary assumption into biology and their development into a coherent theory was a long and subtle process which we shall not examine in detail. The important point is that even in its first tentative outlines, and before there was any question of its general acceptance, the concept of evolution had an immediate effect on biological thought. Mere awareness of the possibility that living organisms change during descent, and that affinity could therefore be an expression of actual genetic relationship, opened wider vistas and fresh lines of research. The search, still empirical or intuitive, for the principles of natural classification, was given new life and rationality. Identification and naming of species remained a central task, but emphasis shifted from observation of a limited number of characters regarded as essential for identification and classification, to the investigation of species in the round with the aim of attaining as full a description as possible in terms of morphology and anatomy, complemented by the study of other important aspects of living organisms, including their physiology, development and relations to the environment. In botany this represented a return to the comprehensive programme of Ray and Grew, which had been narrowed by the dominance of floristic research. It is noteworthy that the need for a more balanced approach to botanical research was robustly stated in several articles on botany and botanical topics in the *Grande Encyclopédie* (1751), which clearly helped to determine the direction of French botany in the years that followed.[19]

The remarkable progress in all branches of French biology during the late eighteenth century owed a great deal of its impetus to the germinal idea of the Enlightenment, born in France, and widely disseminated through the energy and genius, erratic but stimulating, of Buffon. Although Buffon's descriptive writings were mainly concerned with animals,[20] his influence on botany was no less far reaching than on zoology. The significance of his evolutionary speculations for the problem of botanical classification has been touched on, but equally important was his insistence on the need to accumulate accurate factual knowledge as a pre-condition for theorizing. This was certainly a factor in causing the marked expansion of observation and experiment in botany which took place—not only in France—in the decades after Buffon became, in 1739, director (*intendant*) of the Jardin du Roi.

The existence of this institution, which had been founded by Louis XIII in the seventeenth century, was a further cause of the theoretical and practical lead of French biology throughout the eighteenth century. It enjoyed official material support from successive royal governments and was the first, and for over a hundred and fifty years, the only national biological research institute in Europe. In 1793 it became the Muséum d'Histoire Naturelle, but continued to receive support on an increased scale from the various revolutionary and post-revolutionary governments. At the Jardin du Roi there was a permanent staff of salaried scientists, who could devote all or most of their time to research and teaching, and who had assistants, work rooms, collections of specimens (living and preserved) of animals and plants, museums, glasshouses and a lecture room, facilities unrivalled elsewhere.[21] As time went on, related subjects such as chemistry, mineralogy, geology, human anatomy, horticulture, were added to botany and zoology as fields of study. The Jardin, with its group of scientists working together for long periods in relatively favourable conditions, gave French natural history a decisive advantage—very evident in the progress of botany—to the detailed consideration of which we now turn.

The interest of French botanists in natural classification went back to Magnol, who, inspired by Ray's "most natural and philosophical" method, had proposed the family as a natural taxonomic grouping and had discussed the criteria for defining it with extreme acumen. Magnol even seems to have come close to an evolutionary view, when he said that he employed the name family because it includes both kinship and affinity (*ideo nomine familiae, quod cognationem, et affinitatem includit, usus sum*). The attractive simplicity of Tournefort's artificial system damped down interest in natural methods for a time—Magnol himself retreated by devising a system based on the calyx in isolation[22]—but interest was re-awakened after Tournefort's death. Signs of the future appear in the work of Antoine de Jussieu, Tournefort's successor as Professor of Botany at the Jardin du Roi.

In a memoir to the Academy of Sciences in 1718, notable for its precise observation and balanced interpretation, de Jussieu described some fossil plants from coal measures of the Lyonnais region. After weighing the evidence with scrupulous care he concludes that the impressions cannot be anything but those of ancient plants, whose parts were deposited from sea-water (this follows from the abundance of marine shells in neighbouring strata). He dismisses as absurd and unnecessary those theories which would make the impressions bizarre sports of nature or remains left by a universal deluge. Close examination shows many of the plants to be ferns, but they are not species native to France or even to Europe, resembling most nearly tropical ferns growing at the present time in the East and West Indies. The facts and inferences are firmly stated, but the reader is left to draw out the wider implications. More important is de Jussieu's 1728 memoir, already mentioned (Chapter 7), in which he proposed the establishment of a new class of plants, *Plantae Fungosae*, to include both fungi and lichens. His arguments are so interesting that they deserve to be summarized. Fungi and lichens are alike in general form and internal structure, and in lacking the usual plant organs; they have similar habitats on trunks of trees, or rotton wood and decaying vegetable matter; both show rapid growth and the capacity to dry and re-wet [the facts are muddled here!]; they have a common mode of producing seed. That the seed of agarics, puff-balls (*Lycoperdon*) and *Hypoxylon*, can be seen with a lens, links fungi with other plants. That fungi are specific, self-reproducing organisms and not merely diseased excrescences of other plants, is shown by their specific form and structure, and by the fact that particular types are constant from year to year in different countries and habitats. The significant feature of de Jussieu's discussion is that he is here already using multiple affinities, not all, or necessarily, based on morphological characters, to establish fundamental taxonomic relations. He does this as a matter of practical inductive procedure, without discussion, since he was following a method already validated and made familiar by Magnol, who had been his teacher at Montpellier, where he had taken his doctorate in medicine.

Antoine was the first of five eminent botanists who bore the name de Jussieu. The family dominated French botany for three generations and well over a century, and played a remarkable collective part in establishing the principle, and the methods, of natural classification of plants.[23] Antoine combined a successful medical practice with his part-time job at the Jardin du Roi, making a considerable fortune which helped to enable other members of the family to devote themselves almost wholly to botany. Although Antoine's published botanical output was small, he was active and conscientious in supervising and expanding the garden and in teaching. He was a man of wide scientific views, and clearly exerted a very tangible influence on the outlook and aims of younger botanists.

Among these was his brother Bernard, thirteen years younger, whom Antoine had invited, as a lad of sixteen, to join him in Paris. Bernard was trained in botany and medicine by his elder brother and accompanied him on botanical collecting journeys in France and Spain. After this preliminary period of study Bernard took a doctorate in medicine at Montpellier and then another in Paris. In 1722 he was appointed assistant demonstrator of plants at the Jardin du Roi, filling the vacancy caused by the death of Vaillant. For the rest of his life he worked at the Jardin, lecturing, conducting field-courses in the country around Paris, and acting as organizer and leader of botanical research.

All contemporary witnesses are unanimous that Bernard de Jussieu was a teacher of genius who inspired his pupils by his extraordinary depth of botanical knowledge, united with a warm and attractive personality. Among the many French botanists taught by him were Adanson, Duhamel du Monceau, his brother Joseph de Jussieu, the botanical explorer, and his nephew Antoine-Laurent de Jussieu, who was his successor and botanical heir. Buffon is said to have attended his courses, as did a number of notabilities and visiting botanists, of whom Linnaeus was one. Bernard de Jussieu published only three short botanical memoirs, yet through his teaching and personal contacts he had a decisive influence on botanical history, because of his support for the principle of natural classification and his elaboration of the first avowed natural system of plants.

In the memorial address (Eloge) spoken before the Academy of Sciences in 1777 by Condorcet, it is said that Bernard de Jussieu's preference for the "natural method" was based on the belief that it represents a classification of plants "according to the general laws of nature". Unfortunately Bernard left no written account of the development or the final shape of his theoretical ideas: the practical outcome alone was embodied in an arrangement—in "natural-order beds"—of the plants in the royal garden of the Trianon, laid out in 1759. From the record of this arrangement and from other evidence now to be considered, we can nevertheless form a just estimate of his fundamental contribution to establishing the natural classification of plants.

In this context his studies, mentioned briefly in the previous chapter, dealing with the heterosporic ferns, *Pilularia* and *Marsilea* (called Lemma by de Jussieu), merit close attention. Published in 1739 and 1740 as *Mémoires de l'Académie des Sciences*, they not only confirm Bernard de Jussieu's superb ability as an investigator but throw a revealing light on his attitude to classification at this date. It is tempting to dwell on the descriptive part of this work, so far in advance of any earlier account of these plants, but a few words must suffice on this aspect. The description of both plants is monographic, accurate and beautifully illustrated. The structure of the sporocarps is examined by the microscope, the use of which is defended (probably with Ray's admonition in mind) on the grounds that there are entire families, for example, the fungi, whose flowers cannot be seen except with a microscope. By this means he showed for the first time that the sporocarp is not a fruit, as previously thought: he described the internal structure with remarkable precision, observing the microspores, interpreted as stamens and pollen, and the megaspores, interpreted as pistils. The sporocarp he therefore considered to be the equivalent of a flower, composed of stamens and pistil on a common receptacle. It must be said that this recognition of the homology between sporocarp and flower—in some essentials quite correct—was an astonishing insight on the part of Bernard de Jusssieu, more than a century before Hofmeister. What is more, it was not merely fortuitous but based on the fact that he followed the complete development microscopically. He watched the opening of the sporocarps in water and saw the microsporangia liberate the microspores, which seemed to him to behave like pollen grains.[24] In *Pilularia* he observed germination of the megaspores and saw the formation of embryos from them, and the subsequent growth of the embryos into new plants. Since each embryo possessed at an early stage one root and one leaf, de Jussieu classed them as monocotyledonous. Naturally it was impossible for him to observe or interpret the full details of spore development, but it was no mean achievement to follow the whole life cycle through, in outline, with such clarity.

Even greater interest attaches to Bernard de Jussieu's discussion of the systematic relations of *Pilularia* and *Marsilea*, which had been placed by Linnaeus among a rather ill-assorted group of his *Fragmenta Methodi Naturalis*, containing algae, hepatics, lichens and sponges. Bernard follows the example of his brother Antoine, and uses multiple affinities, based on both morphological and non-morphological characters, in a very striking way. He notes that *Pilularia* resembles ferns in the form of its growth and vegetation, the method of production of leaves on the rhizome, the circinnate vernation of the leaves, the characteristic taste and smell, and the form of the "stamen", except that the "stamen" of *Pilularia* does not have an elastic ring [i.e. an annulus, as in the sporangia of homosporic ferns]. For these reasons he concluded that *Pilularia* may well be the head of a special section of the ferns, which differs from the majority of ferns in not possessing "pistils" [i.e. megaspores]. *Marsilea* is so similar to *Pilularia* in the detailed structure of the "flower" [the sporocarp], and shares all the other characters listed above, so that it is evident that both plants belong to the same section of ferns.

So Bernard de Jussieu arrived at a perceptive and correct view of the natural relationships of these puzzling plants, by using the method of multiple affinity that was to become the key to developing the "natural method" of classification. At the same time a sentence in the *Pilularia* paper makes it clear that he was already in 1739 fully cognizant of the theoretical questions at issue, for he remarks that "this is not the place to discover which character (partie) is to serve as a base and foundation for a natural method of plants". He promises to examine the point on another occasion, but apparently never did, at least in writing. We do not know whether he discussed natural classification with Linnaeus during the latter's visit to Paris the previous year, but it seems unlikely that they did not talk about the burning topic of the time. Clearly de Jussieu knew all about Linnaeus's provisional natural orders (the *Fragmenta*) just published (1738) in *Classes Plantarum*, since he speaks of the position of *Pilularia* in Linnaeus's "new method". After Linnaeus went home to Sweden, he and de Jussieu corresponded for many years with the greatest mutual respect. When congratulating Linnaeus on being appointed to the chair of botany at Uppsala in 1742, Bernard expresses the hope that Linnaeus will now be able to devote all his time to Flora "so as finally to bring to perfection a natural classification, which is what all lovers of botany wish and expect". He does not, however, anywhere in the letters touch on their basically different approach to the "natural method", which was perhaps not even apparent to him at that time.

It appears that Bernard de Jussieu continued to develop an inductive approach to classification and that his ideas had taken definite shape by 1747.[25] He made considerable use of character-complexes based on the insertion of the floral parts, but gave equal weight, where appropriate to characters of the vegetative organs. By this time he already gave family names to some of his natural orders, and recognized that genera or species closely related on morphological criteria, often possess similar medical properties.[26]

In 1759 Louis XV entrusted Bernard de Jussieu with the supervision of the royal garden at Trianon, which was, of course, only a private pleasure-garden, not a scientific institution like the Jardin du Roi. Bernard was able to use the opportunity, however, to lay out part of the garden as a living demonstration of his own system. This first attempt at a complete natural classification of plants[27]—for Linnaeus, we saw, had not tried to dispose his natural orders in relation to one another—was never published by Bernard de Jussieu, since he regarded it as tentative, and continued to make gradual changes from time to time in order to improve it, but he dictated the arrangement to Adanson (then an inmate in his house), Claude Richard (gardener at Trianon) and M. de Bombarde (an amateur botanist). The Trianon garden was only open to a privileged few, courtiers and a number of botanists with court connections, so that its general educational effect was small; but Antoine-Laurent de Jussieu,[28] who came to Paris in 1765 and lived with his uncle as pupil and then as intimate associate until Bernard's death, was completely familiar with the arrangement of genera, and with the system and the ideas behind it. It is from Antoine-Laurent that most of our information about Bernard's achievement is gleaned: he first published the full details of the system in 1789, twelve years after Bernard's death. The Trianon demonstration beds only lasted till 1775 when they disappeared to make room for an English garden, which was more to Marie-Antoinette's taste.

The lesson of Trianon was not lost, for in 1774 Antoine-Laurent, already acting professor of botany at the Jardin du Roi, adopted Bernard's system as the basis for the arrangement of plants in new, enlarged demonstration plots there, replacing the long-established system of Tournefort. He published an outline of the new system in the *Mémoires de l'Académie des Sciences*, pointing out that the arrangement adopted at the Jardin du Roi closely followed that at Trianon, but that certain changes had been made (doubtless by himself).[29] It must therefore have reflected Bernard's final ideas rather closely: Bernard was still alive but was now seventy-five and, very sadly, was nearly blind.

The public demonstration of the "natural method" in the Jardin du Roi was the culmination of more than fifty years of critical work and thought by Bernard de Jussieu. It had a very great influence on the further development and popularization of the natural classification of plants, made more effective by the sensible, if almost inevitable decision of Antoine-Laurent de Jussieu to introduce at the same time Linnean nomenclature for genera and species.

Bernard de Jussieu made no secret of the fact that he took Linnaeus's sixty-four natural orders as his starting point:[30] it was a sound and rational thing to do, since the "naturalness" of many of Linnaeus's groupings of genera was manifest to the eye of an experienced botanist once they had been made. Nothing can diminish the genius of Linnaeus in first placing the majority of all the known genera in natural orders. Ironically, it was a decisive step in the progress to natural classification, which his own methods and theories increasingly tended to obstruct. The vital advance made by Bernard de Jussieu was to escape in practice from Linnaeus's essentialism, and to develop his legacy by the inductive methods of Ray, Magnol and Antoine de Jussieu, employing multiple affinities for the purpose of classification. By using many characters, not those of the fructification alone, he began to make gradual improvements in the constitution and boundaries of the natural orders proposed by Linnaeus, and to attempt to place related orders in higher taxonomic classes, which would also represent natural groupings. Many of these changes were ultimately incorporated in the classification published by his nephew Antoine-Laurent in 1789, of which we shall speak later.

Linnaeus had listed his natural orders with scant regard to possible higher groupings; even the division into monocotyledons and dicotyledons was blurred although he had stressed its importance in *Philosophia Botanica* (114). Bernard de Jussieu, however, in his arrangement clearly separated acotyledons (mostly cryptogams, but including some apparently anomalous flowering plants), monocotyledons, and dicotyledons. Comparison of Bernard's arrangement (1759) of families with that of Antoine-Laurent (1774, 1789) shows conclusively that Bernard associated some families together according to the mode of insertion of the floral parts to give higher taxa, a practice which Antoine-Laurent carried further and made explicit. Bernard de Jussieu did not indicate his higher groups by name or definition, only by their position in his arrangement; it is evident, however, that he was feeling his way towards a natural classification that would reflect varying degrees or levels of relationship, as observed in nature.

The distinction of having first analysed and explained the theoretical foundation of natural classification, and, what was even more important, of defining the practical method to be used in seeking such a classification, belongs without question to Michel Adanson. His *Familles des Plantes* (1763, 1764) was a work of historic significance, which gave clarity and coherence to the ideas of the growing number of proponents of the "natural method". It became the main formative influence in developing natural classification in France, and in ensuring its success.

Adanson was born in Provence but his parents went to Paris when he was a young child, and in Paris he grew up and received higher education in theology, classics and philosophy. His interests turned to natural science and he attended classes at the Collège Royale and the Jardin du Roi, becoming personally known to Réaumur, Daubenton, Bernard de Jussieu, and probably to Buffon. The relationship with Bernard de Jussieu, beginning as that of pupil to master, became close and cordial, and Adanson must have been fully conversant with Bernard's thought and methods by the time he left for Senegal in 1748, aged twenty-one, as an employee of the Compagnie des Indes. He spent six arduous but fruitful years in Africa, returning with a remarkable store of information on the geography, geology, natural history, languages, and resources of the country, in addition to thousands of botanical and zoological specimens. Botanically the reward was immense: contact with a tropical flora had profound effect on Adanson. The shock of finding so many plants so different in form and attributes from those of the temporate regions, not fitting into accepted groups or systems, led him to analyse the whole basis of classification in the light of what he had learned from de Jussieu, with a consequent depth of insight which Linnaeus, for all his thoroughness, could not attain.

On his return from Africa in 1754 Adanson was invited by Bernard de Jussieu to live in his house; he remained there ten years, only moving when two of Bernard's nephews—one was Antoine-Laurent—came from Lyon to join their uncle. It was during this household intimacy with Bernard that Adanson wrote *Familles des Plantes*,[31] in which he made Bernard de Jussieu's taxonomic procedure explicit and consistent, and gave it theoretical justification.

In preparation for establishing a natural system Adanson made a thorough investigation of all earlier systems of classification. As a result, he challenged the validity of some opinions expressed by Linnaeus in his survey of earlier systems in *Classes Plantarum* (1738), by drawing attention to the fact that Linnaeus had only considered the extent to which his predecessors agreed with him in using the fructification as the sole basis for classification, and had founded his judgements only in relation to this. Adanson claims that his work differs in two fundamental ways. In the first place he has considered all methods, whether they are founded on the fructification or on other parts of the plant as well. Secondly, he presents in another light some methods, especially those of Cesalpino, Morison, Ray, Knaut, Hermann, and Boerhaave, which have been misunderstood or not sufficiently faithfully treated. All these authors are said [by Linnaeus, Adanson means] to have based their systems on the fructification alone, but this is not so: Cesalpino classified "according to the arrangement, position and form of flowers, the fruit, the radicle, number of cotyledons, latex, flower colour, leaves, and roots", and the other authors likewise "evidently used almost all the other parts of plants". Adanson here includes a long quotation from Magnol in definition of the natural method for which these authors were looking. This historically correct reinterpretation by Adanson, with its implicit criticism of Linnaeus's whole theoretical position, shows how thoroughly he had studied the problem of classification and how much more clearly he saw the issues than Linnaeus ever could. His later opposition to Linnean nomenclature can perhaps be better understood as the expression of the deep philosophic rift between the two men, than as a question of names and priorities.

It is unnecessary to follow Adanson through his exhaustive discussion of the many systems he studied, or in his analysis of the inherent weakness of the artificial systems (including the most popular one, the Sexual System of Linnaeus).[32] He does not dispute that such systems facilitate the acquisition and retaining of a knowledge of plants, or that they can furnish valuable points of view about those parts "whose combination and totality can lead towards the discovery of the natural method", but such systems remain arbitrary and unsatisfactory because based on a small number of selected characters which may be "sufficient to constitute the genera of some families but not sufficient for others". The last phrase is, as will be seen, the clue to Adanson's essentially experimental approach to taxonomy: the characters significant in classification for any group must be found by trial and experience, considering in the first place the totality of all the parts,[33] not just those which seem *a priori* important or essential, and deriving from this totality the particular characters which constitute each family. The opposing view of Linnaeus and Haller, that class characters must only be taken from the fructification, is mentioned by Adanson in order to be rejected.

By his training in the Magnol–Jussieu tradition, Adanson must doubtless already have been a supporter of the natural system before embarking for Africa, but according to his own statement it was his experience of the strange tropical flora of Senegal that convinced him of the inadequacy of the methods of Tournefort and Linnaeus.

> It was necessary to seek in nature for nature's system, if there really was one. With this aim I examined plants in all their parts, without omitting one, from roots to embryo, folding of leaves in the bud, manner of sheathing, development, position and folding of the embryo and radicle in the seed relative to the fruit; in a word, a number of features to which few botanists pay attention.

The intellectual influence of Buffon is in evidence here as in many other aspects of Adanson's work.[34] The method of enquiry he adopted—the detailed systematic study of natural phenomena, without prejudgement but not without purpose—was that of Buffon, and it led Adanson to an unambiguous statement of the principles on which natural classification must be built.

The key to the problem, as Adanson perceived, was to abandon completely the idealist notion of essential parts, that is, of parts which (like the seed or fructification) play such an important role in the life or being of a plant that they constitute its "essence" and are thus peculiarly and exclusively fitted to be the parts on which their classification is based. In rejecting this conception Adanson was, of course, adopting the philosophic view of Locke which had already been forcibly stated in botanical terms by Ray (in the *Dissertatio*) and followed in practice, if less consistently in theory, by Magnol, the de Jussieu brothers and others seeking a natural classification. The special contribution of Adanson lay in the fact that he accepted the non-essentialist, or materialist, view without reservation and spelt out the consequences in the form of a precise strategy for approaching the problem of classification, at the same time giving an illuminating guide to its concrete application by his own delimitation of natural families and genera of plants. No one else attained his theoretical consistency.

Once the philosophical block of essentialist thinking was surmounted, the path was open to the inductive discovery of affinity through multiple relationships, and was described by Adanson with the utmost clarity and with sufficient repetition to drive the lesson home. It will be best to give the substance of his "method" in his own words.

> There is no doubt that there can be only one natural method in botany, that which considers the totality of all the parts of plants. One must consider root, stems, leaves, flowers, fructification, in fact, all the parts, qualities, properties and faculties of plants. From the number, form, position and relative proportion of these parts; from their symmetry, that is, from the comparison of their relationships, similarities and differences, and of their qualities; from this totality is born the conformity, the affinity, which unites plants and divides them into classes or families.
>
> The true science of plants is that which considers relations between all their parts and qualities without a single exception; it unites all plants in families that are natural and unchanging [because] founded on all possible relations.

It is very pertinent that Adanson stresses that microscopical characters must be used if appropriate. Ray, it will be remembered, excluded microscopical characters, although on practical rather than philosophical grounds, since they could not readily be determined in the field.

In many other passages, and by the example of his own systematic treatment of families and genera, Adanson makes the point that affinity is not to be determined from one or a small number of parts, but "by apprehending all the possible relationships in all the parts". The central core of his method is the necessity of looking in the first place at all characters and character-complexes [symmetry], without any *a priori* commitment to the importance of some parts or the exclusion of others. He makes quite explicit that this technique, while non-exclusive, is certainly not to be based on random or accidental features: the characters must always be comparative and taken from the same part or parts in all plants of the same family. Natural classification can therefore only be attained by abandoning essentialist preconceptions and adopting multiple affinity as the foundation, based on an inductive study of as many characters as possible. Adanson adds that this is a general method, not applicable to plants alone, but having the same advantages in other branches of natural history.

It is important to stress—since the point has been misunderstood[35]—that Adanson never held that all characters have equal importance, or equal "weight", in classification. What he insisted was that all characters should be given equal consideration as a first step: there must be no *a priori* selection or rejection. Subsequent study and comparison might show certain characters or character-complexes to be more valuable than others; this value was not absolute, however, but might differ in different families or at different levels of classification. "What is sufficient to constitute the genera of certain families is not sufficient for other families, and neither the same parts nor the same number of these parts invariably furnish these [constituent] characters in each family." In another passage discussing the delimitation of species, he notes that the characters used may be more or less stable, more or less essential, in certain families than in others, so that the number need not be the same nor the choice indifferent. It took Adanson's genius to formulate the principles and methods of procedure that have been the key to taxonomic progress ever since.

The predictive element in natural classification had been recognized to some extent by Cesalpino, Ray and other botanists, but it was Adanson who saw with remarkable penetration, that this element gave systematics a general inductive–deductive, quasi-experimental method by which it could make steady progress. Intuition was not thereby sacrificed, but was incorporated into a scientific technique, which guaranteed the possibility of continuous improvement in classification. That Adanson understood the matter in this way appears from his many discussions of particular groups, and from his stress on the need to establish by experience for each group which characters deserve particular attention, and which can be neglected as minutiae or as superfluous. This is equivalent to saying that the validity of classification can be tested by comparing prediction with reality at each successive step.

Adanson was deeply impressed by the advantages of the "natural method", which he claimed as the only one capable of revealing the classes and divisions really existing in nature, because founded on as unbiased and comprehensive a survey of the phenomena as possible. The result is a stable system, presenting the known facts with the greatest generality, without limiting them by the arbitrary *a priori* selection or exclusion of any. New facts lead to reinterpretation of the system but not to its overthrow. The natural system needs to be completed by the knowledge of many species still lacking but does not require knowledge of all. Adanson is here making a principled criticism of Linnaeus, who admitted that the perfect classification, founded on fructification only (the essence of the plant), was only attainable with complete knowledge of all existing species. At the time of writing he was still an admirer of Linnaeus; these remarks show that he was already more clearly aware of the differences between Linnaeus and the new directions in biology, than were most of his contemporaries.

Having laid down the basic principles for building a natural classification, Adanson devoted the remainder of the *Familles* to an exposition of his own classification of plants, arrived at in accordance with these principles. An account of his scheme has recently been given by Stafleu and a detailed treatment is unnecessary here.[36] Adanson divided plants into fifty-eight families, of which fifty-two contain the known flowering plant genera, the other six containing gymnosperms and cryptogams. The cryptogamic classes show nothing new; the time was not ripe for progress in these groups. His flowering-plant families are in general not very different from the natural orders of Linnaeus and Bernard de Jussieu. The real difference between Adanson and all his predecessors is that he made his method of procedure explicit, showing how he arrived at the constitution of his families and why, after considering all available characters, he held certain characters or character-complexes to be critical in the definition of some families but not of others. Finally, Adanson gave—as Linnaeus and Bernard de Jussieu had not done—a detailed circumscription of each family; he regarded these circumscriptions as his own special contribution to taxonomy, as they undoubtedly were. These critical definitions of families are astonishingly comprehensive and "modern" in form; they were an epoch-making advance and immediately became a model which profoundly influenced the progress of taxonomy.

In the arrangement of his natural families Adanson tried to place them in a continuous series, in which each family was more closely related by multiple affinity to its neighbours than to others further away. This conception of a continuous chain of relation has some scholastic features, but as Adanson employed it in practice it became a guiding principle for the delimitation of higher taxa and the recognition of wider systematic relationships. Linnaeus, it will be remembered, scarcely attempted any systematic arrangement of his natural orders, and Bernard de Jussieu was only beginning to seek an arrangement that would represent wider affinities.

Within each family Adanson attempted to give critical circumscriptions of the constituent genera and to arrange them in a series expressive of their affinities, in the same way as he had treated the families. In the discussion of the proposed relationships, at family and generic level, he consistently applies the essential principles of the natural method. All the various characters and character-complexes are first considered "in order to use only those which experience shows us to contain solely or most generally the generic characters" [i.e. the characters critical for the definition of taxa at different levels]. Adanson always resists the temptation to give *a priori* or overriding weight to any particular character: the weight to be attached has to be decided by experience, the result of detailed study and comparison of many characters in a wide range of plants and over many taxonomic groups. To give a specific example, Adanson used the union or separation of the petals (gamopetaly or dialypetaly) as an important character, but never considered this distinction as sufficient by itself to delimit higher taxa (as Antoine-Laurent de Jussieu subsequently did). He pointed out that in some natural families, the Liliaceae for example, species with united and with separate petals may be found, and there is no reason to separate them widely or place them in different families on account of this character in isolation.

Adanson's *Familles des Plantes* was the first work to define with philosophical precision the theory and practice of natural classification, and its effect was profound and permanent. Within two decades Lamarck was writing in the *Encyclopédie Méthodique* of Adanson's forming natural families by examination of all parts of the plant from root to embryo, and linking this with Bernard de Jusieu's natural classification as publicly demonstrated by Antoine-Laurent de Jussieu in the Jardin du Roi. The "method" of Adanson very rapidly came to guide the practice of taxonomy, as it has done ever since, whatever philosophical diversions individual taxonomists may have followed in theory. It is essential to stress this point, since history was unkind to Adanson and his name and personal contribution were soon and long forgotten.[37] To some extent he brought about this oblivion himself: by his unexplained failure to publish his later researches, by waste of energy on a vain project for a universal encyclopaedia, by his eccentric personal spelling, and perhaps most of all by his opposition to Linnean nomenclature, which no serious scientist could any longer afford not to use. By the time of his death in 1806 his reputation as a rather odd has-been was unfortunately established. But it is undeniable that Adanson, more than any other single person, effectively established natural classification as a fundamental aim of biology, and explained the simple (but not therefore easy or automatic) technique for its realization at all taxonomic levels.

Immediately on its appearance, *Familles des Plantes* was widely and favourably reviewed, and within a few years was referred to with understanding and approval by such distinguished botanists as Scopoli in Italy and Gaertner in Germany. Adanson's influence on Lamarck was decisive and will be discussed in more detail later. It was, however, through Antoine-Laurent de Jussieu, and his statement and adoption of Adanson's principles in his *Genera Plantarum* of 1789, that they became established as the unassailable foundation of natural classification and of modern systematic botany. De Jussieu, in *Genera Plantarum*, links together Linnaeus, Bernard de Jussieu, and Adanson as the three among many diverse authors who were most successful in revealing the "natural method". It is fair to recall this statement, since Antoine-Laurent has been accused of failing to acknowledge with sufficient candour and generosity his own deep indebtedness to Adanson.[38]

In the course of his exposition of the principles of natural classification Adanson was led into a very thorough discussion of the nature of species, in which he reached conclusions remarkable for their bold originality and their influence on the development of biological theory. I have rather artificially isolated this part of Adanson's argument in order to give it the prominence it deserves. Manifestly following a train of thought initiated by Buffon, Adanson considered the vital problem of the stability of plant species and whether classification—especially natural classification—is meaningful if the basic units, the species, are in process of change. This involves the prior question of whether plant species do in fact change. To this question Adanson, in 1763, gave a cautious but definite yes. He was well aware of J. Marchant's discovery in 1715 (reported in 1719 in the *Mémoires* of the Academy of Sciences) of the first scientifically recorded mutation in plants, found in *Mercurialis*; and he also refers to the peloric forms of *Linaria* described by Linnaeus in 1742, and mentions as well known the production of tulips of varying flower colour by pollination of de-staminated flowers of different colour. Plants are also known to be changed by cultivation, a phenomenon particularly to be remarked in plants brought to Europe from Africa and elsewhere, perennial shrubs sometimes giving rise to herbaceous annuals, and introduced plants changing into scarcely recogizable forms. Many such examples were given by John Ray. Variation in such cases often seems to go as far as new species—is this not also possible in nature? Adanson himself cultivated great quantities of lettuce and basil for several years and believed that he had seen the formation of species and varieties which "become fixed each generation".

From these various lines of evidence Adanson concluded that the nature of plants is less constant and more diverse than that of animals, and that the mutation or transmutation of plant species in nature is not improbable; he suggested that the reason why some plants described by ancient writers are not found today is that these species have disappeared or have changed into others. Adanson was apparently the first to employ the word mutation in connection with evolutionary change. In the *Familles des Plantes* he thus boldly envisaged the possibility that an individual species may change and may in consequence only exist as a taxonomic unit for a limited period of time. The possibility of the transmutation of species does not, however, destroy the foundations of natural classification. On the contrary, even if a particular species were to reproduce itself unchanged for only a few generations, it could still be fully defined and classified by the natural method based on the study of multi-relational affinity. Indeed only the natural method is capable of dealing with this situation, as Adanson is careful to emphasize. From Adanson's arguments emerges the penetrating recognition that, if organisms change during descent, then natural classification expresses a genetic, or more accurately, a phylogenetic relationships between them. Although he did not, of course, use these terms, Adanson clearly grasped, and endeavoured to explain, the connection in principle between classification and phylogenetic relationship. This is evident from his statement that, "even if there are no fixed species", the natural method enables us to "know by the number of differences found between neighbouring species, how many intermediaries are lacking". He is saying that the method of natural classification gives a measure of the genetic difference between related organisms.

Adanson's realization that natural classification is probably the expression of an evolutionary, or phylogenetic, relationship did not remain merely brilliant anticipation, but contributed directly to the growth of evolutionary thought. Lamarck accepted Adanson's "method" for taxonomic investigation early in his career; many years later, in his *Zoologie Philosophique*, his arguments for evolutionary change in organisms show the unmistakable theoretical influence of Adanson, by which he had clearly been stirred and enlightened when a young man. Adanson may have been denied the heady wine of personal success, but few have influenced the science of their time more fundamentally or with more lasting effect.

The importance of Adanson's contribution to the ripening of the concept of biological evolution is not diminished by the fact that he later retreated from the position taken in *Familles des Plantes*. In 1769 he re-examined the question of "whether plant species can change", and concluded from his own experiments with wheat and barley, and from a reconsideration of the earlier described mutants of *Mercurialis* and *Linaria*, and of the more recently discovered unifoliate mutant of *Fragaria*, that the observed changes were not due to hybridity nor did they breed true: therefore "the transmutation of species does not take place in plants, any more than in animals".[39] From the vantage point of the present we can comprehend that Adanson was right on both counts, both in contemplating the transformation of species during descent, and in thinking that incontrovertible evidence for the formation of new species was still lacking. Posterity recognizes a personal and scientific integrity in Adanson which struck his contemporaries as plain awkwardness and robbed this remarkable man of the recognition that was his due.

It fell to Antoine-Laurent de Jussieu to make natural classification a universally accepted concept and primary aim in botany. The principles of the method and an impressive example of the result of applying them to all known plants, were published in his *Genera Plantarum* in 1789, making that year as decisive a turning point in biology as it was in the social and political history of Europe. Possessed of a less original mind than Adanson or his uncles Antoine and Bernard, Antoine-Laurent[40] was the fortunate inheritor of their ideas and many-sided knowledge of plants, while as pupil and assistant of Bernard, and close personal asssociate of Adanson, he must also have had constant daily practice in using the "natural method". To this legacy Antoine-Laurent added brilliant talents as a systematic botanist, and the advantage of a detailed study of the enormous number of new plants, often representing hitherto unknown families, which poured into the herbaria during his lifetime from the many voyages of exploration.[41] At the same time, his scientific common sense caused him to adopt the Linnean nomenclature, already the indispensable tool of serious taxonomy, and in consequence the *Generic Plantarum* was a far more effective means of winning adherents for Adanson's method than were his own writings.

The long period of preparatory study undoubtedly gave the *Genera Plantarum* strength and authority which assisted in carrying its message. In a monographic treatment of the *Ranunculaceae*, presented to the Académie Royale des Sciences in 1773, de Jussieu had clearly outlined his theoretical approach to taxonomy, and this remains virtually unchanged in the preface of the *Genera Plantarum* of 1789, and in his last account of the natural method of classifying plants, written in 1842 for the *Dictionnaire des Sciences Naturelles*. Fundamentally he accepts, and employs, the principle of Adanson that natural relationship is determined by multiple affinity, and that affinity is found by considering many (all possible) stable characters, without excluding any *a priori*, but later giving varying weight or value to characters in different groups in the light of experience. The method of multiple affinity is explained by de Jussieu in almost exactly the same terms as those used by Adanson, and he uses it to define species, genera and families. Following Adanson, de Jussieu gave a full diagnostic description of all family groupings of the *Genera Plantarum*, a vitally important practice which henceforth became normal in taxonomy. De Jussieu, like Adanson, emphasized the relative stability of groupings—especially the families—established by the natural method.

After the appearance of de Jussieu's work the "method" of Adanson became simply the normal method of defining species, genera and families, which does not mean, of course, the elimination of differences of opinion about the limits of taxa in particular cases. The great contribution of de Jussieu was to make clear the technique of natural classification and to demonstrate its power and practicality by the hundred families of plants he defined. Of these, ninety-four are flowering plants, and it is a tribute to A.-L. de Jussieu's botanical flair and to his skilled use of Adansonian techniques, that most of the families he included are considered natural at the present day.[42]

In most essential ways A.-L. de Jussieu based himself on Adanson but in two respects he diverged from him. In one direction he attempted to develop the natural classification of plants further than Adanson had envisaged by defining higher groupings, that is, groupings of families (classes, divisions). Ray had already discovered the division into monocotyledons and dicotyledons, and realized that it was associated with other characters in a way suggesting that this was a natural division. De Jussieu accepted the division into monocotyledons and dicotyledons, and tried to find other natural, suprafamily groupings of the same kind. This was a laudable thought. In fact he divided the monocotyledons into three classes, and the dicotyledons into eleven classes, based exclusively on the relative positions or degree of union of the corolla or stamens. Some of these classes were founded on those adopted by Bernard de Jussieu in the Trianon garden, and Antoine-Laurent says it was Adanson who first regularly cited the attachment of the corolla as a character in classification, following Bernard's lead. In striving to form higher taxa A.-L. de Jussieu significantly extended the field of research in taxonomy.

Unfortunately he took a step backward at the same time. By an odd inconsistency of thought he abandoned Adanson's use of multiple affinity when it came to higher taxa. His higher classes are based on single floral characters selected because he held them to be essential.[43] This was not just a matter of taking a single diagnostic feature for convenience, since he argues at length that some characters or character-complexes are essential to plants in a way others are not, and that higher taxa—called by him "primitive divisions"—can only be legitimately founded on such "essential characters drawn from the principal parts". De Jussieu did not fail to mention that Adanson had rejected this view entirely and recognized "no part essentially existent" (the words are those of de Jussieu). If he retreated a little from the complete logic of Adanson's position, de Jussieu was at least absolutely honest and clear-sighted in explaining the theory behind his own. We must also admit that in proposing higher classes he attempted a bold advance which Adanson had foreseen, but had only carried out in so far as he had placed related families side by side in what he considered to be a continuous chain of natural affinity.

The result of the intrusion of essentialist concepts was that de Jussieu's higher classes lack the natural character of his families. Although foreshadowing a new and necessary stage in the extension of classification, these rather artificial divisions proved to some extent (in the flowering plants to which alone they were applied) a barrier to progress, and have been largely abandoned. Despite a partial concession to essentialism, the *Genera Plantarum* of A.-L. de Jussieu was the work which placed natural classification in the forefront of systematic botany, and ensured that the principles outlined by Michel Adanson in *Familles des Plantes* became the Ariadne's thread[44] to guide botanists through the labyrinth of form in the plant kingdom.

In the second half of the eighteenth century the growth of floristic studies continued and increased, providing a mass of information on the range of form, local and world distribution, economic uses, and specific habitats, of plants, from which new branches of botany sprang later, but which for the time being did not break new ground in theory or technique.[45] Plant geography was the creation of the following century, although mention should be made of the chapter on the history of plants in K. L. Willdenow's botanical textbook, *Grundriss der Kraüterkunde* (1792), which was the first attempt to explain the world distribution of species in a scientific manner. In addition to floristics, there were certain other movements in botany, deriving their impulse more directly from the spreading wave of influence of the French biologists of the Enlightenment, and which deserve to be considered in greater detail.

An important, at first sight surprising, development that affected the subsequent course of botanical history, was the number of German botanists who began to report valuable research. In a curious way this advance of German botany seems to be connected with the very backwardness of the conglomeration of petty statelets comprising Germany at the time, which might have been expected to stop scientific activity altogether. In fact, opposing tendencies were at work. The political disunity and the economic and agrarian stagnation of the Holy Roman Empire tended to check both arts and science, yet at the same time almost every ruler of a bankrupt grand-duchy dreamed of making his capital a little Paris (often with a little Versailles too). One odd result of such small-town ambitions—important for science—was that in the seventeenth and eighteenth centuries more new universities were founded in German lands than in either France or Italy. These institutions were often pitiably endowed but most of them had a medical faculty in which botany would have a place in the curriculum, and there was usually a chair of botany and a university garden. The possibilities of material support for botany in Germany were thus appreciably enlarged. The new German universities differed from the long-established foundations of Europe (including England and Scotland) in one important feature. From the beginning they were under close and direct state control; their purpose was to train officials and professional men for service of the local state. This was no great advantage to science in the early days, but the existence of a relatively large number of universities having a direct link with the apparatus of state was to prove a very important factor in the great advance of German science, including botany, during the nineteenth century.[46]

The oppression of German conditions had another double-edged effect. To many of the intelligentsia every road to political freedom or social improvement seemed hopelessly blocked, even the personal satisfaction of a worthwhile career in public service was unattainable. The psychological result in some of the keenest minds was an intense prepossession with theoretical problems in every sphere, a compensation for their impotence in practical affairs. Goethe is the classical case in point but the less universally gifted were affected likewise. This mental attitude gave a distinct philosophical cast to German science, characterized by a constant search for unifying theory, of which the negative accompaniment was sometimes a preference for cloudy

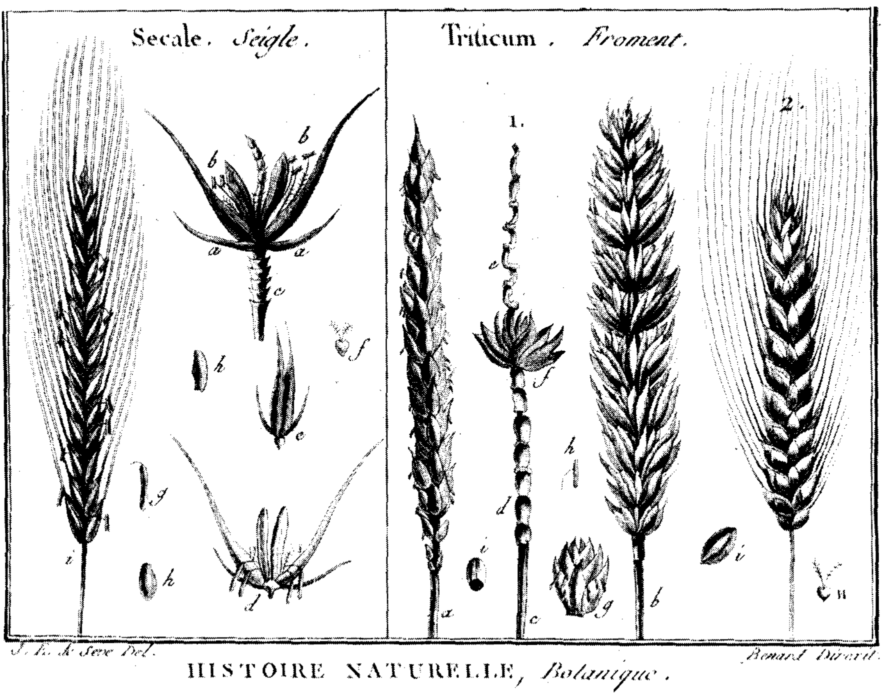

Figure 18 Figures of rye and wheat from the botanical section of the *Encyclopédie Méthodique* (1791) edited by J. B. Lamarck.

abstractions in place of hard facts.[47] These tendencies, however, came more clearly to the fore towards the end of the century; the advances now to be discussed rather reflect the inductive impulse of Locke and Buffon, and the electrifying upsurge of science in France.

We have seen how slight was the experimental follow-up of Camerarius's proof of sexuality in plants. In 1752 J. G. Koelreuter, son of a Tübingen apothecary, and at the time a medical student of nineteen beginning his three final qualifying years at the town's university, published a survey of all the experiments on sex in plants that had been carried out since Camerarius.[48] The need for confirmation and extension of work on the subject evidently impressed Koelreuter, for in 1759, when he became custodian of the natural history collections in the Imperial Academy at St Petersburg, he began his own experimental studies on pollination. He returned to Germany after only a year, continuing his experiments at Calw, Berlin, Leipzig, and after 1764 in Karlsruhe, where he had been appointed professor of botany and director of the botanical and grand-ducal gardens. Between 1761 and 1766 he published a series of detailed reports of his experiments under the title, *Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuche und Beobachtungen (nebst Fortsetzungen).* Koelreuter used only the simple techniques that Camerarius had used earlier, abscission of the stamens or stigmas and some limited observation with lens or microscope, but the work was superb in logical planning and execution and opened a new field of biological experimentation.

Camerarius had pointed out that sexuality in plants implied the likelihood of plant hybrids. Koelreuter realized that to demonstrate the existence of hybrids would be the strongest possible proof of sexual reproduction, and he was horrified at the easy way some botanists, including the great Linnaeus himself, accepted certain plants as hybrid without genuine evidence.[49] Some of these supposed hybrids were between species of different genera, and from the very beginning Koelreuter's experiments had convinced him that hybrids were in general only possible between closely related species of the same

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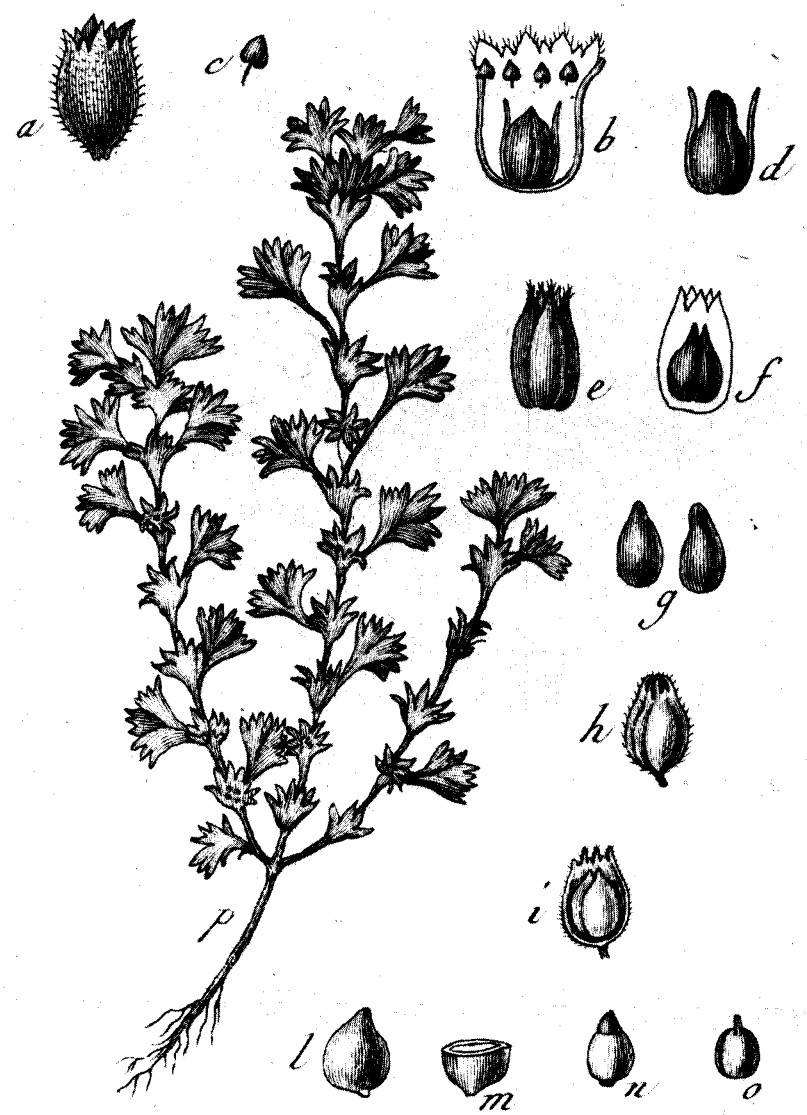
Figure 19 Figure of parsley piert (*Aphanes*) from *Encyclopédie Méthodique* (1791).

Aphanes. *Percepier.*



genus. He therefore set himself the aim of producing plant hybrids by strictly controlled methods, using castration and artificial pollination. His first experimental hybrid was obtained in Russia in 1760 between two species of *Nicotiana*, by using the pollen of *Nicotiana paniculata* to fertilize castrated flowers of *Nicotiana rustica*. The hybrid progeny (F_1) all belonged to a single, distinct species, which shared characteristic features of both parent species, as Koelreuter showed by a thorough descriptive analysis, character by character. The hybrid plants grew well but were sterile owing to failure to form normal pollen. Later, after some unsuccessful tries, he managed to make the reciprocal cross (pollen of *N. rustica* on stigmas of *N. paniculata*), and found that the progeny was identical with that from the original cross. In further experiments over the years he obtained hybrids between other species of *Nicotiana*, and between species of *Dianthus, Matthiola, Cheiranthus, Hibiscus, Hyoscyamus, Datura, Cucurbita, Verbascum* and *Aquilegia*. Most of the hybrids were sterile, but a few, rather to his surprise, were self-fertile.

The importance of these observations cannot be overestimated; they not only established the formation of plant hybrids by controlled experiments, "many times repeated", as Koelreuter emphasized, but they showed that the form of the hybrid is as distinctive and stable as that of its progenitors. In other words, hybrid formation is governed by definite and ascertainable laws; a science of genetics was therefore possible. That Koelreuter recognized this profound implication of his results is manifested by his own attempt to formulate a theory of inheritance. He assumed that two homogenous substances, the male and female seed, are requisite for the (sexual) reproduction of plants. "The combination and mingling of these two substances takes place in the closest and most orderly fashion, and in definite proportions, and from the union arises another substance of intermediate character." This third substance

> either becomes the beginning or firm foundation of a living machine immediately after combination is complete, or produces it [a living machine] after a short interval. On this foundation and on its organizing activity, which must necessarily differ according to the different character of the two germinal materials in each specific type of living machine, rests the whole progressive formation . . . of the future plant.

Koelreuter stands incontrovertibly as one of the great forerunners of modern genetics and of scientific plant breeding.

During the course of his extensive work on plant hybrids, Koelreuter observed for the first time a number of carefully recorded phenomena whose full significance was only to be understood much later. He discovered re-conversion of hybrid to parental forms by back-crossing, that is, the gradual transformation of a hydrid back to one of the original parents by repeated fertilization in successive generations with the pollen of the respective parent, a phenomenon which impressed him profoundly, because it represented an actual transmutation of one species into another.

The apparent absence of hybrids in nature intrigued him, and his explanation was acute and well-founded. His own experiments had convinced him that, as a rule, only closely related species are able to form hybrids. Since related species almost always occupy distinct, often widely separated, habitats, the chance of hybrid pollination is generally remote, but might be expected to be higher in botanical gardens where many different species are grown in unnatural propinquity.[50] Koelreuter had also found that hybrid formation does not normally occur when a plant receives its own and foreign pollen on the stigma at the same time, and he saw that here was another reason for the rarity of natural hybrids.

As an integral part of his studies on hybridization Koelreuter also made a series of precise and highly original observations on fertilization and on the method of transfer of pollen from anther to stigma (pollination). By counting the total number of pollen grains produced in a single flower, and then applying varying numbers of pollen grains to the stigma, he showed that far more pollen grains are produced than are needed to fertilizer all the ovules, and that in favourable conditions one to two pollen grains per ovule suffice to fertilize every ovule. These remarkable experiments were done with *Hibiscus*, in which there are about thirty ovules in a single ovary, and with *Mirabilis*, which has only a single ovule per ovary.[51] The results suggest that one pollen grain fertilizes one ovule but Koelreuter made no comment on this point. He went on to examine whether, in plurilocular ovaries, all the stigmas (which are often divided and may even be borne on completely separate styles) are necessary for fertilization, and found that excision of all but one still permitted every ovule to be fertilized. He makes the point that this only applies to syncarpous ovaries; in apocarpous ovaries (as in Ranunculaceae) each compartment of the compound ovary must have its stigma and style intact.

With the microscope he carefully observed the form of pollen grains and of the stigmatic surface, and watched the behaviour of pollen on the stigma. He concluded that, contrary to de Jussieu, Needham had others, the pollen grains only burst if they take up too much water and that normally they remain intact on the stigmatic surface. He saw in some cases what was evidently the beginning of the outgrowth of the pollen-tube, but did not see or suspect its continued growth into the tissues of the style. The problem was the old one, raised by Camerarius, that the pollen and ovules did not appear to come into contact, yet his own results with hybrids showed that the embryo received elements from both male and female. Koelreuter perceived the double wall of pollen grains (intine and exine) and interpreted the spines and pits present in the exine of some types of pollen as openings through which the male fertilizing substance, which he thought to be of an oily nature, exuded on to the stigma.[52] Here he believed that it met and combined with the female substance that had passed up the style from the ovules. Finally the combination formed by the male and female substances passed down the style into the ovules, where it formed the embryo from which a new plant originated. The actual fertilization was thus assumed by Koelreuter to take place on the stigma. The interesting point about this theory is (as Julius Sachs shrewdly pointed out) that it reflects the chemistry of the day: the combination of male and female fluids gives a product with properties related to but distinct from both, just as acid and alkali combine to form a neutral salt. The linking of fertilization and the development of heritable characters with a material substance—even as vaguely qualified as an "oily fluid"—marked an advance over vital principles and vivific effluvia.

When Camerarius proved the sexual and reproductive function of pollen, he realized that he was raising a new biological problem, that is, how pollen is transferred in nature from the ripe anthers to the stigma, and he discussed this at length. In sum, he pointed to the close proximity of male and female organs in many hermaphrodite flowers, and to dispersal of pollen by shaking and by wind, as the means by which pollination seemed to be ensured in nature. Subsequently several authors (Vaillant, Blair, du Hamel, and others) noticed explosive movements of stamens or anthers in some flowers, and concluded that they helped in pollination. Thereafter the question was strangely neglected until Koelreuter began to look into it properly. He listed the types of pollination mechanism that appeared to exist and observed the phenomena of dichogamy (maturation of stamens and pistil at separate times in the same flower), self-sterility (in *Verbascum*), and movement of the stigmatic lobes in some flowers. Koelreuter's greatest achievement, however, was the discovery of insect pollination. It is true that in 1721, Philip Miller had noticed the transference of pollen between flowers by insects, and there were a few similar isolated observations by others, but Koelreuter established insect pollination, by systematic observation and experiment, as a general feature of whole orders of flowering plants. He described in detail the visits of bumble-bees and other insects to flowers, and the deposition of pollen on the stigma; and investigated the properties of nectar and made clear its role as an attractant. He showed experimentally that in many flowers insect pollination is obligate and cannot be replaced by the wind if insects are excluded, and that it is highly efficient, giving as good a seed-harvest as did pollination by hand. At the same time, he recognized that in some plants insect pollination may be supplemented by other mechanisms. Koelreuter's appreciation of the biological role of widespread insect pollination was very acute. "I was astonished when I first made this discovery, that the reproduction of plants is a matter of chance, a lucky accident. But astonishment changed to admiration of the method—at first sight accidental, but in fact certain—used by the wise Creator to ensure their reproduction." He remarks further that many plants are so dependent on insects for reproduction that if insects perished the plant would perish also.

Koelreuter was quite clear in his own mind about the fundamental theoretical conclusions of his work as a whole. He claimed that facts finally proved the existence of sexuality and hybridity in plants, and the correctness of the old Aristotelean view that reproduction involves both male and female seed. On the other hand his hybrids conclusively disprove the theory of preformationism, that fertilization is merely the activation of a ready-made embryo (either in the ovule or in the pollen grain). The great significance of his work was unfortunately little understood at the time, and his later years were saddened by frustration and poverty. He could hardly foresee the harvest that the future would raise from the seed from his modest garden.[53]

Sporadic progress continued in the study of cryptogamic plants in the second half of the century. A monographic account of seaweeds, *Historia Fucorum* (1768), was published by S. G. Gmelin in St Petersburg, but although containing careful descriptions and accurate illustrations of many marine algae, it added nothing that went beyond the earlier excellent study of *Fucus* by Réaumur.

The most important advances in knowledge of the cryptogams were made by J. Hedwig,[54] who spent many years of his life studying the bryophytes (mosses and liverworts). He laid the foundations for the systematic treatment of the mosses and produced the first classification of this group of plants based to a considerable degree on natural groupings. This work, *Species Muscorum Frondosorum* (1801), published two years after his death, was later accepted as the valid starting point for the nomenclature of mosses. Hedwig showed the close relation between mosses and liverworts, and also defined clearly, for the first time, the characters which separate these two groups. His most significant theoretical results were published in *Fundamentum Historiae Naturalis Muscorum Frondosorum* (1782) and in *Theoria Generationis et Fructificationis Plantarum Cryptogamicarum* (1784), which gave the first complete and essentially correct account of the life cycle of bryophytes, illustrated by the most accurate and beautiful figures of cryptogams yet produced by anyone.[55] It was his correct interpretation of the course of development and reproduction of these plants which enabled him to recognize their close fundamental relationship. Two factors helped Hedwig to success: first, his own technical skill in improving the magnification and optical performance of his microscope (he attained magnifications of almost $\times 300$ and usually stated the magnification of individual figures); and second, the long period of close study of a single group of related plants. In his many figures vegetative parts, leaf cell with chloroplasts, setae, capsules, sexual organs, are all shown, often in section, with remarkable accuracy of detail. He describes the operculum and peristome of the moss capsule (for which his terms are still used) and the four-valved dehiscence of the liverwort capsule. His figures of the antheridia of *Sphagnum* clearly display the accompanying paraphyses, which he called mucilage threads (*fila succosa*); later, he used the term paraphyses to describe analogous structures in fungi. Hedwig equated the antheridial branches with male flowers and the antheridia with anthers producing pollen; he observed the liberation of "corpuscles" from them and assumed that they were male fertilizing elements (he could not have seen the spermatozoids with his microscope). He regarded the archegonial branches as female flowers in which the archegonia correspond to pistils, the neck of the archegonium being equated with a style and stigma. He assumed, but did not actually prove, that "pollen" from the antheridia ("anthers") fertilized the archegonia; he did, however, see the subsequent development of the spore-capsule (the sporogonium) within a calyptra (Hedwig's term) formed by growth of the fertilized archegonium wall.

In both mosses and liverworts Hedwig followed the growth of the sporogonium to maturity and the final production and liberation of spores, which he designated "seeds". He notes that in mosses it could take a year for the formation of the capsule, but that such a delay in "gestation" is to be observed in other plants. The life cycle was completed by sowing the spores. Hedwig did not fail to observe that in mosses the first product of germination is a green filamentous stage [the protonema] with colourless rhizoids, and that new moss plantlets of typical mature form arise as buds from the protonema.[56] Upholding the parallel with flowering plants, Hedwig called the green protonema cotyledons, and the rhizoids radicles. In spite of the pitfalls of analogy, Hedwig made a fundamental clarification of the developmental cycle of bryophytes, a large and very widely distributed division of the cryptogams, and this was a most important advance towards the comprehension of all non-flowering plants. With other groups analogy was bound to lead him badly astray. In ferns Hedwig tried to find male organs on the sporophyte, and increased confusion by pitching on the foliar glandular hairs as anthers; similarly in the horsetails (*Equisetales*) he imagined that the elaters formed from the spore wall represented anthers. Nor could he make anything of the higher fungi although his figures were a step forward in revealing their structure.

In some algae, however, Hedwig provided better evidence of the occurrence of a sexual process. Conjugation in *Spirogyra*, which had been observed by Gaertner in 1788, was figured by Hedwig in 1797 with the comment that it presents at least certain indications of sex. He also illustrated *Chara* and identified the antheridia and oogonia as male and female sexual organs, again by analogy referred to as "anthers" and "pistils" (and also as male and female flowers). More detailed studies of *Spirogyra* were reported by J. P. E. Vaucher in 1803, in *Histoire de Conferves d'Eau Douce*, where he definitely accepted conjugation as a case of sexual fertilization.

The fairly strong evidence for sexuality in bryophytes and algae (and as he thought in other cryptogams too) led Hedwig in 1797 to query the suitability of Linnaeus's name for these plants: the details of impregnation might be hidden but the occurrence of marriage was not. Might not cryptogynum be a better name than cryptogam for such plants? This tentative suggestion was not taken up, but it marks an important development in thought for which Hedwig's careful work gave the impulse: this was the growing conviction that both flowering and non-flowering (cryptogamic) plants shared common methods of reproduction, a conviction which prepared the way for the energetic investigation of structure and development of cryptogams which began in the following century.

The life cycle of ferns, which defeated Hedwig, was not elucidated for another sixty years, but a solid contribution to its eventual understanding was made by J. Lindsay, a doctor in Jamaica, who had kept his eyes open and saw what he guessed to be the germination of fern "seed" on open ground on the forest floor. He proceeded to do simple culture experiments, observed with a microscope, and showed that the "seed" of some eighteen species of tropical fern germinated to form what we now know as prothalli, from which grew plantlets with the characteristic leaves and form of the adult parent fern. Lindsay gave an accurate description of the germination of the spores, and of the growth and appearance of the prothalli as a distinct stage, preceding the outgrowth of recognizable fern plants. He did not discover the sexual organs on the prothalli, but he confirmed Morison's 1699 findings, that the spores of ferns are indeed reproductive bodies, and finally dispelled any lingering doubts on the matter.[57]

The work of Josef Gaertner, an almost exact coeval and close friend of Koelreuter—they were fellow medical students at Tübingen—lay in the conventional field of descriptive botany, but was distinguished by a quite unusual breadth of theoretical outlook. Gaertner was a man of ability and had a varied career;[58] after 1770 he was in sufficiently easy circumstances to devote his life to the self-imposed task of making a comparative study of all known fruits and seeds. For this purpose he visited Joseph Banks in London and C. P. Thunberg in Rotterdam, receiving specimens from them, and also from A.-L. de Jussieu in Paris and from many other sources. The first volume of *De Fructibus et Seminibus Plantarum* appeared in 1788, the second in 1791. This work, which Gaertner sometimes called his "Carpologia", contains finely observed analysis, with related figures, of the structure of the fruit and floral parts of over a thousand genera of plants; it became a source of valuable information which extended the resources of systematics, providing many additional, hitherto unrecorded characters that could be made use of. Gaertner was convinced of the correctness of Adanson's approach to classification. He refers to Adanson on a number of occasions, and considered his own observations as material for advancing and improving the natural classification of plants.

Gaertner's work was well received, especially in France, where its appearance coincided with A.-L. de Jussieu's natural system, whose influence and further development it certainly assisted. Its historical importance springs, however, even more from the introductory chapters where Gaertner discussed some morphological questions in a fresh and luminous way.

The confusion between naked seeds and indehiscent one-seeded fruits was of very long standing, and even such great botanists as Linnaeus and A.-L. de Jussieu were not clear on the distinction (or if they were, had not adjusted their terminology accordingly). Vaillant had come very close to an understanding. Gaertner had studied Vaillant, and quotes his dictum that "no seed can be called naked that possesses a style", but it was the great range of material that he personally examined which enabled him to distinguish the categories of fruit and seed with scientific precision for the first time.[59] He employed the term *pericarpium* in a special but generalized sense to denote the modified ovary (and other floral parts) surrounding the fertilized seeds at maturity, and in this way made clear the true fundamental nature of the fruit. Nature never produced naked ovules or seeds in plants, says Gaertner—it must, of course, be remembered that he is speaking only of flowering plants—but the nature of the pericarp can be very different in different species, one extreme being the exceedingly fine covering of the so-called naked seed. In the case of such seeds the pericarp is often qualified by Gaertner as insignificant (*pericarpium* *nullum*). He was the first correctly to describe the "naked seeds" of Graminae, Compositae, Labiatae, etc. as fruits. This was not simply a minor matter of terminology: the correct interpretation had fundamental consequences for classification, floral morphology, and the study of pollination.

Gaertner threw light on two other areas of morphology. As a result of examining so many seeds and dissecting them, he recognized the endosperm as a definite organ of the seed, distinct from the embryo with its cotyledons, which represents the new plant; he noted that not all seeds contain endosperm, the presence or absence of which is therefore a character of value for classification. It is scarcely surprising that Gaertner, looking almost entirely at mature seeds, did not perceive the distinction between endosperm and perisperm, and used the designation perisperm for both.

In considering the "seeds" of non-flowering, cryptogamic plants, Gaertner made the shrewd observation that they differed from the seeds (*semina*) of flowering plants not just in their minute size but in the absence of a complex organized embryo. To emphasize the difference he reserved the term *gemmae* for the spores of cryptogams (ferns, club mosses, bryophytes, fungi). In the same year Hedwig used the word spore (*sporos*) for these reproductive bodies and it was this term that came to be generally adopted in preference to gemma. It was Gaertner, however, who perceived the fundamental distinction between seeds and spores, and thereby took a not inconsiderable first step towards elucidating affinities within the plant kingdom as a whole.

Pollination of flowers by insect seems to have been widely accepted as a fact of nature, following Koelreuter's observations, without, however, exciting much interest or remark. In 1787 a Lutheran pastor, who worked as a teacher, became fascinated by the process of pollination when he noticed hairs on the petals of *Geranium sylvaticum* and wondered for what good reason the wise Creator had put them there. Christian Konrad Sprengel was an amateur botanist—not even medically trained—but for five or six years devoted himself with complete absorption to examining and recording the relations between flowers and their pollinating insects. He published the results of his quiet observations under the title "Revelation of the secret of nature in the construction and fertilization of the flower",[60] and they were quite revolutionary. Sprengel had read Koelreuter with close attention and understood the importance of his discovery of the preponderant role of insects in pollination; he also understood exactly what was new in his own contribution: he had realized, as Koelreuter had not, that there was more to the matter than chance, even divinely directed, and that "nature had arranged the whole structure of the flower for this method of fertilization". Sprengel was correct. His remarkable analysis of nearly five hundred species showed flower structure to be adapted in the most minute detail to ensure effective pollination, in most cases by insects, although he showed the adaptive features of some wind-pollinated flowers as well.

Sprengel perceived for the first time, and described in accurate detail, all the principal adaptive floral mechanisms concerned with pollination; and he illustrated them by over a thousand engraved figures for which he did the drawings himself. The step-by-step account of how he reached his conclusions, and his descriptions of the structure of individual flowers, still make fascinating and profitable reading; but we must be content to draw attention to the two generalizations which he drew from his work, and which, not at the time but later, profoundly affected biological thought. The first, already mentioned, was the universal occurrence in plants of a most effective and precisely organized form of adaptation, not just to physical factors of the environment (which had long been recognized), but to a set of complex biotic relationships. Ideas of adaptation can be traced back to Aristotle and Theophrastus, but Sprengel's discovery placed the phenomenon in a totally new and unforeseen light. The second generalization related to dichogamy, whose existence Koelreuter had first established. Sprengel noticed that dichogamy—namely, any floral structure or behaviour which favours cross-pollination—is extremely frequent. Since monoecious and dioecious plants, where the stamens and pistils are in separate flowers, are also rather common, Sprengel drew the conclusion that "nature appears not to have intended that any flower should be fertilized by its own pollen". If we replace the "intention of nature" by adaptation, Sprengel's astonishing insight is manifest. Our admiration for this pious and kindly man is all the greater, because he recorded a well-founded generalization from the facts, without trying to explain it by speculation.

The significance of Sprengel's conclusions went beyond the comprehension of botanists at the time; even his facts awakened little interest, and he was so discouraged that a second planned volume on pollination was never published. The information on the biology of insects was welcomed and quoted by entomologists, but botanists almost entirely neglected his discoveries until the subject was re-opened by Charles Darwin.[61]

We now turn to a very different field and to a series of historic investigations, which at long last removed the uncertainty surrounding plant nutrition by revealing the central process on which it is based—the assimilation of carbon from carbon dioxide by green plants in the light. It will be convenient to refer to this process summarily as photosynthesis, although the word was not used until over a hundred years later. The discovery, in principle, of the nature of photosynthesis was one of the greatest scientific triumphs of the age, fraught with technological and theoretical consequences as fateful as those which stemmed from chemistry or electricity.[62] The experiments of van Helmont, Boyle, Hales and others, show how difficult it was to make progress in this question with the existing state of chemical knowledge. The true nature of plant nutrition could scarcely be investigated or understood except in the light of modern chemistry, effectively founded as a new science by Lavoisier between 1786, when he made his decisive attack on phlogiston, and 1789 when he expounded in his *Traité Élémentaire de Chimie* the principles which brought about, in his own words, "a revolution in an important area of human knowledge".[63] The unravelling of the complexity of photosynthesis grew out of, and also contributed to, the formation of the new ("antiphlogistic") chemistry, an interaction of which the full details belong to the history of chemistry. Here it is enough to note that the unravelling of photosynthesis began almost fortuitously from experiments in chemistry, and only assumed the character of an independent plant-physiological problem as the theory and methods of chemistry became adequate for its solution.

In outlining the researches which led to an understanding of plant nutrition I shall use modern chemical names for the elements and compounds mentioned, in order to avoid unnecessary confusion. The reader must, however, bear in mind that Lavoisier did not establish what was essentially modern chemical nomenclature until 1787–89, and that, therefore, Priestley, Ingen-Housz, Senebier, and others, writing before that time, could of necessity only use provisional names reflecting the fog of uncertainty through which the leading investigators were trying, with such brilliant eventual success, to make their way. Thus oxygen was dephlogisticated air or pure air; nitrogen was phlogisticated air, carbon dioxide was fixed or sometimes fixable air, and in mines choke-damp; whilst nitric oxide, which played a key role in the estimation of oxygen, was called nitrous air. I shall also use the word gas in its present-day physical sense, although this usage only became clearly established about 1780.

Historians seem to be agreed that the long and painstaking researches on the nature of gases ("the different kinds of air") carried out by Joseph Priestley from 1767 to 1786 were the experimental foundation on which modern chemistry was built. In the course of this work he made some observations which, at the same time, opened the scientific study of plant metabolism and of the process that sustained life on the earth, and with it, the material fabric of human society. It was appropriate that this beginning should have been made by one in whom the fearless search for truth, for the benefit of all, was the moving force of his being.[64] We shall now examine Priestley's experiments with plants, and the reasons why he undertook them.

Priestley not unreasonably started his exploration of the nature of gases by studying the most familiar, the prototype of all, "common air". When he began, atmospheric air was still generally thought of as a uniform substance, an element, as it had been for thousands of years, although there was already suggestive evidence against so simple a view. Priestley knew of the common observation that air in a closed container was changed by a burning candle, by the breathing of an animal; the residual air, after the candle went out or the animal died, was "vitiated" or "noxious", and no longer supported a flame or respiration. Priestley carried out many such experiments in an inverted vessel over water; in these conditions there was a diminution of about one-fifth of the volume, which he realized was due to the loss of part of the air [oxygen] and the production of fixed air [carbon dioxide] which dissolved in the water and could be detected by the lime-water test, discovered by Joseph Black. He devoted much unsuccessful effort to attempts to "revitalize" or "restore" the vitiated air, that is, to make it once more capable of supporting combustion and respiration: a problem that excited interest at the time. It was in connection with the problem of vitiated air that Priestley was led to experiment with plants. During 1771 he placed a sprig of mint in a glass jar inverted over water, confidently expecting that the air would be vitiated. To his surprise the mint remained healthy and continued growing for some months, but the air "would neither extinguish a candle, nor was it at all inconvenient to a mouse". Thus plants, in contradiction to animals, did not vitiate air even over long periods of time. Priestley at once set about to answer the obvious question: do plants actually restore vitiated air? This time he placed the mint in air vitiated by a burning candle, and found that in ten days the air was completely restored; it once more supported the flame of a candle and the breathing of a mouse. This experiment with mint was done in August and was repeated about ten times with the same result.

In the following summer Priestley carried out more experiments with plants. It is typical of his careful thoroughness that he now prepared the vitiated air in another way, by allowing mice to die in it, although he knew quite well that both burning and respiration remove oxygen (dephlogisticated air) and produce carbon dioxide (fixed air). He also used groundsel and spinach, besides mint, as experimental material, and he found the same result as before—the plants removed carbon dioxide and restored oxygen to the enclosed air. Priestley had revealed some of the essential features of plant metabolism but had not yet fully realized the role of light. He connected the production of oxygen by plants more with growth, which of course depended on light, as common observation showed, than with light itself. Priestley can hardly have failed to recognize the inference from his own experiments that carbon dioxide was the food of plants. This conclusion was clearly expressed by Sir John Pringle in his address to the Royal Society in 1773, when Priestley was awarded the Copley Medal for his researches. In this somewhat high-flown tribute to Priestley, Pringle refers to the winds conveying vitiated air to plants "for our relief, and for their nourishment".[65] In the previous year Pringle and Benjamin Franklin had been witnesses of Priestley's experiments with mint. Furthermore Thomas Percival, a friend of Priestley, took up the question experimentally during the next few years, and showed that the growth of plants was improved by supplying the leaves with carbon dioxide "in a due proportion". Percival concluded that carbon dioxide (fixed air) "may justly be deemed a pabulum of plants".[66] But Priestley was always very cautious in drawing theoretical conclusions—he had a modest view of his own talent, which lay, he felt, in providing well-established facts to excite the curiosity and stimulate the researches of others—and it was some years before he fully accepted Percival's conclusion. His reluctance was bolstered by his own observation that plants died when exposed to pure carbon dioxide, which must therefore be regarded as noxious and not a food.

For some years after 1772 Priestley's researches were on chemical lines; they included the preparation of pure oxygen and led to very important advances. In 1777 he repeated his earlier experiments with plants and began a fresh series. This resumption of work with plants was partly motivated by the fact that Scheele, in the meantime, had obtained seemingly contrary results, finding that germinating seeds caused vitiation of the air by forming carbon dioxide instead of removing it. The contradiction was, of course, only apparent, the result of ignorance of the precise part played by light and chlorophyll. When Priestley in 1778 extended his experiments to various parts of plants and to rooted plants in soil he obtained some contradictory results for the same reasons, but at the same time he stumbled on a simple new technique that was destined to be used by plant physiologists for a long time. By immersing ten sprigs of mint completely in water in a glass jar, he was able to collect the gas bubbles formed by the plants and to show that they were almost pure oxygen. This was clearly a most important and decisive result, since it proved that oxygen was the sole produce of the plant's activity, which his previous methods could only demonstrate with high probability.

Unfortunately Priestley was thrown into temporary confusion by observing oxygen production in glass jars standing in sunlight in which no sprigs of mint had been placed. The cause was soon traced to a "green kind of matter" [an algal growth] on the walls of the jars. It is unnecessary to follow in detail the further experiments by which Priestley, with his usual pertinacity and acumen, established beyond doubt that the green matter was a microscopic plant which entered his vessels in the form of minute "seeds" floating invisibly in the air.[67] He then investigated the growth of the alga and showed that it was absolutely dependent on light. If carbon dioxide were present in the water, he found that the alga caused it to disappear, forming only the purest dephlogisticated air [oxygen].

By 1779 Priestley was thus very close to defining the essential components of photosynthesis, and his letters show that despite his doubts about the role of carbon dioxide as a plant food, he was thinking of "plants imbiding phlogistic matter" as part of their nourishment, and of air being purified by passing through the plant and leaving its phlogiston in the plant as nourishment. It is probable that he would have carried on experiments with plants but for the prior publication of the results of Ingen-Housz, which cleared up precisely the question he was looking into during the same summer.

Jan Ingen-Housz was three years older than Priestley, and he had known him personally since arriving in London fifteen years earlier. Ingen-Housz was born in the Netherlands and had studied medicine at Leiden and Edinburgh; he was a Fellow of the Royal Society, as was Priestley, and was a man of wide interests and thoroughly in the scientific swim. He spent twenty years as physician to the imperial court at Vienna; and the summer in England in 1779, when he did his experiments, was only a break in the long residence in Austria. One wonders whether his interest in plants was awakened by his father-in-law N. J. Jacquin, the distinguished professor of botany in Vienna. Ingen-Housz makes clear in his book that he had read Priestley's work with close attention, and that his own experiments were directly inspired by it. His *Experiments upon Vegetables* was published in the autumn of 1779 and was at once recognized as a very important advance.[68] In brief, he showed that oxygen evolution by plants is absolutely dependent on light and that it only occurs from those parts which are green. This demonstration owed a good deal to his lucky discovery that isolated leaves, immersed in water and illuminated, produce oxygen just as effectively as whole plants or whole sprigs. The proof that light and green tissues are both essential for oxygen production finally cleared up the apparent contradictions and variable results of earlier experiments. Priestley was "much pleased" with Ingen-Housz's experiments and pointed immediately to the salient facts that he had established.

It should be noted that the work was physiological, not aimed primarily at extending chemical knowledge as Priestley's experiments always were; but Ingen-Housz based himself on the latest chemical theory and methods he knew. He gave an explanatory list of chemical terms, which shows his grasp of contemporary knowledge, and lays stress on the use of the eudiometer, regarding it as "perhaps one of the most remarkable inventions ever made; to determine the purity or fitness for respiration of any air"; the discovery of which is "owed to Dr Priestley". The use of Priestley's apparatus, which was both a specific test for oxygen and a quantitative (or at least semi-quantitative) method of estimating it, gave firm chemical support to Ingen-Housz's conclusions.

The principal facts established by Ingen-Housz were as follows. The evolution of oxygen (dephlogisticated air) takes place only in the light and only from the green parts of plants—leaves, petioles and stems, not from roots, flowers or fruit. The evolution of oxygen ceases at once in the dark, but carbon dioxide (fixed air) is produced from all parts of plants, green or non-green, in darkness. The production of oxygen during the day far exceeds the production of carbon dioxide by night. The evolution of oxygen depends on light intensity but not on growth of the plant: it depends on the light but not on the heat of the sun, as Ingen-Housz showed when he raised the temperature in darkness to that attained in sunlight, and found that no oxygen is formed. Oxygen is only produced by living leaves in the light, not by leaves killed by drying or in other ways. Immature leaves are less active in producing oxygen in light than are mature leaves. Oxygen evolution is mainly from the lower surface of most leaves.

Ingen-Housz also proved to his own satisfaction, by experiment, that the oxygen evolved by leaves is not derived from the water itself [that is, from oxygen already dissolved in it; the chemical nature of water was not known until three years later] nor from air already in the leaves. It only arises after having undergone a "purification or kind of transmutation". In this conclusion, which unlike almost all his others is not based on any experimental evidence, Ingen-Housz reveals the main weakness in his work—the absence of any observations on the relation beteen carbon dioxide and oxygen production. He can hardly have been unaware of the growing evidence for the involvement of carbon dioxide and indeed makes some remarks showing his recognition of a cosmic balance between oxygen and carbon dioxide maintained by the activity of plants. It is strange that he so completely neglected this question in his experimental approach, since he had himself confirmed the decisive fact for understanding green plant metabolism—the evolution of oxygen in light and carbon dioxide in darkness.

Ingen-Housz repeated Priestley's investigations with "green matter", using material obtained by scraping the sides of a horse-trough, and finding that it produced oxygen in sunlight. He recognized this matter as vegetable but advanced the theory that it was formed from water by the action of sunlight, a return to the theory of spontaneous generation (*generatio aequivoca*) already abandoned by the vast majority of biologists. This rather strange suggestion by Ingen-Housz led Priestley to undertake the experiments on the subject to which reference was made above.[69]

The impact of Ingen-Housz's book was great and immediate, and it was soon translated into French, German and Dutch. The Paris edition of 1780 was read by Jean Senebier in Geneva, and stimulated him to set about an experimental study of the effect of light on plants, a project which he claims to have had in mind before he knew of Ingen-Housz's work. There is indeed no reason to doubt his statement. Senebier was an amateur, a clergyman who became librarian of Geneva, but his interest in science was quite genuine and deep; he had undertaken formal training in chemistry. His experiments were carried out mainly in 1781 and published in 1782; in the event they were naturally planned in relation to the discoveries made by Ingen-Housz, to whom Senebier pays frank and warm tribute, defending himself for publishing similar results on the grounds that his work contains careful experiments on a new and interesting subject, provides a second witness to facts worth being contemplated twice, and contains some facts which escaped Ingen-housz, as well as some opposing views.

Senebier was a careful observer in matters of fact and an excellent experimenter, but he could be long-winded to exhaustion and sometimes over-speculative in discussion. He took precautions to use healthy plant material and to maintain standard conditions as far as he could; he made quantitative measurements of gas changes and increased their accuracy by simple technical improvements, such as using a more or less conical inverted collecting vessel to which a narrow graduated measuring tube was sealed above. His confirmation of the main results of Ingen-Housz also extended them in a valuable way, because his procedures were in general more critical than those of Ingen-Housz and he explored a wider range of conditions.

The greatest advance made by Senebier was his proof in many experiments that the evolution of oxygen by green plants in light was absolutely dependent on a supply of carbon dioxide, one of the key points whch was not sufficiently examined by Ingen-Housz. Senebier did not establish an equivalence between carbon dioxide supplied and oxygen produced: his experimental conditions, in which submerged plant material absorbed dissolved carbon dioxide, would not naturally lead him to this conclusion or offer a means of quantitative determination. Furthermore, Senebier had made quantitative measurements of the solubility of common air and of carbon dioxide in water, and the far greater solubility of the latter convinced him that it must normally be taken up by plants in solution in water—another reason why he did not think of making measurements by volume. But he showed that a leaf produced no oxygen in sunlight if the surrounding water was entirely free of carbon dioxide, and that the rate of oxygen production was five or six times greater than normal if the water was saturated with pure carbon dioxide. Senebier did not, incidentally, fail to do the control experiment of showing that no oxygen is formed by illuminating water saturated with carbon dioxide but with no leaf present.

For the rest, Senebier added considerably to the precision and generality of what was known. He showed more rigorously that light, not heat, is the factor causing oxygen emission, and concluded that the amount of oxygen formed is dependent on the product of intensity and duration of light. By taking leaves from many species of plants (herbs, trees and shrubs) derived from many habitats (native lowlands, Alpine meadows, the tropics) he proved that photosynthetic oxygen formation is of universal occurrence in green plants, except in very young leaves or mature leaves that are senescent. He noted the formation of carbon dioxide, "by fermentation", in senescent leaves. By more precise dissection of plants than Ingen-Housz had performed, Senebier confirmed that oxygen production in light is strictly confined to green tissues, in fact, to green parenchyma; it does not occur in colourless pith or epidermal cells, or in etiolated leaves.

Senebier was very anxious to be sure that leaves in air behave in the same way as when submerged in water; he carried out many experiments with whole plants kept in containers, above water, to which carbon dioxide was introduced, and obtained evidence of growth and oxygen production, as long as the plants could be maintained in a healthy state. He continued to believe, however, that carbon dioxide always entered the plant dissolved in water, either by way of the roots or drawn off from the atmosphere "with the humidity in which it is dissolved, and for which the leaves are very avid".[70] One experiment has a modern ring: he showed that when branches of water plants, rushes, mint or persicaria, were kept in sunlight in hydrogen, over water containing carbon dioxide, there was an increase in volume of the gas and it became explosive when sparked. Plants kept in hydrogen without any carbon dioxide soon languished.

Finally mention must be made of Senebier's tests with "green matter", undertaken as a sequel to the observations of Priestley and Ingen-Housz. He identified the green matter without hesitation as a plant which had been called by Haller *Conferva caespitosa filis rectis undique divergentibus,* although not described by Linnaeus. The plant required water, carbon dioxide and light in order to grow; and it produced oxygen from carbon dioxide even at temperatures that scarcely rose above freezing point. Its apparently spontaneous origin was an illusion, as was proved by cutting off communication between the experimental vessel and the atmosphere by a mercury seal. When this was done, the water remained sterile for as long as two months, if no *Conferva* were introduced initially, proving the plant came from without in the form of minute air-borne germs.

As a result of the experiments of Priestley, Ingen-Housz, Percival and Senebier, the essential facts of photosynthetic plant nutrition had been assembled by about 1782. The idea of phlogiston was still dominating chemistry, however, and the confusion of chemical theory made rational synthesis and interpretation of the facts almost impossible, and halted profitable investigations in this area for well over a decade. During this time there was intense activity and a complete revolution in chemistry. The new chemistry of 1789 from which phlogiston was banished provided the basis from which physiology could advance again. In the first place there was now a clear language in which the descriptive observations of chemistry could be expressed —the language of chemically defined elements and compounds, applicable to their interactions everywhere, whether in living or non-living systems. The general law on which the new chemistry was built—the conservation of matter, expressed in the chemical equation—gave meaning and emphasis to the use of quantitative methods in investigations of the metabolism of living organisms. Directly connected with the growing understanding of the physics of vaporization and the chemistry of combustion, were Lavoisier's studies of heat and the introduction of the calorimeter by Laplace to measure heat quantitatively. There followed the investigations of Lavoisier and Laplace into animal physiology. By measuring simultaneously the carbon dioxide and the heat produced by a guinea-pig in a calorimeter it was proved that the long-assumed, but vaguely conceived, relation between respiration and combustion was based on a precise chemical reaction, the combination of carbon (and hydrogen) with oxygen, common to both processes, and characterized by the evolution of the same amount of heat in each case.

With the establishment of these fundamental chemical and physical principles, and the fresh insight they permitted, particularly into animal physiology, the way was opened for the elucidation of the key physiological processes in plants. In 1796 Ingen-Housz wrote an essay on the nutrition of plants for the English Board of Agriculture in which he re-interpreted his own earlier results in conformity with the new (non-phlogistic) chemistry.[71] The basis of plant metabolism—embracing both nutrition and respiration—was, however, established by a younger man, educated in a world where the ideas of Lavoisier were already triumphant, although their author had fallen a victim to the great Revolution with which his deepest sympathies lay.

Nicholas Theodore de Saussure was born and brought up in Geneva, a city having traditionally close intellectual links with Paris. The son and personal scientific assistant of a distinguished geologist and geographer, and familiar with Jean Senebier, his father's intimate friend, young de Saussure might seem selected for the task he undertook. Owing to revolutionary disturbances he quitted Geneva in 1790 and spent some time in London, making acquaintance with scientific developments there, before returning to Geneva where he spent the rest of his life, taking an active part in public affairs but devoting his professional time to research in plant physiology. He was officially professor of mineralogy and geology, but gave no formal lectures in these subjects. He was thoroughly versed in the new chemistry, which was the foundation of the methods he used in his experiments, but his outlook was definitely that of the modern plant physiologist, and the range of his enquiry (including soils, composts, mineral nutrition of plants) reflects an impulse from agriculture. It is from about this time we may indeed date the beginning of those attempts, sometimes on a state basis, to apply science to agriculture, which stimulated the rise of plant physiology and related branches of botany during the nineteenth century.[72] De Saussure began his research on plants shortly after returning to Geneva from England, publishing in 1797 an account of experiments on carbon dioxide metabolism, in which the facts concerning respiration and carbon assimilation, and the relation between the two processes, was already clearly stated.

The decisive work of de Saussure was published in 1804 under the title *Recherches Chimiques sur la Végétation*, and consisted of a number of classic research papers which laid the foundation of plant nutrition and of the methodology of plant physiology.[73] The latter point may be dealt with briefly, although de Saussure's work marked an important methodological advance, not only because of the full-scale entry of quantitative physical and chemical methods, but also because he greatly refined and extended the specifically biological technique adopted by Hales. His experiments were also carefully planned with a defined aim and with attention to the maintenance of conditions that are at the same time controlled and consonant with the need to keep the experimental plants normal and healthy. Full use is made of controls, duplicates, sub-samples for determining the state and quantity of the initial plant material, repetition of experiments with different species of plants, and "balance-sheet" experiments. Quantitative results are fully recorded and provide us today with valuable witness to his remarkable accuracy and complete scientific probity; the actual figures which sometimes led him astray show that he never succumbed to the temptation of improving his results. In summarizing his researches I shall not follow the order in which he presented them, nor refer to experimental details unless they have some special interest.

In relation to the gas exchanges of plants, the great advance made by de Saussure was to exhibit the isolated facts, already known in outline, as the proof of a complex but integrated interchange of matter between the plant and its surroundings, essential for its life and growth. The liberation of carbon dioxide by plants he recognized as the equivalent of respiration in animals, investigated by Lavoisier. During the germination of seeds (peas, beans) de Saussure found that oxygen disappeared and was replaced by an equal volume of carbon dioxide, as Lavoisier had shown by the combustion of carbon. The loss in dry weight of seeds was greater than would have resulted from loss of carbon only, and he concluded that some of the hydrogen must have been lost as well. Respiration was not only carried out by every part of the plant, as Ingen-Housz's observations had indicated, but was absolutely essential to maintain every part in health and activity. He showed that seeds required oxygen for germination and for further growth and development, that roots of intact plants died if kept in nitrogen or hydrogen, even though the shoot was in air and light, and that whole plants only survived when deprived of oxygen if their leaves were left on and they were exposed to light. An atmosphere of nitrogen and carbon dioxide proved unfavourable to plants: they appeared to require some free oxygen. Many quantitative experiments with detached leaves kept in the dark convinced him that these organs respire continuously, but that their respiration is concealed by the simultaneous assimilation of carbon dioxide in the light.

Respiration was thus established as a process as essential to the life of green plants as to the life of animals, a botanical—and biological—fact of the greatest significance. De Saussure assumed that the function of the process must be the same in plants as in animals "to procure a liberation of caloric [heat] by the union of oxygen with the carbon of the plant". Such a liberation of heat is a necessary result of the combination of oxygen and carbon; but it often escaped notice in plants by reason of the small quantity of heat evolved and the opposing effect of transpiration.

De Saussure was the first to demonstrate the photosynthetic assimilation of carbon by green plants. He used five different species in the experiments. Plants were enclosed in glass vessels containing ordinary air to which known volumes of carbon dioxide were added, and were then exposed to sunlight for several hours. He measured the disappearance of carbon dioxide and the appearance of additional oxygen quantitatively by means of the eudiometer, and determined the increase in dry matter and carbon content of the leaves during the period of the experiment. The increase in carbon content was determined by carbonizing the plant material at high temperature in a closed iron crucible from which air was completely excluded. De Saussure thus proved by direct chemical methods that fixed carbon appears in the leaf simultaneously with the disappearance of carbon dioxide from the surrounding atmosphere and its replacement by oxygen: a brilliant feat of critical experimentation. Repeatedly in these experiments he found that the dry matter fixed corresponded to roughly twice the weight of carbon fixed. Since there was no increase in dry matter if the leaves were illuminated in water without carbon dioxide, he concluded that carbon assimilation from carbon dioxide always involves the fixation of water as well. This discovery is a remarkable tribute to his experimental skill and scientific acumen.

If one looks closely at the results of his gas analyses it is evident that they showed the uptake of carbon dioxide and the evolution of oxygen clearly enough, but were not sufficiently accurate to show their equivalence: the amount of oxygen formed was generally lower than carbon dioxide taken up by the leaves, and there was often a small apparent rise in nitrogen.[74] Hence de Saussure thought that some of the oxygen of the carbon dioxide was possibly assimilated also and that some nitrogen was liberated from the tissues, in proportion to the carbon dioxide decomposed. These mistaken suggestions arising from imperfect techniques cannot detract from de Saussure's immense achievement in establishing experimentally the central facts of carbon assimilation in light.

In other experiments de Saussure proved that leafy shoots with their stalks in distilled water assimilated large amounts of carbon from the free atmosphere. This was a particularly important observation since it disproved Senebier's belief that the main source of carbon dioxide to plants was in water absorbed by the roots or in dew absorbed by the leaves.

De Saussure also removed confusion concerning the injurious effects of carbon dioxide on plants by showing that artificially high concentrations of the gas (he used 7 to 8 per cent by volume in air) which stimulated growth in the light were adverse to the germination of seeds and to mature green plants kept in the dark.

In one matter de Saussure fell into a serious misconception. He recognized that non-green tissues do not assimilate carbon but thought it

> . . . not necessary to infer that green colour is either an essential character of parts decomposing carbon dioxide or the necessary result of that decomposition, since the red variety *Atriplex hortensis* produces in five or six hours as much pure oxygen (containing only 15% nitrogen) as the green variety.

De Saussure had used the microscope to see that microscopic organization of seeds appeared the same whether the initial swelling in water took place in the presence of oxygen or not; it is therefore extraordinary that he failed to note that the red colour in *Atriplex* leaves is confined to the cells of the epidermis and that the mesophyll is green. This oversight on the part of a man so highly regarded engendered doubts which unfortunately persisted for a long time, even though the link between green tissue and carbon assimilation was accepted as the general rule.

After establishing that carbon, the main component of the substance of plants, comes entirely from the atmosphere (except for minimal amounts through the roots), de Saussure considered the source of other elements found in the plant body. Only oxygen and carbon dioxide are known to be absorbed from the air: his own experiments showed that gaseous nitrogen is not absorbed, although nitrogen is an essential component of every part of the plant (wood, extracts, green tissues) as it is of both flesh and bones of animals. Therefore nitrogen, and the salts, earths and metals found in the ash, must enter the plant in aqueous solution through the roots; and he showed by extremely careful experiments that silica in fine suspension did not enter plants at all during the period of a month, although it is a common constituent of plants, which it must therefore enter in solution. In experiments repeated each year for five years de Saussure grew beans, peas and cress in very pure washed sand through which abundant distilled water was allowed to flow. Growth was very limited, and although the plants usually managed to flower the seed never ripened. He concluded from this that although the salts normally taken up by plants from soil only account for a very small proportion of the dry matter formed "they have as nutrients, despite their very small quantity, a very powerful influence on growth".

De Saussure carried out a further series of experiments in which he measured, by precise chemical methods, the rate of uptake of various salts and mixtures of salts from solution. He used whole, rooted marsh plants, because their roots are accustomed to immersion, and before the experiment began kept them for a few days in distilled water until their roots started to elongate, in order to be sure that he was using healthy plants. The roots absorbed salts and water together, the salts less rapidly in proportion than the water, unless the roots were excised, when the total solution was drawn into the plant. Plants do not absorb all substances present in solution in proportion, but selectively;

he thought that the less viscous solutions are absorbed in greater quantity.

Finally de Saussure made the most accurate and extensive series of analyses of the ash of plants yet attempted, besides surveying the information already available on the subject. The most important elements of ash he found to be salts of potassium and sodium, phosphate of calcium and magnesium, silica, carbonate of calcium, silica, oxides of iron and manganese; many others were present in amounts too small for analysis. All the elements of ash are present in soil and, in greatest proportion, in soil extract; the elements in the ash of a plant are nearly always related to those in the soil in which it is grown. Seeds contain the same amounts and proportions of the elements as plants in the first stages of vegetation; younger tissues contain higher amounts of phosphorus than older tissues. De Saussure drew no conclusions from this survey but simply presented the facts as a contribution to the further study of the mineral nutrition of plants, of which his physiological experiments had laid the theoretical foundation. Two omissions may be noted. De Saussure did not mention sulphur among the mineral elements, nor did he investigate the form in which nitrogen is absorbed, merely suggesting vaguely that it may be supplied by ammoniacal extracts of animal or vegetable matter in the soil.

The laconic résumé of plant nutrition given by de Saussure[75] at the end of his researches recorded the completion of a revolution in botany which led to a vast extension of its field of enquiry during the nineteenth century. The *Recherches Chimiques sur la Végétation* marked the advance of plant physiology from the simple exploration of facts to the status of a science, with its own basis of integrated theory and specific methodology.

Some important changes beginning to affect science as a whole can be detected, at least in embryo, in the investigations of plant metabolism with which we have been dealing. The link with the larger revolution in chemistry reflects a movement towards unity and interdependence of the separate sciences which from this time forward was continually strengthened by the growth of unified technology in the most advanced industrial countries. At the same time industrialization drew many more people into scientific research, at first as "amateurs", like Senebier, Ingen-Housz and Priestley himself, but later increasingly as professionals and specialists like de Saussure. The literary sources of the time reveal in addition a host of minor experimenters—in botany as in other fields—whose work was known to their greater contemporaries and doubtless contributed to progress but is now forgotten. This expansion of science led to the appearance of specialized journals of science in the late eighteenth century, normally concerned with a limited field and acting as the means of rapid communication between individual researchers and as the immediate repository of their results. These journals did not replace the long-established transactions and proceedings of the academies, or the individually produced memoir or monograph, but they supplemented these forms of publication, and acquired a specific and indispensable function in the advancement of science whose importance steadily increased. The first specialist journal devoted to botanical science, the *Magazin für die Botanik,* appeared in 1787 in Zürich; in 1791 it became the *Annalen der Botanik,* and a year or two later publication was transferred to Leipzig, where it continued to appear until 1800. This journal published original research papers and communications, abstracts from other publications, general articles, reviews of books, new items; it included material on every aspect of contemporary botany, giving marked attention to plant physiology.[76] It played a considerable role in the development of botany in this period, and was the harbinger of the botanical journals which proved so powerful a factor in the progress of botany, especially in Germany, in the following century.

No historian of the subject can omit the unique incursion into botany of Johann Wolfgang Goethe, nor avoid the issue of his essay (the description was his own) on the metamorphosis of plants, an essay on botanical theory by an amateur who discovered no new facts about plants but who happened to be one of the most intelligent men of his day, and a writer and poet of supreme genius as well. The fundamental question is whether Goethe had a significant influence on botany, and this I shall try to answer as directly as possible.[77]

Die Metamorphose der Pflanzen (1790) was Goethe's attempt to provide a theory of plant morphology. It was derived from simple observations on flowering plants such as every field botanist could make, and some greenhouse experiments which he carried out during one whole summer and which showed that the development cycle of annual plants from germination to fruiting could be lengthened or shortened, or otherwise altered, by changing external conditions.

Goethe recognized the homology between cotyledons, foliage leaves and the floral parts; and was impressed by the regular change of successive organs during ontogeny, and by the occasional irregular production of abnormal forms, seemingly intermediate between foliage leaves and floral parts, facts which gave additional support to the idea of morphological homology.

This view was not an entirely original discovery: Goethe himself noted with pleasure that C. F. Wolff[78] had expressed similar ideas thirty years earlier, speaking of the floral parts as modified leaves, and it can hardly be doubted that other botanists were thinking along the same lines.[79] However, Goethe was the first to express what became a much debated concept in plant morphology, and he deserves to have it recorded in his own words.

> Whether the plant produces leaves, flowers or fruit, it is always only the same organs which, in manifold determinations and often in changed forms, fulfil nature's demands. The same organ which on the stem is extended as a leaf, and has assumed a highly complicated form, is contracted together in the calyx, extended again in the petal contracted in the sexual organs, only to extend itself for the last time as the fruit.
>
> (*Metamorphose*, 115)

Many years later Goethe quotes Robert Brown, whom he called "this acknowledged greatest of botanists", as saying that he (Brown) "holds all floral parts to be modified leaves", and Goethe accepts this as a succinct and useful statement of the essence of his own doctrine. But Goethe's original formulation, quoted above, was more logical and accurate, and shows that he had a very clear understanding that homology of the adult form is based on a deeper homology of developmental processes and their interrelations during ontogeny. Goethe saw that the term "modified leaf" used by Wolff is in principle misleading because no actual leaf can be said to become, for example, a petal: the reality is that a common initial process can be modified so as to go to different final ends. A new word is required for the morphological reality: if all the organs of the vegetating and flowering plant are viewed in terms of one, namely the leaf, then says Goethe, "it is obvious that we really need a general word with which to designate this organ, which exhibits so many different forms, and by means of which we may compare all the forms it takes." (*Metamorphose*, 120).[80]

The passages I have quoted show that Goethe had an inductive, materialist conception of morphology, based on the concrete processes of development of the plant. The relation between the mature form and the process by which it arises, between morphology and ontogeny, was central to his thinking.[81] But his fundamental notion of "laws of transformation" by which nature can produce "the most varied forms by modification of a single organ" (*Metamorphose,* 3), went much further than the recognition of an intrinsic feature of ontogeny to which little attention had yet been given (important as this was): the production of varied forms by modification was connected by Goethe with the transformation of living organisms in the course of descent, a transformation which he regarded as something highly probable, if not certain.[82] In other words, his view of modification—or "metamorphosis"—included modification during evolution, and thus linked comparative morphology with phylogeny.

These ideas, clearly implicit in the *Metamorphose* and developed more fully and plainly in his later comments on it, add up to a coherent attitude which represented his mature convictions. But Goethe's protean nature did not make for scientific or philosophic consistency; despite an unshakable materialism at bottom, he was not immune to idealist–speculative trends of thought, especially current in Germany, which gave the language of the *Metamorphose* a certain enigmatic and ambiguous quality. There is throughout the work a deep and unresolved confusion, arising from the use of metamorphosis in two meanings never distinguished: to denote a real phylogenetic process in time, and to express the abstraction in thought of a morphological category from a series of forms with common features. This contradiction in Goethe's thought, or at least in his expression of it, was in conflict with his own deepest apprehension of reality. The effect was to make it possible for readers to draw very divergent conclusions.

Late in life Goethe collected together many references to the *Metamorphose* during the forty years after its appearance. No one who studies this material can doubt that the work made a great impression on botanists and was widely discussed. Its formulations were certainly taken up in their more equivocal and idealist sense by the academic nature-philosophers in Germany and France, and inspired some really appalling nonsense. Goethe himself protested that H. F. Link had reduced metamorphosis to meaningless abstraction. In my opinion Goethe's influence on botany was, on balance, positive and far greater than has generally been admitted. He evidently regarded the "foliar" nature of the floral parts as the kernel of his doctrine, and this was what struck his contemporaries. Whatever limitations and refinements we might now put on the statement that the floral parts are modified leaves, it was published at a juncture which made it an illuminating and fruitful new concept. Great progress had been made in disinguishing the form and function of the various organs of the flower. When, therefore, Goethe emphasized that they are not, nevertheless, organs *sui generis* but homologous parts, it was a valuable contribution and stimulus to the further analysis of the nature of the flower: at the same time it also opened the eyes of botanists to the significance of comparative morphology, a field of investigation already being explored in animals, and which was soon to lead to great theoretical advances in the study of plants. Goethe appears to have been the first to use the term morphology, and there is no doubt that he did a great deal to show the perspectives opened by comparative morphology, and the need to base it on detailed investigations of development and not on adult form alone. In 1822 a reviewer remarked with approval that, in contradiction to that of Linnaeus, Goethe's developmental view of the plant organism contained within it a definite "genetic" concept of species, that is, acceptance of "the transformation of one plant into another". It is evident that Goethe also played a modest part in strengthening the rise of evolutionary thought.

The great theoretical advance in biology during the eighteenth century was the definition of the principles, and the techniques, of natural classification by affinity, a process in which botanists unquestionably played a key role, perhaps because plant classification was felt to be more difficult than that of animals, since plants seemed to present fewer diagnostic features, a view often expressed, from Cesalpino onwards, and repeated even by Lamarck. Once relationships within the plant and animal kingdom were no longer a matter for intuition but could be analysed and established by strict scientific methods, the profound implications of natural classification, already apprehended by a few, were brought into the open. Two fundamental ideas thus emerged from embryo to become the future guide-lines for biology—the physiological unity of all living organisms no matter how apparently diverse in form, and the transformation of living organisms during descent. It was as if, in biology as in human affairs, revolution completed the work of enlightenment.

The new theoretical principles of biology were first completely expressed—in a way revealing their origins with remarkable clarity—by J. B. Lamarck in his *Philosophie Zoologique* (1809), the first fully committed statement of evolution by a distinguished and professional scientist.[83] It is not necessary to discuss this famous work at length, but a few words about its relation to botany are in order. We must remark to begin with that Lamarck was himself one of the great botanists of his time, and that his treatise on botany in the first four volumes of the *Encyclopédie Méthodique* (1783–93) had already done a great deal to advance botany to the status of the integral discipline which it became in the following century. It is not surprising, therefore, although it seems often to have been overlooked, that the *Philosophie Zoologique* drew very heavily on botanical knowledge and evidence to support its most essential ideas. In the first place Lamarck used the existence of affine relationship, for the analysis of which he goes back specifically to Adanson, A.-L. Jussieu and the natural classification of plants, as one of the leading and most convincing arguments in favour of evolution. He repeats, in slightly different words, Adanson's definition of affinity, as those features of analogy or resemblance between two objects compared in their totality; and adds that affinities indicate a sort of kinship between the living bodies which show them. Further, "the perception of the importance of affinities was the origin of the attempts in the last few years to determine the natural method, which is only tracing by man of *nature's proceeding in bringing her productions into existence.*" Lamarck says specifically that it was through the study of affinities [i.e. Adanson's method as elaborated on plants] that he was led to make the changes in animal classification proposed in *Philosophie Zoologique*—and which were in fact a considerable advance towards a more natural classification of animals.

Much of the evidence for the actual transformation of species, a process which he accepted must be very slow and therefore not readily observed, Lamarck believed could be found in plants, and instanced among others, Koelreuter's hybrids, the intergrading species of many plant genera (e.g. *Fucus, Carex, Poa, Piper, Euphorbia, Erica, Hieracium, Solanum* etc.), the well-known changes of plants under cultivation and in gardens, and the fact that cultivated wheat *Triticum sativum* is never found in nature. Lamarck has often been criticized for his hypothetical assumptions on the effect of use and disuse as a source of variation in animals: it is interesting that he left the origin of variation in plants more open, merely implying that the environment brings about changes. "If the seed of a grass of a damp meadow is transferred to a hillside, then after growing there for a time, on dry, almost barren ground on a mountain side, after a number of generations it will have become so altered that botanists would erect it into a separate species."

In his generalized account of the evolution of living organisms on the earth Lamarck stressed that growth is the basic property that unites them all, simple or complex, plant or animal. It is growth which, under the influence of changed conditions, gives rise to different kinds of production and greater complexity of organization. This was an important statement of the physiological and evolutionary unity of behaviour of plants and animals. Lamarck did not, however, understand the great advances made by de Saussure in plant physiology, because he never accepted Lavoisier's chemistry; hence his attempt to relate the physiology of animals and plants in a more detailed way was not successful.

The *Philosophie Zoologique* opened a new epoch in the comprehensive science of "living bodies" foreseen by Lamarck, and given by him the name biology. In this historic work the highest theoretical achievements of botany during the eighteenth century were a creative and essential element.

Notes

1. The word evolution in eighteenth-century biological literature was synonymous with preformationism (see Note 22, Chapter 7).
2. The rise of comparative philology is an example outside natural science. That languages change and develop, that relationship between them may be evidence of divergence from a common origin, were evolutionary conceptions which initiated the scientific study of languages, differing completely in its aim and methods from the work of the ancient grammarians.
3. The Enlightenment had its roots in the efforts of the bourgeois classes in

various countries of Europe to destroy the power of the landed aristocracy and the remains of feudal order. It drew inspiration from the political and economic theories of England and Holland where the bourgeoisie had gained effective supremacy, but intellectually was the product of France where the Third Estate had still to win power. In consequence, the Enlightenment became, as its opponents then and later well understood, the ideological preparation for the French Revolution. French philosophers, writers and scientists attacked ignorance, obscurantism and blind authority in the name of reason, science and social progress. The men of the Enlightenment were especially concerned with the purpose and mode of development of society and its institutions, and to many the industrial and material progress of England in particular seemed to be a living model of social change according to natural law. The spectacle of changing human institutions opened their eyes to evolutionary change in the world of nature.

4. The concept of evolutionary development in time was brought to life again by the Enlightenment. Understood by the Ionian philosophers, and later by Epicurus, it was lost during the Middle Ages and replaced by the apprehension of time as a sombre union of transience and stability. Thus Boethius (in Chaucer's translation): "It is certain and established by lawe perdurable, that no-thing that is engendered is stedefaste ne stable."
5. The direct knowledge of more primitive peoples and forms of society, discovered during exploration and colonization, had a profound effect in stimulating evolutionary thinking by scientists of the Enlightenment.
6. The name of the new science, geology (géologie), was proposed by J. A. de Luc in 1778.
7. In his book *De Solido Intra Solidum Naturaliter Contento,* based on studies in Italy, Steno recognized the true nature of fossils and put forward clear ideas on the deposition of geological strata from water, the beginning of stratigraphy, on which the whole science of geology may be said to be founded. Steno was an ardent convert to Roman Catholicism and there seems no doubt that his recognition of the conflict between the conclusions arising from his researches and the doctrine of the Church, was an important factor in his decision to abandon science in favour of his ecclesiastical vocation.

   Ray met Steno at Montpellier in 1665.
8. Ovid, *Metamorphoses* Book 15: "Vidi ego, quod fuerat quondam solidissima tellus, / Esse fretum. Vidi factas ex aequore terras / Et procul a pelago conchae jacuere marinae."
9. It was suggested that fossils were formed by internal growth by some plastic force (*vis plastica* or *vis lapidifica*) in the same way as crystals or stalactites, or were produced from minute seeds or rotting plant remains which penetrated the rock through minute fissures.
10. Ray wrote to his geologist friend Edward Lhwyd: "I am inclined to think that they are vestigia or impressions of plants themselves. . . . Yet . . .

there follows such a train of consequences as seem to shock the Scripture-history of the novity of the world; at least they seem to overthrow the opinion generally received, and not without good reason, among Divines and Philosophers, that since the first creation there have been no species of animals or vegetables lost, no new ones produced."

11. G. L. Leclerq, Comte de Buffon (1707–88), was the unquestioned leader and organizer of French biology of the Enlightenment; something of his contribution to the general progress of botany is dealt with in the text. He was exactly of an age with Linnaeus, of whom he became very critical, regarding him, not without some justification, as destroying the observed continuity of nature by artificial divisions and "systems". A full account of this dispute is given by P. R. Sloan in *The Buffon–Linnaeus controversy. Isis* **67**, 356–75 (1976). It had very little, if any, effect on the course of botanical history. Buffon's criticisms of Linnaeus were often neither clear, consistent, nor fair, and the details seem to me to have only minor interest. At bottom, Buffon was protesting, sometimes a bit illogically, at Linnaeus's static view of nature, and clearing the way for the new ideas that came to dominate biology, first in France and then in the rest of Europe.
12. The conception of geological time was prepared in the first volume (1749) of Buffon's *Histoire Naturelle*, which deals with the theory of the earth and its development in time under the influence of natural, still existing processes. This was followed by the historic *Époques de la Nature* (1774). Buffon suggested 75,000 years for the age of the earth, a figure based on his calculations of its rate of cooling, but in his manuscript notes he extended the estimate to 3 million years; he considered that the "more we extend time, the nearer we are to the truth".
13. It was doubtless the existence of the mule and the hinny which caused Buffon to include his postulate of evolution at this point. His difficulty was the apparent fixity of the species observed in nature.
14. The only equivocation in this passage is the use of the conditional "if" which can be interpreted in three ways: as a means of self-protection, as an expression of genuine doubt, or as indicating the need to look for experimental evidence.
15. See Diderot: *Rêve de d'Alembert* (1769).
16. La Mettrie's work was published in Berlin whither he had betaken himself to avoid attacks from the religious hierarchy in France who disliked the open materialism of *L'Homme Machine* (1747). I think that by 1753 Buffon must have read *Système d'Épicure* but it would need closer investigation to be sure. La Mettrie in his book refers to Buffon's new and ingenious hypothesis, but by this he means Buffon's belief that there exists a special kind of organic animated matter diffused through all

animal and vegetable substances, serving equally for their nourishment, growth and reproduction. This suggestion appears in the second volume of the *Histoire Naturelle* (1749).

17. There can be no doubt of the big effect of the *Système d'Épicure*. It was immediately (1751) published in London in English translation, without the author's name and with an exculpatory preface, thus disavowing La Mettrie's notoriety and profiting by it at the same time. It was published in Amsterdam (with La Mettrie's other writings) in 1751, 1752, 1753 and 1764, and once more at the end of the century, in 1796, in Berlin.

    Another, less complete, sketch of evolution was given by Maupertuis in his *Système de la Nature* (1751), where he speaks of the possible occurrence in individual organisms of repeated variations from which would have arisen the infinite diversity of organisms seen today.

    This is not the place to do more than mention the observations on human heredity made by Maupertius, and the brilliant anticipations of post-Mendelian genetic theory which he drew from them. Unfortunately this work was unappreciated at the time and fell into oblivion.
18. Evolutionary thought was not absolutely forgotten; occasional recollections can be traced even during the Middle Ages. See R. E. D. Clarke: *Darwin: Before and After* (1958).
19. Several of the botanical articles in the *Grande Encyclopédie* are from the hand of Daubenton; they deplore the fact that botanists waste too much time on nomenclature, i.e. on use of specific and generic descriptive epithets, instead of concentrating on complete systematic description (this was before the Linnean reforms), and on studies of the method of cultivation of plants, and of their properties and behaviour. Special attention is given to methods of transporting exotic plants, so that they can be introduced elsewhere.
20. Buffon had studied botany and medicine at the university of Angers. In 1734 he translated Hales's *Vegetable Staticks* into French. Most of his researches between 1734 and 1740 were concerned with botany and forestry. He reported on the tensile strength of timbers at the instigation of the French navy, and published a work on the culture of forests.
21. Almost all the great figures in French botany of the eighteenth century, and many lesser ones, were associated with the Jardin du Roi or the Muséum d'Histoire Naturelle. Among the directors were Tournefort, Antoine de Jussieu, Buffon (1739–88) and Antoine-Laurent de Jussieu, whilst Vaillant, Bernard de Jussieu and Lamarck worked there. Adanson had a post in the Académie des Sciences, but there were always close connections between the Académie and the Jardin.
22. *Novus Character Plantarum* (1720), published posthumously.
23. The following branches of the de Jussieu family tree will help to make clear the relationship between the botanists among them (in italic)

Laurent (1651–1718) of Lyon
(M.D., M.Pharm., 16 children)

- Christophe (1685–1758) (Pharmacist, botanist at Lyon)
  - *Antoine-Laurent* (1748–1836)
    - *Adrien* (1797–1853)
- *Antoine* (1686–1758)
- *Bernard* (1699–1777)
- *Joseph* (1704–79) (Explorer)

A few words may be added about Joseph, not mentioned in the text. He was trained in medicine and joined a South American expedition (1735–43) as physician and naturalist. He sent living and dried plants to Paris. Antoine-Laurent made use of Joseph's collections from which he founded a number of new genera. Joseph played an important part in early studies on *Cinchona*. He did not return from America until 1770.

24. He evidently observed the liberation of antherozoids from the microspores, and as he had previously seen the bursting of pollen grains in water, he concluded that he was seeing the same thing. Hence he equated the microspores with pollen (male elements).

    The megaspores formed embryos and must therefore represent ova or female elements. During germination the gametophyte in these heterosporic ferns develops as a small beak protruding from the megaspore. De Jussieu saw this and thought it represented a stigma without a style. His identification of the megaspore with a pistil was thus eminently reasonable.

    De Jussieu lays stress on his discovery that the sporocarp (which he calls "capsule" or "shell") is not a fruit as previously held, but a flower, since it contains male and female organs, stamens and pistils. His claim is quite justified in terms of contemporary knowledge. His observations and analysis of the situation were masterly.
25. The evidence comes from a thesis by one of his students, N. S. Blot, published in 1747. For details see F. Stafleu: *Linnaeus and the Linneans*, p. 277. I have not myself been able to see this thesis.
26. It is worth noting that Bernard de Jussieu explicitly rejected the imaginary medical properties of plants—the alleged heat, coldness, or fermentation. See his preface to the 1725 edition of Tournefort's *Histoire des Plantes qui Naissent aux Environs de Paris*, which he edited.

27. The distinguished Russian botanist Timiriazev wrote somewhat poetically: As if to justify its name, the natural system first saw the light not in the dust of a library nor the pages of a Latin folio, nor among the dried leaves of a *hortus siccus*, but living, open to the sky and the spring sunshine, in the beds of the Trianon garden.
28. Antoine-Laurent trained as a doctor, taking his M.D. at Paris in 1770, but was immediately appointed as assistant to Lemonnier, who was court physician to Louis XV and also Professor of Botany at the Jardin du Roi. The young de Jussieu was virtually acting professor from the beginning, although not appointed professor officially until 1793; his entire life was thus devoted to botany.
29. According to A.-L. de Jussieu, in *Mémoires de l'Académie des Sciences* (1774), the system was "less perfect" than that of the Trianon, because some exceptions were included. He notes that some features from Tournefort were incorporated (divisions based on the petals, e.g. apetalae, monopetalae, polypetalae) and other features from Linnaeus (divisions based on characteristics of the stamens). Linnean nomenclature was adopted.
30. He removed Linnaeus's sixty-fifth order (corals and madrepores) because he had shown that these are animals.
31. Adanson's book contains much more than the title indicates. The prefatory chapters include a highly original survey of the whole field of botany which must have been as valuable and stimulating at the time as it is interesting today. Adanson shows a keen knowledge of the literature: a revealing point is that he stresses Camerarius's experimental evidence for sexuality in plants, to which Linnaeus (and many others) paid less than due attention.
32. Adanson (like Buffon and many French botanists of the Enlightenment) tended to use the word system to mean an artificial classification based on *a priori* selected characters, and to use the word method for either artificial classification based on a limited number of characters taken from nature, or for natural classification based on all possible characters. Method, by its practical overtones, emphasized for Adanson the inductive–experimental way of looking at systematics. Present-day usage is different: system tends to have a wider meaning, and the distinction between system and method is not keenly felt. I have not tried to follow Adanson's usage.
33. Adanson here introduces a physical analogy. Physicists cannot treat things only in relation to attraction or gravity, but must consider the totality of mechanical principles; similarly botanists must consider all parts together.
34. The debt was not all on Adanson's side, however; Buffon in the *Histoire Naturelle* cites many observations on Adanson's authority.
35. Some proponents of "numerical taxonomy", for example, have adopted

the term Adansonian to refer to their methods. Numerical taxonomy is obviously one valid and doubtless useful method of approach: it can provide some of the many possible sets of characters than can be used in classification. But this is only the beginning of the Adansonian method, and is on the same level as any other method for accumulating the initial observations.

36. F. A. Stafleu: Adanson and the "Familles des plantes". In *Adanson*, (G. H. M. Lawrence, Ed.), Vol. 1, pp. 123–264 (1963).
37. The "rediscovery" of Adanson dates from 1960 when his manuscripts and library, till then in family possession, came into the market and were bought by the Hunt Botanical Library, which staged an international symposium on Adanson and his work in 1963.
38. In 1824, towards the end of his life, A.-L. de Jussieu gave an account of the principles of the natural method of classification of plants, in an article in the *Dictionnaire des Sciences Naturelles*. He mentions Magnol, Linnaeus, Bernard de Jussieu and Adanson, as the principal founders of natural classification by their delimitation of families, and recognizes his own work as completely based on theirs.

He considers that Bernard de Jussieu's arrangement of families was the best and most natural. Linnaeus did not attempt to place his families in a natural arrangement. "Adanson shows similar drawbacks, but his family diagnoses are very detailed and show many happy conformities [*rapprochements*], and their arrangement is not so distant from present admitted principles as that of Linnaeus's *Fragmenta*, although one cannot recognize on what basis it is founded." De Jussieu notes correctly that Adanson did not characterize his delimitation of families explicitly, and adds, somewhat enigmatically, "this omission, combined with other causes, probably prevented this work [i.e. *Familles des Plantes*] from being adopted by botanists living at that time." He also remarks that it is surprising that Adanson, who knew the arrangement of families at Trianon, did not profit by it.

In treating natural classification de Jussieu adopts in all essential ways the position of Adanson, basing classification on the use of total affinity, with subsequent weighting in the light of experience, but he discusses much more fully the general principles by which the relative value of characters may be judged. He also gives special attention to the endeavour to define higher natural taxonomic groupings, whereas Adanson only tried to place related families in proximity.

I do not know that we are called on to judge A.-L. de Jussieu's behaviour in relation to Adanson but I will venture a comment. It is evident that de Jussieu had not for Adanson the warm affection and veneration he felt for his uncle Bernard, but I do not believe that he meant to be unfair to Adanson's scientific achievement. To de Jussieu it must have appeared that Adanson was to a great extent using Bernard's methods, and de Jussieu's own philosophic limitations (remnants of essentialist thinking to which we drew attention in the text) would tend to blind him to the really decisive advance—the complete break with essentialism—made by Adanson.

39. M. Adanson: Examen de la question si les espèces changent parmi les plantes; nouvelles expériences tentées à ce sujet. *Mémoires de l'Académie des Sciences* 383–419 (1769).
A. N. Duchesne: *Histoire Naturelles des Fraisiers.* Paris (1766).
40. A curious example of his limitations is that he did not unite lichens with fungi in his classification, although his uncle Antoine de Jussieu had demonstrated their close relationship long before.
41. Expeditions from France brought plants from the Levant, Syria, Lebanon, North Africa, French Guiana, the Pacific Islands. De Jussieu also received plants from Sir Joseph Banks.
42. Seventy-six of A.-L. de Jussieu's one hundred family names are now conserved under the International Rules of botanical nomenclature. According to Stafleu, de Jussieu took eleven family names from Linnaeus, forty-six from Bernard de Jussieu, six from Adanson, and used thirty-four names for the first time.
43. Even in relation to the division according to cotyledons he gives a curiously tortuous argument to prove that the number of cotyledons is an essential characteristic, because it is involved in the plant's development. Ray had been quite clear that the significance of mono- and dicotyledony lay in their respective association with contrasting character-complexes.
44. Linnaeus: *Philosophia Botanica* (156). Filum ariadneum Botanices est Systema, sine quo Chaos est Res herbaria.
Adanson would have written *methodus naturalis* in place of *Systema.*
45. Basically this flow of information resulted from the exploitation of the new techniques of nomenclature (Linnaeus) and classification (Adanson and A.-L. de Jussieu), sustained by the influx of new species from the world flora. It was summed up by the descriptions and magnificent plates of plants in the *Encyclopédie Méthodique* (1783–1823) for the early volumes of which Lamarck was responsible, and which became the standard work on systematic descriptive botany for a long time.
46. For a fuller discussion of the role of German universities in the eighteenth century and later, see W. H. Bruford: *Germany in the XVIII Century* (1935).
47. There was, naturally, another reaction: some recoiled from theory altogether and stuck to the gathering of facts. Some of the popularity of botany, and of the Linnean sexual system, in late eighteenth-century Germany may have been connected with this, as Goethe's fascinating account of botany in Weimar suggests.
48. That Koelreuter took up this question is an interesting example of local scientific continuity. R. J. Camerarius had been professor at Tübingen. S. G. Gmelin, the son of a Tübingen apothecary, trained in medicine at

Tübingen, and then after spending fifteen years in Russia at St Petersburg, returned to his native town as professor of botany. In his inaugural lecture in 1747 Gmelin dealt with the evidence for hybrids in plants in the light of Camerarius's *Epistola*, which he re-published (in 1749), with the text of his own lecture. In the lecture Gmelin expressed the view that long years of experiment would be required to establish with certainty the existence of plant hybrids, and for the present he leaves the question open. Koelreuter entered the university in 1748 and graduated in 1755, the year of Gmelin's early death. He must have been a student of Gmelin and was clearly fired by the latter's enthusiastic admiration for Camerarius. Gmelin could not have known Camerarius personally since he did not enter the university until three or four years after his death, but the memory and teaching of Camerarius would still be very much alive.

49. Koelreuter wrote acidly: "The plants boldly claimed as hybrids by some recent botanists can from this point of view only be qualified as premature births of an over-excited imagination. How can they present them as hybrids before they have been produced by the most reliable experiments?"
50. This view was based on his own experience. He had observed many intermediate forms (hybrid swarms) between *Nicotiana paniculata* and *N. rustica* when the two species were growing close together. This was an additional reason for his belief that species formation by hybridization did not occur in nature: the hybrids were usually sterile as well, and would reconvert to the parental forms by back-crossing.
51. Koelreuter's patience and experimental skill are shown by his results. In *Hibiscus* he counted a total of 4863 pollen grains in a flower, and found that only fifty to sixty are required to ensure that all the thirty or so ovules in the ovary are fertilized. With fifteen to twenty pollen grains he found that ten to sixteen ovules were fertilized, but using less than ten pollen grains no seeds matured. These results were obtained at the best time of the year. When the weather was cooler, later in the season, considerably more pollen was required to get complete fertilization.

    In *Mirabilis* only one to three perfect pollen grains were required to fertilize the single ovule.
52. He examined the pollen of many plants and found that each species has its specific form of pollen, and that closely related species usually have similar pollen, but that there are some marked exceptions to the rule.
53. The metaphor is sadly ironic. His experiments in the gardens of the Markgraf of Baden were subject to the ill-will and the interference of the gardeners. After the death of the Markgräfin, who supported him by her personal interest, Koelreuter gave up in despair and transferred the work to his own small private garden.
54. J. Hedwig (1730–99) trained as a doctor in Leipzig and then spent twenty years in medical practice in Chemnitz before returning to Leipzig in

1781, where he remained for the rest of his life. Hedwig was led to an interest in mosses by the gift of a microscope and some botanical books from J. C. D. Schreber, Professor of Botany at Erlangen, who was a former student of Linnaeus. After 1789 Hedwig became Professor of Botany and Director of the botanic garden at Leipzig.

55. The *Theoria* is actually a slightly modified version of the *Fundamentum*, rather hastily put together as a prize essay in a competition organized by the St Petersburg Academy of Sciences. Hedwig published a second edition of the *Theoria* in 1797 containing some additional information and plates.
56. Hedwig made it clear that he was not the first to get a new plant from sowing the spores of mosses: he mentions that C. Meese had done it with *Polytrichum commune* in 1767.
57. This was still said to be a matter of doubt in the *Encyclopaedia Britannica* (Third Edition, 1797). Lindsay's work was published in the *Transactions of the Linnean Society* **2**, 93–100 (1794). Lindsay was a former student of Professor John Hope of Edinburgh to whom he first communicated his observations before they were published.
58. J. Gaertner (1732–91) was the son of a court physician and was early orphaned. After taking his M.D. at Tübingen he travelled to Italy, France and England, and attended Adrien van Royen's botanical lectures at Leiden. He was subsequently Professor of Anatomy at Tübingen and Professor of Botany at St Petersburg; he travelled in the Ukraine and described many new plants. In 1770 he returned to his native town of Calw to write his great monograph on fruits.
59. Gaertner's precise characterization of the nature of the fruit will be clear from the following brief passage translated from the introduction to *De Fructibus*.

    "Pericarpium is a special name of the fruit by which not only is the determinate form of the mature ovary expressed, but above all its difference from the naked seed is indicated. Hence the containing-wall (*conceptaculum*) formed from a single mature ovary is generally called a pericarpium, because the seeds within it are hidden, and their actual form cannot be seen unless they are liberated from within the containing-wall."

    "Nature never produces either a naked ovum or a naked seed in plants. [There is simply a gradation] to the extremely thin covering (*ad tenuissimam cuticulam*) of a so-called naked seed."

    Gaertner did not realize that naked seeds do exist, not in flowering plants, but in conifers and in gymnosperms generally. He includes the seeds of *Pinus* and other conifers among fruits, assuming that they possess a very thin pericarpium.
60. *Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blume*. Berlin (1793).

    Poor Sprengel devoted so much time to the details of pollination that he·was forced to resign his post of Rektor (headmaster) at Spandau for neglecting his duties.

61. M. Proctor and P. Yeo: *The Pollination of Flowers*, p. 26 (1973).
62. Once carbon assimilation was understood in principle, the clarification of the remaining aspects of plant nutrition was more straightforward. This first and most difficult step led to the adoption of rational manurial techniques in agriculture, the use of artificial fertilizers, and their industrial production on a vast scale: a technological revolution with incalculable effects on the progress of human society. At the same time the theoretical basis was established, on which physiology and ecology could develop as independent methods of investigation within plant science as a whole.
63. The transformation of chemistry into practically a new science was an almost direct result of the industrial revolution, the "take-off into self-sustained growth", which most economic historians consider began during the 1760s and accelerated remarkably in the 1780s. The necessity of bringing chemical research to the study of industrial problems was pointed out in his *Philosophical Commerce of Arts* (1763–65) by Dr William Lewis, who was known to Priestley.

    It is of special interest in relation to the history of botany, to note the extent to which the theoretical reconstruction of chemistry depended on evidence from experiment and research in plant and animal physiology. To examine this dependence in detail is, however, beyond the scope of a note.
64. F. W. Gibbs: *Joseph Priestley: Adventurer in Science and Champion of Truth* (1965), gives a sympathetic and discerning account of Priestley's life and work. It is particularly valuable in showing how his unshakable integrity was founded in deep attachment to progressive principles in religion and politics, an attachment which gave him the reputation of a dangerous agitator in some quarters and brought him both persecution and distress.
65. In his speech Sir John Pringle clearly suggests the existence of a world-wide circulation in which sunlight, vegetation, the atmosphere and the ocean, all play a part, a hint of what we should call today the carbon cycle. One must assume that this idea of a cosmic circulation expresses Priestley's own surmise, or at least that he had discussed such an idea with Pringle.
66. Thomas Percival (1740–1804) was one of the first students at the famous Dissenter's Academy at Warrington, where Priestley became a tutor just at the time that Percival completed his studies there and moved on to do his medical traning at Edinburgh and finally at Leiden. Percival became a life-long friend of Priestley. Percival spent his life in medical practice in Manchester, where he founded the Manchester Literary and Philosophical Society in 1782; he was active in promoting legislation to improve sanitation and public health.
67. The decisive finding was that the alga never grew in fresh-distilled water

exposed to the sun, if access of air was blocked by a mercury seal; there had to be an open connection to the atmosphere for algal growth to occur.

68. The full title of Ingen-Housz's book was: *Experiments upon Vegetables Discovering their Great Power of Purifying the Common Air in the Sunshine and of Injuring it in the Shade and at Night.*
69. Priestley seems to have been very disturbed by this theory of Ingen-Housz which he thought completely wrong-headed. In 1803, after settling in America, he went to the trouble of repeating his experiments, confirming his earlier results. The work was published eventually in the *Transactions of the American Philosophical Society* (1809).
70. This idea reflects the view of Charles Bonnet that plants absorb dew from the undersides of their leaves. Bonnet (1720–93) had discovered parthenogenesis in aphids and became, in consequence, a proponent of preformationism. He made some excellent observations on insect metamorphosis and on regeneration in lower animals. Later in life he tried to investigate the behaviour of plants, but was without any critical experimental talent, as Julius Sachs pointed out, and his reputation only gave longer currency to some confused ideas, but did not advance botany. He wrote extensively, and his contemporaries regarded him as a considerable philosophical thinker. It seems to me that he had an eclectic propensity for reflecting many disparate intellectual tendencies of his time, both progressive and retrogressive, without much tangible effect; his inconsistency defeated his occasional shrewdness. Bonnet adopted Buffon's hypothesis of a special universal "living matter" (see Note 16, above) and combined it with a "catastrophic" theory of development of the world and organic creation.

    Senebier knew Bonnet personally and much admired the older man.
71. This essay was translated into German in the same year by Alexander von Humboldt.
72. The demands on the science of botany that began to be widely voiced at the end of the eighteenth century, are exemplified by the remarks of Henry Hume, Lord Kaimes, cousin of David Hume, in *The Gentleman Farmer*: "After much labour bestowed on botany, and many volumes composed on that subject, it appears very little advanced above infancy: no other science has made so slow a progress. I praise the diligence of our botanists: some of them have great merit. But as far as I understand, their study has been mostly confined to give names to plants, and to distribute them into classes; not by distinguishing their powers and properties, but by visible distinguishing marks. This is an excellent preparation for making a dictionary: but it leaves us in the dark as to the higher parts of the science, such as are the most proper to engage a thinking and rational mind. . . ."

    "Were we acquainted with the nature of different plants, we should be able to account for the difference of size, of leaves, of roots, of colour, and of seed. We should also be able to explain why some plants spring early, some late: why some are adapted to a hot climate, some to a cold; why some thrive best in dry soil, some in wet; why some produce flowers before leaves; and why some never shed the leaf."

"This speculation opens a wide field for observation and experiment, that may worthily employ the most acute philosophers."

73. It was a sign of a new phase in the growth of science that de Saussure's first experiments were published (in 1797) as a paper in a scientific journal, the famous *Annales de Chimie*.
74. De Saussure employed potassium sulphite or phosphorus to absorb the oxygen. The reaction is slower than that between nitric oxide and oxygen which Priestley had used, and one may guess that absorption of oxygen was not always complete.
75. He lists the main nutrients of plants as water, carbon (in greater quantity from the carbon dioxide in the atmosphere than from any other source), nitrogen, salts and earths.
76. The *Magazin für die Botanik* was published four years before *Curtis's Botanical Magazine* (London), which is sometimes said to be the first botanical journal. The *Magazin* also covered the whole field of botany whereas *Curtis's* only provided fine illustrations of new plants.
77. The immense literature of comment on Goethe's essay prompts the immediate answer, that it obviously made botanists think about plant morphology.

    A translation of the *Metamorphosis* into modern English by Agnes Arber will be found in *Chronica botanica* **10**, 67–124 (1946).
78. C. F. Wolff (1733–94) trained in medicine at Berlin and Halle. After service as an army surgeon during the Seven Years War, he lectured in the medical faculty at Berlin but came into conflict with the professors and in 1764 accepted an appointment in the Imperial Academy at St Petersburg. He remained working in Russia until his death. His chief work is *Theoria Generationis* (1759) in which he defended epigenesis and attacked preformationism. In 1768 he published observations which conclusively showed the epigenetic course of development of chick intestine.

    His work on plants is in *Theoria Generationis*: he tried to continue the work of Grew and Malpighi on plant tissues but his techniques were much inferior to theirs, and nothing of value emerged. The only positive feature of his investigations was that he raised the question of how new cells are formed in the growing parts. He thought that new vesicles and vessels [the two cell-types recognized by Grew and Malpighi] arise between older ones.
79. Goethe refers to collaborative work with A. J. G. Batsch, who was Professor of Botany in Jena (1761–1802).
80. The term phyllome has been used by some modern plant morphologists very much in the sense proposed by Goethe.

81. In 1817 Goethe quoted, with approval, C. F. Wolff's insistence "that organic development must be accurately [i.e. microscopically] observed, and that the history of the mature part must precede any description of it."
82. A passage written in 1819 will show Goethe's approach to the evolution of plants (and he had, of course, similar ideas about animals).

    After speaking of the triumph of "physiological metamorphosis" in which families, genera and individuals are split, divided and transformed, he continues: "This activity of nature goes on to infinity; it can neither rest nor remain unchanging, yet not everything it produces can be preserved or maintained. We have indeed the most definite relics of organic creatures which could not immortalize themselves in living reproduction. On the other hand there constantly develop from seeds diverging plants which organize the relation of their parts differently, of which reliable observers have told us a great deal, and will certainly bring more to our knowledge as time goes on."

    "How important all these considerations are, we may finally be convinced when we once more recall how families are separated: for here again, how close are formation and malformation. Who could blame us if we called the Orchidaceae monstrous Liliaceae."

    In the *Geschichte meines botanischen Studiums* (1817) he wrote: "The variability of plant form, the specific course of which I had followed for a long time, brought me to the conception that the plant forms around us were not determined and established in the beginning, but rather that they were given, besides a stubborn generic and specific permanence, a fortunate mobility and flexibility, so that in the many conditions affecting them over the face of the earth, they are able to adapt and transform themselves accordingly."

    Goethe states that while thinking about the *Metamorphosis* he was helped by discussions with Herder about the development of organic creatures since the beginning of the world.
83. As is well known, Erasmus Darwin put forward a remarkable outline of evolution in his *Zoonomia* (1794). Many people believe that Lamarck had read Erasmus Darwin. It seems almost impossible that he could not have done so, in view of the enormous popularity of *Zoonomia* and its speedy publication in French, German and Italian; and Darwin may well have helped Lamarck to shape his own ideas. But Lamarck's acquaintance with the idea of evolution and with evidence supporting it began thirty years before Darwin's book and, as we have seen, can be traced to Buffon and Adanson.

9

Establishment of a Unitary Theory of the Structure and Life Cycle of Plants (1809 to 1851)

If we are to describe what a body is, the whole cycle of its alternations must be studied; for the true individuality of body does not exist in a single state but is exhausted and displayed only in this cycle of states.

Hegel (1830)

At the beginning of the nineteenth century science in Europe was held back for a time by the constraints of war and the political reaction which followed, but well before mid-century there began an expansion and acceleration of scientific activity on a scale hitherto unknown. It was connected with the growth of industrial capitalism, the aftermath of the French Revolution and of its social and economic gains, which the Napoleonic conquests had helped to bring to many parts of Europe. Industrialization tended to link science more closely with technology, and this in turn gave an impetus to scientific research and education, and in the long run caused a fundamental change in the position of science in the economy. From being a fortunate, but merely adventitious, bonus in improving industrial and agricultural methods, science became an indispensable element of production.[1] The technical problems of production influenced the internal progress of the pure sciences. The concurrence of many disparate processes in industrial production helped to break down accepted mental barriers between the sciences and to foster wider generalization, whilst within each science the interplay of various processes presented itself in the form of new fields of specialized enquiry, extending the scope and deepening the content of each particular science.

Botany was caught up in the general expansion of science, and though less directly affected than chemistry,[2] physics, or geology, it too was influenced by the growing involvement of science with technological change. Before considering the progress of botany in detail, it will be useful to glance at the broad deployment of botanical effort in the nineteenth century.

The leading position of French science in the eighteenth century was established still more firmly by the Revolution. Irrespective of chãnges in their political aims, the successive revolutionary and post-revolutionary governments systematically increased state support for all branches of science.[3] Old institutions were reformed, and new ones set up in order to improve research, training and education in science; and during the Napoleonic era these set the pattern of scientific organization in Europe wherever French arms or influence extended.

Botany and plant physiology constituted one of the ten sections into which the Mathematical and Physical Class of the Institut National (replacing the old Académie des Sciences in 1795) was divided. Each section consisted of six salaried members; and botany had therefore the same status as mathematics, physics, chemistry, geology, or anatomy and zoology.[4] At the Jardin des Plantes, reconstituted as the Muséum d'Histoire Naturelle in 1793, the number of professorships was increased to twelve, three being in botany, and facilities for research and teaching were extended. The existence of these institutions raised botany to a new level of scientific and economic importance in France.

The perspectives of science at the dawn of the nineteenth century were still those of the Enlightenment, but its new status and professional organization were the legacy of what Goethe called "the splendid French Revolution". It was in Germany, now breaking out of its long political and economic stagnation, that the new role of science was most fully realized. The defeat of Prussia by Napoleon at Jena, in 1806, and the formation of French-controlled states on the Rhine, opened Germany to French influence. The twin flood of industrialization and nationalism was still only in its first beginnings, but already the expansion of science was seen as the key to progress. The existing state-supported universities were injected with new vigour; efforts were made to fill the professorial chairs in science with the most capable men; new chairs were created and the first university laboratories for teaching and research in science were built. The University of Berlin was founded in 1807–10 by W. von Humboldt—brother of Alexander von Humboldt, the greatest German scientist of his time—with a strong science faculty, and it set the pattern of organization and development for universities throughout Germany and the world. In addition, polytechnics (technische Hochschulen), modelled on the École Polytechnique in Paris, were established in a number of German cities.

Thus began the remarkable expansion of science in Germany which was to rival that in Britain and overtake that in France. In botany Germany soon assumed a leadership which was maintained unchallenged for a century. Although progress in botany, as in other sciences, now came increasingly to depend on the work of numerous professional scientists in more than one country, the high quality and sheer volume of German botanical research was outstanding, and was matched by the intellectual eminence of a number of leading German botanists who made fundamental advances in almost every branch of the subject.[5] By contrast, official botany in Britain stuck largely in the groove of floristic and systematic studies, and the recording of the wealth of plants accumulated from Britain's vast colonial empire.[6]

Turning to the detailed progress of botany, the very outset of the nineteenth century was marked by a revival of interest in the internal structure of plants, which proved to be of the greatest significance. From this revival originated an increasing number of investigations, based primarily on the microscope, extending into, and linking together, many related aspects of the life forms and processes of plants. This became the most important field of botanical research during the first sixty years of the century, and the results led to a completely new understanding of form, structure and development in the plant kingdom as a whole.

The subject of plant anatomy had fallen into neglect after Grew and Malpighi; in the whole of the eighteenth century almost nothing had been added to their work, except for the researches of Hedwig mentioned earlier. In his attempts to disprove preformationism and establish the case for epigenesis (*Theoria Generationis* (1759), German version, 1764), C. F. Wolff used evidence from both animals and plants, and studied plant material microscopically for himself. His

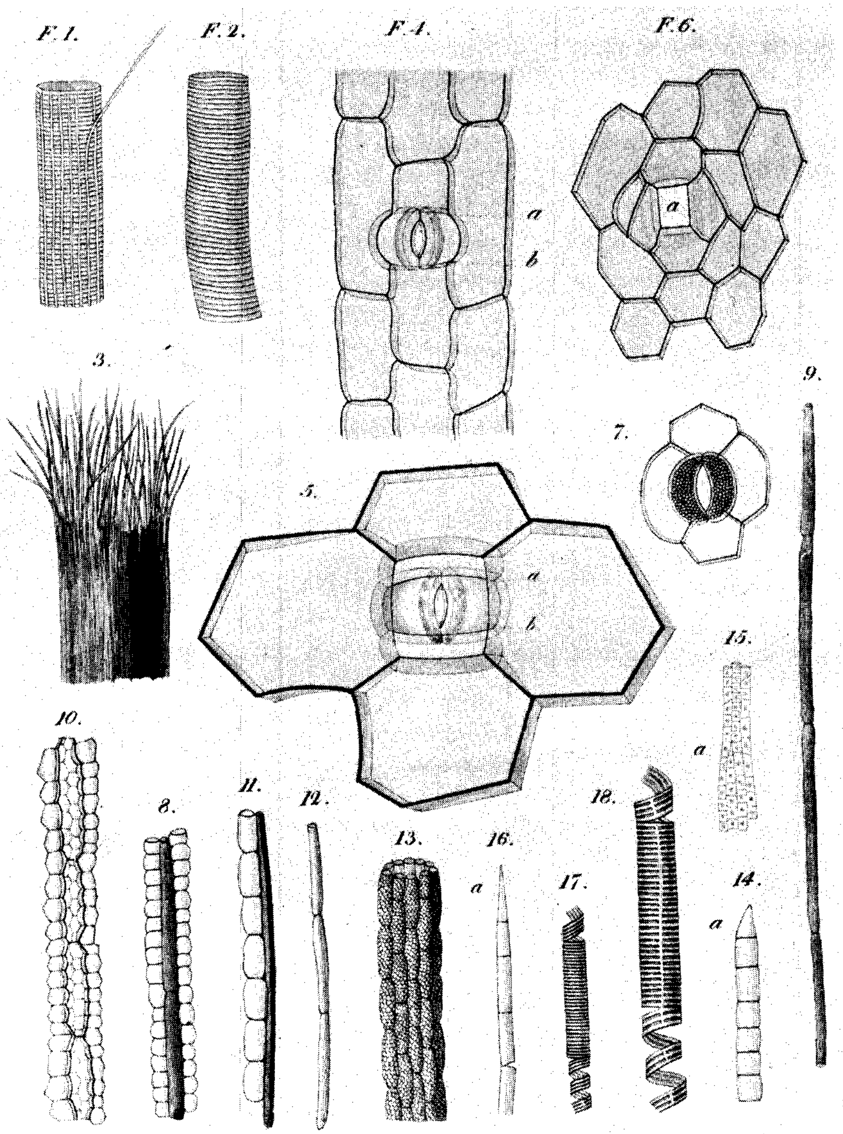


Figure 20 Cells of maize isolated by Moldenhawer by maceration. *Beiträge zur Anatomie der Pflanzen* (1812).

observations were poor and show nothing that was not better and more fully illustrated by Grew, to whom, and to Malpighi, he refers. Wolff's discussion was, however, well argued and theoretically important; botanically it had the merit of drawing particular attention to the meristem or growing point as the region where new cells and new organs (leaves) evidently arise.[7] Now Grew had observed the origin of new leaves around the growing point far more accurately, and stated quite clearly that new cells (bladders) must be "generated" there, but his technique did not allow him to see how this happened and he refrained from guessing. Wolff dared to guess—his figures are quite worthless—and developed a theory that the living plant body consists of homogenous gelatinous material at the growing apices, and that within this small bubbles of liquid arise and gradually enlarge. At first there is a thick mass of gelatinous ground substance between adjacent bubbles, but as they expand this becomes thinner and eventually forms the single thin wall which Wolff considered to exist between the mature cells; the cells are, however, in connection by pores. The details of the theory are of little moment; its historic interest is that it stimulated the French botanist C. F. Boisseau-Mirbel to a general investigation of plant structure, the first attempt at a comprehensive study since the work of Grew and Malpighi. Probably another reason for the renewed interest in plant anatomy was a series of technical improvements in microscopy between 1780 and 1800. Achromatic lenses began to be introduced about 1800, and the use of thin glass cover-slips, enabling tissues to be observed immersed in water or other fluids, instead of in air, was gradually adopted.[8] The effect of these advances was not dramatic, for the main problem of spherical aberration was still unsolved, but there now seemed the possibility of making further progress in a field that had come to a dead end.

Mirbel proposed a view of cell formation in plants[9] in 1801 that was very similar to the theory propounded by Wolff, and in 1802 published a general account of the mature cells and tisues of plants in his

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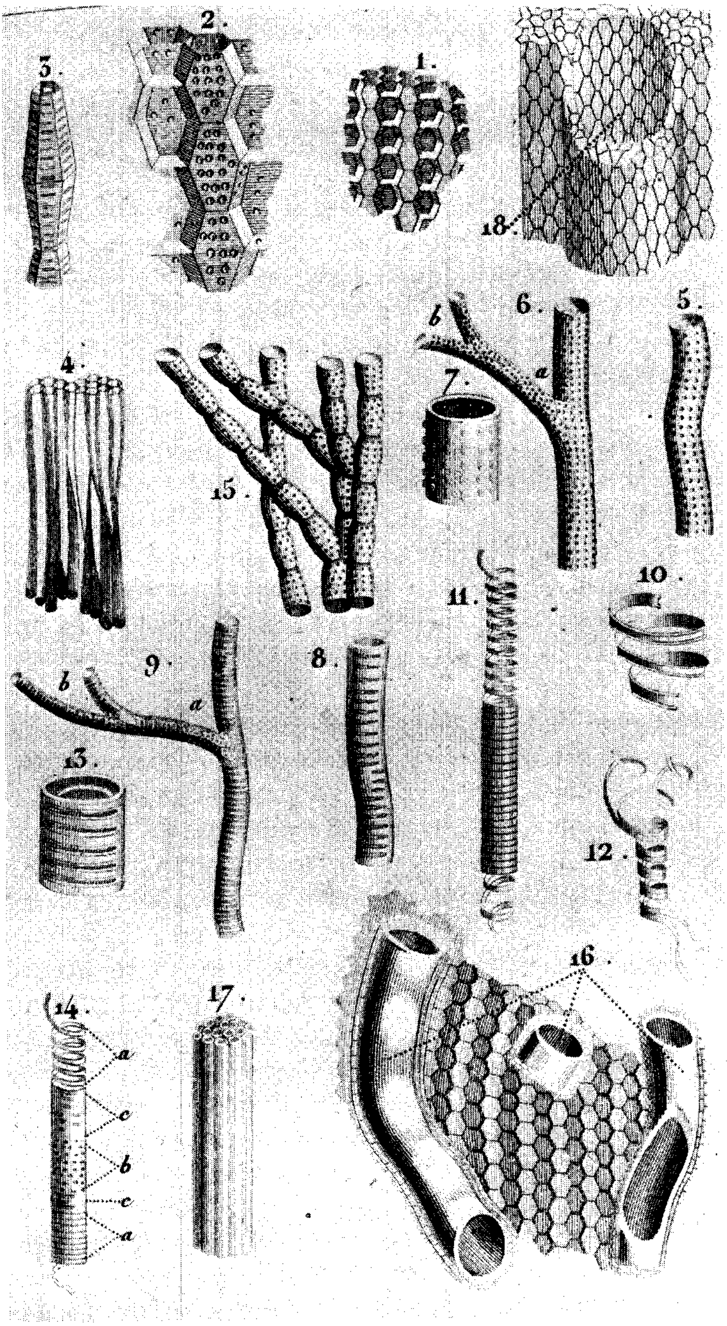
Figure 21 Plant cells figured by Mirbel in *Elémens de Physiologie Végétale* (1815): "Elementary organs, seen with the microscope, considered hypothetically as being distinct and separate from the surrounding tissue".



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Traité d'Anatomie et de Physiologie Végétale. This work excited great interest and was followed by quite an outburst of anatomical researches by French and German botanists, accompanied by much controversy about the results. In spite of their efforts, progress was slow because of the technical limitations of microscopy. Mirbel was without doubt a balanced and unprejudiced observer, but the figures in his earlier papers are certainly no advance on those of Grew. The difficulties of interpretation facing these early students of plant structure are shown by his long-held opinion that the spiral thickening of xylem vessels represented a hollow tube spiralling through the tissues with only the ends fixed, or by Sprengel's belief that starch grains were vesicles which expanded to form new cells. Starch grains were indeed a constant source of misconception, until the discovery of the starch–iodine reaction in 1824 made them the most easily recognizable object in plants. This first period of investigation of plant structure was therefore one of considerable confusion, sometimes made worse by unchecked speculation inspired by the *Naturphilosophie* of Schelling.[10] Yet there was at least active interest in the field and from the uncertainty and controversy some basic facts and concepts were slowly established.[11]

Obervations by L. C. Treviranus in 1806, confirmed Grew's suggestion that xylem vessels arise from columns of elongated cells by dissolution of the transverse walls. Treviranus also made out the true nature of spiral (helical) thickening in xylem vessels, and from this he saw that vessels with other types of thickening (pitted, scalariform, reticulate) must be formed independently and not by the transformation of spirally-thickened vessels, as H. F. Link, K. Sprengel and others imagined to be the case. The key advances in the knowledge of plant structure in this first period were undoubtedly made by J. J. P. Moldenhawer, who published the results of eighteen years of research in 1812.[12] He was a most careful observer who was able to free himself from the influence of older ideas more readily than his contemporaries; in addition he discovered and used a new technique of investigating plant structure, that of maceration. Supremely simple—for it merely consisted in keeping plant material in water until it began to disintegrate and could be broken up completely by gentle pressure—the technique answered a number of questions troubling plant anatomists of the time. During maceration the middle lamella (the common connecting wall, usually very thin, formed between new cells arising by division) is dissolved and the whole tissue can be completely dispersed into individual cells. Every cell, including the elongated fibres, to which Moldenhawer paid laborious attention because their cellular nature had been denied by Link[13] and others, could be seen to be a separate unit completely enclosed by a continuous wall without visible pores.[14] Only mature xylem vessels appeared as open tubes, but these had been shown by Treviranus to arise from cells, and maceration clearly confirmed this and enabled many details of their structure to be seen.

Moldenhawer thus provided concrete evidence that the mature plant body is built up entirely of cells, of varied shapes and sizes, each with a complete wall without pores: a most important conceptual advance. He emphasized that this view is quite distinct from the mature structure implied by Wolff's theory of cell formation, in which there can be only a single common wall between adjoining cells, whereas observation shows that each cell has its own wall, so that even the thin adjoining walls of paranchyma cells are actually double.[15] It is rather strange that Moldenhawer did not explicitly consider the problem of how cells are formed initially in development, since he denies that they arise within other cells as Wolff and Mirbel suggested. He realized that there must be a thin layer which cements adjoining cells together, and thought he could see a tissue of very fine threads between cells. His figures give no evidence that he really observed the middle lamella, but his belief that such a layer existed was correct. Although Moldenhawer recognized in general that cells have gelatinous or fluid contents, his attention was primarily directed to the form of the wall, and this was the essential element in his view of the cells.

Other advances followed from the combination of maceration and microscopy. Perhaps the most significant was his descriptive analysis of the vascular bundle, showing that several distinct types of cells are regularly associated within it. From this he was led to make a fundamental distinction between ground tissue (parenchyma) and vascular tissue, a concept which broke sharply away from the ancient division into bark, wood and pith, and proved very illuminating in the investigation of vascular plant anatomy.

At a more detailed level, Moldenhawer was the first to give a basically correct account of secondary thickening and the formation of annual rings in dicotyledons. He recognized that the cambium is cellular (Grew had been unable to make out its true nature), and that the tissue and cells of the wood, including the medullary rays, are formed internally, and those of the bast externally, from the cambial ring. This was a key advance in the clarification of the process of secondary thickening, even though the mode of origin of new cells was left uncertain; the prevalent view (held by Link, for example) was that the bast underwent hardening and transformation into wood on the inner side. Moldenhawer was emphatic that new tissues always remain in the position where they are first formed, a penetrating observation, the truth and significance of which took a long time to be fully appreciated by plant anatomists.[16] He noted the difference in diameter of vessels of spring and summer wood, defining the annual rings, and the absence of annual rings in the wood of tropical plants, whose vegetation is uninterrupted. Of special importance was his clear recognition that in dicotyledons, the structure of vascular tissue and its manner of increase by cambial activity follow essentially the same pattern in herbs as in trees.

Moldenhawer also correctly interpreted the stoma, showing that it was not, as thought, a pore in the wall of a single cell, but consists of two cells with a space or orifice between them. The structure was later confirmed in leaf-sections by Treviranus (1821) and Amici (1824). The opening and closing movements of the stomatal pore had been discovered by A. Comparetti in 1791.

The work of Moldenhawer seemed for a time to have exhausted the technical possibilities for further progress in elucidating plant structure; Moldenhawer himself published no more and turned to fruit-tree culture. In 1817 botanists were made aware of a hitherto unknown activity of plants, when L. C. Treviranus (in collaboration with his brother) reported protoplasmic circulation (cyclosis) in the cells of a species of *Chara*. This was, in fact, a rediscovery, for B. Corti had already published an account of the phenomenon in 1774,[17] but his work had apparently been unnoticed. Corti's observations were indeed more thorough than those of Treviranus, for after the discovery of cyclosis in *Chara*, he published a second paper two years later, describing its occurrence in the leaves of many higher plants, both aquatic and terrestrial. He used slices of healthy leaf-tissue mounted in water, and notes that patience is required. It seems that either Treviranus's technique or his patience fell short, for he failed to observe cyclosis in many leaves he tried. However, within a year Amici had seen cyclosis in the leaves of several plants and in stigmatic hairs, and its frequent occurrence soon became an accepted fact.[18] Since its discovery, cyclosis in plant cells has remained a strangely isolated phenomenon, of whose mechanism and physiological significance we have remarkably little understanding even today. Amici suggested that it was caused by "galvanism", and later it was considered a fundamental property (motion, irritability) of living protoplasm, showing the close physiological relationship between plants and animals. One result of the startling discovery of organized movement within the cavity enclosed by the cell walls, was to draw attention away from the walls alone and towards investigation of the contents, that is, the structure of the cell as a whole—a new direction in research that was taken up in earnest a few years later.

Before following the further microscopical investigations of plant structure, it will be in order to consider the progress of plant classification, interest in which was sustained by the economic possibilities of the constant accession of new plants from expanding exploration.[19] The scientific rationale of natural classification was now generally accepted, although there was some old-guard rivalry from adherents of the Linnean Sexual System.

Significant advances in natural classification were made in the first decade of the century by Robert Brown and Auguste de Candolle—close contemporaries, knowing each other's work, whose paths were yet strikingly independent. De Candolle was very much the direct successor of Antoine-Laurent de Jussieu, and his work is therefore dealt with first.[20] He outlined his views in *Théorie Élémentaire de Botanique* (1813, second edition 1819), "an exposition of the principles of natural classification and of the art of describing and studying plants". In the introductory portion he follows Magnol, Adanson and A.-L. de Jussieu in defining the natural method, of which the requisite basis is rigorous observation of the totality of all organs. He makes the point that truly natural classes are necessarily the same whether established on one set of functional characters or another. This is a practical test of whether a class is natural: two routes should arrive at the same result. Recognition of this does not, however, in de Candolle's opinion, destroy the preference given to the organs of fructification—the subordination of other characters is founded on the practical reason that, up to now, the fructification is the best known organ and therefore most suited as the basis for classification.

Thus, although de Candolle recognizes in principle the possibility of using physiological characters for classification, he accepts that morphological criteria are the essential ones in practice. Furthermore he noted that, while individual organs may be very greatly modified by adaptation for special physiological functions, the specific positional relations of organs, which are an expression of their developmental relations, remain basically unaltered, forming as it were a ground-plan common to a group of related species. He used the term symmetry for this concept of morphological relationships, and applied it with particular success to the analysis of floral structure.[21] Symmetry can be disturbed in three ways: by the abortion, loss of function or complete disappearance of particular organs, by the modification of organs (termed degeneration by de Candolle), and by the adherence or fusion of organs (which, with remarkable penetration, he relates to the frequent formation of natural grafts between identical or related species in forests). In spite of these disturbing processes, the type of basic symmetry can be recognized by the observation of cases of abnormal or monstrous growth, and by carefully following the stages of normal development. Further aid in interpretation may be gained by analogy and induction. The nature of staminodes in certain Scrophulariaceae is revealed, for example, by their position in relation to the petals and other organs; whilst the fact that in *Scabiosa* the calyx extends into a pappus is evidence that the pappus in Compositae is equivalent to the calyx.

De Candolle's doctrine of symmetry had a profound effect on the development of floral morphology, and of the natural system at generic and family level. This is demonstrated in the successive editions of the *Théorie Élémentaire* and in the description of dicotyledons and conifers to specific level in his great *Prodromus Systematis Naturalis regni Vegetabilis* (1824–41, completed by his son 1841–73). He increased the number of well-defined plant families to more than twice the number recognized by A.-L. de Jussieu.

Surprisingly, de Candolle made no serious attempt to classify families into higher groups of natural character. He merely arranged the families in a linear series, which is "consequently artificial", to use his own words, uniting them in a small number of large groups, almost all defined by a single character. One of his main groups, the Endogens or Monocotyledons, unites such diverse plants as true monocotyledons, cycads and ferns, and is based on an anatomical character, the supposed endogenous formation of vascular bundles, which is fictitious, the result of a misinterpretation of monocotyledonous anatomy by Desfontaines.[22]

Robert Brown, born in Montrose, Scotland, a son of the manse, trained in medicine at Aberdeen and Edinburgh, proposed no complete system and gave no account of general principles, but his studies of particular families or genera led to fundamental advances in the determination of natural affinities, whilst at the same time he made a number of brilliant observations of plant structure and how it arises, which were the starting point for a new era of botanical—and biological—researches on the problem of development.[23] The reports of these discoveries were for the most part included, almost as appendices, in papers dealing primarily with some floristic topic. Brown's established eminence as a systematic botanist fortunately guaranteed that they received immediate attention from his contemporaries, whilst his combination of healthy native caution with an unerring philosophic eye for the essential in things, gave unusual scientific weight to his conclusions. This was the case with his discovery of Brownian movement which had momentous theoretical results in physics.[24]

Brown made his first contributions to the Scottish flora at the age of eighteen, but for several years botany could only be a leisure occupation during his service as an army surgeon, part of the time in northern Ireland. Whilst thus employed he made the acquaintance of Sir Joseph Banks, whose friendship, help and influence made it possible for him to devote the rest of his life entirely to botany. Banks secured the appointment of Brown as botanist to accompany Matthew Flinders on a voyage to Australia (then New Holland). The expedition was in some ways ill-fated, but allowed Brown to study the flora of South Africa, Australia and Tasmania, whence he returned in 1805 after nearly five years collecting, to London, where he then worked until his death.

The results of this experience were published in his earliest works—on Proteaceae, on Asclepiads, on the flora of Australia, *Prodromus florae*

Novae Hollandiae (1810), and on the Compositae—which established his reputation as "botanicorum facile princeps", in A. von Humboldt's words, and form at the same time a practical exposition of the natural method of classification as enriched and made more critical by his insight. The fact that he used de Jussieu's natural system in the *Prodromus,* in preference to the Linnean, gave it great impetus; his special contribution, however, was to show that in trying to "arrange plants according to the sum of their affinities", it was necessary to employ many morphological features in addition to those hitherto used. Such characters could be derived from a critical study of the various plant organs, and his own researches provide examples of minute, sometimes microscopic characters of fruits, seeds, stamens, anthers, stigmas, of contrasting types of aestivation of perianth members, of degrees of freedom or adnation of floral organs, which can be useful in establishing natural affinities. In particular, he stressed the need to examine immature organs to discover characters that may be only manifest during development.

In floral morphology Brown adopted a view which in principle anticipated that of symmetry, arrived at later, and in more explicit terms, by de Candolle. His most important theoretical contribution was his interpretation of floral organs developmentally, as modified leaves. This may be considered in a sense as a revival of Goethe's "metamorphosis" theory, to which Brown does not refer, or of ideas expressed by Linnaeus and Link,[25] whose influence he acknowledges. However, the conception was given an entirely new concreteness and authority by the profound knowledge of floral structure and development with which Brown supported it. Points to note are his opinion that all plurilocular ovaries represent syncarpellary structures composed of a ring of "polyspermous follicles" surrounding the imaginary axis, and more or less closely united; and that with few exceptions (such as *Nymphea, Nuphar, Butomus*), the pollen and ovules are always borne on the margin of modified leaves. For the latter statement he adduces evidence from abnormal morphology (conversion of one stamen into a pistil), and from the comparative vascular systems of stamens and ovaries. Brown was, I think, the first to use vascularity in studying the homology of floral organs. Whether his interpretation was correct is still uncertain, but its effect on the study of comparative morphology and phyletic relationships has been profoundly stimulating and fruitful.[26]

In 1827 Brown published a microscopic study of the development of unfertilized ovules, describing the detailed structure (hilum, integuments, microphyle, nucellus, enbryo-sac) and the origin of endosperm and perisperm, which he thereby distinguished for the first time. This work was doubly important in revealing new seed-characters of high systematic value and as a step towards understanding the process of fertilization; it no doubt also aided Brown in his recognition (quietly announced in the same paper, primarily devoted to a study of the Australian genus *Kingia*) that the ovule (seed) in Cycads, Conifers, *Ephedra* and *Gnetum*, is truly naked and not at any stage enclosed in an ovary.[27]

This was an epoch-making discovery. Recognition of the fundamental distinction between Gymnosperms (conifers and cycads) with naked ovules and seeds, and Angiosperms (flowering plants) whose ovules and seeds are enclosed in an ovary until fertilized, was in itself a profound advance in natural classification. At the same time it opened a new stage in the analysis of morphological and developmental relationships within the plant kingdom.

Ever since Camerarius had proved pollen to be the male element, the problem of how it actually fertilized the ovule had remained a mystery. Interest in the question was revived when, in 1823, J. B. Amici of Florence, a mathematician and accomplished microscopist, observed the pollen tube growing out of pollen grains lodged on the stigmatic hairs of *Portulaca oleracea*; in the next few years he found pollen tubes in other species and saw them penetrate the tissue of the style, pass into the ovary and apply themselves closely to the ovules. These observations were repeated and confirmed by Adolphe Brongniart who concluded that the pollen tube conveys "spermatic fluid" to the ovule. In 1831 Brown gave a long account to the Linnean Society (published in 1833) of his morphological and microscopical studies of fertilization in Orchideae and Asclepideae, in which he described changes in the cells of the stigma and style during development, the passage of the pollen tube down the style, the entry of its tip into the ovule through the micropyle, and the subsequent formation of the embryo in the embryo-sac. This work, soon widely confirmed, filled the gap between ovule and pollen which had been the great puzzle in sexual reproduction of higher plants: by demonstrating physical contact between ovule and pollen, it placed fertilization in plants on a par with the process in animals, where the necessity for physical contact between ovum and sperm, was beginning to be generally accepted.[28]

In the same paper Robert Brown also reported observations on the "areola or nucleus" in plant cells. These observations are held, correctly, to constitute the discovery of this essential organ of the cell, although with his scrupulous regard for others Brown points to indications of the nucleus in recent work of other botanists, including Meyen, Purkinje and Brongniart. He remarks, however, that "so little importance seems to be attached to it, that the appearance is not always referred to in the explanations of figures in which it is represented". His own thorough investigations showed that the nucleus is a definite organ, present in most, if not indeed in all cells, and therefore implied that it must, on the contrary, be an important vital organ of the plant. He noted the distinct and regular form of the nucleus, globular or lenticular; its occurrence, usually singly per cell, in the cells of every kind of tissue examined, in both dicotyledons and monocotyledons; and believed that it consisted of "granular matter held together by an enveloping membrane".

In pollen [pollen mother-cells] he saw that a single nucleus is present at first, but later there are four. He extracted the nuclei from the cell by pressure—a striking anticipation of a very recent technique—and noted that the extracted nuclei retained their form. In some cells movements of the cell contents could be seen between the surface of the nucleus and that of the cell, convincing him that the nucleus does not adhere to the wall.

The microscopical studies of Robert Brown, revealing the nucleus as a constant organ of the cell and providing the first firm knowledge, at cellular level, of the development of the reproductive organs and of the mode of fertilization, were so germane to the key problems of current enquiry, and so accomplished in execution, that they were a powerful factor in a renewed expansion of research into plant structure, beginning in the 1830s in Germany. Two technical developments also contributed: the availability of cheap microscopes of high quality, factory-made in Germany, Austria and France, and more important, the gradual introduction, following J. J. Lister's theoretical treatment in 1830, of lenses (made by combining achromatic doublets) free from spherical aberration. The effect of these optical advances is evident in the very marked improvement in figures of plant cells and tissues published after 1835.

Study of all aspects of plants by the microscope was taken up with enthusiasm and became the most exciting area of progress. Many more workers became involved in the field, and the organization of botanical research assumed its modern form as a community of professionals, in close and rapid touch across national boundaries through an increasing network of specialist journals.[29] The resulting investigations, employing new methods of observation and experiment, began the foundation of fact and generalization on which the modern science rests. Before outlining the results, we must mention an event which had a profound effect—acknowledged by all contemporary botanists—in stimulating a new outlook and direction in botany. This was the appearance in 1842 (with repeated improved editions in the next few years) of M. J. Schleiden's *Grundzüge der wissenschaftlichen Botanik*, translated into English in 1849 as *Principles of Scientific Botany*.

When he wrote the *Grundzüge*, Schleiden had already published microscopical studies on the development of the ovule and the formation of cells in the embryo-sac. These researches were inspired by Robert Brown, for whom Schleiden repeatedly expressed his admiration as the first to see that the history of development is the leading principle in understanding the morphology and nature of plants. The careful study of development, "not omitting a single stage or the result will be insecure", must be the foundation of scientific botany, in Schleiden's opinion, replacing the mixture of aimless empiricism and pseudoscientific speculation then dominant, if botany was to take its place beside chemistry and physics. It was therefore with deliberate polemical intention that Schleiden wrote what became the first textbook of botany that is modern in form and spirit. Even today one can still catch what must have been the shock and excitement of its impact, rousing a whole generation of young botanists to new perspectives.

Merely in content and arrangement, the difference from any previous general treatment of botany was startling. Almost no attention is given to the detailed systematics of higher plants, which, Schleiden complained, had formerly occupied botanists to the exclusion of far more important topics. Instead, the first chapter deals with the chemical constitution of plants, the main elements present, the chief classes of organic substance formed, the substances absorbed (carbon dioxide, water, ammonia) to form organic matter (with a closely argued rejection, based on quantitative figures, of the view that humus is an important plant food).

The structure of the individual cell is then described, and the types of association of cells in tisues, the physiological activities of individual cells (absorption, assimilation, excretion, motion, reproduction) and of tissues. Morphology is treated in relation to development and in this way Schleiden demolished many misleading interpretations, and showed the need for a strict terminology based on general principles. In discussing special morphology, simpler forms (algae, fungi) are treated before more complex (mosses, lycopods, ferns, phanerogams), not in the reverse direction from phanerogams to cryptogams (as was the usual practice for historic reasons) which leads to blindness and confusion, and is in effect a barrier to the investigation of the lower plants. Finally a description of the specialized organs (vegetative and reproductive) of plants, is combined with an account of their physiological activities: physiology is indeed stressed throughout as the essential complement to structure and development.

In spite of his strictures on systematics, Schleiden makes some perspicuous and fruitful observations of morphological and developmental characters, valuable in separating the primary natural divisions of plants.

Throughout the book established facts and divergent views are discussed with vigour, but Schleiden is not dogmatic, except in dismissing what he considers nonsense, and does not draw conclusions when the answer is *non liquet*—further research is needed. He rejects empty concepts like "vital force", always coming back to the facts of physics and chemistry and plant development as the framework of hypotheses in botany. Schleiden states categorically that he follows "the school of chemists, of Leibig, Mulder and Dumas", in holding that the laws of inorganic chemistry apply to all chemical processes in the plant body, that the elements of the plant cell obey the same laws within as outside it. He refers to the power of nitrogenous bodies to effect catalysis [Berzelius had defined and named it in 1835], to chemical activity *in statu nascendi*, the ready decomposition of water, a major constituent of plants, and the possibility of deriving "the impulse to an endless chain of chemical processes" from the destruction of one equivalent of water, as examples.

For Schleiden, the task of directing botanists into the true "inductive" path of natural science was a philosophical as much as a scientific problem, and he prefaced his book with a "methodological introduction" which amounts to a philosophical manifesto. The Philosophy of Nature of Schelling had not been without some positive benefit to science, by stimulating comprehensive theorizing, in face of tendencies to take refuge in pedantic empiricism, but his reliance on "intuition" as the source of theoretical knowledge inevitably caused this aspect of his teaching to degenerate into "nature-philosophy" and to become, in Hegel's words, "an instrument for superficial thinking and fanciful imagination". Unfortunately nature-philosophy had considerable influence on German botanists, and few French, leading to much word-spinning and absurd theorizing, especially in anatomy and morphology, with adverse effects even on empirical observation. Schleiden set out to eradicate nature-philosophy from botany, and was highly successful, employing some robust ridicule, but showing in each particular case how the formal and idealist theories thought up under its influence, were inconsistent with the simple facts of development.[30]

Against such trends Schleiden took the philosophic position of Kant, in so far as the latter was concerned with the systematic method and procedures of natural science. Fundamentally Kant accepted Locke's view of the origin of knowledge from experience, from the results of observation and experiment; but in the light of the progress of science since Locke's day, he was able to specify the desiderata of scientific method more adequately. The essential addition made by Kant was his insistence that scientific investigation must be critical: a requirement which included, at the empirical level, the separation of clear facts from the unclear or doubtful, of the essential from the accidental; the use of theories which admit of confirmation or refutation by experiment, as means of seeking precise information from nature and arriving at rational synthetic judgement (general theories) from empirical data; and recognition that the "strife of dialectic is a necessity of reason", and that science is advanced by mutually tolerant, rational polemic between opposing views.

Kant defined the attitudes and general methods which became the accepted norm (not always practised, of course) for scientific research.

Schleiden brought the critical methodology of Kant into botany, raising it to the same status as the other branches of natural science.

The metaphysical aspects of the Kantian critique were of little interest to Schleiden, and he had no time for Hegel, whom he treats with derision.[31] Yet Hegel profoundly advanced understanding of the nature of developmental processes, and of the causal interconnections and inner dialectic of progressive change, which he perceived in every form of existence, whether in the material world, in human society, or in the operations of thought. His philosophy, with its emphasis on the historical and conditional determination of all phenomena, had an immense influence, and one cannot fail to recognize its reflection in the actual course of botanical investigation, with its decisive turn towards the processes of plant development, the relations between development and environment, and the integration of different levels of structure and activity within the plant body. Carl Nägeli, one of the most original and able botanists of the period, had studied under Hegel as a young man, and tried to apply his thought to scientific methodology.

As if to draw the philosophic moral in practical terms for the working scientist, Schleiden included in his book a section on techniques and interpretation in microscopy, warning of possible errors and giving valuable hints on the critical use of this new research tool, which was conquering the field. It is ironical that the very force of his mind led Schleiden seriously astray in his own microscopical work.

Schleiden's textbook also had a decisive influence in establishing "cell-theory" as the guiding principle in botany. In originating and formulating this conception, Schleiden, arguing from botanical evidence, had indeed played a major part. Cellular structure in plants, however variously interpreted, had been recognized since the seventeenth century, owing to the universal presence of visible cell-walls in plant tissues; the terms cell and vessel were in common but ill-defined use. In zoology, cell and cellular were only applied to areolar connective tissue, in other animal tissues only various confused appearances and artefacts could be seen, described vaguely as globules. The plant cell was given sharper definition by Brown's discovery of the nucleus, but it was Schleiden who grasped its significance as the basic formative element of the plant. The recognition of the dual role of the cell, at once structural and developmental, was the kernel of the cell-theory.

Several lines of evidence seem to have led Schleiden to consider the cell as the fundamental organ of the plant. Following up Brown's observations, he was impressed by the constant presence of the nucleus in young cells, which always appeared to consist of nucleus (cytoblast) with mucilaginous granular matter (cytoblastem) around it. Since very rapid formation of new cells takes place in the embryo-sac after fertilization of the ovule, this was what Schleiden studied. [He was actually observing what is now termed free cell-formation, a type of cell-division which is rather unusual in plants, except in the ovule during growth of the endosperm.] Although Schleiden's account of the process proved quite wrong in detail, he correctly inferred that each new cell is organized in connection with a nucleus.[32] The importance of the cell was probably heightened for him by the fact that the mucilaginous ground-substance stained yellowish-brown with iodine, indicating protein compounds, the biological significance of which was just being revealed by the chemists: Mulder coined the name protein in 1838, the year Schleiden's paper was published.

Schleiden did not extend his work to animals, but in 1837 he dined with Theodore Schwann, a brilliant animal physiologist, who like Schleiden was working in J. Müller's laboratory in Berlin, and communicated to him his new theory on the role of the nucleus in the development of the plant cell. Schwann took Schleiden into the laboratory to show him nucleated plant-like cells in the chorda dorsalis of tadpoles of *Rana esculenta*. This discussion with Schleiden moved Schwann to embark on a thorough investigation of many animal tissues, which convinced him that the basic cell structure of animals is analogous to that of plants. The results were communicated to the French Academy of Sciences in 1838, and published in 1839 in a famous book, where for the first time a unitary concept of the constitution of all living organisms was expounded.[33] Schwann adopted the name "cell-theory" for this concept, which envisaged "a common formative principle for all organic productions": the principle being "cell-formation".

By his part in developing cell-theory and placing it in the forefront of botany, Schleiden defined the most important field of investigation for many years to come, and made a theoretical advance which far outweighed some palpable blunders he made in his own researches.[34]

The study of plant structure now entered a wide-ranging exploratory phase, in which the form and mode of production of cells, the anatomy and arrangement of tissues, and the cellular details of reproduction in different classes of plants, were the leading objectives of enquiry. It is convenient to consider these questions separately, although their elucidation was the result of many overlapping and interdependent observations.

When Schleiden and Schwann made "cell-formation" the basis of all living organisms, their generalization relied on a very imperfect knowledge of how new cells are formed. In the early years of the century Mirbel, as we saw, adopted C. F. Wolff's idea that cells arise by enlargement of vesicles within a homogeneous matrix. He returned to the question in 1835 in a classical paper on the liverwort *Marchantia*, which illustrates among other notable features the progress in microscopy in the intervening period; the figures of spore germination and of mature thallus tissues are beautiful and accurate, albeit attention is centred on the cell walls with only sketchy indications of the cell contents. Mirbel stated very clearly his understanding that all distinct types of mature cells (including "vessels and tubes") arise by differentiation of young cells which are very similar in their "original simplicity"; he concludes that the general facts of [cell] development are the same in phanerogams and cryptogams, and even speculates that the process is the same in animals and plants. When it comes to the origin of new cells, however, Mirbel did not consider the possibility of cell division, which his own excellent figures of spore germination might well have suggested. He still remained under the spell of Wolff but thought that new cells arise in three ways: (1) in the outer surface wall of old cells, (2) within the conjoint wall of old cells, the new cell growing without any break in continuity, as in parenchymatous tissues, and (3) on the internal face of the wall of old cells, which he thought to be the method of gemma formation in *Marchantia*.

This third possibility leads to the growth of a number of new cells within a mother-cell; Mirbel conceived that the wall of the mother-cell either dissolves to leave a connected tissue of new cells [as he thought, wrongly, happened in the gemma], or the new cells remain within the undissolved mother-cell wall [as in sporangia]. It is evident that in 1839 Schleiden adopted Mirbel's third method of cell-formation as the model of the process observed by him in the embryo-sac, the only essential difference being Schleiden's emphasis on the role of the nucleus. According to his interpretation the first step was the formation of nuclei out of granular material; a new cell was then organized by each nucleus around itself, gradually increasing in size and finally developing its own wall. Schleiden considered this to be the universal mode of cell-formation, in tissues and elsewhere; he believed that the nucleus was organized on the inner wall of the old cell within which new cells were formed, and that it remained attached to the wall—a surprising assumption in view of Brown's conclusive evidence that the nucleus lies free. Schleiden's reverence for Brown did not extend to reading him with attention to detail, but Schleiden's strength was always in principle rather than in details.

This theory of Schleiden—actually based on imperfect observation of a special case—was widely accepted for a time, and defended by him with some stubbornness. Yet Hugo Mohl (later von Mohl) had already described cell-division in *Cladophora* and other filamentous algae, and he was a most skilled and careful investigator for whom Schleiden repeatedly expressed the highest regard. By 1841 F. Unger had found cell-division to be the most usual process of cell-formation in the root tip and stem tip and adjacent regions of many plants, and he remarks that von Mohl had made many similar observations. Unger defines the process as "the formation of cross-walls in young cells, in a word, division"; and he says that in vegetative tissues he has never seen the production of cells within cells as Mirbel claims to have done. Although Schleiden is not named, this was the first direct challenge to his theory of cell-formation. Three years later, in a study based mainly on *Tradescantia*, Unger brought further evidence that in vegetative tissues new cells arise only by division, and introduced the term meristematic for this mode of cell-formation. It is indicative of Schleiden's intellectual domination that Nägeli for several years continued to accept his description of cell-formation as applying to the tissues of higher plants, whilst recognizing cell-division in algal cells and at the tetrad stage in the development of spores and pollen. However, in 1846 Nägeli published a paper (ironically, in the journal founded by Schleiden and Nägeli to cover advances in the "new" botany) which finally demolished Schleiden's theory and drew the conclusion that "in vegetative cell-formation comprehensive researches show one universal law, that two secondary cells originate in one parent cell, in other words, that one cell divides into two".

In the first accounts of cell-division by von Mohl and Unger the nucleus was not considered nor even depicted in the figures: the striking fact to them was the division of the contents of an existing cell by the formation of a new single-layered wall or septum. In *Cladophora* and other algae the septum developed from the outer wall inwards, and for some time von Mohl thought this was the rule. Later, Nägeli, Unger and von Mohl himself, recognized that in higher plants the septum is normally formed at the centre first, joining up with the old wall by outward extension.

Schleiden's principle—correct in essence although owing perhaps more to intuition than to strict observation—that new cells are organized by (or around) the nucleus, raised the question of the role of the nucleus in division. The fact that the nucleus sometimes seemed to be absent in older cells, caused doubt, expressed by Unger and von Mohl among others, whether it could have a direct effect on cell division, but Nägeli was early of the opinion that cell-formation only occurred if a nucleus were present, and that its absence indicated cessation of growth. In 1844 Nägeli (making use of iodine staining) showed the presence of the nucleus in all types of cells of every class of plants, algae, bryophytes, Lycopodiales, Equisetales, ferns, phanerogams; in the last, the nucleus is present in all young cells and, if apparently absent from some older cells, can always be found in other individual cells of the same kind. Only in fungi and lichens was Nägeli unable to detect nuclei with certainty. In this paper Nägeli showed very clearly that in several algae, division of the nucleus precedes the formation of the septum and the complete division of the cell. These observations pointed to division of the nucleus as the essential step in cell division, but Nägeli was still not quite certain whether cell-division was universal or whether Schleiden's account of cell-formation might not be true in some cases (e.g. the so-called "free cell-formation" in the embryo-sac of flowering plants or the gametangia of algae).

In his 1846 paper Nägeli had made up his mind: his extensive observations proved that cell-division is universal, and that Schleiden's

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Figure 22 Cell division first observed in higher plants by F. Unger in apical meristem and tissues of the grass *Campelia Zanonia*. *Botanische Zeitung*, **2** (1841).

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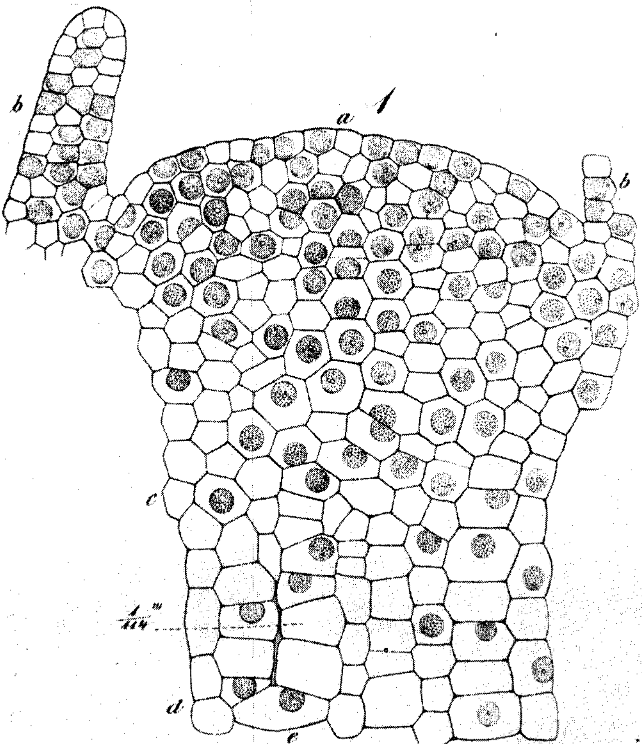

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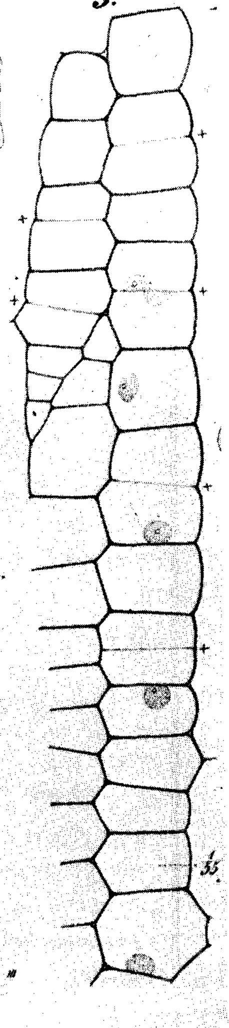

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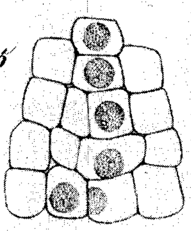

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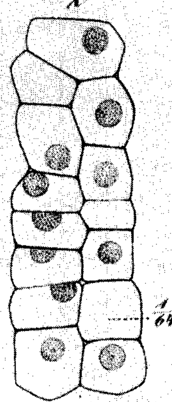

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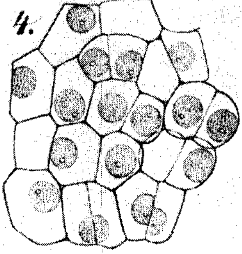


theory of cell-formation must be wrong, because it was inconsistent with the facts. Nägeli distinguished two types of cell-formation: vegetative, as in the meristems and young tissues of higher plants, and in filamentous and thalloid algae, where two cells are formed within one parent cell and become separated by a new wall; and reproductive cell-formation, as in the embryo-sac of flowering plants or the reproductive organs (gametangia, sporangia) of cryptogams, where various numbers of cells originate within a parent cell. In both types of cell-formation, however, the fundamental process is the same, consisting in division of the contents of the parent cell, accompanied by a corresponding division of nuclei. This was in fact a recognition—in the plant kingdom—of the fundamental tenet of cell-theory, that cells only arise from previously existing cells: a principle which in the phrase "omnis cellula e cellula", acquired universal currency following the zoological observations of R. Remak (1852–55) and R. Virchow (*Cellularpathologie* (1859)).

There is no doubt that Nägeli regarded the nucleus as a constant and essential component of the cell, reproduced when the cell divides; but his references to the process of nuclear division reflect uncertainty about the facts. He speaks of seeing a nucleus divide into two, with the subsequent formation of a septum between the nuclei; and in studies of pollen development he saw "transitory cytoblasts" during the formation of two nuclei from a single parent nucleus (almost certainly the earliest observation of chromosomes); but he also speaks of the dissolution of a primary nucleus in the parent cell, and the formation of new nuclei, around each of which a cell is organized. It is indeed obvious that until the discovery of more specific nuclear stains than iodine, the continuity of nuclear material during division could not be established, nor could the difference between division and the "dissolution" of one nucleus and the *de novo* "formation" of two nuclei have real meaning. In his first paper in 1847 Hofmeister reported nuclear division in the embryo-sac of *Oenothera*, "one half of the cell contents collecting round each daughter nucleus"; and in 1848 he saw more details of nuclear division in pollen, including the dissolution of the nuclear membrane before division, a "granular plate" [presumably the chromosomes] between the daughter cells, and the re-formation of the membrane round each daughter nucleus. By the time of his review of cell-structure in 1851 von Mohl recognized the simultaneous doubling of the nucleus and of the cell, but thought that division of the nucleus was less common than its dissolution and re-formation.

The primacy of the cell content in division gave sharper definition of the concept of the cell. Nägeli particularly emphasized that the cell content, i.e. the cell, secretes the wall at its surface: the wall is thus a secondary formation, differing markedly in chemical composition from the "albuminous" substance of the cell itself (Payen had found in 1844 that all plant-cell walls consist of cellulose). In 1846 von Mohl adopted the word protoplasm,[35] to provide a physiological designation for the albuminous ground-substance of the cell, and to obviate the confusion of chemical names that were being applied to it. He further clarified the nature of the plant cell by demonstrating the existence of a distinct outer layer of the protoplasm, which could be readily seen if the cell were plasmolysed and to which he gave the name primordial utricle, corresponding roughly to the modern plasmalemma. Von Mohl also followed the growth of young cells behind the apical meristem and observed that small vacuoles appear in the protoplasm, which gradually enlarge and coalesce to form the single central sap-filled vacuole of the mature parenchyma cell.

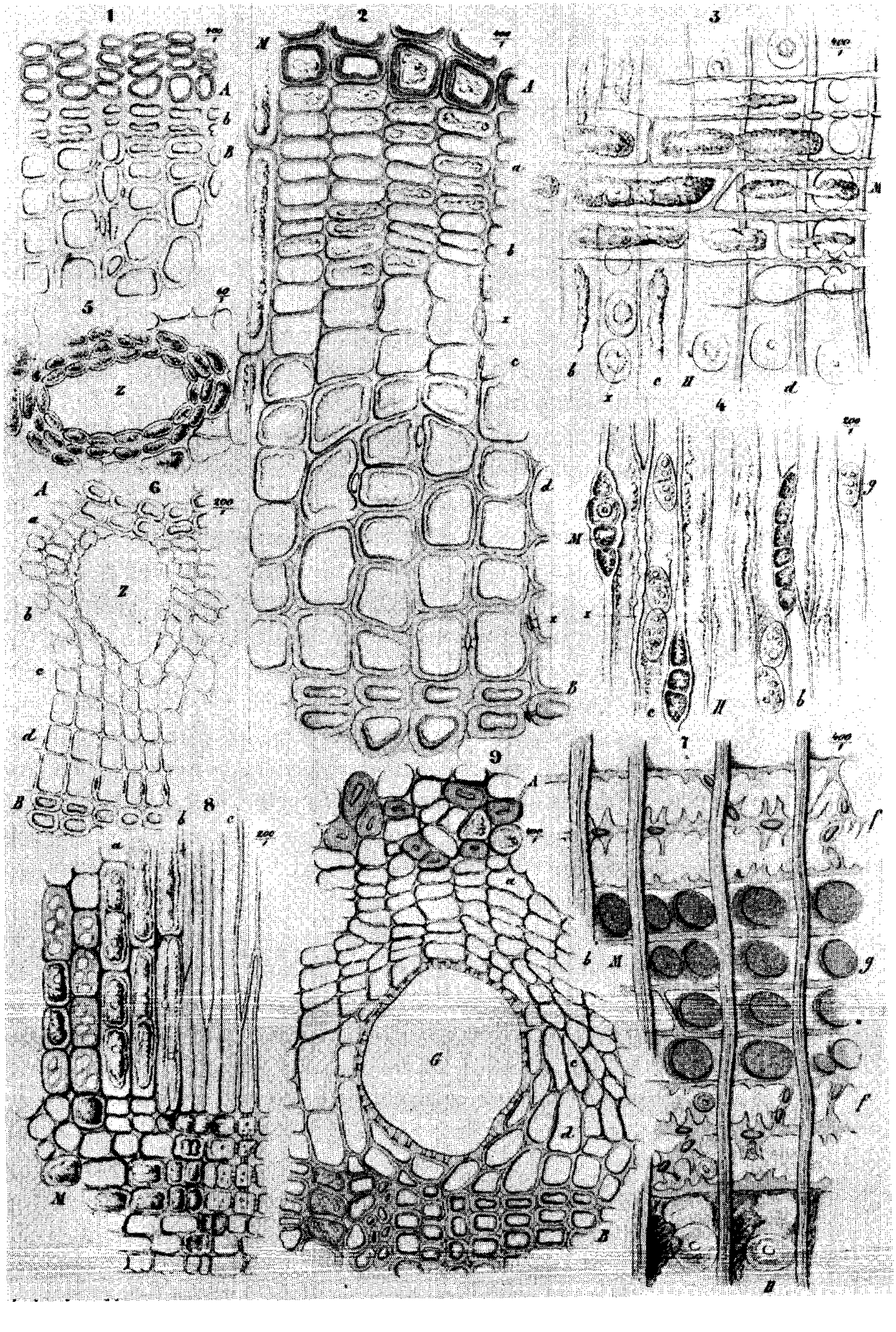
Knowledge of the process of wall formation was largely the result of von Mohl's painstaking developmental studies. He proved the essential fact (still in dispute till he settled the question with brilliant finality), that thickening is laid down internally to the earliest wall of the cell, in successive layers towards the centre; and he recognized in principle the modern distinction between middle lamella, primary wall and secondary wall, and elucidated the mode of formation of pits and of intercellular spaces. By showing that pits extend only through the secondary walls and that the primary wall is, except in special cases, without visible pores, he settled another long controversy.

These observations were the basis for understanding the differentiation of all types of mature plant cell, as von Mohl showed in detail. They thus linked up with the problems of tissue formation, a topic on which we need not dwell since it received relatively little attention in the period when the cell was the all-absorbing interest. The main advance was made, once again by the indefatigable von Mohl, in a monograph on the mature anatomy of the palm, already mentioned above. In this work, a model of its kind, he gave the first accurate account of the course of the vascular bundles in monocotyledons and destroyed all basis for assuming their "exogenous" production. At the same time he brought out the important fact that the constitution and internal tissues of the vascular bundle are essentially the same in monocotyledons and dicotyledons, despite the very different arrangement and course of the bundles in the stem in the two groups. He later extended his anatomical studies to tree ferns, cycads and conifers, bringing out the connection of the leaf traces with the vascular system of the stem.

In 1851 von Mohl summed up, in a monograph on the plant cell (*Die vegetabilische Zelle*), the remarkable advances that had been made in the space of some thirty years. The vague notion of "utricles and vessels", defined almost entirely by their walls, had given place to a clear concept of the plant cell, based on a firm body of knowledge of its structure, reproduction, range of mature form, mode of differentiation, and even of its chemical constituents.[36]

Investigation of the chemistry of animals and plants—the beginning of organic chemistry—had been taken up vigorously by French chemists after 1808, when Dalton's atomic theory made effective progress possible. It soon became generally accepted that whilst "organic" compounds may have a character and complexity peculiar to products of life, they obey the same basic chemical laws as the better known inorganic compounds. Nitrogenous or albuminous substances, compounds with a definite range of elementary composition, and having characteristic physical and chemical properties, were early recognized as a primary constituent of both animal and plant tissues, and as an indispensable requirement in the food of animals; because of their evident importance to life, such compounds were called proteins [first substances] by the Dutch chemist G. J. Mulder.[37] By 1850 the elementary composition of a number of plant constituents was known approximately, and many could be identified by a combination of physical, chemical and staining tests. The ability to characterize protein, cellulose, lignin, cutin, pectin, starch, inulin, chlorophyll, tannin, alkaloids, etc. became the foundation for later developments in physiology.

Figure 23 Anatomy of pine stem (*Pinus sylvestris*) illustrated by H. Schacht in *Die Pflanzenzelle* (1852).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The chemical study of plants was at first not closely linked with physiology; it contributed chiefly to the interpretation of cell structure, as we have seen, and had the invaluable effect of causing microscopists to enlarge their art with chemical methods and so develop new revealing techniques. At the same time Schleiden, Nägeli and a few like minds revolutionized the outlook of botanists by directing their attention to the cell as a physical and chemical system, and prepared the way for the surge of interest in plant physiology which ensued in the second half of the nineteenth century. In the period under discussion there were few notable advances in physiology and these may be conveniently mentioned at this point.

In 1806 T. A. Knight, the son of an iron-master but himself an estate-owner and agriculturalist and one of the last gentlemen scientists of the eighteenth century, hit on the bright idea of testing the response of growing plants to gravity by attaching them to a wheel rotated in a vertical plane. The apparatus he used was driven by a small water-wheel turned by a stream in his garden; later, Julius Sachs was to convert it into the klinostat, a device for eliminating the directional influence of gravity, which has remained an essential piece of equipment in investigations of geotropism ever since. Knight's experiments proved what was hitherto only inference, that both the normal upward growth of the main stem and the downward growth of the primary root, resulted from a direct and directing influence of gravity on the plant. Moreover these effects of gravity were shown to be replaced by a sufficiently strong field of "centrifugal force" due to rotation. These experiments evoked great interest and were repeated by a number of continental botanist, including Dutrochet, who corresponded with Knight. The invention of the klinostat marks the beginning of the scientific investigation of geotropism; it enabled Knight to distinguish between geotropic and hydrotropic reactions of the root, and opened the whole question of tropic responses, of their physical basis and adaptive significance in the life of plants.

The most important advance in plant physiology came from R.-J.-H. Dutrochet, who had studied medicine in Paris, but then for thirty years devoted himself to physiological research mainly, but not entirely, with plants. His final results appeared in 1837 in a book entitled *Mémoires pour Servir a l'Histoire Anatomique et Physiologique des Végétaux et des Animaux*, replacing a series of earlier published papers which he considered "null and void". Dutrochet's fame rests on his discovery of osmosis, to which he gave the name.[38] Whether others can claim to have seen the phenomenon before him is immaterial; Dutrochet first investigated osmosis systematically and grasped its fundamental significance in living organisms. His attention was drawn to osmotic processes by seeing the swelling of the sporangium of an aquatic fungus, followed by liberation of aplanospores [not zoospores, as is sometimes wrongly stated]; some time later he saw similar behaviour in sperm packets of slugs. Investigation showed that osmosis depends on the quantity of substance in solution, but most specifically on the nature of the membrane separating the solution from pure water. Dutrochet concluded that osmosis is only found in organic beings, because "osmotic" membranes were only found naturally in animals and plants, although an artificial membrane could be made from china clay.

By supporting natural membranes on a perforated metal disc and attaching a mercury manometer, Dutrochet set up the first osmometer and made quantitative measurements of osmotic pressure. In some experiments he attained pressures of two atmospheres with strong sugar solutions, considerably lower than the true value, but striking enough at the time and in view of the difficulty of these pioneer measurements. As membranes he used hen's caecum or the bladders of domestic animals, and from plants the calyx of *Colutea* or scales of onion. Of all plant substances he found sugar to have the greatest "osmotic power"; acids gave confusing results, for reasons which we can now understand. His quantitative measurements showed that "osmotic power" increased with the amount of solute dissolved in the water: Dutrochet thought, quite reasonably, that there was a direct relation of osmotic power to density; the relation to concentration escaped him.

Although Dutrochet could not explain the cause of osmosis, he did not doubt that it was a physical process and was of very great importance in vital phenomena. He pointed out the probable role of osmosis in the uptake of water by the root, in bleeding from the cut stem, in the rise of sap to the leaves, in maintaining turgor, and in certain irritable and periodic movements of plants. Many of his suggestions proved to be correct; in any case, they had a profound effect in stimulating the later development of this fundamental branch of physiology.

Dutrochet made admirable observations on the responses of plant organs to external stimuli[39] in which he sought a physical explanation of these activities. These researches were the basis for much subsequent work, but their most immediate result was the more general one of weakening the hold of vitalist philosophy in botany. Dutrochet felt very strongly on the misuse of "vital force":

> the fairly common opinion that vital force is due to an agent quite foreign to non-organic bodies has always seemed to me unworthy of the philosophy of science . . . The time will soon come I hope when the occult and mystic causes by which phenomena are explained, will be replaced by an account of the physical laws to which they are due.

His own well-designed experiments were influential in expelling vital force from plant physiological research.

The basis of plant nutrition seemed to have been so thoroughly settled by de Saussure that for a long time botanists gave the subject no serious attention. Even de Saussure devoted himself to other problems, such as trying to measure heat production from plant respiration, and the impetus passed to agriculturalists and chemists, at a time when rising industrial population, linked with changes in rural economy, provided the incentive for applying science to increasing the output of agriculture. One of the first chemists to be involved was Humphrey Davy, who began to deliver an annual course of lectures on chemistry and agriculture at the request of the Board of Agriculture of the government. The lectures were brought up to date each year and published in book form in 1813. This work, *Elements of Agricultural Chemistry,* became the standard textbook in Britain and Europe for nearly thirty years; it was an effective step in the development of agricultural science, and raised questions such as the relation between plant growth and the physical and chemical state of the soil, which were to assume great importance. Davy based his treatment on de Saussure's researches on plant nutrition and respiration, and so brought the elements of plant physiology to the notice of agriculturalists. Unfortunately he also adopted the "humus theory", at that time widely accepted by agriculturalists, which assumed that plants gained both carbon (in addition to that derived from carbon dioxide by photosynthesis) and nitrogen, from humus in the soil. The increase in yield of crops after manuring with dung and other organic material was *prima facie* evidence in favour of this view, and de Saussure had been rather vague about the source of "ammoniacal" nitrogen to plants, implying that some at least came from organic remains in the soil. Davy's eminence as a chemist gave wide currency to the humus theory, which is often quoted in botanical writings of the period but was not critically investigated by botanists. The humus theory caused confusion and uncertainty; in particular, it delayed full understanding of the unique role of photosynthesis in green plant nutrition.

The issue was not clarified till 1840, when the great chemist Julius Liebig published a book in which he applied the latest advances in chemistry to the problem of plant nutrition.[40] Liebig, like Davy, took de Saussure's account of plant nutrition as the starting point. He devoted his opening chapter, however, to demolishing the humus theory, showing by a series of cogent arguments that it was inconsistent with the known physical and chemical properties of humus. Furthermore quantitative estimates of the amount of humus in soil and of the annual production of plant material, showed that even if all the humus were utilized (for which there was no evidence), it could only account for a minute fraction of the carbon and nitrogen of the crop.

The sole source of nitrogen in Liebig's opinion was ammonia, which he showed to be formed by the breakdown of organic matter of all kinds, and to be constantly present in the soil water, in rain-water, and in the ascending sap of trees. The recognition of ammonia as the source of nitrogen for plants was a great advance. Liebig appears to have observed the formation of nitrate from ammonia in the soil, but he did not (at this time) think of nitrate as a source of nitrogen for plants, nor does he mention nitrate in the numerous soil analyses in his book. It was more than ten years later that Boussingault showed, by numerous careful experiments (1851–55), that plants assimilate nitrogen from nitrates. The tardy recognition of nitrate is very curious, for the favourable effect of nitre on plant growth was quite well known to the sixteenth and seventeenth century gardeners.

For some reason Liebig assumed that there was always a sufficient supply of ammonia in the soil to maintain plant growth, and his consequent omission of nitrogen led to the failure of his first field experiments with artificial (inorganic) manures.

Like de Saussure, Liebig realized that metals and salts play an essential part in plant nutrition; he went further, however, and by making many analyses of plants he judged that potassium, calcium, magnesium, phosphate and sulphate are especially important.

Liebig's chemical onslaught on plant nutrition was valuable clarification of existing knowledge, and had an enormous effect on the practice of agriculture and its development on scientific lines. The stimulus —and the irritation—generated by Liebig, awakened botanists to the need for experimental study of plant nutrition using the up-to-date chemical knowledge and methods. This need was recognized by Schleiden and carried into execution by von Mohl, followed by Julius Sachs and many others, who became the first professional plant physiologists. Liebig expressed forthright contempt for botanists on account of their failure to understand chemistry and to use experiment, "an art which can only be learned in the chemical laboratory". But Liebig himself lacked understanding of many biological matters, and was sharply attacked by botanists for, among other things, his stubborn insistence that carbon dioxide evolution by plants resulted from oxygen injury, and not from respiration: so perhaps scores were even in the not very illuminating polemic exchanges which ensued.

It is now time to give an account of the researches into fertilization and sexual reproduction, which were the counterpart and complement of the investigations of cell structure and formation.

Any lingering doubts about sexual fertilization in higher plants had been largely removed by the discovery of pollen tubes in flowering plants and conifers, since they provided the means of material contact between the male and female elements which Spallanzani's experiments in 1785 had shown to be essential in animals. Moreover K. F. Gaertner (son of Josef Gaertner), between 1827 and 1838, had repeated and extended Koelreuter's work on plant hybrids, so completing the experimental confirmation of Camerarius. Two closely connected questions naturally arose; one related to the mode of reproduction in cryptogams, and whether it did or did not involve sexual fertilization; the other, to the details of fertilization in phanerogams at the cellular level.

Among cryptogams Hedwig had recognized the sexual function of the antheridium and archegonium in the bryophytes (liverwort and mosses) and of the male and female gametangia in the alga *Chara,* equating them with the anthers and pistils of flowering plants, and he had suggested, as Vaucher did later, that conjugation in *Spirogyra* was probably a sexual process. The occurrence of sexual fertilization in these cryptogams was assumed on reasonable grounds, but had not been actually seen or demonstrated with certainty. In other algae and in the higher cryptogams (ferns, lycopods, horsetails) sexual reproduction was not known.[41]

The motile cells of lower plants were first observed in the 1820s. They were often called swarm-cells because of their production in large numbers simultaneously, and there was much confusion about their nature; some regarded them as animals (monads, infusoria) because of their power of movement, others considered them as the transformation of plants into animals (and the reverse), an idea deriving from nature-philosophical speculation.[42]

The cilia of *Vaucheria* zoospores were seen by F. Unger in 1826; although the report was not published till many years later, it is probably the first record of cilia in plants, and was followed by Unger's discovery of ciliated antherozoids in mosses in 1834. Even so intelligent and careful an observer was sufficiently influenced by nature-philosophy as to interpret both cases in the first instance as animals; within three years, however, Unger had realized the true state of affairs and stated his conviction that the antherozoids were the male elements. Production of motile ciliated cells was shown by Thuret to occur in several kinds of green and brown algae.

Then in 1844 Nägeli followed the development of antheridia on the fern prothallus and described the production of ciliated antherozoids. This was an unexpected discovery to botanists at the time. It had long been known, that the spores of ferns are reproductive bodies, germinating to form a "proembryo" [prothallus] from which the embryo of a new plant appears. The spore thus corresponded to the seed, and it was quite expected that, as in mosses, male organs ("anthers" or antheridia, the latter term was already current) would be found associated with spore production. Yet though frequently sought on the fern plant, male organs had never been found; indeed hairs, indusia, scales, even stomata, had all at different times been taken for male organs, only to be rejected. When Nägeli found what certainly appeared to be antheridia, in complete isolation from the "seed-bearing" fern plant, it was therefore very puzzling. To us, the surprise is that Nägeli, who was one of the outstanding investigators of his time, failed to notice the female organs (archegonia) at the same time. Two years later he observed antherozoid production by microspores of *Pilularia*.

The production by plants of ciliated cells obviously analogous to spermatozoids of animals, created an immense impression on botanists. The zoologists Dumas and Prévost had already in 1824, gathered together a great deal of experimental and inferential evidence that in animals the spermatozoid itself is the effective male element. The presumption—widely held but still disputed—that in mosses and liverworts the antheridia and antherozoids are the male organs and fertilizing elements respectively, was much strengthened in consequence. Now Nägeli's observation on ferns suggested the occurrence of male organs in the higher cryptogams also: the difficulty was that the corresponding female organs had not been found.

In parallel with these discoveries in cryptogams a more intensive study of fertilization in higher plants was started by Schleiden with results characteristic of his erratic talents. In 1837–38 he published researches on the origin and development of the ovule in flowering plants, described by von Mohl as "numerous and excellent" and by Sachs as "certainly the best and most thorough of his day", which were directed to answering the key questions of the moment. His observations removed all doubt of the correctness of Amici's conclusion that in fertilization a single pollen tube enters the micropyle and that the tip is applied to the end of the embryo-sac. Unluckily, when following the early stages of embryo formation Schleiden evidently mistook the suspensor for an extension of the pollen tube pushing into the embryo-sac by invagination. He thus formed the belief, and stuck to it with tenacity, that the long-accepted sex roles in higher plants must be reversed, that the anthers are really female organs since each pollen grain could give rise to the embryo of a new plant, and that the embryo-sac merely acted "dynamically" and is therefore the male principle, "unless one assumes more correctly that it has simply a nutritive function". Schleiden thought his view was confirmed by the development of the megaspores in *Pilularia* and *Salvinia*, and he became entangled in inextricable confusion in trying to bring phanerogams, bryophytes and these heterosporic ferns into a common pattern consistent with his misguided interpretation.

The theory excited strong controversy for over ten years. There were real difficulties in bringing a new technique of observation to bear, and Schleiden was not a man to retract an opinion until the facts against it could no longer be disputed. Several workers claimed to have made observations supporting Schleiden, and some were prepared to defend his position on theoretical grounds, but the most experienced microscopists were against him and began to accumulate evidence that finally carried the day. Between 1842 and 1847 Amici made a series of careful observations of fertilization in orchids which left no doubt that, in this family, the embryo originates from a single well-defined cell, the ovum, already present in the embryo-sac before pollination, and that the pollen tube does not enter the embryo-sac. These observations were confirmed by von Mohl in 1847 (also in orchids, where details of the embryo-sac can be seen in the intact ovule). Amici and von Mohl effectively destroyed Schleiden's interpretation, although Schacht published supporting figures as late as 1851 but withdrew them immediately afterwards. Between 1847 and 1849 the basic facts of fertilization in flowering plants were firmly established and placed in a wider theoretical context by Hofmeister, of whose work we shall give a full account in a moment.

Amid the political storms that swept Europe in 1848 the world of botany was shaken by what Hofmeister called the "brilliant discovery of the presence of female organs on the fern prothallus at the same time as the antheridia found by Nägeli". The discovery was made on prothalli of *Pteris serrulata* by the Polish Count J. Leszczyc-Suminski, who showed fresh preparations of his material during the course of the work to Profesors Münter, Ehrenberg and Link of Berlin University. A full account of the work, with plates, was published by the Berlin Academy of Sciences. The paper received some sharp criticism, for Suminski went astray in a number of details, especially in describing the development of the antheridia and archegonia,[43] where he fell into "self-deception" (Hofmeister's comment), largely because he was still under the influence of Schleiden's view on cell-formation and the origin of the embryo from the male element. There was not the slightest doubt, however, of the truth of his basic discovery—he demonstrated the female organs (archegonia), saw the entry of antherozoids, and described the subsequent formation of an embryo within the archegonium and its development into a new plantlet.

We are now so familiar with the fern life cycle that von Mohl's description of Suminski's finding as "fabulous" may seem exaggerated, but to botanists at the time it was no less. Since very ancient times it had been guessed that the spore-dust of ferns functioned as "seed", and this had been proved when spores were seen with the microscope and shown to germinate and form a "proembryo" [prothallus] from which a new fern plant grew.[44] The astonishing discovery was the finding of sexual organs on the "proembryo" and not, where expected, on the mature fern plant which formed the "seed".

The full significance of the discovery was at once perceived by Wilhelm Hofmeister (1824–77), the most outstanding figure among a constellation of brilliant botanists of the century, and one of the great botanists of all time, ranking with Theophrastus, Cesalpino, Ray and Linnaeus. A few words must be said about the man himself. The son of a bookseller and occasional publisher in Leipzig, Hofmeister attended the local Realschule where the basis of instruction was physics, chemistry, mathematics and geography, instead of the classics, which were the main study in the Gymnasia. On leaving school he spent three years in Hamburg as learner-apprentice with a music publisher, and then at the age of seventeen he entered his father's business to take charge of foreign correspondence. He never studied at a university and never received any formal instruction in botany. An early interest in natural history was doubtless awakened by his father, who was an amateur botanist; in Hamburg he became acquainted with Professor Gustav Reichenbach, an expert on the orchids, who encouraged his botanical interest. He was deeply moved by reading Schleiden's *Grundzüge,* and studied other botanical literature including von Mohl, whom he recognized as far superior to Schleiden as an investigator. Towards 1847 Hofmeister began the microscopical researches which were the foundation of his scientific reputation and of the great theoretical advance embodied in the theory of alternation of generations. Hofmeister did a full-time job in his father's firm; his research was almost entirely done between four and six o'clock in the morning, before the normal day's work—a remarkable feat. In 1863, at the age of thirty-nine, Hofmeister was invited to the chair of botany at Heidelberg, although he was without formal qualifications in the subject. At Heidelberg, and later at Tübingen where he followed von Mohl, he continued active in significant research, and trained many young botanists who later distinguished themselves, including Karl Goebel, T. W. Engelmann and the talented Russian K. A. Timiriazev.

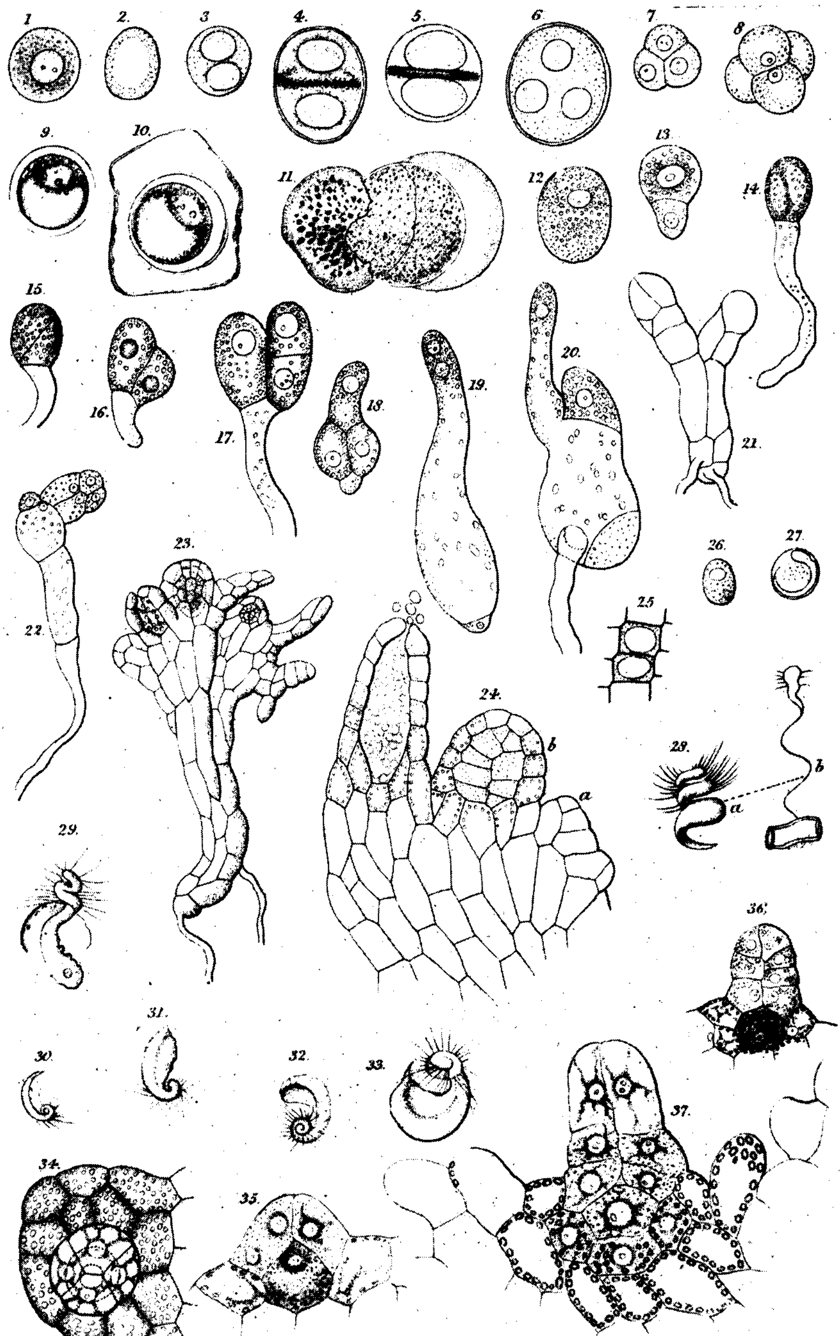
Hofmeister was active until a few months before his untimely death, but it is his earliest, truly classical studies of the structure, development and reproduction, of the angiosperms, gymnosperms and higher cryptogams, which constituted his most important work, and which raised the science of botany to a new stage. His theoretical genius was firmly based on a consummate mastery of microscopical technique, unique powers of observation and critical interpretation, and an ability to delineate what he saw with impressive accuracy and beauty. He gave the most conscientious attention to the results of other workers and made full use of them, but always confirmed the facts himself, not failing to examine (if possible) several representatives of each group of plants studied. His almost monographic descriptions of all the main groups of higher plants were so complete and authoritative that they made his theoretical conclusions unassailable.

In his first paper Hofmeister showed in seven species of Oenotheraceae (Onagraceae) that the embryo is formed from the ovum in the embryo-sac, not from the pollen tube as Schleiden imagined: this confirmed what Amici and von Mohl had found in orchids. This work was followed by a comparative study of pollen and ovule development in flowering plants, illustrated by fourteen superb plates, and dedicated to von Mohl. From an examination of forty species taken from nineteen families, spread across dicotyledons and monocotyledons, Hofmeister elucidated the basic facts beyond doubt. Although unable to follow the divisions in the embryo-sac in complete detail, he established the constant presence at maturity of the egg apparatus, consisting of ovum and two synergids, and of the antipodal cells, usually three, but numerous in the Graminae; he described the mode of development of the suspensor and embryo, and of the endosperm. As we noted earlier, an incidental result of this work was to strengthen the evidence for simultaneous division of cell and nucleus in the formation of new cells. The firm knowledge of the process of reproduction in angiosperms thus acquired, proved to be the essential complement to the studies of reproduction in cryptogams to which Hofmeister devoted himself with incredible industry after the discovery of the female organs of the fern by Leszczyc-Suminski.

It had been known for some time, from the observations of G. W. Bischoff and others, that the spores of other higher cryptogams besides ferns germinate to form prothalli. After Suminski's paper appeared, several botanists therefore began to look for sexual organs on the prothalli of Equisetaceae and Lycopodiaceae. Only Hofmeister grasped the far wider implications of Suminski's discovery. He saw in the first place that it was evidence of a regular alternation of two generations in the complete life cycle of a fern: a generation "preceding impregnation" on which sexual organs (antheridia and archegonia) arise, and a "fruit-forming" generation producing spores [in modern terminology, which I shall use for clarity, a gametophyte and a sporophyte generation]. This alone was a great advance in understanding, but even more fundamental was Hofmeister's recognition that a strictly homologous alternation of generations occurs not only in the life cycle of all the higher cryptogams (ferns, Equiseta, lycopods) but also in the bryophytes, gymnosperms and angiosperms as well. This was an insight of genius.

Hofmeister evidently began to entertain the concept of an alternation of generations very soon after Suminski's discovery and whilst in the middle of researches on which he founded his exposition of the theory in 1851. In a footnote to his 1849 paper on the embryo-sac he records his conviction that formation of the embryo in conifers corresponds, in many important points, to the development of the spore and embryo plant of the Lycopodiaceae and Rhizocarpae [heterosporic ferns]. In a paper on the higher cryptogams in the same year, he gives a preliminary discussion of analogies between bryophytes, ferns and conifers, and promises a fuller contribution on this question later. This paper is notable for Hofmeister's statement that he regards reproduction in the heterosporic forms *Pilularia, Salvinia* and *Selaginella* as the key to understanding reproduction in higher plants, and for his correction of Schleiden's errors of observation and interpretation of these plants. A brief statement of his ideas was included in a book review in 1850, but the full exposition of alternation of generations in higher plants formed the concluding section of Hofmeister's book entitled *Comparative Researches into Growth, Development and Fruit-formation of the Higher Cryptogams (mosses, ferns, Equisetaceae, Rhizocarpae and Lycopodiaceae) and Seed-formation in Conifers* [which I shall abbreviate to *Comparative Researches*], published at Leipzig in 1851 by his father's firm.[45]

Figure 24 Hofmeister's figures of the development of prothallia antheridia and archegonia of *Equisetum arvense*, from the *Comparative Researches* (1851).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The work begins characteristically without any introduction, plunging straight into the description of *Anthoceros* and fourteen other liverwort genera, mosses, ferns, *Equisetum, Pilularia, Salvinia, Selaginella*, and conifers. Hofmeister repeated Suminski's investigation of *Pteris serrulata* and included three other genera of ferns in addition. It is instructive to compare the respective figures and to see how superior in accuracy and detail are those of Hofmeister. The descriptions are remarkably thorough, covering morphology, apical meristems, anatomy of cells and tissues, details of reproduction, spore germination, embryology, and are illustrated by thirty-three plates. The literature is referred to and compared in detail with Hofmeister's own results.

Only when all the factual evidence is complete does Hofmeister sum up his epoch-making view in half a dozen pages. He begins by remarking that comparison of the development of mosses and liverworts on the one hand, with that of the ferns, Equisetaceae, heterosporic ferns and Lycopodiaceae on the other, discloses a complete uniformity between the formation of the sporophyte on the one hand, and of the embryo on the other. The archegonia and antheridia of moss or liverwort correspond exactly to those on the fern prothallus, while the product of fertilization of the moss—the sporogonium—is equivalent to the frond-bearing fern plant (the fern in the ordinary sense), and the leafy plant of the moss is equivalent to the prothallus of the fern. Thus "mosses and ferns offer one of the most striking examples of a regular alternation of two generations that differ widely in their organization". There is a clear alternation between the first (sexual) generation which bears antheridia and archegonia, and the following (asexual) generation "destined to produce spores in far greater number than that of incipient fruits [i.e. fertilized embryos] produced by the first generation".

The heterosporous cryptogams (*Pilularia, Salvinia, Selaginella*) form a link with the gymnosperms and angiosperms. They produce spores of two kinds; the larger ones (megaspores) form gametophytes bearing only female organs (archegonia); the smaller microspores form gametophytes bearing only male organs (antheridia); moreover, the gametophytes develop wholly or partially within the spores. In gymnosperms and in angiosperms the megaspore, represented by the embryo-sac, remains throughout its development within the sporangium, represented by the ovule, in which it is produced. The prothallus develops wholly within the megaspore (empryo-sac), being represented in gymnosperms by the endosperm; in the angiosperms the prothallus is highly reduced and represented only by the cells present in the embryo-sac at fertilization. The pollen grains in gymnosperms and angiosperms correspond to microspores; prothallus development is here represented only by the growth of the pollen tube and the one or two divisions by which the generative nuclei are formed.[46]

Hofmeister's exposition is a masterly example of succinct statement which it is difficult to compress further, nor is it possible in a summary to do justice to the many brilliant perceptions of homology which illuminate his discussion. One extraordinary insight which became a prediction was his suggestion that perhaps ciliated fertilizing elements might be formed in pollen tubes of conifers. Hofmeister looked for them in vain, but twenty years after his death swimming sperm were found in the gymnosperms, not indeed in conifers, but in the cycads.

Perhaps only a botanist familiar with all the detailed facts, many first observed and recorded by Hofmeister, can fully appreciate the transformation brought about in botanical science by the *Comparative Researches* and the theory of alternation of generations which it announced.[47] It can only be compared to the revolution in chemistry caused by Mendeleev's Periodic Law. The demonstration of a basic unitary pattern of life cycle in the plant kingdom was, in the first place, a great advance towards an all-embracing natural classification of plants. It showed the genetic relationship which underlies the diversity of plants, and destroyed such traditional divisions as cryptogams and phanerogams, now seen to be purely artificial and mere labels for lack of knowledge. At the same time, it pointed to new natural groupings of plants, based on characters of development and structure. This extension of natural classification to higher taxonomic groupings could not fail to foster the growth of phylogenetic and evolutionary ideas.[48]

The unitary concept of higher plant development had also a deep influence on the study and interpretation of comparative morphology, for which it provided the theoretical foundation and methodology, no longer seeking to force lower plants into categories derived from the more highly organized, but using lower forms as a guide to comprehending the higher. The cell was finally recognized as the key to plant organization and development in all its forms.

The comparative studies of meristematic growth by Hofmeister were of particular significance in relation to morphology and tissue formation. For some years Nägeli had been convinced, by observations of algae and mosses, that growth by division of a single apical cell was universal in plants. Hofmeister showed, however, that multicellular meristems, without a special apical cell, are normal in most higher plants except ferns. This work marked the beginning of interest in the internal factors controlling cell division and organ formation.

The concept of alternation of generations led to a clear and logical picture of the morphology, reproduction and natural affinities, of vascular plants and bryophytes, but still left the algae and fungi untouched. Different kinds of motile and non-motile spores had been seen in algae, including tetraspores of red algae, whose resemblance to pollen mother-cells and pollen did not escape von Mohl, but their reproductive role was not clear. Only in *Chara* was the reproductive cycle known with certainty, and Hofmeister was able to make a perceptive comparison between it and the basic life cycle of higher plants. As the concept of alternation brought order into the ontogeny of higher plants, it gave the impetus to a spate of investigations into the great assemblage of lower plants which systematic botany was beginning to discover.

With the appearance in 1851 of von Mohl's comparative study of the plant cell, and of Hofmeister's researches establishing an alternation of generations in higher plants, a unitary theory of plant structure, development and reproduction, was completed in its main outlines. It became a stimulus and guide during the further expansion of botany.

Notes

1. In 1869 T. H. Huxley wrote: "As industry attains higher stages of its development, as its processes become more complicated and refined, and competition more keen, the sciences are dragged in, one by one, into the fray"; and Karl Marx at about the same time: "modern industry . . . makes science a productive force distinct from labour and presses it into the service of capital".
2. Chemistry, of all sciences, made the most direct contribution to indus-

try, especially through its many applications in textile manufacture and dyeing, and became in consequence the science to which the greatest effort was devoted. In France, and later in Germany and the Netherlands, investigation of the chemistry of "natural products" began, the results of which opened new areas of research in animal and plant physiology.

3. Plans for the development of science were drawn up early in the Revolution by the Committee of Public Instruction of the Convention, and although held up during the critical period of the "terror", these plans became the basis on which the subsequent reforms and institutions were established. Scientists made themselves popular by the practical help they gave in saving the Republic during the most dangerous days of foreign intervention. The prestige of science was enormously increased, and leading scientists (including Lamarck and Antoine-Laurent de Jussieu among the botanists) were given responsibility for detailed planning of the scientific reorganization that was carried out.
4. The first members of the botany section were Lamarck, A.-L. de Jussieu, Adanson, L'Heritier, Desfontaines and Ventenat. The éclat enjoyed by members of the Institut was not equalled by their salaries, and most of them undertook teaching or other work in order to supplement their pay!
5. The leading position of German botany was certainly related to the large number of universities and to the fact that natural science was given equal weight with traditional faculties such as theology, law, and medicine. There were simply more professors and lecturers (Dozenten) in botany in Germany than in any other country. In the eighteenth century chairs of botany were often still subordinate to medical teaching; indeed Goethe tells us that at Jena the chair of botany was regarded as a perquisite of the senior medical chair and no botanical courses were ever given, until Goethe himself induced the incumbent of the time to give one. But in the nineteenth century the position was quite different, and botany in almost every German university was treated as an independent discipline. Other factors in the upsurge of German botany were the close links between botany and agriculture in Germany, and the growth of the German optical industry which made available excellent, but much cheaper, microscopes.
6. The one-sided development of British botany due to imperialism was noted by F. O. Bower in *Sixty Years of Botany in Britain* (1938). All the resources of Kew, the British Museum, Glasgow and Edinburgh were concentrated on floristic exploitation of the British Dependencies.
7. Wolff used the term *punctum vegetationis* for the meristem. He figures it (in *Brassica*) without distinguishable cells, and with young leaves arising as tiny mounds of tissue upon it. He states his general principle of epigenesis thus: "Every organic body or part thereof, is produced at first without organic structure, and is later made organic." He bases this on developmental observations of seeds and growing points in plants, and embryos

in animals; both plants and animals have a common structure of cells and vessels, he says.

8. The first record of the use of glass cover-slips in microscopy was published by J. Ingen-Housz in 1789, and it seems probable that he learnt about them during a visit to Italy. See note by H. E. Hoff in *Bulletin of the History of Medicine* **36**, 365 (1962).
9. Briefly, Mirbel (1802) distinguished "tissu cellulaire", consisting of "cells", and "tissu tubulaire", consisting of "tubes" or vessels, as the two fundamental components of plant structure [this closely follows Grew]. The plant is formed of a basic "organizing substance" which at first, that is, at the stem or root apex, is mucilaginous and fluid, and without cells or tubes. These arise as small bubbles, and once formed they grow until the hardening and thickening of their walls puts an obstacle to their development.
10. The question of nature-philosophy and its influence in science is too complex a subject to be treated adequately in a general history such as this. Schelling's philosophy was certainly not at first without positive effects on science, but its negative tendencies were always present and became accentuated with time. Among botanists (biologists) Agassiz, Braun, Oken and Schimper had been pupils of Schelling and were affected by nature-philosophy to varying degrees.

    The influence of nature-philosophy soon disappeared in physics and chemistry, but lasted much longer and was much greater and more confusing in botany: possibly owing to the absence of quantitative experiment and methods in botany, a point suggested by Schleiden's discussion in *Grundzüge der wissenschaftlichen Botanik*.
11. It is to be noted that from this period onward, advances in botany represent the resultant or summation of the contributions of large numbers of investigators of whom only a few are mentioned by name.
12. J. J. P. Moldenhawer: *Beiträge zur Anatomie der Pflanzen*. Kiel (1812).

    Moldenhawer was Professor of Botany and Fruit-tree Culture at Kiel for thirty-six years, although first trained in theology and classics. As a young man he published a commentary on the first three chapters of Book I of Theophrastus' *Historia Plantarum*, in which he combined textual criticism with botanical notes: this work was highly thought of by F. Wimmer, the editor of Theophrastus.

    Moldenhawer gives some information about the five microscopes he used: "two from Weickert; an English one whose lenses could be used as a simple microscope, very good; an old English one put together by Culpeper; but superior to all, a factory-made English one by Wright, with a stock of 8 lenses, with 6 others of the same artist which I added for completeness. The Wright instrument magnifies three-hundred times."

    Moldenhawer examined a wide range of plants to confirm his ideas, but very sensibly used a single favourable and easily grown material, the maize plant, for most of the foundation work.

13. In his *Grundlehren der Anatomie und Physiologie der Pflanzen* (1807).
14. The absence of pores was confirmed by showing that individual cells with coloured sap do not transfer their sap to adjacent colourless cells when the tissue is pressed with a needle. Moldenhawer demonstrated this with tissue of *Fritillaria* and epidermis of *Tradescantia*.
15. To emphasize the distinction between his interpretation and Wolff's, Moldenhawer says that "tissue" is an inappropriate term for the aggregates of cells which make up the plant body, and proposes "cell substance" instead. Perhaps it is fortunate that this term was not adopted, and "tissue" remained in use.
16. The idea of intrusive growth of one plant tissue into another haunted plant anatomy for over a century. In fact true intrusive growth of tissues is absent or very exceptional in plant development where co-ordinated growth is the rule. Some specialized cells (laticifers, sclereids, fibres) do show intrusive growth, or more accurately, a combination of co-ordinated and intrusive growth. Moldenhawer's grasp of the essential basis of tissue development was very acute: the facts of observation convinced him of the absence of tissue movement (Verrückung) and intrusion (Einschnürung).
17. B. Corti: *Osservazioni microscopiche sulla Tremella e sulla circolazione di fluido in una pianta acquajuola*. Lucca (1774).
18. In 1851 von Mohl says [not quite accurately] that motion of the protoplasm, "long thought to be peculiar to water plants, is now shown to be a universal phenomenon".
19. Sir Joseph Banks had persuaded the British government to accept the principle that a naturalist should accompany naval voyages of exploration. Thus Banks himself with D. Solander, and later, great botanists like Robert Brown, William Hooker, his son Joseph Hooker, and of course Charles Darwin, were enabled to collect material and experience which shaped their ideas. Other countries adopted a similar policy. The great expansion of knowledge of the global flora not only advanced taxonomy and plant geography, but resulted in vast economic changes, and crops were transferred and acclimatized in new areas of the world.

    The Royal Botanic Gardens at Kew became the scientific centre for movements of plants that had far-reaching economic and political results.
20. Augustin Pyrame de Candolle (1778–1841) grew up in the French-oriented scientific atmosphere of Geneva, his interest in botany being awakened by J. P. E. Vaucher. He spent eighteen years in France, first in Paris in botanical researches and in editing a new edition of Lamarck's *Flore Française*, and then as Professor of Botany at Montpellier. He became professor in Geneva in 1816 and remained there for the rest of his life. His *Prodromus Systematis regni Vegetabilis* 1824–41 (completed by his son Alphonse between 1841 and 1873) is a classic descriptive account of dicotyledons and gymnosperms to specific level.

21. De Candolle's concept of symmetry undoubtedly reflects the powerful influence of Cuvier and his treatment of animal anatomy.
22. The error was cleared up by Hugo von Mohl in a careful study of the anatomy of palms, *De Palmarum Structura*. Munich (1831).
23. For a biographical account of Robert Brown (1773–1858) see the obituary in the *Proceedings of the Royal Society* (1859). One point of special interest deserves mention, namely Brown's determined study of German as a youth. His mastery of the language gave him ready access to the most copious contemporary botanical literature and close contact with leading German botanists (A. von Humboldt, Schleiden) whom he knew personally on visits to Berlin. It was Brown who drew Darwin's attention to C. K. Sprengel's work on the adaptation of flowers for pollination by insects.
24. It is nightmarish to think of the possible interpretations Brown might have made had he been influenced by nature-philosophy. He discovered Brownian movement in burst pollen of *Clarkia* when looking for sperm-like male elements in plants. Fortunately he experimented instead of jumping to conclusions, and soon satisfied himself that the movement is not confined to living matter, but is found in many kinds of suspended material with particles whose diameter he estimated with remarkable accuracy to be about 10^{-5} cm. He cautiously suggested that the particles were "active molecules" universally present in matter. The kinetic explanation of Brownian movement was given by Sir William Ramsay fifty years later.
25. C. Linnaeus: *Prolepsis Plantarum* (1749).
    H. F. Link: *Philosophia Botanicae Novae*. Göttingen (1798).
26. Brown was the least dogmatic of men, and only a few years later he wrote that "the structure of both anther and ovaries [in *Rafflesia*] is not obviously reconcilable with any hypothesis hitherto proposed to account either for the origin, or for a common type, of the sexual organs of phanerogams."
27. Brown had begun to suspect the true nature of gymnospermy some eleven years earlier: his studies of seed development made him certain. Later he published a study of ovule development in gymnosperms which brought awareness of the crucial differences in development between gymnosperm and angiosperm seeds. With his usual fairness Brown records that J. C. Trew had suggested in 1767 that the seed in *Pinus* is not enclosed in an ovary; [what Trew actually wrote was: Individual seeds, or rather germs, have a stigma just as if they had a female organ (singula semina vel potius germina stigmati tanquam organo feminino gaudent)].
28. The first decisive experiments with animals (frogs, toads) were reported in 1785 by Lazzaro Spallanzani. He showed that physical contact between spermatozoids and the ovum was essential for fertilization, and that it was not accomplished by an "emanation"; nevertheless he continued to

believe that the actual "fertilizing power" was in the seminal fluid.

His experiments with plants (an attempt to repeat Camerarius) ran into confusion, partly through failure to realize that occasional bisexual flowers are produced on dioecious plants, partly through lack of strict precautions against accidental pollination. His negative results, it may be added, could not at this stage undermine botanists' belief in the sexual fertilization of flowering plants.

29. The growth of specialist journals of botany is illustrated by the following list (not complete) of some newly founded in this period.

1804–7	*Botanische Zeitung* (Revived as *Flora*).
1818	*Flora*. Regensburg.
1824	*Annales des Sciences Naturelles*. Paris.
1826	*Linnaea*. Berlin.
1843	*Botanische Zeitung*, (Edited by von Mohl) Tübingen.
1844–47	*Zeitschrift für wissenschaftliche Botanik*, (Edited by Nägeli and Schleiden).
1835	*Wiegmann's Archiv für Naturgeschichte*.
1858	*Pringsheim's Jahrbücher für wissenschaftlicher Botanik*.

30. For example, Schleiden showed the absurdity of the views of Du Petit Thouars (who explained secondary thickening of the stem as an extension downwards of vascular tissue from the buds) from the simple fact that "the cells of the bud are organized into vascular bundles from the vascular bundles of the stem upwards into the bud, and not in the reverse direction."
31. To some extent Hegel brought misunderstanding on himself. The extreme idealism he adopted, the resulting ambiguity of expression about the reality of the material world, even his diffuse and tortuous language, all made his exposition difficult. Moreover the crucial importance he attached to science was compromised by an early period when he was much influenced by Schelling. Although later he tried to distance himself from nature-philosophy, in his specific comments on botany Hegel unfortunately relied for information on men like Schelver, Schulz and Oken, who had succumbed most completely to nature-philosophy in its worst absurdities, and brought botany and philosophy alike into disrepute. Hegel's comments on botany sometimes have a kernel of penetrating truth but founder in what Sachs called a quagmire of error.
32. M. J. Schleiden: Beiträge zur Phytogenese. *Müller's Archiv* (1838).
33. Theodor Schwann: *Mikroskopische Untersuchungen über die Übereinstimmung in der Struktur und dem Wachstum der Tiere und Pflanzen*. Berlin (1839).
34. Schleiden's statement of the evidence for cell-theory in plants, given in his textbook, is of considerable historical interest. The following points are made. The simplest plants, e.g. Protococcus, consist of a single cell, others consist of single cells united together. In all algae and fungi a naked spore is the reproductive element. Single-celled gemmae of mosses re-

produce the whole plant; in higher plants a single cell, or a very few cells, of the leaf can give a new plant. Hence the essential life of a plant must be contained in the cell.

Schleiden suggested the use of algae as experimental material for physiological investigation, saying that it is essential to examine the physiology of single cells.

By 1846, such was the rate of progress in research, Unger was able to give a much fuller account of cell structure of plants in his book *Grundzüge der Anatomie und Physiologie der Pflanzen*. Vienna.

35. Originally taken from theology, the word protoplasm had already been applied to the common ground substance of animals by the Czech physiologist J. E. Purkinje.
36. H. Schacht: *Die Pflanzenzelle*. Berlin (1852).

    This book is more detailed and compendious than von Mohl's, to which it forms a useful complement. The twenty plates, drawn by the author from nature, illustrate many cell types from algae, fungi, bryophytes, ferns and higher plants. A notable feature is the description and use of microchemical methods to identify starch, cellulose, lignin, cutin, protein, etc.
37. Mulder determined the average composition of protein to be represented by the formula $C_{40}H_{62}N_{10}O_{12}$ (the modern estimate would be $C_{40}H_{65}N_{11}O_{13}$). This basic unit he thought combined either with sulphur or phosphorus. G. J. Mulder: *Versuch einer physiologischen Chemie*. Braunschweig (1843).
38. Dutrochet usually placed the osmotic solution inside the membrane and pure water outside so that water moved inwards. Hence he called the process endosmosis; this is the usual term in the older literature, only later did "osmosis" become the general form. He derived the term from the Greek ὤσμη "impulse".
39. He made the first systematic study of the movements of *Mimosa pudica*, the Sensitive Plant, in relation to external stimuli, recognizing transmission of the stimulus to a distance, and the presence of a turgor mechanism in the pulvinus.
40. J. Liebig: *Die organische Chemie in ihrer Anwendung auf Agricultur und Physiologie* (1840).

    The work was many times reprinted with additional matter, greatly stimulating the development of agricultural science.
41. Bernard de Jussieu's early study of *Pilularia* seems to have been forgotten.
42. Hence the term zoospore, still in scientific use, its nature-philosophic origin forgotten.
43. The word archegonium was first used in 1835 by G. W. Bischoff, for the female organ of mosses. The name was adopted for the homologous organ in ferns and other higher cryptogams when it was discovered.
44. The name prothallus was introduced by Hofmeister.

45. The full list of W. Hofmeister's publications in this crucial period of his career is as follows.
    - 1844 Untersuchungen des Vorgangs bei der Befruchtung der Oenothereen. *Botanische Zeitung*, Vol. 5.
    - 1848 Ueber die Entwicklung des Pollens. *Botanische Zeitung*, Vol. 6.
    - 1849 *Entstehung des Embryo der Phanerogamen*. Leipzig.
    - 1849 Ueber die Fruchtbildung und Keimung der höheren Kryptogamen. *Botanische Zeitung*, Vol. 7.
    - 1850 Short statement of alternation of generations [Generations wechsel]. In review (signed Wm. H.) of C. E. Merklin's book on fern prothallia. *Flora*, Vol. 33.
    - 1851 Zur Entwicklungsgeschichte des Embryo der Personaten. *Flora*, Vol. 34.
    - 1851 *Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen (Moose, Farne, Equisetaceen, Rhizokarpeen und Lycopodiaceen) und der Samenbildung der Coniferen*. Leipzig.
46. In the enlarged 1862 edition of the *Comparative Researches* Hofmeister added an interesting expansion of his earlier discussion, pointing to flowering plants as the upper terminal link of a series containing the conifers and cycads, the vascular cryptogams, the mosses and liverworts, and the Characeae. Within this series, he says, the extension and independence of the vegetative existence of the spore-bearing generation [sporophyte] increases in proportion to the descending rank of the generation bearing sexual organs [gametophyte].
47. Karl Goebel wrote in 1905: "The alternation of generations is in very truth the greatest discovery that has ever been made in the realm of plant morphology and taxonomy."
48. Rather strangely, Hofmeister did not mention the evolutionary implications in his 1862 discussion of his theory.

10

Laying the Foundations of Modern Botany (1851 to 1912)

Botany is the science of the transformation of matter in the form of plants.
M. J. Schleiden

Life is the mode of existence of protein bodies, the essential element in which consists in continual metabolic interchange with the environment outside them. . . . This metabolism is the necessary condition for their existence.
F. Engels

In the second half of the nineteenth century botany entered a period of very vigorous and exciting growth. In the space of fifty years botanists established an immense body of interconnected facts, from which could be deduced, for the first time in the study of plants, a "synthetical unity" (in Kant's terminology) of general relationships embracing the totality of plant structure, activity and modes of development. On the knowledge accumulated during these years of intense activity the modern science came into being—it is the permanent substratum of facts and principles contained in every textbook of botany today. A notable feature of the period was indeed the publication of several splendid textbooks, which presented the whole of botany, or one of its major subdivisions, in a comprehensive and theoretically coherent way.[1]

An important factor in the rapid progress and consolidation of the natural sciences at this juncture was the establishment of research schools in the universities, formed in the first place around some leading scientist, whose fame and personality attracted ardent students.

The special conditions which gave the study of botany a pre-eminent position in the German universities naturally caused the first research schools in botany to arise there. Keen students who could afford it flocked to Germany for the privilege of studying and pursuing research under men of international reputation.[2] The result was a remarkable increase in the productivity of botanical research. Many students carried back with them the inspiration and advanced methods of German botany when they returned home.[3]

The recognition of a common protoplasmic and cellular basis to the structure and development of all living organisms, and the clarification of the life cycles and natural relationships of plants by the concept of alternation of generations, gave a powerful stimulus to the further systematic study of plants from these fundamental aspects. These concepts acquired even greater relevance after the theory of "descent with modification through natural selection" was announced by Charles Darwin in 1859 in the *Origin of Species*. The doctrine of evolution manifestly offered a simple explanation for the unitary features of plant structure and development, which now appeared as the natural consequence of a real phyletic unity based on variation during descent from common ancestral forms. Natural selection of better adapted variants, as proposed by Darwin, also offered a rational mechanism by which the evolution of new forms was brought about. The brilliant achievements of a generation of botanists, culminating in the work of von Mohl, Nägeli and, above all, Hofmeister, were in effect preparatory to Darwin's theoretical synthesis and became an integral part of it; not surprisingly, therefore, most leading German botanists adopted with enthusiasm the idea of evolution through natural selection, as did Joseph Hooker in Britain, Asa Gray in North America and Timiriazev in Russia. From this time evolutionary theory dominated botany, just as it did all branches of biological science.[4]

It would be superfluous to analyse the origin and impact of Darwinism, or attempt to add to the mountain of exegesis that has accumulated around it. I shall content myself with emphasizing a few aspects in which the emergence of modern evolutionary theory was directly connected with the history of botany.

During the first half of the nineteenth century the mutability of species, assumed by Erasmus Darwin and Lamarck, was becoming more frequently considered as a possible explanation of the growing fossil evidence for the appearance and extinction of species in earlier geological epochs, and of links between natural classification and the facts of terrestrial distribution of plants and animals.[5] The idea of the evolution of plants gained force through studies of fossil plants in Europe and North America between 1820 and 1850. Adolphe Brogniart hints at this in his important *Histoire des Végétaux Fossiles* (1828), notable for the careful comparison of living and fossil forms, and for the use for the first time of anatomy as a diagnostic feature.

> By studying ancient floras . . . and comparing them with present day floras . . . we can . . . make presumptions of the nature of the climate under the influence of which ancient plants developed. Perhaps by such study we may be able to illuminate some of the most important points of the history of the earth and give greater probability to theories at present considered to be simple hypotheses.

Unger, whose important contributions to cell structure and anatomy have already been mentioned, also studied fossil plants for twenty years and showed that the component forms of the fossil flora changed in successive epochs, and that the groups of higher plants, with more complex organization, are absent from the earliest formations, appearing and becoming dominant in the more recent (*Versuch einer Geschichte der Pflanzen*, 1852). He gave an enlightened discussion of possible explanations of the observed succession of plant forms, indicating his own view that new forms appear by transformation during descent, "according to some great, at present but dimly perceived law of development." Nägeli had already accepted the transmutation of species by the time the *Origin* appeared, writing in that very year: "External reasons from comparison of floras of successive geological periods, and internal reasons from the physiological and morphological laws of development and from the variability of species, leave little doubt that species have arisen one from another." Botanical opinion was clearly receptive to one component of evolutionary theory—the mutability of organic forms—when Darwin's complete statement shook the intellectual world.

The hypothesis of mutability was not compatible with strict belief in the biblical account of creation, but if this account were held to be in some degree symbolical then it was possible to accept transformation of organisms in time ("descent theory" as Strasburger distinguished this aspect of evolution from "Darwinism", which included the theory of natural selection) without coming into open conflict with religion. So mutability of species in a rather undefined form hovered as a cautious hypothesis in biological thinking, only becoming a decisive influence in science when Darwin suggested, and was able to adduce a mass of factual evidence in proof, that natural selection of better adapted variants is the mechanism of change. Darwin was replacing the vague operation of God's purpose or some teleological final cause, by the action of a material cause or combination of material causes alone. This was the reason for the immediate scientific impact of Darwinism, and also the explanation of the extremely bitter opposition it aroused in some quarters; Darwin himself, as we know, was more than cautious in seeking to avoid the religious issue, but it was impossible to conceal that natural selection, which in his own words "acts on the whole machinery of life", invoked only material causes and brought vital phenomena wholly within the purview and laws of natural science. The process of evolution as envisaged by Darwin had, therefore, a scientific standing and completeness lacking in all earlier evolutionary theories; moreover, it was supported by the wealth of fact and scrupulous argument in the *Origin*, to which his established reputation gave immense authority. The triumph of Darwinism was built on this double foundation.

In the *Origin of Species* Darwin used evidence from plants very freely to support his argument, drawing on many sources, including in particular the experience of practical plant breeders from T. A. Knight onwards, information on plant dispersion and distribution from Augustin de Candolle and his son, the "large store of knowledge and excellent judgement" of Joseph Hooker, and his own botanical observations and experiments. Darwin called himself an ignoramus in botany, but this only meant that—perhaps fortunately—he had not been academically trained in the subject and did not possess the detailed knowledge of plant systematics which was still considered the hallmark of the true botanist.[6] In fact, he made important contributions to botany which are referred to below. Here it is sufficient to note the very great part played by contemporary botanical knowledge and theory in the formation of Darwin's theory of evolution and in its acceptance by scientific opinion. The complementary evidence from both plant and animal kingdoms provided the strongest possible support for Darwin's thesis.

Joseph Hooker was Darwin's most intimate friend and was involved in the crystallization of his evolutionary ideas from their first beginnings, revealed to Hooker in a famous letter in 1844. The first explicit acceptance of Darwinism by a leading scientist was in Hooker's *Flora Tasmaniae*, published only a few months after the *Origin*. In an introductory essay Hooker discussed the facts of natural relationship and geographical distribution of plants which pointed to evolution by selection, and gave an account of Darwin's views and of some problems and difficulties. Hooker's candid, judicial treatment, and the seal of his approval, were powerful advocates for the new theory.

Darwinism had an almost immediate effect on every branch of biology,[7] as is evident from the writings of many botanists of the time. It profoundly influenced the aims and strategy of research and the interpretation and integration of the results.[8] Natural classification and comparative morphology had far greater and more exciting meaning when seen as the reflection—however imperfect, and the imperfection was itself a productive challenge—of the real relationships of organisms that had been modified in the course of descent "from some one primordial form, into which life was first breathed." The phylogenetic view (the expression is Strasburgers's) opened extremely fruitful and unifying perspectives, even if it sometimes led to trivial speculation. The great morphologists, men like Strasburger himself, de Bary, Goebel, and others, were well aware of the limitations and pitfalls of using comparative morphology as a guide to possible phyletic relations, but they also understood its value and the illumination it could bring. The critical phylogenetic approach was of vital service in the formation of modern plant morphology: its neglect in recent times has been unfortunate.

Even within the strict confines of morphology, the evolutionary view made for deeper understanding. It had been a great advance in the study of plant form when morphological categories came to be defined by the mutual relations of organs in their position and development within the plant body, but these categories retained a certain idealist character, and as a result some morphologists treated particular categories of plant organ (e.g. leaf, shoot, carpel, etc.) as fundamental and unchanging units of plant construction, without regard to the facts of ontogeny. From the standpoint of evolution, the morphological categories could be seen not just as mental labels, but as the expression of actual inherited regularities in the differentiation of form within a group of phyletically related organisms. At the same time, since evolution entailed changes in morphological organization with time, notions of fixed and absolute morphological categories, isolated from development, could no longer be entertained.[9] The possibility of experimental morphology, to be realized in the century following, could at last be envisaged.

The role of natural selection in evolutionary change made it possible to comprehend, and hence to explore, the unitary of structure and function in the plant body and in its individual organs and tissues; in this way physiology was brought into close connection with the facts of morphology. Adaptation, viewed as the consequence or obverse of natural selection, was freed from the mystery of teleology and final causes, and became open to investigation in terms of the physics and chemistry, the material structure and metabolic activities, of living plants in their environment: plant physiology was stirred into new and vigorous life. Darwin's researches also extended the concept of adaptation by including the complex relations between organisms and the climatic, edaphic and biotic conditions of the environment, and from the study of these relations developed the new sciences of ecology and plant geography.

In preparing the projected work which, in the event, became the *Origin of Species*, Darwin carried out pioneering experiments with plants. He was first to test the effect of sea-water on the flotation and viability of seeds and fruits, and so to demonstrate that a significant proportion of the present-day land flora would be able to spread in course of time across at least a thousand miles of ocean, assuming the direction of winds and currents to be favourable. By observing the degree of hybridity in the progeny from adjacent plots of several varieties of cabbage and other species, he confirmed C. K. Sprengel's surmise that even in hermaphrodite flowers cross-fertilization is favoured by nature. He also experimented with sowings of mixed varieties of wheat and sweet-peas continued from year to year, the total seed from each plot being harvested and re-sown, in order to follow the changes in population as natural selection operated. This simple approach opened a new era in the experimental investigation of many ecological and related problems.

After the *Origin of Species* Darwin devoted much time in the last twenty years of his life to botanical researches.[10] The apparently unconnected topics were united by the common aim of supporting and elaborating principles already enunciated in the *Origin*. Although isolated from the main stream of botany of the period, Darwin's researches aroused great interest because he used his extensive and mainly novel observations to show what startling adaptive modifications occur in nature. His account of "various contrivances" for insect fertilization of orchids, and his discovery and explanation of heterostyly in the primrose and other plants, were landmarks in floral morphology. They were the first studies of floral adaptation to insects since Sprengel, and mark a big advance by reason of Darwin's realization that flowers are not only adapted for pollination by insects (as Sprengel had shown), but specifically for cross-pollination, a discovery which put the whole question in a fresh light.

In parallel with study of floral mechanisms favouring cross-pollination, Darwin set up many experiments over a period of ten years, showing that the benefit from cross-fertilization (which in 1862 he called "some unknown good") was a reality that could be measured in the progeny as more rapid and vigorous growth, greater height of plants, and increased production of fertile seed. These results were of the greatest theoretical and practical importance in genetics and plant-breeding in the long term; more immediately, they provided firm experimental evidence of the evolutionary significance of cross-pollination and the mechanisms that promote it. The study of pollination mechanisms received a great stimulus from Darwin's work, and in the half-century following, botanists gathered a mass of detailed information on the subject from all over the world.[11]

Darwin's studies of climbing and insectivorous plants are characteristic examples of his thorough treatment of a particular subject. The climbing habit and the adoption of insect nutrition are considered as adaptive responses to the environment, in the one case as a means to gain light with the greatest economy of stem material, in the other as a form of accessory nutrition in a particular type of habitat. The complex co-ordination of structure and behaviour involved is described by Darwin in minute and graphical detail, and his analysis of these examples of adaptation made a great impression and added a new dimension to the interpretation of physiological facts. Almost the last work of

Darwin was a study of plant movements to which we shall refer later.

Between 1851 and the end of the century the mere accumulation of facts about plants outstripped the gatherings of the previous five thousand years. In our account the work of many memorable botanists must, alas, be anonymously subsumed in the smoothed curve to which the intriguing conflicts and adjustments of research are here reduced. All the lines of investigation of plant structure and reproduction which found a temporary consummation in Hofmeister's *Comparative Researches*, continued without pause, extending and branching into wider territories opened by the vision of Hofmeister and Darwin, and made accessible by a series of novel procedures and technical improvements in microscopy, introduced from about 1870 onwards. The optical performance of the light microscope was raised practically to its limit by the Abbé substage condenser and the new apochromatic lenses, produced by the firm of Zeiss in Jena, and capable of working with oil immersion. On the preparative side the use of fixed, in place of living, material was combined with wax-embedding and mechanical sectioning, making it possible to see the structure of complete organs and tissues in serial sections, aided by differential staining with products of dye-chemistry. A phase of extraordinary progress was opened by these technical advances, in which not the least important factor was the incredible skill, patience and critical insight of the leading microscopists.

The remarkably rapid growth of plant physiology[12] was the most momentous new development in botany after the mid-century. Within a few years plant physiology changed from the personal interest of a few isolated investigators, and sprang to life as a fundamental division of botany, co-equal with morphology and systematics. The internal theoretical reasons for the increasing turn to physiology have been touched on. In addition a cogent practical impulse spread into botany from agricultural research, which was naturally concerned with physiological questions. Although state-aided agricultural research had begun in England and France, it was in Germany where it first took off on a large scale, partly under Liebig's energetic influence, but mainly because the special circumstances of German industrial expansion awakened the authorities in a forcible way to the need to increase crop production. Agricultural departments were added to a number of universities, and agricultural research stations were established, the first being at Möckern near Leipzig in 1851. Many others quickly followed and by the end of the century over eighty agricultural stations were active in Germany. This policy did much to give Germany the great lead in plant physiology which was maintained for more than fifty years. Julius Sachs, whose researches, teaching and writings make him the unquestioned founder of modern plant physiology, carried out his pioneer investigations in physiology during the eight years he was employed, first in the Agricultural and Forestry Institute at Tharandt near Dresden, and then at the Agricultural College of Poppelsdorf in Bonn. Hugo de Vries, whom Sachs regarded as his best student, worked for some years for the Prussian Ministry of Agriculture. The closer links between agriculture and botany which existed in Germany were undoubtedly productive for both sciences. One vital contribution to plant nutrition, the discovery by H. Hellriegel and W. Wohlfahrt of symbiotic fixation of nitrogen by leguminous plants (published in 1888), came from a research institute devoted to improvement of the sugar-beet industry.

It is an indication of the extraordinary intellectual gifts of Hofmeister, Nägeli and von Mohl, the main architects of the unitary theory of plant structure and ontogeny, established in principle by 1851, that all three made further significant advances, both within developmental morphology and in attempts to extend the physiological understanding of plant structures and processes. They were leaders in the turn to physiology, and in striving to bring it and other areas of botany together in a single field. This endeavour, an essential element in the formation of modern plant science, inspired the most brilliant of their immediate successors, Julius Sachs, Anton de Bary and Eduard Strasburger, whose wide-ranging researches and comprehensive views exercised a dominant influence on the ensuing course of botany.[13]

To display the interrelations between the diversifying branches of enquiry that now began to proliferate is beyond the bounds of a general history; we can only try to isolate the most important ones and to follow their development in the barest outline, noting those discoveries and interpretations that appear in retrospect as nodal points of growth.

The nature of protoplasm was a question at the centre of both morphology and physiology. Investigation of its properties was tremendously stimulated in 1859 by de Bary's account of the slime-fungi[14] (Myxomycetes, Mycetozoa), in which he recognized the plasmodium as a mass of protoplasm "resembling in every detail the circulating protoplasm of plant cells", yet devoid of cell walls. De Bary emphasized that the plasmodium is cellular in the biological sense, since it possesses nuclei, internal organization and a differentiated external layer [plasmalemma], which, following von Mohl, he termed the primordial utricle. A single plasmodium of *Aethalium septicum (Fuligo septica),* very common in tan-yards and garden compost, could weigh a kilogram or more, so that relatively large amounts of "protoplasm" were easy to obtain. Within a few years knowledge of the chemical composition, physical properties, vital behaviour and structural differentiation of protoplasm had reached a level from which there was little fundamental advance for nearly a century. Hofmeister's treatise on the plant cell (1867) opens with a long chapter on protoplasm, based to a considerable extent on his own observations. It is characteristic of the new outlook of "experimental botany" that he not only made a thorough study of the effect of external factors on cyclosis, but made the first quantitative measurement of the rate of movement of the flow. In 1862 Hofmeister had suggested that protoplasm could best be understood as a colloidal system, following up the definition and naming of the colloid state by Thomas Graham in the preceding year.

During the 1850s Nägeli took up the water-relations of plant cells, neglected since Dutrochet. He revived interest in osmosis and in the property of imbibition exhibited by several biological materials. From an exhaustive study of the structure, swelling and physical properties (especially the birefringence[15]) of starch grains and cell walls, Nägeli arrived at an interpretation of their molecular structure and behaviour that was highly original and, in essential features, is still held to be valid. This was the micellar theory, which conceived "organized substances" as consisting of

> crystalline, birefringent molecules (themselves made up of numerous atoms) which lie freely, yet with a definite regular arrangement, alongside one another. As a result of a preponderating attraction, each is surrounded, when moist, by an envelope of water; when in the dry state, they touch one another.

In this first statement of his theory Nägeli used "molecule" for what later (when chemistry had clarified the distinction between atom and molecule) was better described as a multimolecular aggregate, for which Nägeli then coined the word "micella" or "micelle". This theory was greeted with considerable enthusiasm by botanists, since it seemed to offer a clear picture of the structure of cell walls and other biological materials, and of the processes of growth by which the final structure was attained. Later, for rather adventitious reasons, the theory found less favour and, in botany, fell into temporary oblivion, only to be revived as a fruitful guide to investigation a hundred years later.[16]

The micellar concept was originally developed by Nägeli in relation to solid materials, but in 1865 Sachs and Hofmeister independently pointed out that protoplasm, a semi-fluid, could be interpreted as an organized substance in Nägeli's sense, consisting of micelles, formed by the union of many protein-type molecules, each surrounded in the imbibed state by an envelope of water. This was a very important advance on existing notions of protoplasm as a "formless fluid". Sachs pointed to the doubly essential role of water in protoplasm—as a basic element of structure and as the medium in which the chemical and enzymic reactions of the cell take place. Nägeli accepted the extension of his theory to protoplasm, and stressed the peculiar suitability of micellar structures for carrying out several vital functions; he also postulated that "micellar associations" are formed in the protoplasm.

The connection between the osmotic properties of plant cells and the semi-permeability [differential permeability] of the protoplasm was elucidated in principle by Pfeffer and by de Vries in 1877, who both recognized the function of the plasmalemma in the control of entry of solutes into the cell.[17] The formation of a new cellulose wall by extruded protoplasts of some algae was already well known, and Strasburger showed that cellulose is secreted by the plasmalemma during thickening of the primary wall by apposition. Strasburger introduced the useful terms cytoplasm and nucleoplasm, and within the latter he distinguished, by selective staining, the hyaloplasm, or clear ground substance of the nucleus, from the chromatin which is concentrated in the chromosomes during division. The important discovery of amyloplasts [leucopasts] and their relation to chlorophyll bodies [chloroplasts] and the formation of starch grains, was made by A. F.

W. Schimper in 1880. It was already known that chloroplasts grow, change their shape and position in the cell, and increase in number by division, so that Sachs was able to point to plastids as semi-independent organized structures forming part of the protoplasm;[18] he also saw within the homogenous ground protoplasm very small granules, which he called microsomes, and which almost certainly were mitochondria. The account of the physical and chemical nature of protoplasm, and of its vital structure and behaviour,[19] given by Sachs in his famous series of lectures published in 1882, was an excellent and balanced presentation, very firmly linked to the physico-chemical and physiological facts then known. It remained the basis of knowledge on the subject for a long time.

After the micellar theory fell into the background other ideas of protoplasmic structure were propounded, in which protoplasm was variously held to be fibrillar, vesicular, granular, or foam-like. These ideas arose from appearances presented by fixed material; they were not founded on the physico-chemical properties of living protoplasm and in consequence led nowhere. Not till the end of the century did the next fundamental advance begin. Then in 1899 C. E. Overton discovered the general permeability of cells to fat-soluble substances, and hence inferred the preponderantly lipid constitution of the plasmalemma. The significance of Overton's observation was not immediately appreciated, but it opened the way to an understanding of cell permeability, presaging a flood of investigation that is still in full spate.

In addition to the work of Nägeli and Hofmeister mentioned in connection with the study of protoplasm, there are other indications of growing movement in wider areas of physiology. In 1850 Link watered plants with a dilute solution of potassium ferrocyanide, easily detectable by the "Prussian blue reaction", and thus provided direct evidence that water (and dissolved salts) moves from root to leaves in the vessels and tracheids of the xylem. A few years later, Hofmeister showed that the "empty" vessels of intact plants contain only rarefied air, not, as had been long assumed, air at atmospheric pressure. These observations showed that the vessels serve to conduct water, and put an end to the view, dating from Malpighi, that they supply the internal tissues with air. This idea was still entertained by Sachs as late as 1865, although he abandoned it soon after. Hofmeister also showed that exudation from cut stems of rooted plants [root pressure] is a general phenomenon, exhibited in suitable external conditions by both trees and herbs, concluding from this that osmotic forces are concerned with the passage of water from the root into the xylem. The opening and closing of stomata was proved by von Mohl to result from changes in turgor of the guard-cells. Thus understanding of the water economy of plants at last began to advance beyond the point reached by Stephen Hales.

It was, however, the earliest researches of Sachs, between 1859 and 1865, which decisively launched the new physiology and determined the direction of its development.

These researches fall into three groups. In the first place Sachs took up the method of water culture, used by Du Hamel exactly a century before but subsequently forgotten, and turned it into a critical technique for investigating the mineral (inorganic) nutrition of plants. He analysed the advantages of the method in a classical paper in the *Botanische Zeitung* (1860), where he described results showing that plants could be grown from seed to the stage of flowering and seed formation in water culture if supplied with appropriate mineral salts and nothing else except carbon dioxide and light. Some botanists at first frankly disbelieved him, and even accused him of cheating, so certain were they that soil must be necessary to support the proper growth of plants. Sachs used the simple, but revolutionary technique, to establish the essential mineral elements required by plants as potassium, calcium, magnesium, phosphorus (as phosphate), sulphur (as sulphate), and iron (essential in very much smaller amounts).[20] The elements sodium, chlorine and silicon, although nearly always present in plant ash, were shown by him not to be essential for normal growth. He also established the fundamental facts of nitrogen nutrition by showing that both nitrates and ammonium salts are the natural and most readily available sources of nitrogen for plants, although most plants flourish best when supplied with nitrate. From this work of Sachs, and the methods he devised, all subsequent advances in the mineral nutrition of plants ultimately derived. The historic results in the development of agriculture and the rise of great fertilizer industries were far-reaching, but lie outside the scope of the present discussion.

The study of carbon assimilation by green plants had scarcely advanced since de Saussure until Sachs again made it the subject of systematic enquiry, making use of the progress in chemistry and microscopy attained in the intervening years. Skilfully combining evidence from observation and experiment, Sachs showed that in most plants[21] starch is the first product of photosynthesis to accumulate—not necessarily, or even probably, the first product formed, as he was very careful to point out. From starch all other carbon-containing substances of the plant (carbohydrates, proteins, fats) must be formed.

He confirmed and extended the basic facts of photosynthetic carbon-assimilation by showing that the primary formation of starch only occurs in association with chlorophyll in the chloroplasts, and is absolutely dependent on the immediate action of light and the presence of carbon dioxide in the atmosphere. He demonstrated graphically, by shading portions of a single leaf or withholding carbon dioxide, that starch formation is strictly confined to areas where both light and carbon dioxide are present. A few years later a pupil of Sachs made the first quantitative measurements of starch formation in leaves of plants growing in the field, and found that the increase was sufficient to account for the rate of accumulation of dry matter in the whole plant.

Sachs observed the dissolution of starch in the chloroplasts of previously illuminated leaves kept in the dark, showed that the starch is converted to sugar in which form it can be transported, and saw the re-formation of starch grains in other tissues. By studying the germination of many seeds, he observed the transformation of oil into starch, of starch into sugar, and of storage protein (aleurone crystals) into soluble nitrogen compounds; he ascribed the changes to the action of enzymes, whose essential role in plant metabolism he was the first to appreciate.

These extensive researches of Sachs led to the first integrated account of carbon metabolism in green plants. They gave botanists a vivid understanding of the central role of photosynthesis in plant nutrition and of its relation to the chemical transformations of materials in the plant body as a whole. Sachs made a distinction between plastic substances (proteins, carbohydrates and fats) which are the "constructive materials" in growth, reserve substances (starch, aleurone crystals, oil, etc.) whose metabolic role is shown by the fact that they are formed, dissolved and re-formed within the plant, and secreted substances (cellulose, lignin, wax, pigments, etc.) which may be very useful to the plant but are inert when once formed. This distinction was of the greatest value in developing a comprehensive view of plant metabolism; it is an example of Sachs's unrivalled genius in drawing pregnant conclusions from an array of quite simple observations. At the root of all his work is a passionate striving to reach a general theory; this is the source of his strength and his success, and is the reason why his writings still have freshness and excitement for the reader of today. Sometimes he could be stubbornly wrong, but Sachs's errors were more productive than the cautious correctness of lesser men.

Sachs's other investigations in his early years were concerned with the effect of external conditions, principally temperature and light, on various plant processes, including germination, growth, transpiration, chlorophyll formation, and the origin and growth of plant organs. This systematic study of the relations between the developing plant and the external environment became the starting point for many important developments, of which only two will be briefly mentioned. The concept of a maximum, minimum and optimum temperature for growth and for many individual plant processes, is due to Sachs, and became of key significance in physiology and in the development of ecology and plant geography. His studies also revealed many unsuspected facts about the response of plants to light, and stimulated research into its photosynthetic, morphogenetic and phototropic effects.

The researches of Sachs had an immense influence as a result of the wealth of new information they produced, the clear and firmly based conclusions, and the novel and successful experimental methods employed. They were the foundation of the volume entitled *Experimental-Physiologie* which Sachs contributed to Hofmeister's *Handbuch der physiologischen Botanik* in 1865. This volume of Sachs was the first textbook of plant physiology. In 1868 Sachs published a general textbook of botany (*Lehrbuch der Botanik*) in which plant physiology was given equal treatment with the general and special morphology of plants, systematics, and an account of Darwin's theory of evolution in relation to plants. All Sachs's brilliant gifts of exposition and theoretical clarity are displayed in this work, which had a powerful influence on the emergence of botany as a comprehensive discipline, with its own laws and its own techniques of enquiry.

There was a veritable outburst of physiological research after 1865, to which Sachs (now at Würzburg) and his students made contributions in many directions, notably to the study of growth, where Sachs discovered and analysed the "grand period", to the morphogenetic effects of light (etiolation, flower formation), to the geotropic, phototropic and hydrotropic responses of plants, and to the correlative growth which results from their joint operation in natural conditions.[22]

The understanding and investigation of tropisms was greatly forwarded by A. B. Frank in 1868, when he showed that whatever the nature of the exciting stimulus, all tropic curvatures result from differential growth between opposite sides of the responding organ.[23] In 1881 Charles Darwin and his son Francis demonstrated that the perception of light is located in the stem or root tip, whilst the tropic response (curvature) takes place distally, and they therefore inferred that something must be transmitted through the intervening tissues in order to elicit it. The importance of this work and the conclusion drawn from it was appreciated by Pfeffer, who cited it in his textbook of plant physiology, but Sachs rejected the evidence and the question was not followed up at the time.[24]

In 1882 Sachs gave a synoptic account of thirty years of active progress in his *Vorlesungen über Pflanzenphysiologie* (translated into English by Marshall Ward in 1887), to which the *Pflanzenphysiologie* (1881) of his talented pupil Pfeffer was in many respects complementary. These two works were the foundation for all subsequent teaching and research in plant physiology. Sachs had, to the highest degree, the capacity of uniting the essential elements in the work of many investigators into a general theory, which, whether later proved right or wrong, was always rational and stimulating and a pointer to fresh initiatives in research.[25] The whole course of modern plant physiology bears the unmistakable stamp of his incisive mind; he established its reliance on accurate, controlled, quantitative experiment, on the use of the most advanced physical, chemical and observation techniques available, supplemented by more unconventional, improvised methods, that must often be specially invented, in order to probe the complexities of living matter. Whilst seeking the physical and chemical basis of plant behaviour, Sachs always insisted that plant physiology is an independent science, with its own laws and methods which arise from the evolutionary history and adaptive relations of every living plant.

Plant physiology came of age with Sachs's brilliant synthesis. The period that followed was one of consolidation, adding detail and definition to what was known without breaking much new ground. In the 1890s work in Pfeffer's laboratory in Leipzig removed all doubt of the correctness of the Darwins' view that curvatures due to light or gravity result from the passage of a stimulus from a localized region of perception to a more distant region of response. It was not till 1910, however, that Boysen-Jensen showed that the stimulus would pass through a block of watery gelatine placed between a stimulated, excised tip and the stem below—an observation that strongly suggested that the "stimulus" must be a diffusible substance, and started the search which led to the first isolation of a plant hormone.

In 1891 Strasburger published an extensive anatomical description of the conducting systems (xylem and phloem) in higher plants, combined with a thorough experimental study of water movement, the whole forming a landmark of anatomical and physiological precision. His demontration in intact plants of continuing water transport through a long stretch of "killed" xylem was an observation of critical importance, since it showed that water movement in this region could not have any immediate dependence on the living cells of the xylem. Three years later Dixon and Joly proposed the cohesion theory of the ascent of water through the xylem—the most brilliant and original contribution yet made to this central problem of plant physiology.[26]

At the turn of the century G. Haberlandt reported the first attempts at plant tissue culture, a prelude to fundamental developments which did not come to maturity until nearly fifty years later. The researches of G. Klebs (1896 to 1913) on environmental control of the genetically determined cycle of development ("the powers lying dormant in the specific structure" in the words of Klebs) in both lower and higher plants, opened a branch of physiology with vital implications for genetics, ecology and the practice of agriculture and horticulture. A new stage in the application of physical and chemical theory to plant physiological problems began in 1905 with the publication of F. F. Blackman's paper on "Optima and limiting factors", and with the researches which followed.

The investigation of plant anatomy was taken up with assiduity by many botanists after 1850. In a survey (1868) of stem and root structure in numerous plants, Nägeli arrived at several clarifying generalizations of great value. He established the distinction between meristematic and permanent tissue, and between primary and secondary meristems, and showed that primary roots always have initially an alternating radial arrangement of xylem and phloem strands, with centripetal differentiation of the primary xylem, completely different from the typical anatomy of the stem. Perhaps the most important advance made by Nägeli was his recognition of the phloem as a fundamental tissue, characterized by containing sieve-tubes, and always associated with xylem to form a vascular bundle. Sieve-tubes as such had been discovered by Theodor Hartig in 1851 and considered by him and by von Mohl as "special elementary organs", but the latter interpreted the sieve-plate as an area of lattice-like thickening. In 1861 Nägeli proved, by watching with a lens the flow of slime from cut sieve-tubes in the stem of *Cucurbita*, that the sieve-pores are open and permit conduction. He was the first to suggest that the sieve-tubes are the paths of movement of elaborated products (proteins as he thought, an idea adopted by Sachs).

The puzzling features of bordered pits were elucidated by Schacht in 1860, whilst Sanio described the structure of mature xylem with astonishing accuracy and detail, and followed the ontogeny of cambium and the formation of annual rings.[27] The so-called "anomalous" thickening of a few monocotyledons was clarified by Millardet. De Bary and his pupils made many anatomical studies, and in 1877 he gathered the results of twenty-five years in his *Comparative Anatomy of Ferns and Phanerogams*, where an enormous mass of information was put into superb order. It was de Bary who applied the systematic terminology which, in all essentials, is still in use. He discovered and named the endodermis, the more or less specialized layer of cells which delimits the vascular system in almost all roots and in many shoots.[28] This comprehensive treatment by de Bary established the principal features of mature plant anatomy on a secure foundation.

With his usual insight, Hofmeister had already recognized the need to look more deeply at the processes by which the mature, differentiated structure is attained. In a paper in 1863 he raised the problem of integrated growth as follows.

> The growth of single cells of an organ in the earliest bud-stage is subordinated to the general growth of the organ. The growth in mass of the organ, directed towards the attainment or expansion of definite forms, cannot be understood as the sum of the innate and individual formative tendencies of single cells. It must be assumed that growth-increase and form-changes of individual cells only occur to an extent determined by the general direction of growth of the organ.

He studied the origin of leaf and branch primordia at the stem apex, and the order of divisions and position of cross-walls in the cells of the apical meristem, with the aim of finding general laws to explain co-ordinated development.[29] Some years later Sachs was moved to make observations along similar lines.

The most important addition to de Bary's classical picture of plant structure was the discovery of plasmodesmata, fine protoplasmic strands extending through the cellulose walls and bringing the protoplasm of adjacent cells into direct connection. This discovery was made in 1880 by E. Tangl, a somewhat obscure professor of botany in Czernowitz, who nevertheless understood very clearly the full significance of what he had found, and in further investigations provided evidence of the passage of wound-stimulus and of enzymes through the plasmodesmata. The subject was taken up by Sachs and his student W. Gardiner, who continued to work on it after returning to England. It was believed for some time that the phasmodesmata were formed at the site of spindle-formation during cell division, but in 1901 Strasburger made a thorough study of plasmodesmata (to which he gave the name) and showed that they arise after cell division is complete by the penetration of opposed protoplasmic threads through the primary walls.

Other viewpoints on plant anatomy resulted from Schwendener's analysis (1874) of the part played by certain tissues in conferring mechanical stability on the plant body, in which he showed how the form, distribution and physical properties of "supporting" tissue correspond to known mechanical principles. Haberlandt, who had worked with Schwendener, extended the study of relations between

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Figure 25 Plasmodesmata between endosperm cells of *Strychnos nux-vomica* observed after staining with iodine. E. Tangl in *Jahrbücher für wissenschaftliche Botanik* **12** (1881).

Fig. 8

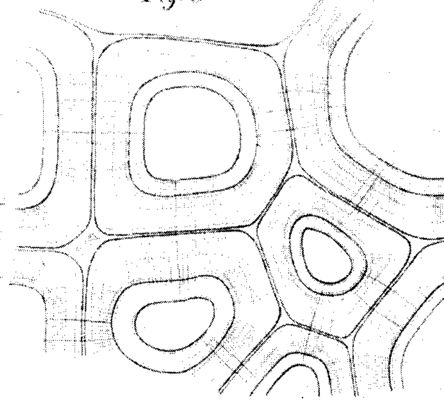


Fig. 9

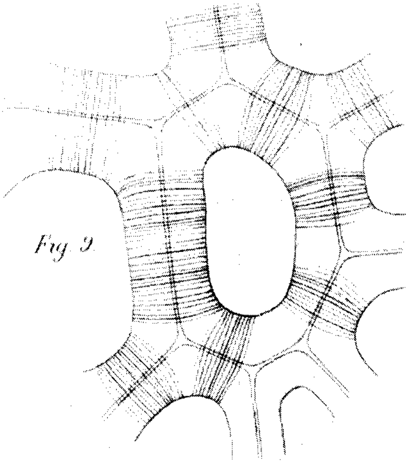


Fig. 10

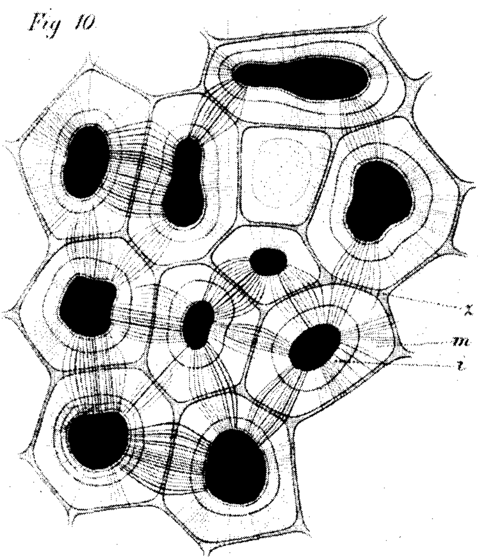


Fig. 13.

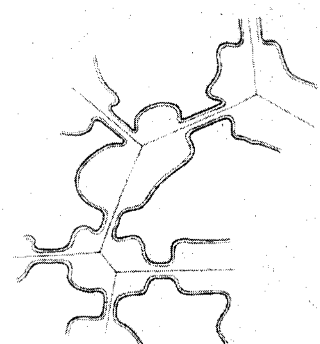


Fig. 11

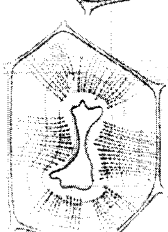
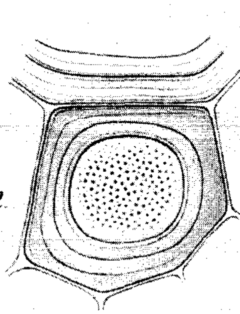


Fig. 12.



anatomical structure and physiological function. In his *Physiological Plant Anatomy*, first published in 1884, he defined twelve or thirteen tissue systems.[30] He regarded physiological anatomy as an "explanatory science", and his treatment evoked divergent judgements among botanists, but it certainly stimulated a fresh and more experimental approach to anatomy.

A similar trend in morphology is expressed by Goebel[31] in his *Organography of Plants* (1898). Recognizing that "morphology studies the results of stereotyped physiology", he stressed the need for ontogenetic investigation of the profound modifications that particular organs may undergo as the result of a change in physiological function. His book re-invigorated enquiry into the problems of plant form and contributed to the rise of experimental morphogenesis.

Progress in the knowledge and description of the world flora, which we shall not attempt to chronicle, brought about a great extension of natural classification at the lower taxonomic levels, without causing any major changes in methodology or in concepts of the status and relationships of higher plants. Advances in knowledge of the algae, however, and especially of the comparative life cycles and types of alternation found among them, led to the recognition of a number of very distinct and not closely related natural groups within the great assemblage of forms covered by this blanket designation. This was a very big step forward in natural classification with implications for the understanding of the evolution of higher plants of the greatest theoretical importance. Two other fundamental developments must also be mentioned. The true nature of lichens, as organisms consisting of an alga and a fungus in specific symbiotic association, was demonstrated by Schwendener in 1867, and thus a source of confusion in morphology and classification was removed. Increasing knowledge of fossil plants revealed in the rich flora of the coal measures several well-marked dominant groups of now extinct plants, having many characteristics in common with living groups of vascular cryptogams (ferns, horsetails, lycopods) yet producing unmistakable seeds. The existence of these ancient lineages caused an exciting shake-up of opinion about the evolutionary origins of flowering plants and gymnosperms, without leading to any immediate solution of the morphological and phylogenetic questions raised.[32]

The advances in physiology and floristics combined to foster the growth of plant geography and ecology as fields of investigation with their own methods and aims. Augustin de Candolle (1820), his son, Alphonse de Candolle (1855) and A. Grisebach (1872) extended and elaborated the pioneering attempt of Alexander von Humboldt to typify plant form in relation to climatic regions. After 1875, as Sachs's work on the effects of environmental factors on plants became widely known, a series of works began to appear in which the distribution of plants was correlated with their physiological response to the environment. This new approach culminated in A. F. W. Schimper's *Pflanzengeographie auf physiologischer Grundlage* (1898). Plant ecology is usually considered to begin with the publication of E. Warming's *Plantesamfund* ("Plant Ecology") in 1895, although the term ecology was proposed much earlier by Haeckel. The development of specifically ecological concepts was further aided by the establishment of the principles of soil science (1890–95) by N. N. Dokuchaev, and by C. Raunkiaer's classification of plant life-forms in the years from 1903 onwards.[33]

The greatest expansion of botany after 1851 naturally took place in the areas of special and general morphology, of development and reproduction, where research was stimulated—directly or indirectly—by the theory of alternation.

An understanding of the patterns of development and reproduction among the Thallophyta (Algae and Fungi) was crucial for the rational extension of Hofmeister's generalization to the whole of the plant kingdom. The acquisition of this knowledge in its fundamental principles was one of the great achievements in botanical history of this period which we can only touch upon. It is significant that Hofmeister turned to the study of diatoms and desmids, and elucidated the main features of their reproductive cycles, whilst at the same time continuing research on the higher cryptogams and the flowering plants.[34] De Bary made an intense study of the Conjugatae and Pringsheim examined many other Chlorophyceae (green algae) in a long series of researches.[35] Systematic knowledge of the life cycles in Phaeophyceae (brown seaweeds) and in Rhodophyceae (red seaweeds) began with the work of the great French amateur G. Thuret and his assistant E. Bornet, published by Bornet (1867–80) after Thuret's death. The immense researches of de Bary and O. Brefeld laid the basis for an understanding of fungal life cycles. As this knowledge of the lower plants grew, it became increasingly possible to correlate patterns of life cycle (alternation) throughout the plant kingdom.

It was Eduard Strasburger who continued the main themes of Hofmeister's work with the greatest insight and clearest grasp of essentials.[36] So many important advances stemmed from his researches between 1867 and his death, that his complete works have been said to comprise the history of botany for this time. Like Sachs he had the ability to carry out research of the highest originality and to combine the results with those of others in a clear theoretical synthesis. As a young men he was trained by Schacht and Pringsheim, both very accomplished microscopists, and was deeply stirred and inspired by hearing Sachs lecture at Bonn, and then by his close association with Haeckel at Jena. This youthful experience contributed to his assured intellectual mastery in every field of botany.

The exact nature of the act of fertilization was still uncertain in 1851, although the necessity of physical contact between the male and female elements was by this time generally taken for granted. Experiments with the heterosporic fern *Salvinia*, with dioecious mosses (C. F. Schimper) and with Fucus (E. Thuret), had shown that contact between the spermatozoids (antherozoids) and the ovum was essential to obtain progeny, and Hofmeister had seen the entry of antherozoids into the archegonium of ferns; but it still seemed possible to both zoologists and botanists that "catalytic" contact could be sufficient. In flowering plants the question was complicated by Hofmeister's demonstration that the tip of the pollen tube reaches the embryo-sac but does not enter it: he ascribed fertilization to the "transudation" of fluid through the cell wall.

An alga provided the first definite evidence. In 1858 Pringsheim followed the complete act of fertilization microscopically in the fresh water alga *Oedogonium*. He established that the male gamete penetrates into the substance of the ovum, with which it becomes so completely mixed that it loses its distinct morphological identity. In the same paper he reported essentially the same course of events in the aquatic fungus *Saprolegnia*, and concluded that fertilization consists in the "material union of two reproductive substances". Pringsheim's observations were almost immediately confirmed by de Bary in *Saprolegnia* and in the Conjugatae, and later Pringsheim saw gametic fusion in other species of algae.

It was soon universally accepted that fertilization involves a union of male and female protoplasts, but the behaviour of the nuclei during the process was a matter of uncertainty for nearly twenty years, until in 1875 Hertwig showed all stages of nuclear fusion in sea-urchin eggs by means of stained preparations; almost simultaneously nuclear fusion was observed by others in the fertilization of mollusca, nematodes, amphibians and mammals.

Within three years Strasburger had shown nuclear fusion in the ovules of gymnosperms and angiosperms. In flowering plants he followed all the divisions involved in the formation of the pollen from the pollen mother-cells and of the mature embryo-sac from the embryo-sac mother-cell. He saw the dissolution of the wall where the pollen tube is in contact with the embryo-sac, the passage of two generative nuclei into the embryo-sac, and the fusion of one of them with the nucleus of the egg-cell. He remarked on the special character of the fusion of one nucleus from each end of the embryo-sac to give the polar nucleus, a fusion which, he says, "seems to balance the opposition between the antipodal cells and those of the egg-apparatus". The only feature which he failed to notice was the extraordinary "triple fusion" of the polar nucleus with the second generative nucleus of the pollen, a phenomenon peculiar to the flowering plants, which was eventually discovered in 1898 by the Russian botanist, S. G. Navashin.

These brilliant and epoch-making researches of Strasburger established our fundamental understanding of reproduction in the higher plants. They were possible because Strasburger had already discovered the details of nuclear division in plants in researches which he began before 1875, and which were the botanical parallel to similar work on animal cells by O. and R. Hertwig, W. Flemming, O. Bütschli and other zoologists. Between 1870 and 1890 their joint efforts established the basic facts of cell and nuclear division, and revealed the astonishing identity of chromosomal behaviour in plants and animals, a proof of the evolutionary unity of living organisms, formally endorsed by the use of the term cytology to denote this new branch of biology.[37]

The foundation of plant cytology was doubtless Strasburger's greatest achievement, but it is important to note that this work originated in a series of researches, inspired by Hofmeister, into the development and reproduction of algae, ferns, liverworts, gymnosperms and angiosperms, which were in themselves permanent and monumental additions to knowledge of the species and groups with which they dealt. In particular his study of gymnosperms, containing the first thorough account of the Gnetales, and his work on the reproduction of flowering plants (already mentioned), became the factual basis for the treatment of these groups. His consideration of the homologies between the reproductive structures of angiosperms and gymnosperms is a model of illuminating interpretation of complex problems, free from dogmatism or mere speculation. It is still a valuable analysis of many questions concerning the morphological, phyletic and genetic relationships of higher plants.[38]

When Strasburger began to examine the precise sequence of cell divisions in the developing archegonium and antheridium of a fern, the mode of entry of antherozoids to the ovum, and the subsequent sequence of cell divisions during embryo-formation, he was roused to the need for clearer information about the structures and changes within the protoplasm.[39] In his first paper on cell formation and cell division (1875) it is strange to find him still entertaining the possibility of "free cell formation" after the manner envisaged by Schleiden, but he very quickly became convinced that cells only reproduce by division, and Schleiden's view is not referred to again. During the next twenty years Strasburger established the facts of plant cytology so thoroughly that for almost fifty years there was little further progress except in matters of detail.[40]

We shall not follow his researches in detail or try to relate their progress to the contemporaneous work with animal cells, of which Strasburger was of course completely aware. By 1882 Strasburger had fully described the stages of karyokinesis [mitosis] and the related process of intercellular wall-formation, had recognized the constancy of chromosome number [karyotype] for each particular species (or genus), and accepted the fact of a reductive division [meiosis] at some stage in the sexual life cycle. For a time he thought that the chromosomes divided transversely at the midpoint during mitosis, but within less than a year he accepted that longitudinal splitting of the chromosomes, shown by Flemming in 1883, was also the rule in plants. In 1888 he demonstrated that in flowering plants a reductive division occurs in the mother-cell of the pollen and of the embryo-sac, a most

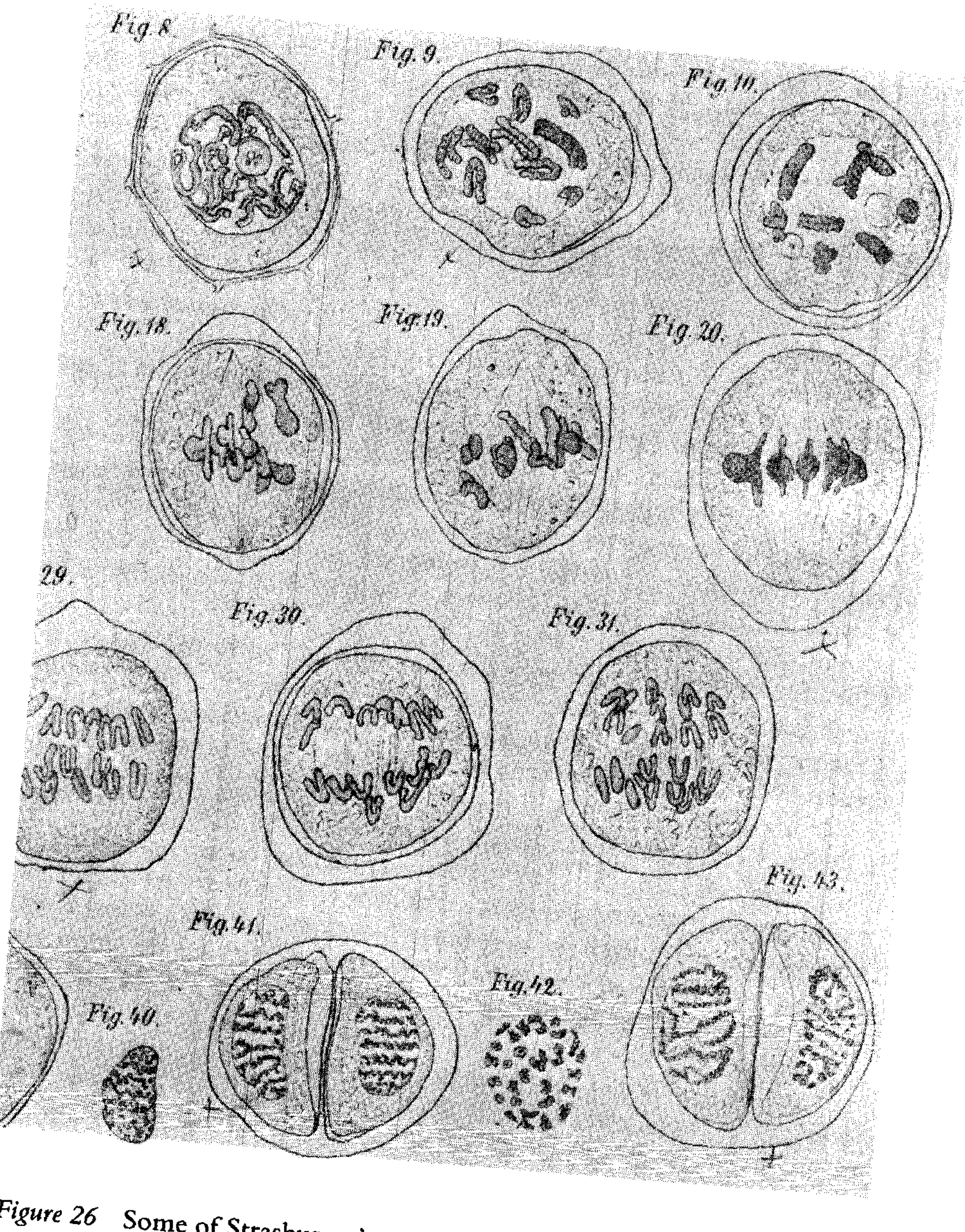


Figure 26 Some of Strasburger's early figures of nuclear division in pollen mother-cells of *Fritillaria imperialis* (1882).

important fact, confirmed by Guignard within the year. Four years later C. E. Overton found that in gymnosperms reduction in chromosome number is likewise attained in the pollen mother-cell and in the embryo-sac mother-cell, and that the cells of the endosperm are all haploid. Overton stressed that there is an indefinite number of divisions in the endosperm before archegonia are formed, in other words, that the whole gametophyte generation is haploid, in distinction from the sporophyte generation [the plant body], whose cells are all diploid. The terms haploid and diploid were introduced by Strasburger, when the cytological difference between the sporophyte and gametophyte generations were found in all groups of higher plants, as well as within the algae, the group in which evidence of the phyletic origin of the higher land plants began now to be looked for.

In whatever branch of botany he was active—morphology, anatomy, physiology, cell-structure, even fossil plants—Strasburger made original discoveries and drew conclusions productive for future work. He perceived that the common pattern of nuclear behaviour in animals and plants, extending to the minutest details, was the most convincing evidence yet found for the descent of all organisms from a common ancestral source, a group of closely related primitive forms, as Darwin had suggested. He was also one among a number of biologists, including O. Hertwig and A. Weisman, who began more or less simultaneously about 1884, to form the view that the nucleus, or some constant part of it, is the material bearer of heredity. As early as 1876 Strasburger was moved to consideration of the problem of hereditary continuity by the contrast between the uniform structure of the plasmodia of myxomycetes and the very distinct type of sporangium produced by each species. There must, he argued, be specific differences within the apparently uniform plasmodia, and these differences cannot lie in change of size of the "molecules" or of their associated water layers—this is a reference to Nägeli's micellar theory—but in the molecules themselves. "These molecules would, however, as is already indicated from various sides, then be conceived as units of very complex construction." By 1884 the constancy in the number and form of the chromosomes in each species, and their exact division ("halving") between daughter nuclei, had convinced him that they are the material carriers of the hereditary characters (Substanz-Elemente). It was in this year that Nägeli published his *Mechanisch-*

physiologische Theorie der Abstammungslehre ("Mechanical-physiological theory of heredity"), a remarkable prevision of the chromosome theory of heredity. The further developments of these ideas fall, however, within the scope of genetics.[41]

In the context of botany, the advances in knowledge of plant cytology led Strasburger to the recognition of a cytological diploid–haploid alternation of generations, which normally accompanies, and is linked with, the morphological-reproductive alternation discovered by Hofmeister. This extremely important concept was stated by Strasburger in 1894 in the *Biologisches Zentralblatt*, appearing in English translation in the *Annals of Botany* of the same year under the title: "The periodic reduction of the number of chromosomes in the life-history of living organisms". An alternation of diploid sporophyte ("asexual" generation) with haploid gametophyte ("sexual" generation) was shown to be the constant pattern in all groups of land plants (flowering plants, gymnosperms, pteridophytes, bryophytes, etc.) and in many algae and fungi. The pattern is not universal in algae, as Hofmeister was well aware when he called *Chara* the lower end of a series in the scale of alternation. With this work Strasburger made a theoretical advance which was complementary, and comparable in magnitude, to that made by Hofmeister: it has had the most fundamental effects on botanical thought and progress ever since.

Perhaps the greatest value of Strasburger's profound synthesis of cytology, morphology and development, lay in the number of questions brought sharply to the fore in relation to the internal and external factors controlling orderly development. One of the most difficult is immediately raised by the very great differences in higher plants between the structure and complexity of the two generations. Even in ferns where the gametophyte (prothallus) has an independent existence, and is not wholly dependent on the sporophyte (fern plant), the contrast between the two generations is very striking. Yet each form has the same genetic constitution, with the sole difference that it is represented twice in each cell of the diploid. Moreover, the exceptional transition from one generation to the other, without the formation of sexual organs (apogamy) or without the formation of spores (apospory), had been observed in both mosses and ferns as early as 1874, and shortly after 1900 several investigators, including

Strasburger himself, showed that in some ferns regular morphological alternation occurs between haploid gametophyte and haploid sporophyte, as well as between diploid gametophyte and diploid sporophyte. The occurrence of apomixis (omission of sexual fusion) was discovered in a number of flowering-plant genera; it was investigated in detail by Strasburger in *Alchemilla*.

These complications did not prevent Strasburger from putting forward his great generalization and they do not lessen its significance. The problems they pose are still with us and are mentioned only as an indication of the productive stimulus to further research which modern botany owes to the genius of Strasburger.

Another approach to alternation was developed by F. O. Bower in 1890 and later in his *Origin of a Land Flora* (1908). Bower considered the differentiation of the sporophyte and gametophyte generations in land plants from an evolutionary–adaptive point of view. He argued that the most advanced and successful groups of land plants are all characterized by the progressive elaboration (dominance) of the sporophyte, with a parallel reduction in the complexity and independence of the gametophyte, and that this trend is an adaptive response, by plants fitted for life in the water, to the physiological problems of growth and reproduction presented by the new habitat—dry land. Bower developed the morphological evidence for his interpretation with skill and insight, linking it with the "antithetic" in opposition to the "homologous" theory of alternation.[42] The antithetic–homologous controversy now appears rather formal, but it led Bower to very important advances in comparative morphology and in the classification of ferns. His adaptive–evolutionary view of the origin of alternation was an illuminating theoretical contribution and merits critical reappraisal in the light of more recent developments in genetical thought.

It is fitting to close our account of the foundation of modern botany with the death of Strasburger, not an end but a beginning, when new paths of exploration were opening as a result of his work and that of a whole generation of talented botanists. This modest, cultivated man, more than any other except the dynamic Sachs himself, left his impress on modern botany—through his technical mastery, his philosophic reflectiveness of thought, his unswerving scientific integrity, and a charm and humanity to which countless students throughout the world responded with grateful affection.

Notes to Chapter 10

Notes

1. The first textbook in modern form and content was J. Sachs's *Lehrbuch der Botanik* (1868), which ran to four editions in ten years and was translated into English in 1875.

   The aim of Hofmeister's *Handbuch der physiologischen Botanik* was to provide detailed treatment of special topics. It appeared in four volumes as follows (titles in English).

   I: Part 1. *The plant cell.*
   Part 2. *General morphology of plants.* W. Hofmeister. (1867,68).
   II: *Morphology and physiology of fungi, lichens and myxomycetes.* A. de Bary (1866).
   III: *Comparative anatomy of ferns and phanerogams.* A. de Bary (1877).
   IV: *Experimental physiology.* J. Sachs (1865).

   Physiology was treated separately in W. Pfeffer's *Plant Physiology* (2 vols, 1881) and J. Sach's *Lectures on Plant Physiology* (1882).

   E. Strasburger's *Kleines* and *Grosses botanisches Praktikum* (both 1884) became the standard guides to botanical laboratory technique at teaching and research levels respectively.

   In 1894 Strasburger, in collaboration with F. Noll, H. Schenk, and A. F. W. Schimper, published the famous *Textbook of Botany for Universities*, which summed up the achievements of an epoch and, in repeatedly revised editions, nurtured generations of botanists.
2. Students were particularly attracted to the laboratories of Hofmeister (Heidelberg, Tübingen), Sachs (Würzburg), de Bary (Strasburg), Pfeffer (Leipzig) and Strasburger (Bonn).
3. British botanists who studied in Germany include Francis Darwin, F. O. Bower, I. Bayley Balfour, D. H. Scott, H. Marshall Ward, S. H. Vines and (from Ireland) H. H. Dixon.
4. Hofmeister, Nägeli, Sachs, Strasburger, were among many leading German botanists who became ardent adherents of Darwinism. Both Sachs and Nägeli later became more critical of Darwin's treatment of variation and natural selection, without, however, questioning the fact of evolution by adaptation during descent. A few botanists never came to terms with the new theory. Only in France was Darwinism smothered in official silence for twenty-five years by the strength of Roman Catholic reaction and the extraordinary personal influence of Cuvier. For details see T. F. Glick: *The Comparative Reception of Darwinism* (1972).
5. Extremely interesting ideas on the relation between natural classification of plants and their geographical distribution were sketched by A. von Humboldt and A. Bonpland in their *Essai sur la Géographie des Plantes* (1807), which has evolutionary undertones. It was one of the earliest attempts to give a rational account of the distribution of plants and to characterize geographical–ecological plant associations and classify the

life-forms of vegetation. At about the same time Robert Brown made observations on the distribution of the Australian flora with numerical estimates of the frequency of natural groups. The observations of these men clearly influenced the direction of thought of J. D. Hooker.

6. Darwin enjoyed the friendship of J. S. Henslow, the Professor of Botany at Cambridge in his student days. Henslow was mainly concerned with systematics, but he evidently helped Darwin to use the microscope on plants (see the *Autobiography*), so Darwin may have been impelled to look more closely into plant morphology and anatomy than he bothered to record. At a later period in his life his acquaintance with botanical literature was adequate enough.
7. As Darwin remarked with singular litotes, "when the views entertained in this volume [the *Origin*] . . . are generally admitted we can dimly foresee that there will be a considerable revolution in natural history."
8. See, for example, Strasburger's inaugural lecture as Professor of Botany in Jena on 2 August 1873: "Ueber die Bedeutung phylogenetischer Methoden für die Erforschung lebender Wesen".
9. Of course, the idealization of morphological categories is not automatically abolished when everyone pays lip service to evolution. Examples can be found in the literature up to the present day.
10. The following are Darwin's botanical works:
    Climbing plants (1865), in *Transactions of the Linnean Society* (1875) enlarged as a book.
    Insectivorous Plants (1875).
    Effects of Cross and Self-Fertilisation in the Vegetable Kingdom (1876).
    Different Forms of Flowers on Plants of the Same Species (1877).
    The Power of Movement in Plants (with F. Darwin) (1880).

    Many short notes appeared in various periodicals and have been collected together in recent times.
11. See especially the work of H. Müller (1879, 1881 and 1883), and P. Knuth, *Handbook of Flower Pollination* (1906, 1908, 1909).
12. Here, as elsewhere, I use plant physiology in its modern sense. In the nineteenth century "physiology of plants" was still often used to include all parts of botany except systematics. Sachs sometimes used "experimental physiology" in order to specify plant physiology.
13. Julius Sachs (1832–97) gained his scientific training at Prague under the influence of the great Czech physiologist J. E. Purkinje, who befriended him on his father's early death. After eight years in agricultural research he spent the rest of his life (1868–97) as Professor of Botany at Würzburg.

    Anton de Bary (1831–88) came under the influence of Alexander Braun (plant morphology), G. Ehrenberg (Infusoria) and J. Müller (physiology) whilst a student of medicine in Berlin, and was later Privat-Dozent (lecturer) under von Mohl at Tübingen. Although remembered, above all, as the founder of scientific mycology, he made distinguished contributions to almost every branch of botany.

Eduard Strasburger (1844–1912) was Professor of Botany at Jena (1866–80) and at Bonn (1881–1912).

Full biographical details of all three, and of many other botanists mentioned in this *History*, can be found in the *Dictionary of Scientific Biography*, to which interested readers are referred.

14. De Bary gave a very acute discussion of the systematic position of slime fungi, rejecting a close relationship with the true fungi (which a superficial resemblance of the sporangia to the Gasteromycetes had suggested to some authors). He thought that they are nearer to animals—hence his preference for Mycetozoa as a name for the group—but thought that the problem was neither very important nor ripe for solution.
15. Von Mohl was the first botanist to suggest the use of plane-polarized light to explore plant structure (*Botanische Zeitung* (1858)).
16. For a full discussion of Nägeli's theory and its history see the monumental study by J. S. Wilkie: Nägeli's work on the fine structure of living matter. *Annals of Science* **16**, 11–239 (1960).
17. In his *Osmotische Untersuchungen* Pfeffer gave an account of the osmotic relations of plant cells, which in essentials remains valid today. He was the first to make accurate measurements of the osmotic pressure of pure solutions and of living cells. His measurements were used by van t' Hoff in 1887 in establishing the physical theory of osmosis. De Vries described and correctly interpreted the phenomena of plasmolysis (to which he gave the name), and introduced the plasmolytic methods for studying the osmotic and turgor properties of plant cells that have become standard techniques. In 1885 de Vries showed experimentally that the plasmalemma bounding the vacuole in plant cells is semi-permeable, like the external plasmalemma of the protoplast. Sound arguments for the exitence of an osmotic barrier round the vacuole had already been given by Pfeffer in 1877.
18. The concept of what are now termed cell organelles was first put forward by Nägeli in 1846, who spoke of "utricular structures". He observed the membrane delimiting the chloroplasts and also their increase by division, but his statements were not immediately accepted.
19. An essential property of living protoplasm was considered to be "irritability". Sachs used the term with a quite definite meaning to indicate the fact that living organisms constantly react to external (and internal) conditions in a characteristic way. The reaction takes place entirely in accord with physical and chemical laws, but shows specific features due to the special structure and adaptive activity acquired by living organisms in the course of evolution. There could be no objection to this concept, which had the merit of drawing attention to specific features of living systems and the need to examine them in physical and chemical terms. Unfortunately "irritability" came sometimes to be used as "vital force" had been, as a verbal substitute for experimental investigation. Later, F. F. Blackman remarked (1908) that Pfeffer's view that every

change in which protoplasm takes part is an activity of an irritable substance "overflowed its legitimate bounds", and the use of the term irritability in plant physiology was largely abandoned.

20. The effect of iron salts in correcting chlorosis was discovered by E. Gris, Professor of Chemistry at Châtillon sur Seine, in 1843. Sachs clearly distinguished the "trace element" function of iron.
21. Sachs was well aware that in many monocotyledons the first product of assimilation to accumulate is not starch but sugar.
22. One of the most important contributions of Sachs was to show that plagiotropic growth (i.e. the growth of organs horizontally or at a characteristic angle to the normal vertical direction of growth of the main plant axis) is also a tropic response to the same stimuli (gravity, light) which determine vertical growth.
23. The observations of Frank were particularly important in bringing positive and negative curvatures under one mechanism; earlier investigators had suggested quite different reasons for the opposite curvature in stem and root.
24. The fact was that Sachs was a bit shocked by what seemed to him the amateurish methods of the Darwins. He was used to using quite elaborate apparatus like the klinostat, and precise physical and chemical methods, and he had some of the professional's distrust of country-house experiments.
25. Many examples could be quoted. One that was not followed up at the time was the suggestion, based on many observations and experiments on the origin of shoot, root and flower initials, that organogenic substances are produced and transported within the plant—a hypothesis which, in many respects, anticipated the plant hormones discovered years later. Again, Sachs had very clear comprehension of the distinctive photosynthetic and morphogenetic effects of light, and of the role of light in assimilation ("chlorophyll is only effective in assimilation when vibrations in the ether in the visible range penetrate into its substance and impart the forces necessary to produce organic substances from carbon dioxide and water"). In this connection he raised and tried to solve questions of the effectiveness of light of varying intensity and wavelength, for the solution of which, as he recognized, the necessary physical methods were not yet available.
26. Dixon had been a student of Strasburger. He derived the physical foundation of the cohesion theory from Joly, who grasped the significance of the observations of Donny and Berthelot on the tensile strength of columns of sulphuric acid and water.
27. Sanio's researches were carried out from 1856 to 1873 and the results were included by de Bary in his comprehensive account of anatomy. Sanio produced a table of comparative wood anatomy of 166 species.
28. De Bary was also first to define the pericycle (which he called the pericambium) with its special role as the origin of the periderm in roots.

29. Hofmeister could hardly reach very definite conclusions but his work was influential in directing future research along objective lines, by the examination of the facts of cell division and organ formation at the apical growing points. He rejected formal ideas like the "genetic spiral" of phyllotaxy developed by A. Braun and C. F. Schrimper, which he showed to be simply inconsistent with the developmental facts. Hofmeister pointed in particular to the remarkable change in the pattern of organ initiation which is frequently observed when vegetative growth gives place to flower formation. A thorough investigation of floral development had been made by Payer in *Organogénie de la Fleur* (1857).
30. Haberlandt distinguished the following principal tissue systems: meristematic, dermal, mechanical, absorbing, photosynthetic, conducting, storage, aerating, secretory, sensory, motor.
31. K. Goebel (1855–1932) was Professor of Botany successively at Rostock, Marburg and Munich. He was trained under Hofmeister, de Bary and Sachs. He was assistant to Sachs for three years and was selected by him to rewrite the systematic part of his textbook in 1882. As a young man Goebel was a student of Hegel's philosophy.
32. The comparative morphology of living and fossil plants was first given critical and illuminating treatment by H. Solms-Laubach in 1887. The recognition that vast numbers of fern-like Palaeozoic plants were actually Pteridosperms came as the result of researches of F. W. Oliver and D. H. Scott in 1903. The exciting discovery of the primitive early Devonian vascular sporangiate plants *Rhynia, Horneophyton* and *Asteroxylon* was not made till 1913. *Psilophyton princeps* had been known since 1859, but its affinities had not been realized.
33. Consideration of the rise of plant pathology during the nineteenth century and of its intimate but complex relations with botany, has been deliberately excluded from this *History*.
34. The extraordinary thoroughness of Hofmeister's work is shown by his examination of nearly two hundred flowering plants, which confirmed the normal regular arrangement of antipodal cells, polar nucleus and egg-apparatus, characteristic of the mature embryo-sac. He did not, however, follow the sequence of divisions leading to the final state; this was done by Strasburger.
35. N. Pringsheim, in the work referred to in the text, speaks of the extreme importance of the algae as a group showing manifold types and primitive structure, which can throw light on the reproduction and life cycles of higher organisms.

    Pringsheim noted the absence of any cellular enclosure of the oogonia as a characteristic of all algae (except *Chara*), distinguishing them from the archegoniate cryptogams. He introduced a uniform terminology (antheridia, oogonia, sporangia, etc.) for the reproductive structures of the algae, which was of enormous value in the investigation and clarification of algal life cycles.

36. It is sad to record that Hofmeister on one occasion treated the young Strasburger with such embarrassing hostility that he was forced to withdraw from a scientific gathering at Innsbruck. The reason seems to have been Hofmeister's resentment at Strasburger's justified correction of his equating the embryo-sac of angiosperms with the archegonium of gymnosperms. This must surely have been an aberration on Hofmeister's part, because in the *Comparative Researches* he quite clearly states the homology between the embryo-sac of angiosperms and the endosperm plus archegonia of gymnosperms. At the time of the unhappy incident Hofmeister was, however, already suffering under the burden of ill-health and family tragedy which caused his early death.
37. In 1882 Strasburger checked for himself that nuclear division follows the same pattern in the cells of *Salamandra* as in the many types of plant tissue he examined.
38. Note, for example, Strasburger's very cautious and balanced attitude to certain resemblances, first pointed out by him, between gametophytic development in the Gnetales and in the angiosperms. He also stressed the very specialized features of embryo-sac development in the angiosperms and the extreme uncertainty of comparisons with endosperm (prothallus) development in gymnosperms.
39. In 1876 he published his first paper on protoplasm as such.
40. Strasburger atttributed the success of his cytological work to the use of fixed plant material with living material for comparison, and to his almost exclusive reliance on stains specifically absorbed by the nuclear substance. The discovery that nuclear division could be watched in living cells of the staminal hairs of *Tradescantia* was crucial in the correct interpretation of fixed and stained preparations.
41. As is well known, Nägeli was the one botanist with whom Mendel corresponded for several years and who had the closest and most direct knowledge of Mendel's work. Nägeli was encouraging to Mendel, but like all his contemporaries clearly had no understanding of the new and significant features of Mendel's work. Nägeli was interested in the genus *Hieracium* and persuaded Mendel to experiment with it. Nothing could have been more unfortunate for Mendel, and the confusing results he obtained with these plants, now known to be apomictic, probably contributed to his giving up research.

    De Vries was one of those who rediscovered Mendel's work in 1900. His observations on *Oenothera* and his Mutation Theory are part of the history of genetics.
42. Roughly speaking, the homologous theory assumed the divergent differentiation in course of time of two morphologically similar gametophyte and sporophyte generations of the ancestral form. The antithetic theory assumed an ancestral form in which the sporophyte generation was represented only by the diploid zygote, which immediately underwent reductive division to start the gametophyte

generation once more. As a result of delay in the occurrence of reduction, a diploid sporophyte generation of increasing complexity was, as it were, "intercalated" in the life cycle. The distinction between the two theories is obviously rather artificial, but the "homologous" picture is closer to modern genetical ideas.

The vital point made by Bower was that the uniformity in the type of alternation found in all the archegoniate cryptogams and in the phanerogams (gymnosperms and angiosperms) is due to adaptation to life on land. He remarked on "the tenacity with which these archegoniate plants (under obvious disadvantages which it entails when their habitat is sub-aerial) retained their aquatic type of fertilization"; and he suggested that the development of siphonogamy [fertilization by pollen tube], by making the phanerogams independent of external water for fertilization, "doubtless contributed to their present ascendency".

11

Botany in the Twentieth Century

Semper in adsiduo motu res quaeque geruntur.
(All things are caught up in ceaseless motion.)

Lucretius

The botanists of the nineteenth century, by their breadth of theoretical vision and the immense range of patient, accurate observations that they recorded, completed the foundations and supporting structure of modern botany. Almost all the far-reaching advances made during the present century grew out of facts, theories and lines of investigation which they established, or from seminal ideas raised by them, which had to await new techniques or some impulse from other sciences before blossoming into active life. To weigh the significance of the many new branches of twentieth-century botany, and to portray their interconnections and their roots in past developments and present problems, would demand a power of historical and scientific judgement to which no contemporary observer, and certainly not the writer, would venture to lay claim. Even the bare catalogue of new discoveries could not be rehearsed without exceeding the proportionate limits of a concluding chapter. For these reasons a detailed chronicle of the growth of botany in our own times will not be attempted. Historically oriented reviews of progress in the main topics of contemporary botany are to be found in the current literature: only the retrospective view of a future historian can gather together all the threads into a grand design. In order to bring to a close this study of the evolution of botanical science through the ages, I shall therefore limit myself to the tentative identification of some more important recent trends, with a glance at their place in botanical theory, their relation to advances in other sciences and in technology, and their potential for further progress in botany and its application to human affairs.

The unparalleled speed of growth of natural science in the last forty or fifty years is a fact that impinges on the life and consciousness of all. This growth was organically linked with the great wave of industrial and economic expansion throughout the world, which supervened on that of the nineteenth century. The increasing involvement and reciprocal interaction of science with industrial and agricultural production, was the ultimate driving force in this sorcerer's transformation of science. In fifty years the global resources devoted to scientific research multiplied several hundred times, with a corresponding, if not quite so spectacular, rise in the number of research workers. The expansion of botanical research, whilst not equalling that in the physical sciences, followed the same general pattern, and this in itself contributed to the great volume of new work which has appeared.

The impetus to botanical progress from state-sponsored agricultural research in Germany during the nineteenth century, was noted in an earlier chapter. In the present century the establishment of agricultural research institutes with direct government or industrial support spread to many countries, resulting in a world-wide stimulus to botanical research, in universities, botanic gardens and many specialized institutions, and going far beyond the immediate needs and problems of agriculture. The very real, practical contributions of botanists to reliable seed production, plant breeding, protection of crops from disease, the study of world plant-resources, the physiology of plant nutrition and crop production, were a powerful lever in raising the status of their science and the degree of official support it was able to attract.

The beginnings of botanical research in regions outside its long confinement to Western Europe,[1] and of very different climate, soils, and indigenous flora, brought fresh problems and sources of information within its purview. This geographical spread (quite distinct, of course, from earlier phases of exploration of the world flora) immeasurably broadened the scope of botanical enquiry and stimulated re-evaluation of many accepted ideas.

Botany, in common with other divisions of biological science, was profoundly affected by closer integration with the physical sciences. The full deployment of physical and chemical knowledge in biological research had been advocated, and practised, by leading investigators during the nineteenth century—notably by Nägeli, Sachs, Pfeffer and de Vries, among botanists—but an essentially different stage was now reached. New and powerful techniques in physics and chemistry became available to penetrate the molecular organization of living systems, whilst at the same time a number of theoretical advances in the physical and earth sciences opened the way to fundamental conceptual and practical advances in biology. Later we shall refer to some of the specific results from contact with the physical sciences at various levels, which transformed our understanding of so many vital processes. Important changes in general outlook also resulted from interaction with the physical sciences, and these are reflected in contemporary botany.

Notions of some indefinable vital force or entelechy were still sometimes entertained in the early decades of the century as a possible explanation of vital phenomena, partly because not all botanists were sufficiently grounded in the physical sciences, partly because the established methods of these sciences were not yet capable of resolving the special complexities of "living matter". The undeniable success of more advanced physical and chemical methods in exploring physiological processes and gaining insight into the molecular structure of protoplasm, areas which had seemed intractable, finally banished vitalist hypotheses from serious consideration, and established a pragmatic materialism as the position of the overwhelming majority of biological researchers.

The advent of more discriminating analytical techniques was heralded as early as 1903, when the Russian botanist M. S. Tswett used chromatography on powdered chalk to separate chlorophylls a and b, carotene and xanthophyll, extracted from leaves in petroleum ether.[2] Although R. Willstätter used Tswett's methods in the researches which determined the structure of chlorophyll, the potentialities of chromatography were not realized until the 1930s. Thereafter it became one of the most widely applied and useful procedures in chemistry. The combination of chromatography with other new techniques—ultra-centrifugation, use of "isotopic labelling", electron-microscopy, among the most important—and the entry of physicists and chemists into biological research in many areas, led to a completely new stage in knowledge of the basic structural elements and the metabolic and reproductive processes of living organisms.

A remarkable unity of structure and functioning at "cellular" and "molecular" level was revealed in all forms of life: animals, plants, fungi, bacteria. The demonstration that the maintenance of living systems, from the simplest to the most complex, involves a common basis of biochemical mechanisms and protoplasmic organization, was the greatest advance in biology of our time. It is the most striking independent proof of the evolution of all existing organisms from a group of common, closely related progenitors;[3] and it marks the realization of that true science of biology, with its own specific basis of general laws, long ago envisaged by Lamarck, Treviranus and others as the goal of the scientific study of living things.

The principles of biochemistry and what has come to be known as molecular genetics, complemented and completed the unitary conception of biological organization, to which cell theory, the chromosome theory of heredity, and evolution, already pointed. This great theoretical advance acted as a potent stimulus to research; it broke down mental boundaries between phenomena traditionally studied in isolation, both by revealing new connections between them, and by providing a range of additional possibilities, both theoretical and experimental, for exploring these connections. The genetics, cytology, metabolism and ecology of plants, in particular, have gained from being viewed in wider biological contexts, whilst closer integration of areas of research in the morphology, anatomy, physiology and systematics of plants led to far-reaching progress in new directions. The strategic combination of many methods of enquiry, old and new, in the solution of fundamental problems, is characteristic of botany today and is the source of its remarkable scope and vigour.

In order to convey some idea of the expanding field of modern botany it is convenient to start from historically established categories, even though recent developments have tended to weaken the justification for them. We will first look at a group of evolutionary topics, touching on aspects of genetics, phylogeny, classification and fossil botany.

Evolution was the background to most botanical research during the grand period of growth in the years after Darwin. Interest in evolutionary problems was given greater intensity at the turn of the century when the working out of the details of nuclear behaviour coincided with the rediscovery in 1900 of Mendel's now famous experiments, to provide the starting point for the gene–chromosome theory of heredity, from which the whole of modern genetics developed. Strasburger, as we have seen, was one of the group of biologists who first suggested that chromosomes are the bearers and transmitters of hereditary characteristics, and his advocacy of this view in his publications between 1900 and his death had much influence in establishing this conception among botanists. Even more significant in the long run were ideas expressed by Nägeli in his mechanical–physiological theory of heredity in 1884, ideas which were then far ahead of their time. Nägeli did not, it is true, locate the genetic material (which he termed idioplasm) exclusively in the nucleus; he thought that it extended throughout the cell in order to fulfil its functions. The idioplasm consisted, in his view, in a series of complex units [Anlagen], each having a specific chemical and micellar structure, all the units being linked together in definite linear order, and being regularly reproduced during ontogeny. Nägeli put forward the further conception that ontogeny (development) is the result of the successive activation of units in response to external and internal conditions. More than twenty-five years after they were first enunciated, Nägeli's penetrating and original ideas found their place as vital elements in genetic theory.

The rise of genetics is both too wide and too specialized a subject to be followed here, but some interrelations with botany are germane. The development of genetic theory falls into two distinct periods. Between 1900 and 1944 the cytological basis of the gene-chromosome theory of heredity was firmly established for higher organisms by a vast assemblage of interlocking facts. The evidence from plants played an essential part, in conjunction with the key researches of T. H. Morgan and his associates on *Drosophila*, and with other work on animals, in establishing the whole web of cytological detail on which the theory was built. The observations (1931) of H. B. Creighton and H. B. McClintock on maize, for example, were crucial in confirming the reality of the interchange of homologous chromosome segments in crossing-over.

The discovery in 1944 of the transference of genetic characters from one bacterial strain to another by means of extracted purified deoxyribonucleic acid (DNA) opened the second phase in genetics. The outburst of investigation into the biochemistry of genetic processes thus set in train, led to the triumphs of molecular biology and to the synthesis of the cytological and molecular aspects of genetics into a single substantive body of theory. It is noteworthy that plants contributed less directly to this second phase of genetics, largely because of two specific cellular features—cell walls and vacuoles, the latter often containing large quantities of secondary metabolites, or cell sap at pH markedly different from that of the cytoplasm. These features of plant cells present unique, although not insuperable, difficulties in studying their biochemistry. Not infrequently this has meant that advances in this area have first been made with more amenable organisms and then confirmed in plants.

Gene mutations, natural and artificially induced, were observed in plants,[4] and this evidence, with similar results in animals, fungi and bacteria strengthened the belief that gene mutations are the principal source of variation on which selection acts to produce evolutionary change—a question left open by Darwin. The combination of cytological studies with systematics brought new concepts in the study of plant speciation when it was shown that polyploidy and hybridization have played a frequent part in plant evolution. The researches of N. I. Vavilov (1915–40) constitute probably the most significant advance in this field, throwing completely new light on the geographical origin and evolutionary history of many economic plants. His recognition that related genera and species, defined by similar morphological characters, also exhibit a similar range of "homologous" variability in both morphological and physiological characters, and that this is an expression of phytogenetic relationship, profoundly influenced evolutionary theory, as well as the strategy of directed plant breeding and the utilization of world plant-resources.

The mode of origin of living from non-living matter now began to be posed as a serious question for science. The techniques devised to cope with bacteria and micro-organisms had finally excluded spontaneous generation of existing life or its imaginable ancestors; yet evolution implied the emergence of primordial life from inorganic matter at some time in the earth's history.[5] The origin of life had special interest for botanists since they most clearly understood the unique role of plants in the primary production of organic matter. As Sachs put it (in 1874), "the substance of the bodies of animals is originally produced in the chlorophyll cells of plants". A few years earlier Nägeli had already concluded that life had arisen from inorganic matter[6] and that the primitive living forms, the "Urbionta", must have possessed chlorophyll; although later he changed this opinion when his own experiments showed some lower fungi to be capable of growth on ammonium salts and organic acids alone. The difficulty of conceiving the first life-forms as possessing the complete apparatus of photosynthesis was sharply revived in the early decades of this century, when plant physiology began to reveal more of the highly evolved complexity of the process. It was, therefore, a decisive event in evolutionary, and specifically in botanical, theory when the Russian biochemist A. I. Oparin published in his book, *The Origin of Life* (1936), an interpretation of the birth of living matter—consistent with a large body of evidence from astronomy, geology, geochemistry, biochemistry and biology—which removed this difficulty, and presented a hypothesis which, in its main principles, has been supported by many later observations and experiments. We must unfortunately forbear analysis of the widespread and pervasive influence of Oparin's work on botany and on its relations to other sciences.

These advances in evolutionary theory were linked with advances in fundamental physics and geology. In the 1920s evidence from radioactivity dramatically extended the age of the earth to at least 3000 million years, and this opened new perspectives and possibilities for biological investigations, including more intensive search for fossil records of life. Perhaps the most exciting result has been the discovery, within the last twenty years, of structural fossils of micro-organisms going back more than 1500 million years prior to the Cambrian era, with evidence of the existence of "living matter" for more than 1000 million years before the appearance of fossilized structures. Vast numbers of the most ancient "Proterozoic" fossils were photosynthetic organisms structurally similar to existing prokaryotic blue–green algae (cyanophyta), but some later forms appear to have possessed eukaryotic cell structure and to have resembled types of present-day green algae.[7] These investigations, which are still only in their beginning, have thus pushed the field of botany more than 2000 million years further back into the past.

The distinction between prokaryotic and eukaryotic organisms represents a phylogenetic and evolutionary dividing line of the greatest importance, separating as it does bacteria and blue–green algae as one group from all higher organisms as another. Its significance was only fully appreciated when basic differences in reproduction and metabolism between the two groups were associated with fine-structural differences revealed by electron-microscopy, but the absence of nuclei in blue–green algae had been noted by C. J. F. Schmitz in 1883, and confirmed by E. Tangl in the same year.

The twentieth century has witnessed rapid and very exciting progress in exploring the fossil record of vascular plants. After the discovery (1905) that many fern-like plants of the Carboniferous Age were in fact seed-bearing, constituting a new order of fossil plants, Pteridosperms or seed-ferns, came the finding of the most ancient vascular land plants yet known, the Psilophytales, from the lower Devonian of Scotland.[8] The distinctive and apparently primitive morphology of these plants gave a new direction to thought on vascular plant phylogeny. Since then evidence of many other types of early vascular plants of Devonian, Silurian and even of Ordovician age, has been growing. At the same time a great assemblage of diverse and hitherto unknown Devonian and Carboniferous plants has been discovered, showing "synthetic" relationships with psilophyte, gymnosperm and pteridophyte stocks, from which, as material continues to accrue, valuable evidence on higher plant phylogeny may be expected.

Light has also been shed on what Darwin called the "abominable mystery" of the apparently abrupt appearance of flowering plants (angiosperms) in the Cretaceous. Detailed comparative studies of Cretaceous floras show the existence of orderly patterns of diversification and radiate evolution, consistent with a monophyletic origin of the angiosperms and their relatively rapid spread thereafter.

The systematics of living plants holds its place as one of the most active areas of study. This is firstly because the task of recording the world flora is still far from complete, surprising as this might seem to the uninstructed, and its very completion is put in doubt by the speed with which natural habitats are being destroyed by human interference. The importance of systematics has been further increased by the need to conserve the store of genetic variation in wild populations for use in plant breeding.

One of the main developments in systematics has been the use for classification, in addition to morphological characters (the *differentiae* of the old botanists), of many diverse characters derived from cytology, anatomy, pollen morphology,[9] embryology,[10] chemical and macro-molecular properties, serology, ultra-structural features, and other indicators. The new *differentiae* do not replace the time-honoured floral and morphological characters, but they are a valuable supplement to them, and are additional sources of evidence of natural relationship. In the 1960s the availability of high-speed computers led to the development of "numerical taxonomy", which provides efficient mathematical techniques for making maximum use of the variety of *differentiae* on which classification can now be based.

A fundamental contribution to systematics was made by the American botanist C. E. Bessey in 1915, in a paper on the phylogenetic taxonomy of flowering plants. He discussed what should be the guiding principles for founding a phylogenetic classification of angiosperms, suggested a number of characters which could be regarded as primitive, and put forward a tentative phylogenetic arrangement based on them. In particular, Bessey considered that the type of flower of *Rannunculus* or *Alisma* and their relatives, came closest among living plants to the primitive angiosperm flower, a view which had been expressed by Nägeli in 1884, but had been overshadowed by the supposed primitive character of the reduced flowers of Amentiferae, an idea due to de Candolle and enshrined in Engler's arrangement in *Die natürlichen Pflanzenfamilien*. Bessey's principles led to a complete change of ideas and, although modified and extended since, were the starting point for a new wave of research and advance in angiosperm phylogeny, within which the work of the Russian systematist A. Takhtajan has been outstanding for its combination of many lines of enquiry in an illuminating synthesis.

Ever since the pioneer work of Alexander von Humboldt, Robert Brown and Joseph Hooker, the distribution of plants over the face of the earth has been recognized as a key question linked directly or indirectly with many aspects of botany, from problems of palaeobotany and evolution to those of comparative physiology. The subject was raised to a new level early in this century by the impact of Alfred Wegener's theory of continental drift (1915), which had an immediate impact on botany. The theory was recognized by E. Irmscher as affording an explanation of most of the perplexing problems of plant distribution, and his account (1922) of the distribution of flowering plants from the Cretaceous to the present, which assumed the occurrence of continental drift according to Wegener, became the foundation for further progress in the evolutionary history, systematics and distribution of the angiosperms. It is interesting that continental drift was accepted by most biologists long before the majority of geologists believed that the geological evidence was convincing.

The rise of ecology to become a major branch of biology is one of the most important scientific advances of recent years. Inevitably, the study of plant associations in natural environments (plant ecology) has had a preponderant influence in the development of ecology because of the status of green plants as the primary fixers of solar energy.

The growth of distinct ecological concepts and methods was at first hesitant, and much work was descriptive. The plant community became established as an ecological unit as the means of recording and describing plant association were improved. The recognition of succession by F. E. Clements and others (1916) began the study of dynamics of plant communities and was the basis for the expansion of ecological research in the 1930s which still continues. Critical methods were brought to bear on the problems of causal analysis of change and stability in natural communities. The quantitative analysis of matter and energy flow in ecological systems has opened new approaches to unifying theoretical principles.

Some general conclusions have emerged very clearly from the mass of research on the environmental relations of plants. The interbreeding population, maintained in each particular case within fairly precise spatial limits by natural conditions, appears as the unit in adaptive change, both evolutionary and ecological. The frequency and immense importance of natural selection, assumed by Darwin, has been abundantly confirmed by observation and experiment. Correspondingly, a host of structures and properties (such as glandular hairs, trichomes, idioblasts, secretions and special metabolites, variations in detailed morphology such as leaf shape, and many other features), which have been sometimes held to be "neutral", have been found to have high adaptive value in natural environments, often in relation to predators or beneficial symbionts. Thus Darwin's emphasis on biotic adaptation (or co-adaptation) as a constant feature in many organisms has been shown to be correct. Biotic relationships, such as the mycorrhizal association normal for very many plants, or the widespread occurrence of root grafts in forest trees, present aspects of physiology and ecology still to be explored.

The study of morphogenesis—of the metabolism of co-ordinated growth and differentiation of cells, tissues and organs, by which the plant body is formed—was begun by Hofmeister, Sachs and Goebel, but was necessarily circumscribed until the breakthrough in biochemistry and genetics of the mid-twentieth century, and advances in plant physiology, created possibilities for experimental approach on a wide front. Before dealing with this concrescent movement of morphology and physiology, some advances in descriptive morphology and anatomy must be noted.

A massive increase in detailed knowledge of plant structure came from examination of the world flora. The accumulated results, whilst not destroying the validity of established categories and relationships, enlarged the known limits of variation and of "aberrant" formations (epiphyllic organogenesis, for example), with important theoretical consequences. Wide-ranging studies of embryology, stelar morphology, stomatal development, differentiation and mature form of xylem elements, and many other anatomical features, produced reliable comparative data which have already thrown fresh light on the systematics and phylogeny of higher plants. Even an additional type of specialized cell, the collecting or transfer cell, has been defined and shown to be commonly associated with the vein-endings and photosynthetic cells in the leaves of many plants.

A feature of recent work has been efforts to follow histogenesis or organogenesis from the meristematic initials to complete differentiation. This renewed interest in the apical meristem has brought impressive evidence of its complex and heterogenous organization, with distinct regions of markedly different physiological activity under strict endogenous control. A very high degree of autonomous regulation resides in the apical meristem, as is shown by the ability of the excised shoot apex to develop into a complete plant when placed in suitable, relatively simple cultural conditions.[11] The function of plasmodesmata in the ordered processes of tissue development is now being seriously investigatd, after a long period of neglect since the observations of Tangl and Strasburger.

Description of the huge territory of fine-structure anatomy revealed by electron-microscopy is only now beginning, the perspectives of which it will need another generation to explore.

The many-sided growth of plant physiology since the 1930s may well be regarded as the biggest advance in modern botany, yet the outlook which guided it and the methods of investigation employed would have been perfectly comprehensible to Nägeli and Sachs and other plant physiologist of the last century, and the results, however

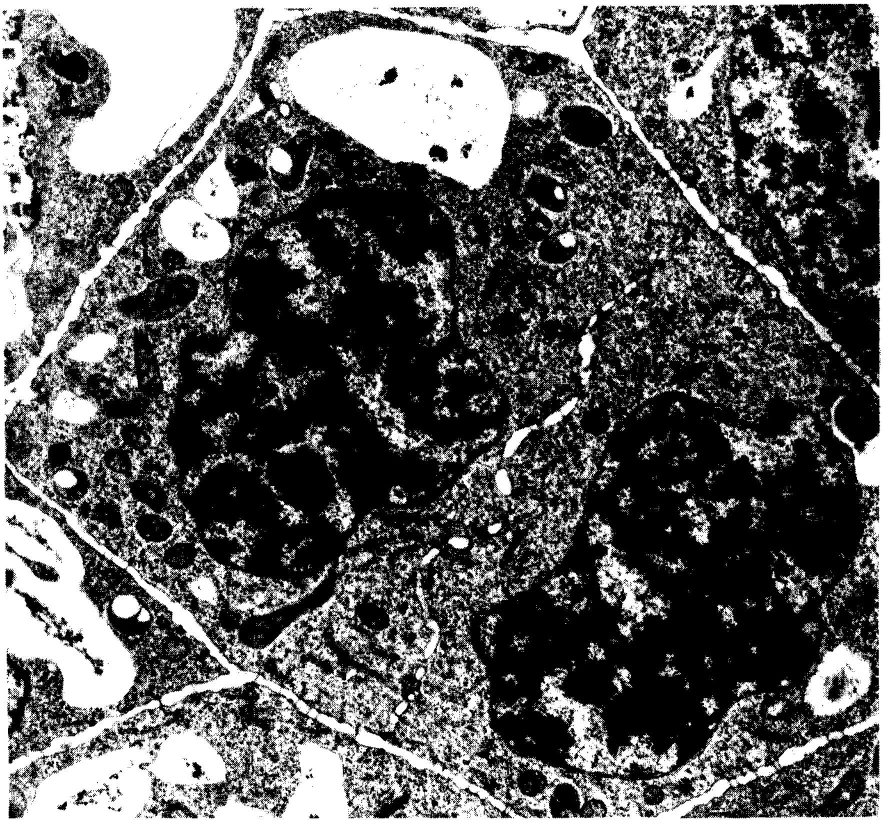


Figure 27 Transmission electron micrograph of a dividing plant cell from ovule wall of *Gibasis oaxacana* D. R. Hunt (Commelinaceae). Late anaphase stage, showing daughter nuclei being separated by a newly formed cell-wall (×13,000). The critical observation of "ultra-structure" opens new vistas in anatomy and its relation to the development and functioning of the plant.

novel, would not, I believe, seem to them to be in contradiction with reasonable expectation.

We have referred to the effect of biochemistry in adding a new dimension to research in plant physiology, but must forego detailed consideration of the interaction between the two modes of enquiry. A supremely important result of their combination has been the remarkable progress in unravelling the mechanism of photosynthesis in green plants. It is difficult to realize that up to 1930, analysis had not gone beyond F. F. Blackman's recognition of "light" and "dark" reactions in photosynthesis—in itself a great theoretical advance—whilst the old suggestion (given chemical support by von Baeyer in 1870) that formaldehyde may be an intermediate in the photosynthetic formation of sugar was still taken seriously. In 1930 a new phase of investigation was initiated by the theoretical impulse of an epoch-making paper by C. B. van Niel, in which he put forward the conception of the "dark" reaction as consisting of the chemical fixation of carbon dioxide followed by its reduction, and of the "light" reaction as consisting of the use of light energy to split water (photolysis) to give products capable of driving the reductive reaction. This idea soon received experimental support from Hill's demonstration of oxygen liberation by isolated chloroplasts illuminated in the presence of suitable electron acceptors, and from the demonstration by Ruben and Kamen (making use of the heavy isotope of oxygen) that the oxygen liberated during photosynthesis by green algae is derived from water, not from the carbon dioxide assimilated. There now began a period of intense research which has substantiated the correctness of van Niel's conception of photosynthesis, and has enormously enlarged our detailed understanding of its constituent reactions and their co-ordination, and of the control of photosynthesis in relation to the functioning of the plant as a physiological unit.

Knowledge of plant nutrition was fundamentally altered by the discovery between 1920 and 1940 of the essentiality of the so-called trace elements (copper, zinc, boron, manganese, molybdenum, chlorine). The results were obtained by classical water-culture experiments, merely using more carefully purified chemicals and stricter operating precautions. This work had incalculable effects in agriculture throughout the world, raising the yield and quality of crops and herbage; it inaugurated a vast amount of research into the metabolic function of the trace elements.

The story of the isolation and study of plant hormones is too involved to tell in summary, and I shall only refer to some fundamental results of this most explosive development in plant physiology. The existence of endogenously formed substances, or groups of closely related substances functioning as hormones or "growth substances" in higher plants, is now well established. The three most important appear to be auxin, the gibberellins and the cytokinins [the rationale of these commonly used names need not be discussed and I shall use them without qualification]. To these should probably be added abscisic acid and ethylene, whilst there may be others not yet characterized. Synthesis of auxin seems to be localized in definite parts of the plant, being especially active in the shoot apex; its direction of movement in the plant is normally strongly basipetal in relation to polarity. Information on the other two hormones is less complete, but they also appear to be synthesized principally in apical regions. Translocation of the gibberellins is rapid but not polar, whilst the movement of cytokinins appears to be more restricted.

Early studies with auxin applied exogenously to whole plants, or to excised organs or tissues, showed that it could affect a very wide range of physiological activities—cell division, cell extension, cell differentiation, root formation, bud growth, apical dominance, abscission, enzyme synthesis and many more—depending on the concentration applied and on the nature and state of the tissue receiving it. Gibberellin and cytokinin were later found to affect many of the same plant activities as auxin, although in different and sometimes antagonistic ways. There is now an immense literature on the physiological effects of auxin, gibberellin and cytokinin, which strongly suggests that much of the regulation of metabolism and development at cellular level depends on the interaction of these three plant hormones. The multiplicity of effects can be unified by the conception that the behaviour of cells at specific positions within the plant body is determined by the local dynamic balance of concentration of endogenous hormones, and the capacity of cells to react to it in specific ways. There is already much experimental evidence of the involvement of plant hormones in morphogenesis and differentiation, although as yet little indication of how their regulatory effects are exercised. Practically nothing is known of the even more fundamental question of how neighbouring cells come to react in totally different ways to the same levels of hormones: this is likely to become a very important line of research in the future.

New insights into both nutrition and morphogenesis have come from researches into the culture of isolated plant cells in defined media. This line of work was begun by Haberlandt, and progress was at first slow and beset with experimental difficulties, but thanks to the persistence of a small number of pioneers it is now possible to culture organs, tissues, embryos, pollen grains, individual cells and even protoplasts, by fully controlled methods. One remarkable result of this work was to show that single plant cells, or cells in unorganized masses, have very complex nutritional requirements, needing vitamins, plant hormones and a variety of carbon and nitrogen compounds to be supplied from without, in order to support growth. Yet when such cells, for whatever reason, succeed in forming a new meristem, the organized mass becomes autotrophic, requiring only the normal mineral salts plus either soluble carbohydrate or the presence of light and carbon dioxide in conditions allowing photosynthesis. Clearly there are nutritional interactions between cells in normal tissues which are destroyed when its organization is broken. Confirmatory evidence comes from embryo culture. Embryos removed from the embryo-sac in very early stages of development will only continue to develop in culture if provided with hormones, vitamins and other complex compounds, whereas embryos removed at a more advanced stage will readily grow and develop autotrophically.

Cell culture also throws interesting light on morphogenesis. The normal processes of morphogenesis are inhibited or disturbed in cell culture; unorganized masses of irregular cells tend to arise, and there is neither internal differentiation of regular tissues nor the formation of plant organs. Reversion to normal morphogenesis can sometimes be induced by the addition of appropriately balanced mixtures of hormones. When this happens, the resumption of normal development is always preceded by the formation of one or more true meristems, which then give rise to perfectly co-ordinated plantlets with the typical morphology of the species in question.

A most important result of experiments in cell culture has been to show that, with few exceptions, every plant cell, even when fully differentiated, retains totipotency, that is, the capacity to return to the meristematic state and give rise to a complete new plant. This retention of the power to de-differentiate and begin the process of ontogeny again, appears to distinguish the cells of higher plants from those of higher animals.

The discovery of photoperiodism, that is, the control of flowering by the relative lengthy of night and day, was made by W. W. Garner and H. A. Allard in 1920, when working with tobacco plants. It opened a new phase in environmental physiology and in the study of the morphogenic effects of light to which Sachs had devoted much attention. A mass of research on the physiology of flowering and on photo-inductive effects on other plant processes such as leaf-fall and seed dormancy, originated from this work. One outcome was the discovery of phytochrome, a protein pigment universally present in low concentration in all parts of higher plants, and believed to be part of the "trigger mechanism" in many light-dependent plant responses.

The belief that phloem is concerned in the translocation of elaborated food substances was established in the nineteenth century on the evidence of its structure and cell contents, its constant association with water-transporting xylem and the results of ringing experiments. The mechanism of phloem transport remained unknown and almost unconsidered. The enunciation of the mass-flow theory of the movement of metabolites in the phloem, made by E. Münch in 1930, was thus one of the most important theoretical advances in physiology of the period, since it was founded on a precise and reasonable physico-chemical mechanism and was consistent with many physiological observations and with the anatomical facts. The explanation of phloem transport is still a matter of much dispute, but Münch's ideas have been a guide and spur to research and, even if considerably modified, seem likely to find a place in the final solution of the problem.

I have selected rather arbitrarily a few of the growing points of physiology of special theoretical interest, whilst neglecting others, and have said nothing of much steady progress in long-established areas. Perhaps it will not be amiss to mention, in conclusion, two topics in which plant physiologists of the nineteenth century were intensely interested, but which have received surprisingly little attention since. The electrical properties of whole plants were the subject of a number of researches at Würzburg under Sachs, although he admits that the results were not very revealing: it is surprising that interest in the question has not been revived. Even more surprising is that the physiological function of the protoplasmic movements, to be observed in almost every section of living plant tissue placed under the microscope, is still a complete mystery, whilst even the physical mechanism of cyclosis is not understood.

Our rapid survey, like the changing views from a *camera obscura*, can give only an impression of the historical movement of contemporary botany, its theoretical energy and wide-ranging activity. At no time in its long history has botany been so directly concerned with the urgent practical needs of human existence. It is now an indispensable tool in improving the culture, productivity and protection of crops, in the technical transformation of agriculture and horticulture, in plant breeding, in the discovery and preservation of plant resources, economic, genetic and pharmacological, and in ecological control of the environment. Wide prospects and challenging problems, in theory and in practice, lie before the fortunate botanists of the future.

"The property of history", said Polybius, "is first, to ascertain what was actually said or done, and second, to discover the causes of success or failure. It is the study of causes which makes history fruitful and a basis for estimating the future and facing coming events with confidence."

With humility, I dedicate this history of botany to the memory of the great company of past botanists, named and unnamed, in the hope that this account of their struggles and failures, of their peaceful labours and hard-spun thought, and of their lasting achievements, will be an inspiration and guide in the future advance of the science which has done so much to lighten and beautify the life of men.

Notes

1. The growth of indigenous botany has been truly world-wide; it includes renewal of the traditional knowledge of India, China and Japan by fusion with modern science, and the contributioin of such rapidly developing countries as Australia and Canada. The biggest developments have taken place in the United States of America, especially after the strengthening of science by the "New Deal" in the early 1930s, and in the Soviet Union after the October Revolution in 1917, when heavy investment in science was seen as essential to building a socialist society, and there was a great

extension of botanical research in every field. It is noteworthy that the progress of botany in the Soviet Union was less affected than other areas of biology by the temporary influence of Lysenko's mistaken notions. In fact Soviet botanists were largely united in active opposition to Lysenko's views on species formation, which were demolished in a series of more than forty articles in the *Botanicheskii Zhurnal* between 1952 and 1955, when discussion was brought to an end by the failure of Lysenko's adherents to produce either evidence or argument to support him.

2. What seems to be the first recorded use of paper chromatography was by the chemist F. F. Runge in 1855, but the general use of chromatography as a method stems from Tswett.
3. The idea of Darwin as purely a "naturalist" is hardly consistent with his remarkable anticipation of the role of biochemical and cytological evidence, penetratingly expressed in the *Origin of Species*. "Analogy would lead me one step further, namely, to the belief that all animals and plants have descended from some one prototype. But analogy may be a deceitful guide. Nevertheless all living things have much in common, in their chemical composition, their germinal vesicles, their cellular structure, and their laws of growth and reproduction. We see this even in so trifling a circumstance as that the same poison often similarly affects plants and animals; or that the poison secreted by the gall-fly produces monstrous growths on the wild rose or the oak tree."
4. The Mutation Theory of de Vries undoubtedly had a very great effect in bringing the conception of mutations into genetics, although the variant forms of *Oenothera* to which he applied this term turned out to be something very different, and confused the issue for some time.
5. Darwin recognized this but was too cautious to say so except in private correspondence to friends. He used the term archebiosis, to refer to the origin of life from non-living matter.

   Lamark had already postulated (in 1820) this mode of origin of life.
6. In his work on heredity, already cited above, Nägeli said that the origin of life from inorganic matter must have involved the spontaneous production of proteins, and that this probably did not take place free, in solution in a mass of water, but in the surface film of fine porous substances such as chalk or sand, the catalytic property of which is well known. The formation of proto-organisms occurred by the association of micelles and the gradual development of co-ordination between growth and reproduction.

   Such ideas anticipate in a remarkable way those developed later by Oparin, Bernal and others. There is a good case for holding Nägeli to be the most profoundly original and versatile thinker of the nineteenth-century botanists.
7. The fossil evidence fits in very well with the evolutionary succession postulated by Oparin, the appearance of atmospheric oxygen at the time

when photosynthetic organisms became dominant, changes in cell organization, etc.

8. See Note 32, Chapter 10.
9. Pollen is well preserved in many natural deposits, and since it can often be identified to genus or even to species, the study of fossil pollen (palynology) has become a valuable means for investigating past changes in the flora and the ecology of particular regions, and the alteration in climate, drainage, or other environmental factors which gave rise to them.
10. An example of the use of such information is Maheshswari's recent observation that the Lemnaceae—a family isolated by their very reduced and specialized morphology—are related to the Araceae by the type of embryo-sac they possess. This is an interesting confirmation of a relationship originally suggested by Engler on other grounds in 1877.
11. The technique of excising and culturing the apical meristem of the shoot (a critical minimum region is required for successful development) is now widely used in horticulture to obtain rapid clonal reproduction, especially of virus-free plants (the apical meristem, even of infected plants, is normally free of virus). A remarkable fact is that excised apices, if quickly frozen in liquid nitrogen, retain their viability in it for long periods.

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Botany is one of the oldest of sciences. While its intellectual origins are in the two ancient disciplines of medicine and magic, it has deeper roots in early Man's developing role as a farmer. Through its long association with pharmacology, agriculture and horticulture, and its important role in the exploration of the world and the supply of food and raw materials, it has had a major effect on human progress. In recent years research in every branch has expanded rapidly and the results have influenced our methods of plant breeding and crop protection and our exploitation of the genetic, medicinal, food and energy resources of plants. The need for a new history of botany in the light of contemporary science and historical method has been evident for some time.

Professor Morton's book describes the development, on a world scale, of scientific thought about plants from its origins to the present day. It is the fruit of years of careful study and reassessment of the principal primary sources, ancient and modern, and brings forward much new or neglected material, giving fresh insight into many aspects of botanical progress. The main theme is the increase in knowledge of plants and the associated development of botanical concepts and theories: however, in order to present an integrated view, the book discusses the relation of botany to world events and social change, to other fields of science, to prevailing philosophical ideas, and, in particular, to the lives and personalities of leading botanists.

Written in a lucid style, with a minimum of technical language, the work is accessible to readers with a general interest in science as well as to professional botanists. For the latter there are numerous notes containing much supplementary information, but the fascinating story of botanical science can be followed without recourse to them. Thus botanists and horticulturalists, biology teachers and historians of science alike will appreciate this book.

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