is a great annoyance to man and beast from the prickly calyx (involucrum) ;" and by Major Denham that from Aghedem to Woodie "it covered the surface of the country, and annoyed the travellers to misery ;" he observes also that the seed is called *Kasheia,* and is eaten.

PANICUM TURGIDUM (*Forsk. Arab., p.* 18 ; *Delile,* [216
Flore d'Egypte, p. 19, *tab.* 19, *f.* 2) is also one of the most common grasses from Tripoli to Bornou.

Of ACOTYLEDONES, the only plant in the collection is *Acrostichum velleum,* found on the Tarhona mountains. Mr. Ritchie's herbarium contains, also, a single plant of the same family, namely *Grammitis Ceterach.*

The foregoing observations have extended much beyond the limits which the number and importance of the plants they relate to may seem to require. I still regret, however, that I cannot add a few remarks on such species as, although not in the herbarium, were observed, either indigenous or cultivated, in the countries visited by the mission, and for information respecting which I am indebted to Major Denham and Captain Clapperton. But it being determined no longer to delay the publication of the very interesting Narrative to which the observations already made will form an Appendix, I am unable at present to enter on this part of my subject.

GENERAL VIEW

OF THE

BOTANY OF SWAN RIVER.

BY

ROBERT BROWN, ESQ., F.R.S.

[*Extracted from the 'Journal of the Royal Geographical Society of London.' Vol. I, pp.* 17—21.]

LONDON:

1832.

GENERAL VIEW OF THE BOTANY

OF THE

VICINITY OF SWAN RIVER.

BY R. BROWN, ESQ., F.R.S.

Read November 22nd, 1830.

THE vegetation of the banks of Swan River, and of the adjoining country to the southward, is at present known chiefly from the report of Mr. Charles Fraser, the botanical collector, who accompanied Captain Stirling in his examination of that district in 1827, and from collections of specimens which were then formed. [17

I have inspected, and in part examined, two of these collections; one of which I received from Mr. Fraser himself, through my friend Alexander Macleay, Esq., the Secretary of the Colony of New South Wales; for the second I am indebted to Captain Mangles.

The number of species in both collections does not exceed 140; and some dicotyledonous herbaceous tribes, as well as grasses, Cyperaceæ, and Orchideæ, are entirely wanting.

From materials so limited in extent, but few general observations can be hazarded on the vegetation of this portion of the south-west coast of New Holland.

The principal families of plants contained in the collections are *Proteaceæ*; *Myrtaceæ*; *Leguminosæ*, such especially as belong to *Decandrous Papilionaceæ*, and to the

Leafless Acaciæ; Epacrideæ; Goodenoviæ; and *Compositæ.* And the more conspicuous plants, not belonging to any of these families, and which greatly contribute to give a character to the landscape, are, *Kingia australis,* a species of *Xanthorrhæa;* a *Zamia,* nearly allied to, and perhaps not distinct from, *Z. spiralis* of the east coast, although it is said frequently to attain the height of thirty feet; a species of *Callitris;* one or two of *Casuarina;* an *Exocarpus,* probably not different from *E. cupressiformis;* and *Nuytsia floribunda,*[1] a plant hitherto referred to *Loranthus,* but sufficiently distinct in the texture and the form of its fruit, and now named in memory of the discoverer of that part of the coast to which this very singular tree is nearly limited.

If an opinion were to be formed of the nature of the country merely from the inspection of these collections, it certainly would be extremely unfavorable as to the quality of the soil; for not only do the prevailing families already enumerated, but the whole of the genera of those families, and even many of the species, agree with those found on the shores of King George's Sound, which, with the exception of a few patches of very small extent, seem absolutely incapable of cultivation.

The opinion so formed, however, would be necessarily modified in noticing the entire want in the collections of 18] tribes, all of which must be supposed to exist, and some even in considerable proportion, in the tract examined; in allowing for the unfavorable season when the herbarium was collected; in admitting the statements in Mr. Fraser's report, respecting the abundance and luxuriance of *Anthistiria australis*—the Kangaroo-grass of New South Wales; from the account given in the same report of the extraordinary size of some arborescent species of *Banksia,* which, in the neighbourhood of King George's Sound, generally form small trees only; and lastly, in adverting to the important fact stated by Captain Stirling in his despatch to Government—namely, that the stock had not only been

[1] Loranthus floribundus. *Labill. Nov. Holl.* i, *p.* 87, *t.* 113.

supported through nearly the whole of the dry season, but that most descriptions of it had even fattened on the natural herbage of the country.

From these more general observations I proceed to make a very few remarks, chiefly relating to the geographical distribution of some of the families or more interesting species, either contained in the herbarium, or distinctly noticed in Mr. Fraser's report.

The striking resemblance in general character, and the identity of many of the species with those of King George's Sound, have been already mentioned. But this portion of the shores of New Holland, extending from Swan River on the west coast to Middle Island, in 123° 10′ east long. on the south coast, may be said to contain the greatest proportion of those genera which form the chief peculiarities of New Holland vegetation.

In comparing the Flora of the district of Swan River with more distant regions of the same continent, it may be remarked, that probably not more than four or five species are common to this part of the west coast, and to the same parallel of the east coast of New Holland; and that even the existence of some of these species at Swan River is not altogether certain.

In the collections which I have examined there is no specimen of *Anthistiria australis*, or Kangaroo-grass of New South Wales; but as this valuable grass must have been well known to the botanical collector, and as it is perhaps the most general plant in New Holland, I have no hesitation in admitting its existence on the authority of Mr. Fraser's report.

Mesembryanthemum æquilaterale is neither contained in the herbarium, nor mentioned by the collector. I find, however, in one of the letters from Swan River, published by Mr. Cross, a plant noticed as a pot-herb, that, from the account of the writer, is probably this plant, which, next to *Anthistiria australis*, is perhaps the most widely diffused species in the Flora of New Holland.

The third species is *Pteris esculenta*, the only fern found by Mr. Fraser, and which is both general and abundant

beyond the tropic in New Holland and in Van Diemen's Land.
19] The *Zamia*, already noticed, if not specifically different from *spiralis*, would furnish another example of a plant peculiar to New Holland, and very generally found in the extra-tropical parts of that continent. I had, however, myself observed on the south coast a *Zamia* of at least ten feet in height, which I suspected might be distinct from *Z. spiralis* of the neighbourhood of Port Jackson, and which is probably the same with that of Swan River.

The *Exocarpus* of the Swan River may possibly differ from *cupressiformis*, though there is nothing in the specimens to make it probable that it is specifically distinct. But *Exocarpus cupressiformis* is found very generally, not only in the southern parts of New Holland and Van Diemen's Land, but also within the tropic.

The last plant in the collection whose range is very extensive remaining to be noticed, I have not been able to distinguish from *Arenaria marina* of the shores of Europe.

Of the families existing in the vicinity of Swan River, the most striking, as well as the most extensive, is *Proteaceæ*, a tribe which, from its general dispersion, and the remarkable forms of its numerous genera and species, includes many of the chief peculiarities of the vegetation of New Holland.

In Mr. Fraser's collection, the principal genera of this order are—*Petrophila*, *Isopogon*, *Hakea*, and *Banksia;* and these are also the most abundant in the districts of King George's Sound and of Lucky Bay. The number of species of the two first-mentioned genera confirms the remark made in the Botanical Appendix to Captain Flinders's Voyage[1]—namely, that in New Holland, at the western extremity of the parallel of latitude in which the great mass of this order of plants is found, a closer resemblance is observable to the South African portion of the order than on the east coast, where those allied to the American part chiefly occur.

This is not the place to enter into a particular account of the new species of this family existing in the collections

[1] (*Antè*, *p.* 41.)

from Swan River. I may observe, however, that the number is considerable, and that their specific characters have been recently published.[1]

The *Myrtaceæ* of Swan River belong chiefly to *Melaleuca*, *Beaufortia*, *Calothamnus*, *Calythrix*, *Billottia*,[2] and *Eucalyptus*.

Of *Eucalyptus* the only species in the collection had been first found in Captain Flinders's voyage at King George's Sound, on the shores of which it was the only useful [20
timber tree, though there of very moderate size. I have named it *Eucalyptus calophylla*.

Mr. Fraser describes it as forming, on the banks of the Swan, a large forest tree, and erroneously refers it to *Angophora*, a genus which is limited to the east coast of New Holland. Other species of *Eucalyptus*, forming the timber of the country, are mentioned in the report, and considered to be some of the common gum-trees of Port Jackson, from which, however, I have no doubt they will prove to be distinct; for I am acquainted with no species of this genus common even to the east and south coasts of New Holland.

I shall conclude with a remark relating equally to the genus *Eucalyptus* and to the *Leafless Acaciæ*, several species of which are found in the collection. This observation I have formerly made in the Appendix to Captain Flinders's Voyage in the following terms[3]:—"These two genera are not only the most widely diffused, but by far the most extensive in Terra Australis, about 100 of each having already been observed; and if taken together, and considered with respect to the mass of vegetable matter they contain, calculated from the size as well as the number of individuals, are perhaps nearly equal to all the other plants of that country. They agree very generally also, though belonging to very different families, in a part of their economy, which contributes somewhat to the peculiar

[1] *Supp.* I, *Prodr. Flor. Nov. Holl.*

[2] A genus distinct from *Leptospermum*, to which the few species hitherto published, namely, *B. marginata*, *flexuosa*, and *linearifolia*, have been referred.

[3] (*Antè*, *p.* 62.)

character of the Australian forests, namely, in their leaves, or the parts performing the functions of leaves, being vertical, or presenting their margin, and not either surface, towards the stem: both surfaces having consequently the same relation to light.

"This economy, which uniformly takes place in the *Acaciæ*, is in them the consequence of the vertical dilatation of the foliaceous footstalk; while in *Eucalyptus*, where, though very general, it is by no means universal, it proceeds from the twisting of the footstalk of the leaf."

To this quotation it may be added that these two genera still more uniformly agree in the similarity of the opposite surfaces of their leaves. But this similarity is the indication of a more important fact—namely, the existence equally on both surfaces of the leaf, of those organs, for which, as I believe them to be in general imperforated, I have adopted the name of *cutaneous glands*, but which by most authors are denominated pores, or *stomata* of the *epidermis*.

In leaves, especially of trees and shrubs, these glands are generally found on the under surface only; while among arborescent plants in a very few instances, as in several *Coniferæ*, they are confined to the upper surface.

21] In addition to the two extensive New Holland tribes here mentioned, there are many other cases in which these organs occupy both paginæ; and I am inclined to think such cases more frequently occur on that continent than in any other part of the world. It is at least certain that on this microscopic character, of the equal existence of cutaneous glands on both surfaces of the leaf, depends that want of lustre which is so remarkable in the forests of New Holland.

BOTANICAL APPENDIX

TO

CAPTAIN STURT'S EXPEDITION

INTO

CENTRAL AUSTRALIA.

BY

ROBERT BROWN, ESQ., D.C.L., F.R.S., F.L.S., &c.

[*Extracted from the 'Narrative of an Expedition into Central Australia, during the years* 1844, 1845, *and* 1846,' *by Captain Charles Sturt, F.L.S., F.R.G.S. Vol. II, Appendix, pp.* 66—92.]

LONDON:

1849.

PLANTS OF CENTRAL AUSTRALIA. [66

My friend, Captain Sturt, having placed at my disposal the Collection of Plants formed in his recent Expedition into the Southern Interior of Australia, I am desirous of giving some account of the principal novelties it contains.

The collection consists of about one hundred species, to which might be added, if they could be accurately determined, many other plants, chiefly trees, slightly mentioned in the interesting narrative, which is about to appear, and to which the present account will form an appendix. I may also observe, in reference to the limited number of species, that Captain Sturt and his companion, Mr. Brown, seem to have collected chiefly those plants that appeared to them new or striking, and of such the collection contains a considerable proportion.

In regard too to such forms as appear to constitute genera hitherto undescribed, it greatly exceeds the much more extensive herbarium, collected by Sir Thomas Mitchell in his last expedition, in which the only two plants proposed as in this respect new belong to genera already well established, namely, Delabechia to Brachychiton, and Linschotenia to Dampiera.

In Captain Sturt's collection, I have been obliged, from the incomplete state of the specimens, to omit several species, probably new, from the following account, in which the plants noticed, chiefly new genera and species, are arranged according to the order of families in the Pro- [67
dromus of De Candolle.

BLENNODIA.

Cruciferarum genus, prope Matthiolam.

Char. Gen.—*Calyx* clausus, foliolis lateralibus basi saccatis. *Petala* æqualia, laminis obovatis. *Stamina:* filamentis edentulis. *Ovarium* lineare. *Stylus* brevissimus. *Stigma* bilobum dilatatum. *Siliqua* linearis valvis convexiusculis, stigmate coronata, polysperma. *Semina* aptera pube fibroso-mucosa tecta! *Cotyledones* incumbentes.

Herba (v. Suffrutex) *erecta ramosa canescens, pube ramosa;* foliis *lato-linearibus remotè dentatis;* racemis *terminalibus.*

1. Blennodia *canescens.*

Loc. In arenosis depressis.

Desc. Suffruticosa, sesquipedalis, caule ramisque teretibus. Folia vix pollicaria paucidentata. Racemi multiflori, erecti, ebracteati. Flores albicantes. Calyx incano-pubescens. Petalorum ungues calyce paulo longiores. Stamina 6, tetradynama, filamentis linearibus membranaceis apice sensim angustato.

Obs. This plant has entirely the habit, and in many important points the structure of Matthiola, near which in a strictly natural method it must be placed; differing, however, in having incumbent cotyledons, and in the mucous covering of its seeds. The mucus proceeds from short tubes covering the whole surface of the testa, each containing a spiral fibre which seems to be distinct from the membrane of the tube. A structure essentially similar is known to occur generally in several families; to what extent or in what genera of Cruciferæ it may exist, I have not ascertained; it is not found, however, in those species of Matthiola which I have examined.

STURTIA. [68

Malvacearum genus, proximum Gossypio, affine etiam Senræ.

Char. Gen.—*Involucrum* triphyllum integerrimum. *Calyx* 5-dentatus, sinubus rotundatis. *Petala* cuneato-obovata, basi inæquilatera. *Columna* staminum polyandra. *Ovaria* 5, polysperma. *Styli* cohærentes. *Stigmata* distincta linearia. *Pericarpia*. . . *Semina*. . .

Suffrutex *orgyalis glaber;* foliis *petiolatis obovatis integerrimis;* floribus *pedunculatis solitariis.*

2. Sturtia *Gossypioides.*

Loc. "In the beds of the creeks on the Barrier Range." *D. Sturt.*

Desc. Suffrutex orgyalis glaber. Folia ramorum alterna, diametro unciali, trinervia; petiolo folium subæquanti, basi in stipulam subscariosam adnatam dilatato. Pedunculi vel potius rami floriferi suboppositifolii nec verè axillares uniflori, juxta apicem folio nano petiolato stipulis 2 distinctis stipato instructi. Involucrum foliaceum venosum, foliolis distinctis, cordatis, punctis nigricantibus glandulosis conspersis. Calyx dentibus acutis, sinubus rotundatis. Petala sesquipollicaria, uti calycis tubus glanduloso-punctata glandulis nigricantibus semi-immersis, purpurea basibus atropurpureis margine barbatis. Columna staminum e basi nuda super ad apicem usque antherifera: antheris reniformibus, loculis apice confluentibus. Pollen hispidum.

Obs. Sturtia is no doubt very nearly related to Gossypium, from which it differs in the entire and distinct leaves of its foliaceous involucrum, in the sharp teeth and broad rounded sinuses of the calyx, and possibly also in its fruit and seeds, which are, however, at present unknown. They agree in the texture and remarkable glands of the calyx, and in the structure of the columna staminum. Senra, which, like Sturtia, has the foliola of its three-leaved in- [69 volucrum distinct and entire, differs from it in having its calyx 5-fid with sharp sinuses, in the absence of glands, in the reduced number of stamina, and in its dispermous ovaria.

3. Tribulus (*Hystrix*) lanatus, foliis 8-10-jugis, fructibus undique tectis spinis subulatis longitudine inæqualibus: majoribus sparsis longitudinem cocci superantibus.

Loc. "In collinis arenosis. Lat. 26°." D. Sturt.

Desc. Herba diffusa, sericea, incana. Folium majus cuiusque paris 8-10-jugum, foliolis ovatis. Flores magni. Calyx æstivatione leviter imbricatâ. Petala calyce duplo longiora. Stamina decem, antheris linearibus.

Obs. I. A species nearly related to T. Hystrix, found on the west coast of Australia, or on some of its islands, in the voyage of the Beagle, may be distinguished by the following character. *Tribulus* (*occidentalis*) sericeo-lanatus, foliis suboctojugis, coccis undique densè armatis: spinis omnibus conico-subulatis longitudine invicem æqualibus. These two species differ from all others in the uniform shape of the spines, which equally cover the whole external surface of the fruit.

Obs. II. The American species of the Linnean genus Tribulus are distinguishable from the rest of the published species, by having ten monospermous cocci, by their persistent calyx, and the absence of glands subtending the 5 filaments opposite to the sepals.

This tribe was originally separated as a genus by Scopoli, under the name of Kallstrœmia, which has been recently adopted by Endlicher.

Another tribe exists in the intratropical part of the Australian continent, to which, nearly 40 years ago, in the Bank-
70] sian Herbarium, I gave the generic name of Tribulopis and which may readily be distinguished by the following characters.

TRIBULOPIS.

Calyx 5-partitus deciduus. *Petala* 5. *Stamina* decem (nunc 5). *Filamenta* quinque, sepalis opposita, basi glandula stipata. *Ovaria* 5, monosperma. *Cocci*, præter tubercula 2 v. 4 baseos, læves.

Herbæ *annuæ prostratæ ;* foliis *omnibus alternis !*

Tribulopis (*Solandri*) foliis bi-trijugis, foliolis subovatis inæquilateris, coccis basi quadrituberculatis.

Loc. In ora orientali intratropica Novæ Hollandiæ prope Endeavour River, anno 1770. DD. Banks et Solander.

Tribulopis (*angustifolia*), foliis 3-4 jugis (raro bijugis), foliolis linearibus, tuberculis baseos coccorum abbreviatis.

Loc. Ad fundum sinus Carpentariæ annis 1802 et 3. R. Brown.

Tribulopis (*pentandra*), foliis bijugis, foliolis oblongo-lanceolatis pari superiore duplo majore, floribus pentandris, petalis lanceolatis.

Loc. In insulis juxta fundum sinus Carpentariæ anno 1803. R. Brown.

4. Crotalaria (*Sturtii*) tomentosa, foliis simplicibus ovalibus utrinque sericeo-tomentosis, petiolis apice geniculatis, racemis terminalibus multifloris.

Loc. "On the top of the ridges in pure sand, from S. Lat. 28° to 26°." D. Sturt.

Desc. Frutex 2-3-pedalis (D. Sturt). Folia alterna, ovata passim ovalia, obtusa, sesquipollicem longa, utrinque velutina ; petiolus teres basi vix crassiore apice curvato. Racemus terminalis ; pedicellis approximatis calycem vix æquantibus apice bibracteatis. Flores sesquipollicares. Calyx 5-fidus ; laciniis lanceato-linearibus acutis subæqualibus tubum paulo superantibus. Corolla sordidè flava, calyce plus duplo major. Vexillum magnum, basi simplici nec auriculata, late ovatum, acutum. Alæ vexillo fere dimidio breviores, basi semicordata. Carina longitudine vexilli, 71] acuminata, basi gibbosa, ibique aperta marginibus tomentosis. Stamina 10 diadelpha, simplex et novemfidum. Antheræ quinque majores lineares, juxta basin affixæ; quinque reliquæ ovatæ, linearibus triplo breviores, incumbentes. Ovarium lineare, multi-ovulatum. Stylus extra medium et præsertim latere interiore barbatum. Stigma obtusum. Legumen desideratur.

Obs. A species very nearly related to C. Sturtii, having flowers of nearly equal size, and of the same colour and proportion of parts, found in 1818, by Mr. Cunningham, on the north-west coast of Australia, and since in Captains Wickham and Stokes' Voyage of the Beagle; may be distinguished by the following character:—*Crotalaria* (*Cunninghamii*) tomentosa, foliis simplicibus ovali-obovatis utrinque sericeo-tomentosis, petiolis apice curvatis, pedunculis axillaribus unifloris.

5. Clianthus (*Dampieri*) herbaceus prostratus sericeo-villosissimus, foliolis oppositis (rarissime alternis) oblongis passim lineari-oblongis obovatisve, pedunculis erectis scapiformibus, floribus subumbellatis, calycibus 5-fidis sinubus acutis, ovariis (leguminibusque immaturis) sericeis.

Clianthus Oxleyi *A. Cunningham in Hort. Soc. Transac. II series, vol.* 1, *p.* 522.

Donia speciosa *Don, Gen. Syst. vol.* 2, *p.* 468.

Clianthus Dampieri *Cunningham, loc. cit.*

Colutea Novæ Hollandiæ, &c., *Woodward in Dampier's Voy. vol.* 3, *p.* 111, *tab.* 4, *f.* 2.

Loc. "In ascending the Barrier Range near the Darling, about 500 feet above the river." D. Sturt.

Obs. In July, 1817, Mr. Allan Cunningham, who accompanied Mr. Oxley in his first expedition into the Western Interior of New South Wales, found his Clianthus Oxleyi on the eastern shore of Regent's Lake, on the River Lachlan. The same plant was observed on the Gawler Range, 72] not far from the head of Spencer's Gulf, by Mr. Eyre in 1839, and more recently by Captain Sturt, on his Barrier Range near the Darling. I have examined specimens from all these localities, and am satisfied that they belong to one and the same species.

In March (not May), 1818, Mr. Cunningham, who accompanied Captain King in his voyages of survey of the coasts of New Holland, found on one of the islands of Dampier's Archipelago, a plant which he then regarded as identical with that of Regent's Lake. This appears from the following passage of his MS. Journal:

"I was not a little surprised to find Kennedya speciosa (his original name for Clianthus Oxleyi), a plant discovered in July, 1817, on sterile, bleak, open flats, near Regent's Lake, on the River Lachlan, in lat. 33° 13′ S. and long. 146° 40′ E. It is not common; I could see only three plants, of which one was in flower." "This island is the Isle Malus of the French." Mr. Cunningham was not then aware of the figure and description in Dampier above referred to, which, however, in his communication to the Horticultural Society in 1834, he quotes for the plant of the Isle Malus, then regarded by him as a distinct species from his Clianthus Oxleyi of the River Lachlan. To this opinion he was probably in part led by the article Donia or Clianthus, in Don's System of Gardening and Botany, vol. 2, p. 468, in which a third species of the genus is introduced, founded on a specimen in Mr. Lambert's Herbarium, said to have been discovered at Curlew River, by Captain King. This species, named Clianthus Dampieri by Cunningham, he characterises as having leaves of a slightly different form, but its principal distinction is in its having racemes instead of umbels; at the same time he confidently refers to Dampier's figure and description, both of which prove the flowers to be umbellate, as he describes those of his Clianthus Oxleyi to be. But as the flowers in this last plant [73
are never strictly umbellate, and as I have met with specimens in which they are rather corymbose, I have no hesitation in referring Dampier's specimen, which many years ago I examined at Oxford, as well as Cunningham's, to Clianthus Dampieri. This specimen, however, cannot now be found in his Herbarium, as Mr. Heward, to whom he bequeathed his

collections, informs me; nor can I trace Mr. Lambert's plant, his Herbarium having been dispersed.

Since the preceding observations were written, I have seen in Sir William Hooker's Herbarium two specimens of a Clianthus, found by Mr. Bynoe, on the north-west coast of Australia, in the voyage of the Beagle. These specimens, I have no doubt, are identical with Dampier's plant, and they agree both in the form of leaves and in their subumbellate inflorescence with the plant of the Lachlan, Darling, and the Gawler Range. From the form of the half-ripe pods of one of these specimens, I am inclined to believe that this plant, at present referred to Clianthus, will, when its ripe pods are known, prove to be sufficiently different from the original New Zealand species to form a distinct genus, to which, if such should be the case, the generic name Eremocharis may be given, as it is one of the greatest ornaments of the desert regions of the interior of Australia, as well as of the sterile islands of the North-west coast.

CLIDANTHERA.

Char. Gen.—*Calyx* 5-fidus. *Petala* longitudine subæqualia. *Stamina* diadelpha: *antheræ* uniformes; loculis apice confluentibus, valvula contraria ab apice ad basin separanti dehiscentes! *Ovarium* monospermum. *Stylus* subulatus. *Stigma* obtusum. *Legumen* ovatum, lenticulari-compressum, echinatum.

74] Herba, v. Suffrutex, *glabra, glandulosa; ramulis angulatis*. Folia *cum impari pinnata*; *foliolis oppositis, subtus glandulosis*. Stipulæ *parvæ, basi petioli adnatæ*. Flores *spicati, parvi, albicantes*.

Obs. Subgenus forsan Psoraleæ, cui habitu simile, foliis calycibusque pariter glandulosis; diversum dehiscentia insolita antherarum!

6. Clidanthera *psoralioides*.

Loc. Suffrutex bipedalis in paludosis. D. Sturt.

Desc. Herba, vel suffrutex, erecta, bipedalis, glabriuscula. Ramuli angulati. Folia cum impari pinnata, 4-5-juga; foliola opposita, lanceolata, subtus glandulis crebris parvis manifestis, marginibus scabris. Spicæ densæ, multifloræ. Calyx 5-fidus, parum inæqualis, acutus, extus glandulis dense conspersus. Corolla: *Vexillum* lamina oblonga subconduplicata nec explanata, basi simplici absque auriculis; ungue abbreviato. *Alæ* vexillo paulo breviores, carinam æquantes, laminis oblongis, auriculo baseos brevi. *Carinæ petala* alis conformes. Stamina diadelpha, simplex et novemfidum; antheræ subrotundæ v. reniformes, valvula ventrali anthera dimidio minore subrotunda. Ovarium hispidum ovulo reniformi. Legumen basi calyce subemarcido cinctum, echinatum. Semen reniforme, absque strophiola; integumento duplici. Embryo viridis; cotyledones obovatæ, accumbentes.

Obs. This plant, which in some respects resembles certain species of Glycyrrhiza, appears to be not unfrequent in the southern interior. It was found in one of the early expeditions of Sir Thomas Mitchell, and Mrs. (Capt.) Grey observed it on the flats of the Murray.

7. Swainsona (*grandiflora*) suffruticosa pubescens, foliis 8-10-jugis inexpansis incano-tomentosis; foliolis oblongis obtusis retusisve: adultis semiglabratis: rachi subincana, racemo multifloro folium superante, bracteolis lanceato-linearibus acutis æquantibus tubum calycis albo-lanati [75
quinquefidi: laciniis acutissimis longitudine ferè tubi, vexillo bicalloso.

Loc. "Common on the rich alluvial flats of the Murray and Darling." D. Sturt.

Obs. This plant is, perhaps, not specifically distinct from S. Greyana, Lindl. Bot. Regist. 1846, tab. 66, of which the figure is a good representation of S. grandiflora in every respect, except in the form and proportions of the teeth of the calyx and lateral bracteæ. In these points it exactly agrees with complete specimens, for which I am indebted to Mrs. Grey, from the banks of the Murray, and Mr. Eyre's station (Moorundi), about 98 miles from Adelaide, where it was first found in November, 1841. The following characters, if constant, will sufficiently distinguish it from S. grandiflora.

Swainsona (*Greyana*) suffruticosa pubescens, foliis 5-9-jugis inexpansis incano-tomentosis ; foliolis oblongis obtusis retusisve : adultis semiglabratis : rachi subincana, racemis multifloris folio longioribus, bracteis lateralibus lanceato-linearibus brevioribus tubo calycis albo-lanati quinquedentati : dentibus obtusiusculis tubo dimidio brevioribus, vexillo bicalloso.

In the second edition of Hortus Kewensis (vol. 4, p. 326), I excluded from the generic character of Swainsona the calli of the vexillum, having observed two Australian species where they were wanting, but which in every other respect appeared to me referable to this genus; for the same reason I continue to introduce the calli, where they exist, into the specific characters, as was done in Hortus Kewensis, l. c. In the generic character of Swainsona, given in De Candolle's Prodromus (vol. 2, p. 271), the calli of vexillum are transferred to the calyx ; this can only be regarded as an oversight, which perhaps has been cor-
76] rected by the author himself, and which, so far as I know, has never been adopted in any more recent work in which the generic character of Swainsona is given.

8. Swainsona ? (*laxa*) glabra, caule ramoso, foliis 6-7-jugis; foliolis oblongo-ovalibus obtusis, racemis elongatis laxis, pedicellis calyce glabro quinquedentato brevioribus, bracteolis subulatis, vexillo ecalloso.

Loc. Statio nulla indicata, in Herb. D. Sturt.

Obs. There is something in the aspect of this plant not entirely agreeing with the other species of the genus; and as the fruit is unknown, and the flowers yellow, I refer it with a doubt to Swainsona.

PENTADYNAMIS.

Char. Gen.—*Calyx* 5-fidus subæqualis. *Vexillum* explanatum, callo baseos laminæ in unguem decurrenti. *Carina* obtusa, basin versus gibba, longitudine alarum. *Stamina* diadelpha; *antheris* 5 majoribus linearibus, reliquis ovatis. *Ovarium* polyspermum. *Stylus* e basi arcuata porrectus, postice barbatus. *Legumen* compressum.

Herba (Suffrutex sec. D. Sturt), *bipedalis sericeo-incana; caule angulato erecto.* Folia *ternata; foliolis sessilibus, linearibus, obtusis.* Flores *racemosi, flavi.*

9. Pentadynamis *incana.*

Loc. "On sand-hills with Crotalaria Sturtii." D. Sturt.

Desc. Herba erecta, ramosa, sericeo-incana. Folia alterna, ternata; petiolo elongato, teretiusculo, foliolo terminali longiore vix unciali. Racemi multiflori, erecti; pedicelli subæquantes calycem. Bracteolæ subulatæ, infra apicem pedicelli, basin calycis attingentes. Calyx 5-fidus; laciniis acutis tubum æquantibus. Corolla flava, calyce plus duplo longior. Vexillum explanatum, basi absque auriculis sed callo in unguem decurrenti ibique barbato auctum. Carina infra medium gibba pro receptione baseos [77
styli. Staminum antheræ majores lineares, basi vel juxta basin affixæ; 5 minores ovatæ, incumbentes. Ovarium lineare, pubescens. Stigma terminale, obtusum. Legumen immaturum incanum, stylo e basi arcuata porrecto terminatum, calyce subemarcido subtensum.

Obs. In the collection of the plants of his last expedition, presented to the British Museum by Sir Thomas Mitchell, there is a plant which seems to belong to the genus Pentadynamis, which is probably, therefore, one of the species of Vigna, described by Mr. Bentham.

10. Cassia (*Sturtii*), tomentoso-incana, foliis 4-jugis foliolis lanceolato-linearibus planis: glandula depressa inter

par infimum, racemo corymboso paucifloro cum pedunculo suo folium paulo superante v. æquante, calyce tomentoso.

Loc. "In sandy brushes of the Western interior." D. Sturt.

Obs. Species proxima C. artemisiæfoliæ De Cand. Prodr. quæ Cassia glaucescens Cunningh. MSS. 1817, cui foliola teretiuscula, et racemus corymbosus cum pedunculo suo folio brevior.

11. Cassia (*canaliculata*), cinerascens pube tenuissima, foliis 2-jugis (raro 1-jugis) foliolis angustato-linearibus canaliculatis: glandula inter par inferius et dum unijuga inter terminale, calycibus glabriusculis, racemis corymbosis paucifloris folio brevioribus.

Loc. "In the bed of the creeks of the Barrier Range, about thirty-six miles from the Darling, in lat. 32° S." D. Sturt.

Obs. Proxima C. eremophilæ Cunningh. MSS. quæ sequentibus notis a Cassia phyllodinea et C. zygophylla, *Benth.* facile distinguenda.

Cassia (*eremophila*), glabra, foliis unijugis rarò passim
78] bijugis; foliolis linearibus canaliculatis latitudine racheos linearis aversæ, corymbis paucifloris folio brevioribus.

Loc. In desertis prope fluvium Lachlan, anno 1817, detexit D. Cunningham.

Cassia (*zygophylla*), glabra foliis unijugis; foliolis linearibus planis rachi duplo latioribus, corymbis paucifloris folio brevioribus.

Cassia zygophylla, *Benth. in Mitch. trop. Austr. p.* 288.

Another species nearly related to C. zygophylla is readily distinguished by the following character:

Cassia (*platypoda*), glabra, foliis unijugis; foliolis linearibus apiculo recurvo duplo angustioribus rachi aversa lanceolato-lineari.

Loc. Juxta fluvium Murray, anno 1841, detexit Domina Grey.

12. Cassia (*phyllodinea*), canescens pube arctissimè adpressa, phyllodiis aphyllis linearibus planis falcatis aversis, calycibus glabris, legumine plano-compresso.

Loc. In Herbario D. Sturt specimen exstat nulla stationis aut loci indicatione, sed eandem speciem ad fundum sinus Spencer's Gulf dicti in sterilibus apricis anno 1802 legi.

Desc. Frutex quadripedalis, ramosissimus. Phyllodia semper aphylla, aversa, linearia, acuta, basi attenuata, plus minusvè falcato-incurva, biuncialia, $\frac{1}{6}$ circiter unciæ lata exstipulata, paginis pube arctissime adpressa canescentibus, margine superiore glandula unica depressa obsoleta. Flores flavi, in umbella axillari 2-3 flora.

Obs. Cassia phyllodinea is one of the very few species of the genus, which, like the far greater part of New Holland Acaciæ, lose their compound leaves, and are reduced to the footstalk, or phyllodium, as it is then called, and which generally becomes foliaceous by vertical compression [79
and dilatation. A manifest vertical compression takes place in this species of Cassia.

A second species, Cassia circinata of Benth. in Mitch. trop. Austr. p. 384, is equally reduced to its footstalk, but which is without manifest vertical compression. To this species may perhaps be referred Cassia linearis of Cunningham MSS., discovered by him in 1817, but which appears to differ in having a single prominent gland about the middle of its phyllodium; Bentham's plant being entirely eglandular.

These two, or possibly three species, belong to the desert tracts of the South Australian interior. In the same regions we have another tribe of Cassiæ closely allied to the aphyllous species; they have only one pair of foliola which are caducous, and whose persistent footstalk is more or less vertically compressed. Along with these, and nearly related to them, are found several species of Cassia, having from two to four or five pairs of foliola which are narrow, but their footstalks are without vertical compression, and their foliola are caducous, chiefly in those, however, which have only two pairs.

PETALOSTYLIS.

Cæsalpinearum genus, Labicheæ proximum.

Char. Gen.—*Calyx* 5-phyllus, æqualis. *Petala* 5 subæqualia, patentia. *Stamina: Filamenta* quinque sepalis opposita, quorum *tria antherifera*, antheris basifixis linearibus, *duo reliqua* castrata. *Ovarium* oligospermum. *Stylus* maximus, petaloideus, trilobus, lobo medio longiore axi incrassata desinente in *stigma* obtusum simplex!

Frutex *glaber, erectus.* Folia *alterna, pinnata cum impari, foliolis alternis.* Racemi *axillares, pauciflori.* Flores *flavi.*

80] 13. Petalostylis *Labicheoides.*

Loc. "In the bed of a creek along with Sturtia." D. Sturt.

Obs. Eadem omnino species exstat inter plantas in Insulis Archipelagi Dampieri juxta oram septentrio-occidentalem Novæ Hollandiæ in itinere navis Beagle dictæ lectas.

Desc. Frutex facie fere Cassiæ et Labicheæ. Folia alterna, cum impari pinnata, foliolis alternis brevissimè petiolatis oblongo-lanceolatis cum mucronulo terminali paulo majore. Stipulæ parvæ caducæ. Racemi pauciflori, axillares, folio breviores. Alabastrum ovali-oblongum acutiusculum. Calyx viridis, sepalis subæqualibus oblongis acutis, æstivatione imbricatis. Petala quinque subæqualia, oblonga, flava, astivatione imbricata, sepalis sesquilongiora. Stamina 3 antherifera æqualia, filamentis abbreviatis, antheris acutis bilocularibus, loculis sulco longitudinali insculptis; 2 reliqua rudimenta parva subfiliformia. Ovarium sessile, lineare, 3-4-spermum. Stylus lobo medio triplo longiore, oblongo-lanceolato, lobis lateralibus auriculiformibus semiovatis obtusis. Stigma imberbe.

Obs. The structure of the style, which forms the only important character of this genus, so far as the specimens enable me to judge, is so remarkable and peculiar, as to render it necessary to state, that I have found it quite uniform in all the flowers I have examined; namely, in four immediately before, and in three after expansion.

PODOCOMA.

Char. Gen.—*Involucrum* imbricatum, foliolis angustis acutis. *Ligulæ* pluriseriales, angustissimæ, femineæ. *Flosculi* pauciores hermaphrodito-masculi. Ligularum pappo capillari, stipitato, denticulato. *Receptaculum* epaleatum.

Herba *humilis, setosa;* caule *densè foliato;* folia *petiolata, cuneata, incisa, setis albis conspersa.*

14. Podocoma *cuneifolia.* [81

Loc. In Herbario D. Sturt absque ulla indicatione loci vel stationis.

Obs. This plant appears to be generically distinct from Erigeron, particularly in its stipitate pappus. The specimens, however, are so incomplete, that I am unable to determine whether what I have considered stem, may not be a branch only.

LEICHARDTIA.

Char. Gen.—*Calyx* 5-partitus. *Corolla* urceolata; tubo intus imberbi; fauce annulo integerrimo incrassata. *Corona staminea* 5-phylla, foliolis antheris oppositis, iisque brevioribus, indivisis. *Antheræ* membrana (brevi) terminatæ. *Massæ Pollinis* erectæ basi affixæ. *Stigma* vix divisum.

Suffrutex *volubilis;* foliis *linearibus, fascicularibus, extra-alaribus;* folliculis *ventricosis ovato-oblongis.*

15. Leichardtia *australis.*

Doubah *Mitchell, trop. Austr. p.* 85.

Loc. "Common on the Murray, and in the interior." D. Sturt.

Desc. Suffrutex pubescens, subcinereus; ramis striatis nec omnino teretibus. Folia sesquipollicaria, linearia, acuta. Fasciculi multiflori. Calycis foliola obtusa, pube tenui cinerascentia. Corolla glabra; tubo absque squamulis denticulisve, ventricoso; limbo vix longitudine tubi, laciniis conniventibus sinistrorsum imbricatis. Coronæ foliola e basi dilatata adnata linearia, indivisa. Massæ Pollinis (Pollinia) lineares.

Obs. Doubah was originally found by Sir T. Mitchell, but with fruit only, in one of his journeys, and also in his last expedition; and, according to him, the natives eat the seed-vessel entire, preferring it roasted. Captain Sturt, on the other hand, observes that the natives of the districts where he found it eat only the pulpy seed-vessel, rejecting the seeds.

82] 16. Jasminum *lineare.* Br. prodr. 1, p. 521.

Jasminum Mitchellii. *Lindl. in Mitch. trop. Austr. p.* 365.

Obs. In Captain Sturt's collection there are perfect specimens of this plant, on which a few remarks may be here introduced, chiefly referring to its very general existence in the sterile regions of the interior of Southern Australia, and even extending to the north-west coast.

The species was established on specimens which I collected in 1802, in the sterile exposed tract at the head of Spencer's Gulf. With these I have compared and found identical Mr. A. Cunningham's specimens gathered in the vicinity of the Lachlan, in 1817; Captain Sturt's, in his earlier expeditions, from the Darling; those of Sir Thomas Mitchell, in his different journeys; and specimens collected in one of the islands of Dampier's Archipelago. In this great extent of range, it exactly agrees with a still more remarkable plant, and one much less likely to belong to a desert country, namely, Clianthus Dampieri.

I have considered Jasminum Mitchellii as hardly a variety of J. lineare, the character of this supposed species

depending on its smooth leaves, and its axillary nearly sessile corymbi or fasciculi, which are much shorter than their subtending leaves; but even in the specimen contained in the collection presented to the British Museum by Sir Thomas Mitchell, the young branches, as well as the pedunculus and pedicelli, are covered with similar pubescence, and in the same degree as that of J. lineare; the specimens from Dampier's Archipelago have leaves equally smooth, but have the inflorescence of J. lineare; and I have specimens of J. lineare in which, with the usual pubescence of that species, the inflorescence is that of Mitchellii. Among Sir Thos. Mitchell's collection at the Museum, there is a Jasminum not noticed by Professor [83
Lindley, which, though very nearly related to J. lineare, and possibly a variety only, may be distinguished by the following character.

Jasminum (*micranthum*) cinereo-pubescens, foliis ternatis; foliolis lanceato-linearibus, pedunculis axillaribus 1-3 floris, corollæ laciniis obtusis dimidio tubi brevioribus.

17. Goodenia (*cycloptera*) ramosissima pubescens, foliis radicalibus serrato-incisis; caulinis lanceolato-ellipticis obsoletè serratis in petiolum attenuatis, pedunculis axillaribus unifloris folia subæquantibus, seminibus orbiculatis membrana angusta cinctis.

Loc. Indicatio nulla stationis in Herb. D. Sturt.

18. Scævola (*depauperata*), erecta ramosissima, ramis alternis; ultimis oppositis divaricatis, foliis minimis sublinearibus: ramorum alternis ramulorum oppositis, pedunculis e dichotomiis ramulorum solitariis unifloris.

Loc. "In salt ground, in lat. 26° S." D. Sturt.

Desc. Herbacea, vix suffruticosa, adulta glabriuscula, erecta, ramosissima. Rami ramulique angulati; ultimi oppositi, indivisi, divaricati, apice diphylli, foliis minimis et rudimento minuto floris abortivi. Folia sessilia, linearia, acuta, brevissima, ramos subtendentia alterna, ramulos ultimos brachiatos opposita. Pedunculi e dichotomiis ramulorum ultimorum penultimorumque solitarii, uniflori, ebrac-

tcati. Calyx: limbo supero quinquepartito; laciniis lineari-lanceatis, æqualibus, pubescentibus. Corolla: tubo hinc ad basin usque fisso; limbo unilabiato, 5-partito; laciniis lanceolatis, æqualibus, marginibus angustis induplicatis, extus uti tubus pubescentibus, intus glabris trinerviis, nervo medio venoso. Stamina: filamenta distincta, anguste linearia, glabra, axi incrassata; antheræ liberæ, lineares, imberbes, basi affixæ, loculis longitudinaliter dehiscentibus. Ovarium biloculare? loculis monospermis, ovulis erectis. Stylus cylindraceus, glaber. Stigmatis indusium margine
84] ciliatum et extus pilis copiosis longis strictis acutis albis tectum v. cinctum.

19. Eremophila (*Cunninghamii*) arborescens, foliis alternis linearibus mucronulo recurvo, sepalis fructûs unguiculatis eglandulosis, corolla extus glabra.

Eremophila? arborescens, Cunningh. MSS. 1817.

Eremodendron Cunninghami, De Cand. prodr. xi, p. 713. Delessert ic. select. vol. v, p. 43, tab. 100 (ubi error in num. ovulorum).

Loc. "In the sandy bushes of the low western interior, not beyond lat. 29° S." D. Sturt.

Obs. The genus Eremophila was founded on very unsatisfactory materials, namely, on two species, E. oppositifolia and alternifolia, which I found growing in the same sandy desert at the head of Spencer's Gulf in 1802, the only combining character being the scariose calyx, which I inferred must have been enlarged after flowering. This, however, proves not to be the case in E. alternifolia, which Mrs. Grey has found in flower towards the head of St. Vincent's Gulf; and from analogy with other species since discovered, it probably takes place only in a slight degree in E. oppositifolia, whose expanded flowers have not yet been seen.

In 1817 Mr. Cunningham, in Oxley's first expedition, discovered a third and very remarkable species in flower and unripe fruit, which he referred, with a doubt, to Eremophila, and which M. Alphonse De Candolle has recently separated, but as it seems to me on very insufficient grounds,

with the generic name of Eremodendron, established entirely on Mr. Cunningham's specimens. A fourth species has lately been described by Mr. Bentham in Sir Thos. Mitchell's narrative of his Journey into Tropical Australia; and [85
some account of a fifth is given in the following article.

These five species may be arranged in four sections, distinguished by the following characters:

α. Folia opposita; sepala unguiculata.

Eremophila oppositifolia. *Br. prodr.* 1, *p.* 518.

β. Folia alterna; sepala unguiculata, eglandulosa; antheræ exsertæ.

E. Cunninghamii.

γ. Folia alterna; sepala brevè unguiculata, eglandulosa; stamina inclusa.

Eremophila Mitchelli. *Benth. in Mitch. trop. Austr. p.* 31.

Eremophila Sturtii.

δ. Folia alterna glanduloso-tuberculata, sepala cuneato-obovata, sessilia, glandulosa.

E. alternifolia. *Br. prodr.* 1, *p.* 518.

This last species might be separated from Eremophila; it is not, however, referable to Stenochilus, with some of whose species it nearly agrees in corolla, but from all of which it differs in its glandular scariose calyx.

20. Eremophila (*Sturtii*), pubescens, foliis angustè linearibus apiculo recurvo, corollis extus pubescentibus limbo intus barbato, staminibus inclusis.

Loc. "On the Darling; flowers purplish, sweet-scented." D. Sturt.

Desc. Frutex orgyalis (D. Sturt.). Calyx 5-partitus, æqualis; sepalis obovato-oblongis, basi angustioribus sed in unguem vix attenuatis, membranaceis, uninerviis, venosis. Corolla bilabiata, tubo amplo recto, labiis obtusis, extus pubescens, intus hinc (inferius) barbata. Labium superius tripartitum; lobo medio bifido (e duobus conflato); laciniis omnibus obtusis; inferius obcordatum bilobum lobis rotundatis, densius barbatum. Stamina quatuor didynama, omnino inclusa. Filamenta glabra. Antheræ reniformes, loculis apice confluentibus. Ovarium densè lanatum. Stylus glaber. Stigma indivisum, apice styli vix crassius.

86] Obs. Species proxima E. Mitchelli *Benth. in Mitch. trop. Austr.* p. 31.

21. Stenochilus *longifolius.* Br. prodr. 1, p. 517.

Stenochilus pubiflorus. *Benth. in Mitch. trop. Aust. p.* 273.

Stenochilus salicinus. *Benth. in Mitch. trop. Austr. p.* 251.

Loc. Nulla stationis indicatio.

22. Stenochilus *maculatus, Ker in Bot. Regist. tab.* 647. *Cuningh. MSS.* 1847.

β. Stenochilus curvipes. *Benth. in Mitch. trop. Austr. p.* 221. Varietas S. maculati, sepalorum acumine paulo breviore.

Obs. M. Alphonse De Candolle, in Prodr. xi, p. 715, refers S. ochroleucus of Cunningh. MSS. 1817, as a variety to S. maculatus; it is, however, very distinct, having a short erect peduncle like that of S. glaber, to which it is much more nearly related, differing chiefly in its being slightly pubescent.

23. Grevillea (Eugrevillea) *Sturtii,* foliis indivisis (nonnullis raró bifidis) augustè linearibus elongatis uninerviis: marginibus arctè revolutis, racemis oblongis cylindraceisve: rachi pedicellis perianthiisque inexpansis glutinoso-pubescentibus, ovario sessili, stylo glabro.

Loc. "On sand-hills in lat. 27° S." D. Sturt.

Desc. Arbor 15-pedalis (Sturt). Rami teretes, pube arctè adpressa persistenti incani. Folia 6-10-pollices longa, vix tres lineas lata, subter pubescentia incana, super tandem glabrata. Thyrsus terminalis, 2-4 uncialis, rachi pedicellisque pube erecta nec adpressa secretione glutinosa intermista. Flores aurantiaci.

Obs. In the collection presented to the British Museum by Sir Thomas Mitchell, of the plants of his last expedition, there is a very perfect specimen, in flower, of Grevillea Sturtii.

The following observations respecting the Grevilleæ of the same collection may not be without interest.

Grevillea Mitchellii, *Hooker, in Mitch. Trop. Austr. p.* [87
265, proves to be Gr. Chrysodendrum, *prodr. fl. Nov. Holl. p.* 379, the specific name of which was not derived from the colour of the under surface of the leaves, which is, indeed, nearly white, but from the numerous orange-coloured racemes, rendering this tree conspicuous at a great distance.

Grevillea longistyla and G. juncea of the same narrative both belong to that section of the genus which I have named Plagiopoda.

A single specimen, in most respects resembling Gr. longistyla, of which possibly it may be a variety, but which at least deserves notice, has all its leaves pinnatifid, instead of being undivided. It may be distinguished by the following character:—*Grevillea* (*Plagiopoda*) *neglecta*, foliis pinnatifidis subtus niveis; laciniis linearibus, stylis glabris.

A single specimen also exists of Grevillea (or Hakea) lorea, *prodr. flor. Nov. Holl. p.* 380, but without fructification.

24. Grevillea (Cycloptera?) *lineata*, foliis indivisis lineari-ensiformibus enerviis subter striis decem paucioribus elevatis uniformibus interstitia bis-terve latitudine superantibus, cicatrice insertionis latiore quam longa utrinque obtusa, racemis terminalibus alternis, pistillis semuncia brevioribus stigmate conico.

Loc. "It takes the place of the gum-tree (Eucalyptus) in the creeks about lat. 29° 30′ S." D. Sturt.

Obs. It is difficult to distinguish this species, which, according to Captain Sturt, forms a tree about 20 feet in height, from Grevillea striata. I have endeavoured to do so in the above specific difference, contrasted with which the leaves of G. striata have always more than 10 striæ, which are hardly twice the breadth of the pubescent in- [88
terstices, and the cicatrices of whose leaves are longer than broad, and more or less acute, both above and below. This is a source of character which in the supplement to the Prodr. Floræ Novæ Hollandiæ, I have employed in a

few cases both in Grevillea and Hakea, but which I believe to be important, as it not only expresses a difference of form, but also in general of vascular arrangement.

25. Ptilotus (*latifolius*) capitulis globosis, bracteis propriis calycem superantibus, foliis ovatis petiolatis.

Loc. "In lat. 26° S." D. Sturt.

Desc. Herba diffusa, ramosa, incana. Folia alterna, petiolata, latè ovata, integerrima. Capitula ramos terminantia, solitaria vel duo approximata. Bracteæ laterales scariosæ, sessiles, latè ovatæ, enerviæ. Perianthium; foliolis subæqualibus, lana implexa alba basi tectis, ante expansionem ungue nervoso tunc brevissimo, post anthesin laminam scariosam enervem fere æquante. Stamina 5 antherifera; filamenta basi in cyathulum edentulum connata. Antheræ biloculares, loculis utrinque distinctis medio solum conjunctis. Ovarium monospermum, glabrum. Stylus filiformis, glaber. Stigma capitatum, parvum. Utriculus evalvis, ruptilis.

Obs. I was at first inclined to consider this plant as a genus distinct from Ptilotus, more, however, from the remarkable difference in habit than from any important distinction in the flower, for its character would have chiefly consisted in the great size of its lateral bracteæ, and in the form of its antheræ.

In a small collection formed during the voyage of Captains Wickham and Stokes, there is a plant very nearly related to, and perhaps not specifically distinct from, Ptilotus latifolius, but having narrower leaves. It was found on one of the islands of Dampier's Archipelago.

89] 26. Neurachne (*paradoxa*) glaberrima, culmo dichotomo, foliis rameis abbreviatis, fasciculis paucifloris, glumis perianthiisque imberbibus valvula exteriore cujusve floris septemnervia.

Loc. Nulla indicatio loci v. stationis, in Herbario D. Sturt.

Desc. Gramen junceum, facie potius Cyperaceæ cujusdam. Folia radicalia in specimine unico viso defuere; ramos subtendentia abbreviata, vagina aperta ipsum folium superante; floralia subspathiformia sed foliacea nec membranacea. Fasciculi pauciflori: spiculæ cum pedunculo brevissimo articulatæ et solubiles, et subtensæ bractea nervosa carinata ejusdem circiter longitudinis. Gluma bivalvis biflora, nervosa, acuta, mutica; valvulæ subæquales septemnerviæ; exterioris nervis tribus axin occupantibus sed distinctis reliquis per paria a marginibus et axilibus subæquidistantibus; interioris nervis æquidistantibus, externis margini approximatis. Perianthium inferius (exterius), bivalve neutrum; valvula exterior septemnervis, exteriori glumæ similis textura forma et longitudine; valvula interior (superior) angustior pauloque brevior, dinervis, nervis alatis marginibus veris latis induplicatis. Perianthium superius hermaphroditum, paulo brevius, pergamineo-membranaceum, nervis dilutè viridibus; valvula exterior quinquenervis, acuta, concava; interior ejusdem fere longitudinis, dinervis. Stamina 3, filamentis linearibus. Ovarium oblongum, imberbe. Styli duo. Stigmata plumosa, pallida?

Obs. Neurachne paradoxa, founded on a single specimen, imperfect in its leaves and stem, but sufficiently complete in its parts of fructification, differs materially in habit from the original species, N. alopecuroidea, as well as from N. Mitchelliana of Nees, while these two species differ widely from each other in several important points of structure.

In undertaking to give some account of the more re- [90
markable plants of Captain Sturt's collection, it was my intention to have entered in some detail into the general character of the vegetation of the interior of Australia, south of the Tropic.

I am now obliged to relinquish my original intention, so far as relates to detail, but shall still offer a few general remarks on the subject.

These remarks will probably be better understood if I refer, in the first place, to some observations published in 1814, in the Botanical Appendix to Captain Flinders's Voyage.[1]

[1] *Antè, p.* 61.

From the knowledge I then had of New Holland, or Australian vegetation, I stated that its chief peculiarities existed in the greatest degree in a parallel, included between 33° and 35° S. lat. which I therefore called the principal parallel, but that these peculiarities or characteristic tribes were found chiefly at its western and eastern extremities, being remarkably diminished in that intermediate portion, included between 133° and 138°, E. long. These observations related entirely to the shores of Australia, its interior being at that period altogether unknown; and the species of Australian plants, with which I was then acquainted, did not exceed 4200. Since that time great additions have been made to the number, chiefly by Mr. Allan Cunningham, in his various journeys from Port Jackson, and on the shores of the North and North-west coasts during the voyages of Captain King whom he accompanied; by Messrs. William Baxter, James Drummond, and M. Preiss, at the western extremity of the principal parallel, and by Mr. Ronald Gunn in Van Diemen's Land. It is probable that I may be considered as underrating these additions, when I venture to state them as only be-
91] tween two and three thousand; and that the whole number of Australian plants at present known, does not exceed, but rather falls short of 7000 species.

These additions, whatever their amount may be, confirm my original statement respecting the distribution of the characteristic tribes of the New Holland Flora; some additional breadth might perhaps be given to the principal parallel, and the extent of the peculiar families may now be stated as much greater at or near its western, than at its eastern extremity.

With the vegetation of the extra-tropical interior of Australia we are now in some degree acquainted, chiefly from the collections formed by the late Mr. Allan Cunningham, and Charles Fraser, in Oxley's two expeditions from Port Jackson into the western interior, in 1817 and 1818; from Captain Sturt's early expeditions, in which the rivers Darling, Murrumbidgee, and Murray, were discovered; from those of Sir Thomas Mitchell, who never failed to form extensive collections of plants of the regions he visited; and lastly, from Captain Sturt's present collection.

The whole number of plants collected in these various expeditions may be estimated at about 700 or 750 species; and the general character of the vegetation, especially of the extensive sterile regions, very nearly resembles that of the heads of the two great inlets of the south coast, particularly that of Spencer's Gulf; the same or a still greater diminution of the characteristic tribes of the general Australian Flora being observable. Of these characteristic tribes, hardly any considerable proportion is found, except of Eucalyptus, and even that genus seems to be much reduced in the number of species; of the leafless Acaciæ, which appear to exist in nearly their usual proportion; and of Callitris and Casuarina. The extensive families of Epacrideæ, Stylideæ, Restiaceæ, and the tribe of Decandrous [92
Papilionaceæ, hardly exist, and the still more characteristic and extensive family of Proteaceæ is reduced to a few species of Grevillea, Hakea, and Persoonia.

Nor are there any extensive families peculiar to these regions; the only characteristic tribes being that small section of aphyllous, or nearly aphyllous Cassiæ, which I have particularly adverted to in my account of some of the species belonging to Captain Sturt's collection; and several genera of Myoporinæ, particularly Eremophila and Stenochilus. Both these tribes appear to be confined to the interior, or to the two great gulfs of the South coast, which may be termed the outlets or direct continuation of the southern interior; several of the species observed at the head of Spencer's Gulf also existing in nearly the same meridian, several degrees to the northward. It is not a little remarkable that nearly the same general character of vegetation appears to exist in the sterile islands of Dampier's Archipelago, on the North-west coast, where even some of the species which probably exist through the whole of the southern interior are found; of these the most striking instances are, Clianthus Dampieri, and Jasminum lineare, and to establish this extensive range of these two species was my object in entering so minutely into their history in the preceding account.

A still greater reduction of the peculiarities of New Holland vegetation takes place in the islands of the South coast.

PART II.

STRUCTURAL AND PHYSIOLOGICAL MEMOIRS.

SOME OBSERVATIONS

ON THE

PARTS OF FRUCTIFICATION IN MOSSES;

WITH

CHARACTERS AND DESCRIPTIONS

OF

TWO NEW GENERA OF THAT ORDER.

BY

MR. ROBERT BROWN, Libr. Linn. Soc.

Read June 20th, 1809.

[*Extracted from 'The Transactions of the Linnean Society of London.' Vol. X, pp.* 312—324.]

LONDON:

1811.

SOME OBSERVATIONS, &c. [312

The account which the celebrated Hedwig has given of the sexes of Mosses seems to be founded on so ample an induction, and is now so generally received, that it must be [un]necessary to notice the arguments which mere theoretical botanists have from time to time produced against it. There is, however, one author, Mons. Palisot Beauvois, who has not only objected to the account of Hedwig, but has proposed a theory of his own, and who, consequently, appealing to actual observations, and appearing to have particularly studied, specifically at least, this tribe of plants, merits some attention. The earliest account of Mons. Beauvois' theory is to be found in the observations added to the order Musci, in the "Genera Plantarum" of Jussieu; and it was soon after more fully given by the author himself in a Memoir on the Sexual Organs of Mosses, published in the third volume of the American Philosophical Transactions: since that time he has, in his different works, occasionally treated of the same subject, and has lately repeated the substance of his original essay, in the introduction to his "*Prodrome des Cinquième et Sixième Familles de l'Æthiogamie*," published at Paris in 1805, a translation of which is given by my friend Mr. Konig, in the second volume of the Annals of Botany. To this work, as it must be in the hand of [313
every scientific botanist, I refer for a full account of M. Beauvois' hypothesis, and confine myself to observing, that what is generally called the capsule of mosses, is by him considered as the containing organ of both sexes; that the granules which Hedwig supposes to be seeds, he regards as pollen; the real seeds according to him being imbedded in

the substance of that body which occupies the centre of the capsule, and to which botanists have given the name of *columnula* or *columella*. The supposed seeds of this author, however, having entirely escaped the two most acute and experienced observers in this department of botany, Schmidel and Hedwig, in all the species of which they have given dissections, it might fairly be concluded that they are not of universal existence, and this alone would be sufficient perhaps to overturn the hypothesis. But it would be more satisfactory, if, while the accuracy of these excellent observers was confirmed in other instances, the cause of that appearance, which I apprehend has misled M. Beauvois, could at the same time be pointed out. The species more particularly described and figured by him in the American Transactions, is *Hypnum velutinum;* which therefore, had it been in a proper state, I should have preferred as the subject of my examination; but as he asserts that his observations were repeated, and with similar results, on all the species of mosses found in the neighbourhood of Paris and Lisle, I have chosen *Funaria hygrometrica,* perhaps the most general plant in existence; which therefore must have been examined by him, and is within the reach of every one.

As, according to M. Beauvois, the action of the pollen on the seeds does not take place till the separation of the operculum, he probably did not conceive it necessary to observe the capsule until it had acquired its full size, and was in fact nearly ripe, or, as he terms it, in blossom. At
314] this period he examined under the microscope a transverse section of the capsule, in which, as appears both from his description and figure, he found a dense stratum of granular matter, which he considered to be pollen, situated immediately within the inner membrane; while in the substance occupying the centre, which he describes as reticulated, he observed scattered granules, in size and appearance like those of the pollen already mentioned: these he regards as the genuine seeds, and the containing organ he calls the capsule.

It is remarkable that he nowhere expressly states the manner in which this capsule bursts: but it may be inferred, from the use he assigns to the peristomium, that he supposes it to eject its contents by the upper extremity: for, if the bursting were lateral, the seeds would at once come into contact with the pollen: but though impregnation would in this way more certainly be accomplished, the motions of the ciliæ could no longer be considered as in any degree assisting it.

Desirous to examine an object as nearly similar as possible to that on which the hypothesis appears to be founded, I in the first place made a transverse section of the full-grown but green capsule of *Funaria hygrometrica*; and, I confess, was both surprised and disappointed to find it, under the microscope, exactly resembling M. Beauvois' figure [18]. But little reflection, however, was necessary to show that these scattered granules might either have been forced into the pulpy central substance, by the pressure necessarily applied to the stratum of pollen in making the section, or, what is more probable, been carried over its surface by the cutting instrument, which had previously passed through this stratum. Accordingly, by repeated immersion in water, and more readily still by the careful application of a small hair-pencil, the greater part of the granules was removed. [315 A transverse section at an earlier stage of the capsule, before the falling of the calyptra, exhibited, as I expected, fewer granules on the substance of the columella, and which were removable in like manner. Lastly, by a longitudinal section, in which, if well performed, the scalpel could not be supposed to carry any part of the pollen over the surface of the columella, I obtained a distinct view of this part, perfectly free from these supposed seeds, and evidently consisting of large cells filled with an uniform pulpy substance; a continuation of which occupied the cavity of the operculum.

From these observations, even added to those of Schmidel and Hedwig, though they seem conclusive against the hypothesis of M. Beauvois, I by no means pretend to reason strictly respecting the whole order: on the contrary, from the conversations I have had with my ingenious and accurate

friend, Mr. Francis Bauer, as well as from some observations of my own, I am disposed to believe that considerable diversities may exist in the placentation of mosses: that in some cases the seeds may be formed in a much greater portion of the columnula than in others: and it is even not improbable that in certain cases its whole substance may be converted into seeds; or, to speak more accurately, that it may produce seeds even to the centre, and that the cells in which they were probably formed may be re-absorbed. This I am inclined to think is the case in *Phascum alternifolium* of Dickson, in the ripe capsule of which there is hardly the vestige of a columnula; and I have observed the same structure in two new species of *Anodontium* of Bridel; which, if it equally exists in the only species of this genus hitherto described, would perhaps considerably strengthen its character. In these cases the inner membrane is also
316] evanescent; and such a structure, it may be remarked, equally militates against M. Beauvois' theory, whether we suppose the columella to have existed at an earlier stage, in the usual form, or not.

As to this organ being tubular, and discharging its contents by the top, it is neither consistent with what has been already observed, nor with the appearance of its remains in the ripe capsule: but, admitting for a moment its tubular nature, there are certain mosses in which no discharge could possibly take place in the way described; the column being elongated even to the apex of the operculum, to which it often continues to adhere, as in *Buxbaumia*, and in the first of the two new genera which I now proceed to describe.

DAWSONIA.

Peristomium penicillatum, ciliis numerosissimis capillaribus rectis æqualibus e capsulæ parietibus columellâque (!) ortis.

Capsula hinc plana, indè convexa.

Calyptra exterior e villis implexis, *interior* apice scabra.

Muscus *hinc arctè affinis* Polytricho, *quocum foliis, floribus* *masculis, et calyptrâ penitùs convenit; indè aliquo modo* Buxbaumiæ *accedens, præsertim figurâ capsulæ, et structurâ columellæ.* Peristomio *autem ab omnibus diversissimus.*

Dawsonia polytrichoides.

Tab. 11 [XXIII].[1] *Fig.* 1.

Patria. Novæ Hollandiæ ora orientalis, extra tropicum.

Statio. Ripæ subumbrosæ rivulorum, ad radices montium, in vicinitate Portûs Jackson.

Desc. *Cæspites* laxi, amorphi. *Radiculæ* tenuissimæ, tomenti instar, caudicem descendentem brevem inves- [317
tientes. *Caulis* simplicissimus, erectus, strictus, 2—3-uncialis, basi reliquiis foliorum squamatus, suprà densè foliatus. *Folia,* e basi dilatatâ semiamplexicauli membranaceâ fuscâ, lineari-subulata, opaca, viridia, marginibus longitudinaliter dorsoque apicis denticulatis, spinulis sursum crebrioribus majoribusque, concaviuscula, patula, siccatione appressa, canaliculata, superiora vix semuncialia, inferiora sensim breviora.

Masculi Flores terminales, discoidei. *Folia perigonialia* cuneato-orbiculata, mucronata, integerrima, semimembranacea, exteriora sensim majora. *Fila succulenta* numerosa, articulata, basi attenuata. *Antheræ* flosculi singuli 6-8, cylindraceæ, brevissimè pedicellatæ.

Femineus Flos in distincto individuo. *Seta* terminalis, solitaria, erecta, lævis, nitens, rufo-fusca, caule ter brevior, foliis terminalibus duplò longior. *Vaginula* cylindracea, stricta, glabra, tegmine pilorum calyptræ exterioris instar instructa.

Calyptra duplex: *exterior* constans pilis intertextis dimidio inferiore tenui flexuoso pallido ramuloso edentulo, superiore ferrugineo stricto denticulato: *interior* membranacea straminea, capsulæ maturæ subulata, suprà longitudinaliter fissa, apice solum denticulata.

Capsula nutans, angulum ferè rectum cum setâ efformans,

[1] The figures within brackets refer to the numbering of this and subsequent plates in the 'Linnean Transactions.'—Ed.

ovata, per lentem reticulata, areolis subrotundis, sordidè fusca, lævis, nonnitens, suprà plana marginibus acutis, subtùs modicè convexa ore coarctato, marginato. Apophysis nulla.

Operculum conico-cylindraceum, capsulâ brevius, apice lateris superioris in mucronem levissimè incurvum producto, basi incrassatâ, cum calyptrâ sæpissimè deciduum.

Peristomium penicillum densum album referens, longitudine circiter dimidii capsulæ, formatum *Ciliis* indeterminatim numerosissimis (200 et ultrà) capillaribus inarti-
318] culatis æqualibus rectis albis opacis, pluribus e capsulæ parietibus ortum ducentibus, centralibus (circiter 50) columellam terminantibus!

Membrana interior capsulæ maturæ exteriori approximata, vasculisque numerosis connexa.

Columella longitudine capsulæ maturæ, in quâ latiuscula, corrugata, colli brevis margine incrassatâ, intra cilias desinens in processum filiformem solidum indivisum apicem operculi attingentem eique arctiùs adhærentem.

Semina minutissima, lævia, in cumulo viridia, seorsùm hyalina.

Obs. I. I have named this remarkable genus in honour of my esteemed friend Dawson Turner, Esq., a gentleman eminently distinguished in every part of cryptogamic botany, and from whom, after he has finished the incomparable work on *Fuci*, in which he is now engaged, we may expect a general history of mosses.

Obs. II. The strict relationship between *Dawsonia* and *Polytrichum* in most respects, and the striking dissimilarity of their peristomiums, may tend, perhaps, in some degree to lessen our confidence in the characters derived from that part; for there seems in this case but little analogy between the two structures. The better to understand that of *Polytrichum*, I was induced along with Mr. Turner to examine it in the unripe capsule: in this state the cavity of the operculum was found completely filled with a cellular pulp, similar to that composing the columella, of which it appeared evidently to be a continuation; to the surface of this pulp the teeth of the peristomium were closely pressed,

but did not adhere: by degrees the pulp dries up, and in the ripe capsule leaves only the membrane or tympanum of an inorganic appearance, and firmly cohering with the teeth by the inner side of their apices. It does not therefore [319
properly belong to the operculum, though in some cases it may adhere to it, as does the analogous process of the columella in *Dawsonia* and in several other mosses.

The affinity of *Dawsonia* to *Buxbaumia* is certainly less strict than to *Polytrichum*, and rests chiefly on the similarity of the figure of the capsule, and in the central process of the columella, which is still more evident in *Buxbaumia*, where it forms part of the Linnean generic character, though unaccountably overlooked by Schmidel in his masterly dissertation; but, if I mistake not, actually represented by him [in fig. 14, b [1]], and confounded with the peristomium, which in this case, I suppose, had adhered to the operculum, as I have repeatedly found it to do, and thus escaped his notice. Hedwig considers the plaited membrane which constitutes the peristomium of *Buxbaumia*, as derived from the inner membrane of the capsule, and quotes the figure just mentioned of Schmidel in proof of this origin. In both species, however, I find it arising from the exterior membrane, though considerably within its margin, which in *Buxbaumia aphylla* is said by Hedwig to be divided into teeth,—an appearance I could not observe in the few ripe capsules I have dissected. In other respects, the two species seem essentially to agree, and therefore ought not to be separated, as Ehrhart and some late writers have done. The generic character comprehending both, I would propose to alter in the following manner.

BUXBAUMIA.

Capsula obliqua, hinc convexior, vel gibba.

Peristomium intra marginem, quandoque dentatum, membranæ exterioris ortum, tubulosum, plicatum, apice apertum.

[1] Schmidel, *Dissertationes Botanici Argumenti*.

320] LEPTOSTOMUM.

Capsula oblonga, exsulca; *Operculo* hemisphærico, mutico.

Peristomium simplex, membranaceum, annulare, planum, indivisum, e membrana interiori ortum.

Musci *dense cæspitosi*. Caules *erecti, annotino-ramosi*. Folia *undique modicè patentia, latiuscula, nervo valido, marginibus integris, revolutis, pilo (quandoque ramoso?) terminata*. Seta *terminalis*. Capsula *erecta v. inclinans, basi in apophysin obconicam attenuata, ore coarctato*. Calyptra *glabra, lævis, caduca*.

1. *L. inclinans*, foliis ovato-oblongis obtusis; pilo simplici, capsulis inclinatis obovato-oblongis.

Tab. 11 [XXIII]. Fig. 2.

Patria. Insula Van-Diemen.

Statio. Rupes et saxa ad latus orientale prope summitatem Montis Tabularis lat. aust. 43°, elevatione supra mare 3000 ad 3500 ped.

Desc. Muscus lætè virens 2-3-uncialis. Caules parùm divisi, infrà tomento denso ferrugineo vestiti, suprà confertim foliati. Folia concaviuscula, per lentem minutissime punctato-areolata, pilo tortili ipso folio quater breviore. Seta fusca, lævis. Vaginula infrà stipata adductoribus pluribus filisque succulentis capillaribus articulatis.

2. *L. erectum*, foliis oblongo-parabolicis obtusis; pilo simplici, capsulis erectis oblongis.

Patria. Novæ Hollandiæ ora orientalis, extra tropicum.

Statio. Rupes prope fluviorum ripas, in regione montanâ; ad fluvios Hawkesbury et Grose.

Desc. Muscus 2-3-uncialis. Caules simplices et subra-
321] mosi, infrà tomento ferrugineo vestiti, suprà densè foliati. Folia siccatione parùm curvata, et simul adpressa.

Seta elongata, fusca, lævis. Capsula æquilatera. Operculum delapsum fuit.

3. *L. gracile*, foliis ovato-oblongis acutiusculis; pilo simplici folium dimidium æquante, capsulis oblongis æquilateris inclinatis.

Patria. Nova Zelandia.

Statio. Umbrosa humida (?) ad Dusky Bay, *Dom. Arch. Menzies.*

Desc. Caules subramosi. Folia siccatione adpressa, areolato-punctata. Seta elongata, lævis. Vaginula cylindracea, filis succosis adductoribusque numerosis cincta.

4. *L. Menziesii*, foliis oblongo-lanceolatis acutis; pilo simplici folio quater breviore, capsulis oblongis inclinatis arcuato-recurvis.

Patria. Americæ Australis Staten-land, ubi anno 1787 detexit *Dom. Arch. Menzies*, cujus amicitiæ hanc et præcedentem speciem debeo.

Statio. - - - -

Desc. Muscus lætè virens, sesquiuncialis. Caules subsimplices, basi ferrugineo-tomentosi, suprà confertim foliati. Folia erecto-patentia, siccatione adpressa, minutissimè areolata v. punctata. Seta caulem sæpiùs superans, erecta, fusca, lævis. Capsula subfalcata ad angulum acutum rariusve ferè rectum inclinans.

Obs. The plants which I have referred to this genus are all natives of the southern hemisphere, and in their habit, in which there is something peculiar, strictly agree with each other, and with *Bryum macrocarpum* of Hedwig. [322] In three of the four species here described, I have had the opportunity of removing the operculum without having been able in any case to observe an external peristomium, which, from the appearance of these plants, might be expected to exist, and which Hedwig has figured in his *Bryum macrocarpum*. Of this plant I have only seen specimens that had lost the operculum: the mouth of the capsule, however, seemed to be very perfect, and was furnished with a membrane, exactly as in the species here described, but I could not perceive any remains of external teeth. In opposition to such authority, however, I do not venture to add it to this genus, to which in every other respect it seems to belong.

The character of *Leptostomum*, derived from the undivided annular process of the inner membrane of the capsule, may to many appear too minute, and perhaps unimportant; and had it been observed in one species alone, I should not have ventured on that account to distinguish it as a genus: but finding it in four species, accompanied too with a habit widely different from that of *Gymnostomum*, to which these plants must otherwise be referred, I have not hesitated to employ it. As, however, Hedwig has actually figured and described an external peristomium in his *Bryum macrocarpum*, whose striking resemblance to *Leptostomum* has been already noticed, there may be still some reason to doubt the sufficiency of the generic character, and it may seem somewhat improbable that Mosses of such a habit should be really destitute of an outer peristomium. But, without questioning the accuracy of Hedwig in this instance, I may be permitted to observe, that the outer peristomium which he has figured in *Bryum macrocarpum* is extremely unlike that of any other genus where the fringe
323] is double: and it may perhaps in some degree tend to strengthen the character of *Leptostomum*, to advert to what appears to be really the case in certain species of *Pterogonium*, in one of which[1] Mr. Hooker has already described the fringe as derived solely from the inner membrane; and I have collected, on the mountains of Van Diemen's Island, a moss with a peristomium decidedly of like origin; a circumstance that appeared to me so remarkable, that I had actually described it as a distinct genus, before I was aware of the similar structure of the Nepal plant described by Mr. Hooker; or of the probability, from Hedwig's own figures, that some at least of his *Pterogonia* were of the same structure; a point that I have not at present

[1] Pterogonium declinatum. *Trans. Linn. Soc.* ix, *p.* 309.

the means of determining, but which I beg leave to recommend to the attention of those botanists who are provided with perfect specimens of the published *Pterogonia*.

Explicatio Tabulæ 11 (XXIII).

Fig. 1. Dawsonia polytrichoides. *a.* Mascula planta magnitudine naturali. *b.* Discus masc. auctus. *c.* Ejusdem flos unicus. *d.* Idem absque folio perigoniali, magisque auctus. *e.* Anthera et filum succulentum maximè aucta. *f.* Femineæ plantæ magn. nat. *g.* Vaginula cum foliis perichætialibus auctis. *h.* Capsula cum calyptrâ exteriori. *i.* Pili calyptræ exterioris magis aucti. *j.* Capsula cum operculo et calyptrâ interiori. *k. l.* Capsula deoperculata cum peristomio. *m.* Capsulæ sectio ejusdem figuram insertionemque ciliarum ostendens. *o.* Calyptra interior. *p.* Operculum cum columellæ processu [321
filiformi. *q.* Columella ciliis suis terminata. *r.* Semina. *s.* Ciliæ peristomii auctæ.

Fig. 2. Leptostomum inclinans, magnitudine naturali. *α.* Ejusdem capsula aucta cum membranâ annulari. *β.* Operculum. *γ.* Idem a basi visum cum annulo cohærenti.

ON

SOME REMARKABLE DEVIATIONS FROM THE USUAL STRUCTURE OF SEEDS AND FRUITS.

BY

ROBERT BROWN, Esq., F.R.S., Libr. L.S.

Read March 5th, 1816.

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LONDON:

1818.

ON
SOME REMARKABLE DEVIATIONS, &c.

The principal part of the following paper was read to the Society in March, 1813. It was then withdrawn with a view of rendering it more perfect by additional facts, which I hoped I might be able to collect. Since that time I have not had it in my power to pay much attention to the subject. As, however, the facts formerly stated appear to me of some importance, and are as yet unpublished, I take the liberty of again submitting them to the Society, along with a few additional instances of anomalies in the structure of seeds and fruits, hardly less remarkable than those contained in the original essay.

It is, I believe, generally admitted by physiological botanists, that the seeds of plants are never produced absolutely naked :—in other words, that the integument through some point or process of which impregnation takes place, cannot properly be considered as part of the seed itself.

That such a covering, distinct from the seed, really exists, may in most, perhaps in all, cases be satisfactorily shown by a careful examination of the unimpregnated ovarium, to a part only of whose cavity the ovulum will be found to be attached.

There are, however, many cases where soon after fecundation, and more remarkably still in the ripe fruit, this integument acquires so complete and intimate a cohesion [144
with the proper coat of the seed as to be no longer either separable or distinguishable from it.

But systematic botanists have generally agreed to term a naked seed not only this kind of fruit, but every monospermous pericarpium bearing a general resemblance to a seed, and whose outer covering, though distinct from the nucleus, is only ruptured after germination commences.

For the purposes of an artificial arrangement this language may perhaps be sufficiently accurate; but in determining the affinities of plants, it is necessary to express by appropriate terms those differences which are no less important than real.

Of the fruits improperly called naked seeds, there are two principal kinds: the first, in which the pericarpium is distinct from the seed, is termed *Akena* by Richard in his excellent *Analyse du Fruit;* the second, in which the pericarpium coheres with the seed, is the *Caryopsis* of the same author.

An *Akena* (or *Achenium*), even in a separate state, may in general be readily determined. But it is not always equally easy to distinguish a *Caryopsis* from a seed. It may indeed be done in certain cases, as in Grasses, by attending to its surface, in which two distinct and distant cicatrices are observable; the one indicating the point of attachment to the parent plant, the other that by which it was fecundated. In certain other tribes, however, this criterion cannot be had recourse to, the surface of the *Caryopsis* exhibiting but one areola or cicatrix, which includes the closely approximated points of attachment and impregnation: in such cases, the true nature of the fruit can only be determined by its examination in an earlier stage.

But although it must be admitted that an ovulum is never produced without a covering, through some part of
145] which it is impregnated; it is still possible to conceive a case in which a ripe seed may be considered as truly naked while retaining its attachment to the parent plant; and this not subsequent to germination, but even preceding the formation of the embryo. For if we suppose, as the immediate effect of impregnation, a swelling of the ovulum without a corresponding enlargement of the ovarium, the consequence will obviously be a premature rupture of the ovarium, and the production of a seed provided with its proper integuments only.

I am not aware that such an economy has hitherto been described; I have observed it, however, in several plants belonging to very different families, and of essentially different structures.

The first of these is *Leontice thalictroides* of Linnæus, *Caulophyllum thalictroides* of Michaux, who has founded his new genus on a difference of fruit, the nature of which he has entirely misunderstood. It is remarkable that its real structure should have escaped so accurate an observer as M. Richard, through whose hands it is generally understood Michaux's work passed previous to its publication; but the fact may at least serve to show how entirely unexpected such an economy must have been even to that excellent carpologist.

My observations were made in the summer of 1812, on a plant of *Leontice thalictroides*, which flowered and ripened fruit in the royal gardens at Kew. An examination of the unimpregnated ovarium proved it to be in every respect of the same structure with that of the other species of *Leontice*; and essentially the same with the whole order of *Berberides*, to which this genus belongs. A careful inspection of the fruit, in different states, proved also that the "Drupa stipitata" of Michaux is in reality a naked seed, that in a very early stage had burst its pericarpium, the withered re- [146
mains of which were in most cases visible at the base of the ripe seed. The first error of Michaux naturally led to a series of mistakes; and the naked seed being considered by him as a drupa, the albumen, which is of a horny texture, is described as a "nux cornea crassissima," and the embryo itself as the seed.

But although this account of the fruit of *Leontice thalictroides* be in no respect similar to that given by Michaux, it may perhaps be considered by some as still differing sufficiently from *Leontice* to authorise the establishment of a distinct genus; and that, therefore, the name *Caulophyllum* may be retained, and its character derived from the remarkable circumstance described, namely, the early rupture of its pericarpium. I believe, however, it will be found more expedient to reduce it again to *Leontice*.

For, in the first place, its habit is entirely that of the original species of the genus. And secondly, though the pericarpium of *Leontice Leontopetalum,* which is the type of the genus, remains shut until the ripening of the seeds, and attains a size more than sufficient for the mere purpose of containing them; yet in *Leontice altaica,* a species in other respects more nearly approaching to *L. Leontopetalum* than to *L. thalictroides*, the pericarpium, though it enlarges considerably after impregnation, is ruptured by the seeds long before they have arrived at maturity.

The accompanying drawing, for which I am indebted to my friend Mr. Ferdinand Bauer, will materially assist in explaining the singular economy now described; and may also perhaps render more intelligible the account I proceed to give of the second instance in which I have observed an analogous structure, but to illustrate which I have at present no drawing prepared.

147] This second instance occurs in *Peliosanthes Teta* of Andrews's Repository and the Botanical Magazine.

In this monocotyledonous plant, which in 1812 nearly ripened seed in Mr. Lambert's collection at Boyton, the ovarium coheres with the tube of the perianthium or corolla, and has originally three cells, each containing two ovula. Soon after impregnation has taken place, from one to three of these ovula rapidly increase in size, by their pressure prevent the development of the others, and rupture the ovarium, which remains, but little enlarged at the base of the fruit, consisting of from one to three naked berry-like seeds.

In the Botanical Magazine Mr. Ker, in describing a second species of *Peliosanthes,*[1] takes the opportunity of altering in some respects the character of the genus he had previously given, and of adding a description of its supposed pericarpium, from an inspection, as it seems, of the unripe fruit of *Peliosanthes Teta.* It is evident, however, that he is not aware of its real structure; and consequently does not succeed in reconciling its appearance with the unquestionable fact of its having "germen inferum."

[1] Botan. Magaz. 1532.

There are some cases in which this early opening of the ovarium, instead of being, as in the preceding instances, an irregular bursting, apparently caused by the pressure of the enlarged ovula, is a regular dehiscence in the direction of the suture. Of this *Sterculia platanifolia* and *S. colorata* are remarkable examples; their folliculi after opening, which takes place long before the maturity of the seeds, acquiring the form and texture of leaves, to whose thickened margins the ovula continue firmly attached until they ripen. Another example of this early and regular dehiscence occurs in an undescribed genus of the same family, which differs from *Sterculia platanifolia* in its pericarpium having a terminal wing and a single seed.

In the specimens of a plant lately sent from Brazil by [148
Mr. Sellow, I observe a similar economy. In this case the ovarium, which is originally unilocular with five parietal placentæ, soon after fecundation opens regularly into five equal foliaceous valves, to the inner surface of each of which an indefinite number of ovula are attached.

The genus *Reseda*, whose capsule opens at top at a very early period, may be considered as affording another instance, though much less remarkable, of the same anomaly. And it is possible that this may be the real structure in certain cases of which a very different view has been taken.

In the instances of naked seeds now given, the bursting of the pericarpium precedes the distinct formation of the embryo, while the proper coats of the seed remain entire till after its separation from the parent plant, and germination has commenced.

It may not be uninteresting to contrast this economy with that of the Mangroves and other plants of tropical countries, which grow on the shores, and within the influence of the tide. In many of these the embryo, long before the seed loses its original attachment, acquires a very considerable size; and the first effect of this unusual development is the rupture, in most cases succeeded by the complete absorption or disappearance, of the proper integument of the seed. In some instances the develop-

ment proceeds still further, and the pericarpium itself is perforated by the embryo, which, while preserving its connection with the parent plant, often attains the length of from eighteen inches to two feet. This happens in *Rhizophora* and *Bruguiera,* or the Mangroves properly so called. In some of the spurious Mangroves, as *Avicennia* and *Ægiceras,* a lesser degree of development takes place, and in general their pericarpia remain entire till they have dropped from the tree. In both cases the final cause of
149] the economy is sufficiently evident; a greater than ordinary evolution of the embryo being necessary to ensure its vegetation in the unfavorable circumstances in which it is unavoidably placed.

But an analogous structure exists in other plants, where the final cause is less apparent, as in certain species of *Eugenia,* in which the integument of the seed is completely absorbed before its separation from the parent plant, and while the pericarpium remains entire.

An economy no less remarkable than that of the Mangroves, but of a nature diametrically opposite, takes place in the bulb-like seeds of certain liliaceous plants, especially of *Pancratium, Crinum* and *Amaryllis;* in some of whose species the seed separates from the plant, and even from the pericarpium, before the embryo becomes visible. This observation respecting some of these seeds was, I believe, first made by Mr. Salisbury; and in such as I have myself examined, I have found the fact connected with one no less interesting, namely, an unusual vascularity in the fleshy substance.

I have in another place,[1] in speaking of this substance, which constitutes the mass of the seed, and in a central cavity of which the future embryo is formed, stated it to be destitute of vessels, and entirely composed of cellular texture. But on a more careful inspection, of those seeds at least in which the separation precedes the visible formation of the embryo, I now find very distinct spiral vessels:—these enter at the umbilicus, ramify in a regular manner in the substance of the fleshy mass, and appear to have a

[1] Prodr. Flor. Nov. Holland. p. 297.

certain relation to the central cavity where the embryo is afterwards formed, and which, filled with a glairy fluid, is distinctly visible before the separation of the seed. It is a curious consequence of this tardy evolution of the embryo, which in some cases does not become visible unless the [150
seed be placed in a situation favorable to germination, that very different directions may be given to its radicular extremity, according to circumstances which we have it in our power to regulate.

There is a fourth kind of anomaly in the structure of certain seeds, which, as I have formerly described it,[1] I shall here notice in a few words. It is that which takes place in certain *Aroideæ,* especially in some species of *Caladium.* In these, the nucleus of the seed is not properly a monocotyledonous embryo, but has an appearance and economy more nearly resembling those of the tuber of a root; for, instead of being distinguishable into a cotyledon, a plumula and radicula, and of germinating in a determinate manner and from a single point, it is composed of a mass whose internal structure is uniform, and on the surface of which frequently more than one germinating point is observable.

None of these anomalies appear to me materially to lessen the importance of the characters derived from the seeds of plants; but they evidently render a minute attention to every circumstance absolutely necessary in all attempts either to deduce affinities or establish genera from this source; and they especially demonstrate the necessity of carefully ascertaining the state of the unimpregnated ovarium; for, while its structure remains unknown, that of the ripe fruit can never be thoroughly understood.

[1] Prodr. Flor. Nov. Holl. p. 335.

EXPLANATION OF PLATE 12 (VII). [151

A.—A branch of the panicle of LEONTICE THALICTROIDES *Linn.* (Caulophyllum thalictroides *Michaux*), of the natural size.

B.—The same magnified, to show at 1, the early rupture of the ovarium, the ovula as yet but little enlarged and only in part protruded: at 2, the same parts in a more advanced state; one seed being nearly ripe, supported by its elongated and thickened umbilical cord; a second ovulum considerably increased in size, but abortive; and the remains of the ruptured ovarium—somewhat enlarged.

C and *D.*—Two longitudinal sections of the nearly ripe seed; exhibiting the vascular cord continued from the axis of the funiculus umbilicalis to the apex of the seed; the remarkable process of the inner integument at the umbilicus (of which another view is given separately at *E*); and the unripe embryo nearly in contact with this process, and as yet undivided.

AN ACCOUNT

OF

A NEW GENUS OF PLANTS,

NAMED

RAFFLESIA.

BY

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LONDON.

April, 1821.

ACCOUNT OF A NEW GENUS OF PLANTS, [201

NAMED

RAFFLESIA.

Read to the Linnean Society, June 30th, 1820.

It is now nearly eighteen months since some account of a flower of extraordinary size was received by my lamented friend and patron the late revered President of the Royal Society, from Sir Stamford Raffles, Governor of the East India Company's establishments in Sumatra.

This gigantic flower, which forms the subject of the present communication, was discovered in 1818 on Sir Stamford's first journey from Bencoolen into the interior. In that journey he was accompanied by a naturalist of great zeal and acquirements, the late Dr. Joseph Arnold, a member of this Society, from whose researches, aided by the friendship and influence of the Governor, in an island so favorably situated and so imperfectly explored as Sumatra, the greatest expectations had been formed. But these expectations were never to be realised; for the same letter which gave the account of the gigantic flower, brought also the intelligence of Dr. Arnold's death.

As in this letter many important particulars are stated respecting the plant which I am about to describe, and a just tribute is paid to the merits of the naturalist by whom it was discovered, I shall introduce my account by the following extract.

"Bencoolen; 13*th August*, 1818.

"You will lament to hear that we have lost Dr. Arnold: he fell a sacrifice to his exertions on my first tour into the interior, and died of fever about a fortnight ago.

202] "It is impossible I can do justice to his memory by any feeble encomiums I may pass on his character; he was in everything what he should have been, devoted to science and the acquisition of knowledge, and aiming only at usefulness.

"I had hoped, instead of the melancholy event I have now to communicate, that we should have been able to send you an account of our many interesting discoveries from the hand of Dr. Arnold. At the period of his death he had not done much; all was arrangement for extensive acquirement in every branch of natural history. I shall go on with the collections as well as I can, and hereafter communicate with you respecting them, and in the mean time content myself with giving you the best account I can of the largest and most magnificent flower which, as far as we know, has yet been described. Fortunately I have found part of a letter from poor Arnold to some unknown friend, written while he was on board ship, and a short time before his death, from which the following is an extract.

"After giving an account of our journey to Passummah, he thus proceeds:

"'But here (at Pulo Lebbar on the Manna River, two days' journey inland of Manna) I rejoice to tell you I happened to meet with what I consider as the greatest prodigy of the vegetable world. I had ventured some way from the party, when one of the Malay servants came running to me with wonder in his eyes, and said, "Come with me, sir, come! a flower, very large, beautiful, wonderful!" I immediately went with the man about a hundred yards in the jungle, and he pointed to a flower growing close to the ground under the bushes, which was truly astonishing. My first impulse was to cut it up and carry it to the hut. I therefore seized the Malay's parang (a sort of instrument

like a woodman's chopping-hook), and finding that it sprang from a small root which ran horizontally (about as large as two fingers, or a little more), I soon detached it and re- [203
moved it to our hut. To tell you the truth, had I been alone, and had there been no witnesses, I should I think have been fearful of mentioning the dimensions of this flower, so much does it exceed every flower I have ever seen or heard of; but I had Sir Stamford and Lady Raffles with me, and a Mr. Palsgrave, a respectable man resident at Manna, who, though equally astonished with myself, yet are able to testify as to the truth.

"'The whole flower was of a very thick substance, the petals and nectary being in but few places less than a quarter of an inch thick, and in some places three quarters of an inch; the substance of it was very succulent. When I first saw it a swarm of flies were hovering over the mouth of the nectary, and apparently laying their eggs in the substance of it. It had precisely the smell of tainted beef. The calyx consisted of several roundish, dark-brown, concave leaves, which seemed to be indefinite in number, and were unequal in size. There were five petals attached to the nectary, which were thick, and covered with protuberances of a yellowish-white, varying in size, the interstices being of a brick-red colour. The nectarium was cyathiform, becoming narrower towards the top. The centre of the nectarium gave rise to a large pistil, which I can hardly describe, at the top of which were about twenty processes, somewhat curved and sharp at the end, resembling a cow's horns; there were as many smaller very short processes. A little more than half way down, a brown cord about the size of common whipcord, but quite smooth, surrounded what perhaps is the germen, and a little below it was another cord somewhat moniliform.

"'Now for the dimensions, which are the most astonishing part of the flower. It measured a full yard across; the petals, which were subrotund, being twelve inches from the base to the apex, and it being about a foot from the insertion of the one petal to the opposite one; Sir Stam- [204
ford, Lady Raffles and myself taking immediate measures

to be accurate in this respect, by pinning four large sheets of paper together, and cutting them to the precise size of the flower. The nectarium, in the opinion of all of us, would hold twelve pints, and the weight of this prodigy we calculated to be fifteen pounds.

"'I have said nothing about the stamina; in fact, I am not certain of the part I ought to call stamina. If the moniliform cord surrounding the base of the pistil were sessile anthers, it must be a polyandrous plant; but I am uncertain what the large germen contained; perhaps there might be concealed anthers within it.

"'It was not examined on the spot, as it was intended to preserve it in spirits and examine it at more leisure; but from the neglect of the persons to whom it was entrusted the petals were destroyed by insects, the only part that retained its form being the pistil, which was put in spirits along with two large buds of the same flower, which I found attached to the same root; each of these is about as large as two fists.

"'There were no leaves or branches to this plant; so that it is probable that the stems bearing leaves issue forth at a different period of the year. The soil where this plant grew was very rich, and covered with the excrement of elephants.

"'A guide from the interior of the country said that such flowers were rare, but that he had seen several, and that the natives called them *Krûbût*.

"'I have now nearly finished a coloured drawing of it on as large drawing-paper as I could procure, but it is still considerably under the natural size; and I propose also to make another drawing of the pistil removed from the nectarium.

"'I have now, I believe, given you as detailed an account of this prodigious plant as the subject admits of;
205] indeed it is all I know of it. I would draw your attention, however, to the very great porosity of the root, to which the buds are attached.

"'I have seen nothing resembling this plant in any of my books; but yesterday, in looking over Dr. Horsfield's immense collections of the plants of Java, I find something which perhaps may approach to it; at any rate the buds of the flower he has represented grow from the root precisely in the same manner; his drawing, however, has a branch of leaves, and I do not observe any satisfactory dissections. He considers it as a new genus; but the difference of the two plants appears from this, that his full-blown flower is about three inches across, whereas mine is three feet.'"

Sir Stamford proceeds:

"Dr. Arnold did not live to return to Bencoolen, nor to fulfil the intentions expressed in the above extract; but we have finished the drawing of the whole flower, and it is now forwarded under charge of Dr. Horsfield, to whom I have also entrusted the pistil and buds.

"I shall make exertions for procuring another specimen, with which I hope we shall be more fortunate.

(Signed) "T. S. Raffles.

"To the Right Honorable
Sir Joseph Banks, Bart., G.C.B., &c. &c."

The drawing of the expanded flower, and the specimens mentioned in the preceding extract, were brought to England by Dr. Horsfield; and, having been put into my hands, I proceeded without delay to examine the smaller flower-bud. In this examination the antheræ, although not at first obvious, were soon discovered, but no part was found which could be considered either as a perfect pistillum or as indicating the probable nature or even the exact place of the ovarium. The remains of the expanded flower [206
exhibited the same structure; and the larger bud, which was examined by Mr. Bauer, whose beautiful drawings of it form the most valuable part of the present communication, proved also to be male.

These materials, it must be admitted, are insufficient even for the satisfactory establishment of the proposed new genus, and in my opinion do not enable us absolutely to determine its place in the natural system.

The curiosity of botanists, however, has been so much excited by the discovery of a flower of such extraordinary dimensions, the male flower is in many respects so singular, and its structure is so admirably illustrated by Mr. Bauer's drawings, that, accompanied by them, even the present incomplete account will probably be thought worthy of a place in the Society's Transactions.

Its publication is the less objectionable, as it may still be a considerable time before the plant is met with in all its states; and however unsatisfactory our present materials may be, either for determining its affinities, or the equally important question, whether it be parasitic on the root to which it is attached, there can be no doubt that it forms a genus abundantly distinct from any that has hitherto been described.

It is proposed, in honour of Sir Stamford Raffles, to call this genus Rafflesia, the name I am persuaded that Dr. Arnold himself would have chosen had he lived to publish an account of it; and it may in the mean time be distinguished by the following characters.

207] RAFFLESIA.

Perianthium monophyllum, coloratum; *tubo* ventricoso; *corona faucis* annulari, indivisa; *limbo* quinquepartito, æquali.

Mas. *Columna* (inclusa): *limbo apicis* reclinato, subtus simplici serie polyandro; *disco* processibus (concentricis) tecto.

Antheræ sessiles, subglobosæ, cellulosæ, poro apicis dehiscentes.

Fem. - - - - - -

Rafflesia Arnoldi.

Tab. 13—20 (XV—XXII.)

Descriptio.

E *Radice* lignea horizontali tereti, lævi, crassitie fere et structura interiore omnino radicis Vitis viniferæ (*tab.* 20 (22), *f.* 8) ortum ducit *Flos* unicus, ante expansionem, dum bracteis imbricatis adhuc inclusus, brassicæ minori figura et magnitudine similis (*tab.* 14 (16)); cum radice parum dilatata connexus *Basi* (*tab.* 15 (17)) modicè convexa, abbreviata, insignita lineolis numerosis, elevatis, nigricantibus, plerisque reticulatim confluentibus, nonnullis brevioribus distinctis, omnibus sulco longitudinali tenui per axin exaratis, apothecia Opegraphæ æmulantibus, superioribus desinentibus in *annulum* modicè elevatum exsulcum, ejusdem fere substantiæ, definientem basin reticulatam.

Bracteæ (*tab.* 14 (16)) supra annulum baseos reticulatæ, numerosæ, densè imbricatæ, subrotundæ, coriaceæ, glaberrimæ, integerrimæ, venis vix vel parum emersis, ramosis, distinctis, nec anastomosantibus, infra apicem evanescentibus, lata basi insertæ ibique crassæ, versus apicem sensim tenuiores, subfoliaceæ; intimæ e latiore basi, $\frac{1}{5}$ usque ad $\frac{1}{4}$ circuli æquante.

Perianthium (*tab.* 13 (15)) intra bracteas sessile, monophyllum, coloratum, ante expansionem depresso-sphæroideum (*tab.* 16 et 17 (18 et 19)). *Tubus* ventricosus, [208
abbreviato-urceolatus, extus lævis, intus ramentis filiformibus simplicibus passimque parum divisis densè tectus. *Faux: corona* annulari integerrima, intus ornata areolis numerosis, convexiusculis, subrotundis transversim paulo latioribus, superioribus omnino lævibus, reliquis margine inferiore aucto ramentis filiformibus brevibus. *Limbus* quinque-partitus (diametro tripedali), *laciniis* æqualibus, (patentibus reflexisve) rotundatis, integerrimis, *extus* lævibus, præter venas parum elevatas, numerosas, dichotomas, passim anastomosantes, ad apicem usque attingentes; *intus* verrucis numerosis, subrotundis, sparsis, inæqualibus, interstitiis lævibus: *æstivatione* arctè imbricatis, exterioribus interiores utroque margine equitantibus (*tab.* 17 (19)).

Columna centralis (*tab.* 18 (20) et 19 (21), *fig.* 1) staminifera, cavitatem tubi perianthii ferè omnino replens, inclusa, solida, carnosa, intus cum substantia ipsius baseos reticulatæ extus cum tubi superficie ramentacea continua; prope basin aucta *annulis* duobus modicè elevatis, rotundatis, ante

expansionem approximatis (*tab.* 19 (21), *f.* 1, 2), in expanso flore remotioribus (*tab.* 20 (22), *f.* 2), *inferiore* paulo crassiore, striis leviter depressis numerosis rugoso, *superiore* exsulco, punctis minutis elevatis inæquali: supra annulum superiorem lævis et sensim angustata in *collum* brevissimum, insculptum *excavationibus* (*tab.* 19 (21), *f.* 2) numero antherarum iisque oppositis, basi angustatis, longitudinaliter elevato-striatis, interstitiis subcarinatis, carinis marginibusque ciliatis: *apex* dilatatus, cujus *discus* planiusculus, tectus *processibus* numerosis carnosis leviter incurvis subcorniformibus, simplicibus apiceve parum divisis, in seriebus pluribus concentricis, interioribus plus minus irregulariter dispositis, nonnullis minoribus sæpe minimis sparsim intermixtis, majorum singulis fasciculo vasculari centrali tenui instructis, omnibus lævibus, præter apices lobulorum qui
209] sæpe hispiduli vel minutè penicillati; *limbus* solutus reclinatus, e basi recurvata, subtus punctis parvis elevatis quandoque piliferis inæquali, adscendens, margine erecto-conniventi, indiviso tenuiter crenulato, substantia et superficie processibus disci similis, intus fasciculis vascularibus simplici serie dispositis et ad basin antheræ singulæ flexura notabili instructis (*tab.* 19 (21), *f.* 2, 3, 7, 8, et *t.* 20 (22), *f.* 6).

Antheræ (*tab.* 19 (21), *f.* 4—8, et *t.* 20 (22), *f.* 4—6) simplici serie dispositæ, æquidistantes, 35 circiter, vix 40, sessiles, excavationibus dimidiæ recurvatæ limbi, cum iis colli continuis, lata basi insertæ, semiimmersæ, apicibus deorsum spectantibus, in respondentibus cavitatibus colli receptis, ovato-globosæ, pisi magnitudine, apice depressione unica centrali demum aperiente umbilicatæ, cellulosæ, cellulis indefinitè numerosis, subconcentricis, longitudinalibus, exterioribus versus apicem conniventibus, passim confluentibus et quandoque transversim interruptis, plenis *Polline* (*tab.* 19 (21), *f.* 9) minuto, sphærico, simplici, lævi.

Pistilli rudimenta nulla certa; processus enim corniculati apicis columnæ staminiferæ, in circulis pluribus concentricis dispositi atque singuli fasciculo vasculari centrali donati, dubiæ naturæ sunt.

To the foregoing description of *Rafflesia* it is necessary to add some observations explanatory of structure; and I shall also offer a few conjectures on certain points of the economy of the plant, and on its affinities.

The great apparent simplicity in the internal structure of every part, especially in a flower of such enormous size, is in the first place deserving of notice.

This observation particularly applies to the *Column*, which is found to consist of a uniform cellular texture, with a very small proportion of vessels. The *cells* or utriculi are [210 nearly sphærical, slightly angular from mutual pressure, and, in the specimens examined at least, easily separable from each other without laceration. I have not been able to detect perforations on any part of their surface; but extremely minute granules, originally contained in great abundance in the cells, and frequently found adhering to their parietes, may readily be mistaken for pores.

The structure of *vessels* either in the column, perianthium or bracteæ, in all of which they are apparently similar, has not been satisfactorily ascertained. They may be supposed to approach most nearly to the ligneous, though certainly unaccompanied by spiral vessels, which do not appear to exist in any part of the plant.

The same internal structure is continued below the origin of the bracteæ, down to the line at which the vessels of the root appear to terminate, and where an evident change takes place (*plate* 18 (20) and 20 (22), *f.* 1).

The *Perianthium* and *Bracteæ* in their cellular texture very nearly agree with the column, except that in their more foliaceous parts the cells are considerably elongated.

I have not found in any part of their surface, or in that of the column, those areolæ universally considered as cuticular pores, and which, though of very general occurrence, do not perhaps exist in the imperfectly developed leaves of plants parasitic on roots.

In the external composition of the column, the part most deserving of attention is the *Anthera;* for in apparent origin, as well as in form and structure, it presents the most singular modification of stamen that has yet been observed.

It appears to me of importance to inquire into the real relation which so remarkable a structure bears to the more ordinary states of Anthera.

211] A satisfactory determination of this point, while it would certainly assist in explaining the nature of the other parts of the column, might also in some degree lead to correct notions of the affinities of the genus; and the question is perhaps sufficiently interesting, even independent of these results.

In this inquiry, it is necessary in the first place to take a general view of the principal forms of Antheræ in phænogamous plants; all of which, however different they may appear, I consider as modifications of one common structure.

In this assumed regular structure or type of Anthera, I suppose it to consist of two parallel folliculi or *thecæ*, fixed by their whole length to the margins of a compressed filament: each *theca* being originally filled with a pulpy substance, on the surface or in the cells of which the pollen is produced; and having its cavity divided longitudinally into two equal cells, the subdivision being indicated externally by a depression or furrow, which is also the line of dehiscence.[1]

[1] A certain degree of resemblance between this supposed regular state of Anthera, and that which in a former essay (on Compositæ, *Linn. Soc. Transact.* xii, *p.* 89) I have considered as the type of Pistillum in phænogamous plants, will probably be admitted; and both structures have, as it appears to me, an evident relation to the *Leaf*, from whose modifications all the parts of the flower seem to be formed.

This hypothesis of the formation of the flower may be considered as having originated with Linnæus in his *Prolepsis Plantarum*, though he has not very clearly stated it, and has also connected it with other speculations, which have since been generally abandoned. It is, however, more distinctly proposed by Professor Link (in *Philos. Bot. Prodr. p.* 141), and very recently has been again brought forward, with some modifications, by M. Aubert du Petit Thouars.

In adopting the hypothesis as stated by Professor Link, I shall, without entering at present into its explanation or defence, offer two observations in illustration of it, founded on considerations that have not been before adverted to.

My first observation is, that the principal point in which the antheræ and

The structure now described actually exists in many [212
families of plants; and the principal deviations from it ovaria agree, consists in their essential parts, namely, the pollen and ovula, being produced on the margins of the modified leaf.

In the *Antheræ*, which are seldom compound, and whose thecæ are usually distinct, the marginal production of pollen is generally obvious.

In the *Ovaria*, however, where, with very few exceptions, the same arrangement of ovula really exists, it is never apparent, but is always more or less concealed either by the approximation and union of the opposite margins of the simple pistillum, and of the compound when multilocular; or in the unilocular pistillum with several parietal placentæ by the union of the corresponding margins of its component parts.

The few cases of apparent exception, where the ovula are inserted over the whole or greater part of the internal surface of the ovarium, occur either in the compound pistillum, as in *Nymphæa* and *Nuphar;* or in the simple pistillum, as in *Butomeæ* of Richard; and in *Lardizabaleæ,* an order of plants sufficiently distinct in this remarkable character alone, and differing also in the structure of embryo and in habit, from *Menispermeæ,* to which the genera composing it (*Lardizabala* and *Stauntonia*) have hitherto been referred.

The marginal production of ovula, though always concealed in the ordinary or complete state of the Ovarium, not unfrequently becomes apparent where its formation is in some degree imperfect, and is most evident in those deviations from regular structure, where stamina are changed, more or less completely, into pistilla. Thus, in the case of the nearly distinct or simple pistillum, it is shown by this kind of montrosity in *Sempervivum tectorum;* in the compound multilocular pistillum, by that of *Tropæolum majus;* and in the compound pistillum with parietal placentæ, by similar changes in *Cheiranthus Cheiri*, *Cochlearia armoracia, Papaver nudicaule,* and *Salix oleifolia.*

In all the cases now quoted, and in several others with which I am acquainted, it is ascertained that a single stamen is converted into a simple pistillum, or into one of the constituent parts of the compound organ: a fact which, in my opinion, establishes the proposed type of Ovarium.

I have entered thus slightly at present into the proof of this type, derived from these deviations from regular structure, partly on account of an observation which I find in the second edition of the excellent *Théorie Elémentaire de la Botanique* of Professor De Candolle, to whom, in 1816, I had shown drawings of most of the instances of monstrosity now mentioned. To these drawings, and to my deductions from them with regard to the structure of pistillum, I suppose the ingenious author alludes, in the passage in question. His views, however, on this subject differ considerably from mine, which he does not seem to have been aware were already published (*Linn. Soc. Trans. l. c.*)

My second observation relates to the more important differences between the antheræ and ovaria, independent of their essential parts.

In the Anthera the vascularity, with relation to that of the Leaf, may be said to be diminished without being otherwise sensibly modified; the pollen is formed in a cellular substance apparently destitute of vessels; and is always produced internally, or under the proper membrane of the secreting organ.

In the Ovarium, on the other hand, the vascularity, compared with that of the Leaf, is in general rather modified than diminished; the principal vessels occupying the margins or lines of production, and giving off branches towards the axis, whose vascularity is frequently reduced. The ovula constantly arise from vascular cords, and, with reference to the supposed original state of the ovarium, are uniformly produced externally; though by the union of its parts, may be stated to depend either on a reduced or increased development of the parts enumerated, on differences in the manner of bursting, or on the confluence of two or more antheræ.

Reduced development may consist merely in the approximation of the thecæ, consequent on the narrowing or entire absence of the connecting portion of the filament, which is one of the most common states of anthera; in their partial confluence, generally at the upper extremity; their paral-
213] lelism either continuing, which is also not unfrequent; or accompanied by various degrees of divergence, as in many genera of *Labiatæ;* in their complete confluence while they remain parallel, as in *Epacrideæ*, *Polygaleæ*, and in some genera of *Acanthaceæ;* and lastly, in the imperfect production or entire suppression of one of the thecæ, as in *Westringia*, *Anisomeles*, and *Maranteæ*.

Increased development may in like manner be confined to the dilatation, elongation, or division of the connecting portion of the filament, of which examples occur in many *Scitamineæ*, *Orchideæ* and *Acanthaceæ;* it may consist in
214] the elongation of the thecæ either above or below the connecting filament; in an increased number of divisions of each theca by longitudinal, transverse, or oblique processes of the receptacle of the pollen, as in several genera of *Orchideæ* and *Laurinæ;* or in the persistence of part of the cells in which the pollen is formed, as in *Ægiceras*.

Reduced and increased development of different parts may co-exist in the same organ, as in the bifid or incumbent anthera with contiguous thecæ; in the extraordinary dilatation of the connecting portion of the filament, while one of the thecæ is abortive or imperfect, as in the greater number of *Salviæ;* or in the thecæ being confluent, while

whether in the simple or compound state, they become always inclosed, and, before fecundation at least, are completely protected from the direct action of light and of the atmosphere.

In *Coniferæ* and *Cycadeæ*, however, according to the view I am disposed to take of them (*Tuckey's Congo*, *append. p.* 454, *antè*, *p.* 138), this is not entirely the case. But these two families will perhaps be found to differ from all other phænogamous plants in the more simple structure both of their ovaria and antheræ.

the polliniferous cells are at the same time persistent, as in certain species of *Viscum*.

The deviations from the regular mode of bursting are also numerous; in some cases consisting either in the aperture being confined to a definite portion, generally the upper extremity, of the longitudinal furrow, as in *Dillenia* and *Solanum;* in the apex of each theca being produced beyond the receptacle of the pollen into a tube opening at top, as in several *Ericinæ;* or in the two thecæ being confluent at the apex, and bursting by a common foramen or tube, as in *Tetratheca*. In other cases a separation of determinate portions of the membrane takes place, either the whole length of the theca, as in *Hamamelideæ* and *Berberideæ ;* or corresponding with its subdivisions, as in several *Laurinæ;* or lastly, having no obvious relation to internal structure, as in certain species of *Rhizophora*.

The regular structure may also be altered or disguised by the union of two or more stamina; the thecæ of each anthera either remaining distinct and parallel, as in *Myristica*, *Canella*, and in several *Aroideæ ;* being divaricate and united, as in *Cissampelos ;* or absolutely separate, by division of the filament, as in *Conospermum* and *Synaphea*.

It is unnecessary for my present purpose to enter into [215
a more minute account of the various structures of stamina, most of which appear to me easily reducible to the type here assumed.

The precise relation of the anthera of *Rafflesia*, however, to this type is so far from being obvious, that at least three different opinions may be formed respecting it.

According to one of these, each actual anthera would be considered as composed of several united stamina. But in adopting this opinion, which is suggested solely by the existence and disposition of the cells of the anthera, it seems also necessary to consider the apparently simple flower of *Rafflesia* as in reality compound, and analogous to the spike of an *Aroidea ;* the pistilla, if present, being consequently to be looked for not in the centre but in the circumference. On attending, however, to the whole external structure of the flower, as well as to the disposition of vessels, this supposition will, I conclude, appear still more improbable than that in support of which it is adduced.

A second opinion, diametrically opposite to the former, would regard the anthera of *Rafflesia* as only half a regular anthera, whose two thecæ are separated by portions of the united filaments, which, being produced beyond the antheræ, together form the crenated limb of the column.

This view, though less paradoxical than the first, will hardly be considered as affording so probable an explanation of structure as the third opinion; according to which each anthera would be regarded as complete, made up of two united thecæ, opening by a common foramen, and internally subdivided into numerous vertical cells by persistent portions of the confluent receptacles of the pollen; a structure not perhaps essentially different from that of certain antheræ more obviously reducible to the supposed type.

Even in adopting this opinion, a question would still
216] remain respecting the limb of the column under which the antheræ are inserted; namely, whether it is to be viewed as an imperfectly developed stigma, or as made up of processes of the united filaments. In support of the former supposition the nearly similar relation of the sexual organs in certain *Asarinæ* may be adduced; and in favour of the latter, not only their disposition and form in other plants of the same natural family, but also the vascular structure of the column itself; the limb deriving its vessels from branches of the same fasciculi that supply the antheræ (*plate* 18 (20), *f.* 1). If this latter view, however, of the origin of the limb were admitted, it might be considered not altogether improbable, that even the corniculate processes of the disk of the column, each of which has a central vascular cord, are of the same nature. For if, on the other hand, these processes are to be regarded as imperfect styles or stigmata, their number and disposition would indicate a structure of ovarium to be found only in families to which it is not probable at least that *Rafflesia* can be nearly related, as *Annonaceæ* and the singular genus

Eupomatia,[1] which I have placed near that natural order.

Another point to be inquired into connected with the same subject is, in what manner the impregnation of the female flower is likely to be effected by antheræ so completely concealed as those of *Rafflesia* seem to be in all states of the flower; for it does not appear either that they can ever become exposed by a change in the direction of the limb under which they are inserted, or even that this part of the column in any stage projects beyond the tube of the perianthium.

It is probable, therefore, that the assistance of insects is absolutely necessary; and it is not unlikely, both as connected with that mode of impregnation and from the structure of the anthera itself, that in *Rafflesia* the same economy obtains as in the stamina of certain *Aroideæ*, in which it has been observed that a continued secretion and [217
discharge of pollen takes place from the same cell; the whole quantity produced greatly exceeding the size of the secreting organ.

The passage of the pollen to the bottom of the flower, where it is more easily accessible to insects, seems likewise to be provided for, not only by the direction of the antheræ, but also by the form of the corresponding cavities in the neck of the column, in the upper part of which they are immersed.

That insects are really necessary to the impregnation of *Rafflesia*, is confirmed by Dr. Arnold's statement respecting the odour of the plant, by which they may be supposed to be attracted, and also by the fact of the swarms actually seen hovering about and settling in the expanded flower.

The structure of *Rafflesia* is at present too imperfectly known to enable us to determine its place in the natural system. I shall, however, offer some observations on this question, which can hardly be dismissed without examination.

As to which of the two primary divisions of phænoga-

[1] Flinders's *Voyage*, ii, *p.* 597 (*Antè*, *p.* 73), *tab.* 2.

mous plants the genus belongs, it may, I think, without hesitation be referred to *Dicotyledones;* yet if the plant is parasitic, and consequently no argument on this subject to be derived from the structure of the root, which is exactly that of the Vine,[1] its exclusion from *Monocotyledones* would rest on no other grounds, that I am able to state, than the quinary division of the perianthium, which in other respects also bears a considerable resemblance to that of certain dicotyledonous orders, the number of stamina, and the ramification of vessels in the bracteæ.

Assuming, however, that *Rafflesia* belongs to *Dicotyledones,*
218] and considering the foliaceous scales which cover the unexpanded flower, both from their indefinite number and imbricate insertion as bracteæ, and consequently the floral envelope as simple, its comparison with the families of this primary division would be limited to such as are apetalous; either absolutely as *Asarinæ;* those of a nature intermediate between the apetalous and polypetalous, in which the segments of the perianthium are generally, though not always, disposed in a double series, as *Passifloreæ, Cucurbitaceæ,* and *Homalinæ*; or those which have a simple coloured floral envelope, but are decidedly related to polypetalous families, as *Sterculiaceæ.*

With *Asarinæ,* the only truly apetalous order to which it seems necessary to compare it, *Rafflesia* has several points of resemblance, especially in the structure of the central column. In *Aristolochia* the antheræ, though only six in number, are in like manner sessile, and inserted near the apex of a column formed by the union of stamina and pistillum. The mere difference in the number of stamina seems to be of no importance in the present question, there being twelve in *Asarum;* and in *Thottea,* a genus certainly belonging to this family, though referred by Rottböll to *Contortæ,*[2] the stamina are not only still more numerous, but are disposed in a double circular series one above the other; an arrangement which may perhaps be considered

[1] Compare the magnified section of the Root, *tab.* 20 (22), *f.* 8, with that of the Vine in Grew's Anat. *tab.* 17.

[2] Thottea grandiflora. *Rottböll in Nov. Act. Soc. Reg. Hafn.* ii, *p.* 529, *tab.* 2.

analogous to the concentric series of processes in the apex of the column of *Rafflesia*.

In all these genera of *Asarinæ* and in *Bragantia* of Loureiro, which is also referable to the same order, the flowers are hermaphrodite; but in *Cytinus*, which, if not absolutely belonging to this order, is at least very nearly related to it, they are diclinous.

The affinity is also in some degree confirmed by the appearance of the inner surface of the tube of the perianthium of some *Asarinæ*, especially *Aristolochia grandiflora*, and by the thickening or annular projection of the faux in the [219
same plant, as well as in a new species of *Bragantia* discovered in Java by Dr. Horsfield.

It may also be noticed in support of it, that some of the largest flowers which were known before the discovery of *Rafflesia* belong to *Asarinæ*, as those of *Aristolochia grandiflora*, and particularly *Aristolochia cordiflora* of Mutis, which, according to M. Bonpland, are sixteen inches in diameter, or nearly half that of our plant.[1]

The first objection that occurs to this approximation is the ternary division of the perianthium in the regular flowered genera of *Asarinæ*, opposed to its quinary division in *Rafflesia*; but in *Cytinus* it is divided into four segments, a number more generally connected in natural families with five than with three.'

A second objection would exist, if it be considered more probable that the ovarium of *Rafflesia* is superior, or free, than inferior, or cohering with the tube of the perianthium.

There is indeed nothing in the structure of the column itself indicating the particular position of the ovarium. But if it be admitted, that a base of a form equally calculated for support should exist in the female flower, as is found in the male, it might perhaps be considered somewhat more probable that such a base should be connected with a superior than with an inferior ovarium.

Even admitting this objection, however, it would be considerably weakened, on the one hand, by allowing that

[1] *Humboldt Bonpl. et Kunth Nov. Gen. et Sp.* ii, *p.* 118.

Nepenthes, which has a superior ovarium, is related to *Asarinæ*, as I am inclined to believe; and on the other, by considering *Homalinæ*, whose ovarium is inferior, as allied to *Passifloreæ*, the order with which I shall now proceed to compare *Rafflesia*.

The comparison is suggested by the obvious resemblance between the perianthium of our genus, and that of certain
220] species of *Passiflora* itself; or of other genera of the order, as *Deidamia*, in which the inner series of segments is wanting. Thus, they agree essentially, and even remarkably, in æstivation of perianthium: the corona of *Rafflesia* may be compared with that of *Murucuia*, and the two annular elevations at the base of the column with the processes of like origin and nearly similar form in some species of *Passiflora*. The affinity is also supported by the position of the stamina on a central column.

The peculiar structure of antheræ in *Rafflesia* can hardly be regarded as an objection of much weight to the proposed association; and it will at least almost equally apply to any other family with which this genus may be compared.

If the concentric processes on the disk of the column in our plant are to be regarded as indications of the number and disposition of pistilla, or of the internal structure of ovarium in the female flower, they present a formidable objection to its affinity with *Passifloreæ*, in all of which the ovarium is unilocular with parietal placentæ. If, however, these processes were considered as inner series of imperfect stamina, the objection derived from their number and arrangement merely, would be comparatively slight; for in some genera of *Passifloreæ*, particularly in *Smeathmannia*,[1] the stamina are also numerous and perhaps even indefinite.

[1] As *Smeathmannia* forms a very remarkable addition to the order in which I have proposed to place it, and is still unpublished; I shall here give its characters, and add a few remarks in support of this arrangement.

SMEATHMANNIA. *Soland. Mss. in Biblioth. Banks.*

Ord. Nat. Passifloreæ. *Br. in Tuckey's Congo, p.* 439. (*Antè p.* 121.)

Syst. Linn. Polyandria Pentagynia.

CHAR. GEN. *Perianthium* duplex, utrumque 5-partitum; *exterius* semicalycinum persistens; *interius* petaloideum marcescens. *Urceolus* simplex, membranaceus, ex ipsa basi perianthii. *Stamina* numerosa, distincta, apici columnæ

It has been already remarked, that there is nothing [221
in the structure of the column in *Rafflesia* to enable us to
determine the position of the ovarium in the female flower; [222
but that from another consideration there seems a somewhat greater probability of its being superior. If, however, it were even inferior, the objection to the affinity in question would not be insuperable, the relationship of *Homalinæ* to *Passifloreæ* being admitted.

If *Napoleona* or *Belvisia* be really allied to *Passifloreæ*,

brevissimæ genitalium inserta. *Styli* 5. *Stigmata* peltata. *Capsula* inflata, quinquevalvis. *Semina* axibus valvularum inserta.

Frutices (*forsan decumbentes*). Folia *alterna simplicia subdentata*, stipulis *lateralibus* (*utrinque solitariis geminisve*) *distinctis, callosis*. Flores *axillares subsolitarii, pedunculis, quandoque brevissimis, basi bracteolatis*. Urceolus *abbreviatus, ore denticulato*. Filamenta *simplici serie, viginti circiter*. Antheræ *incumbentes, lineares*. Capsula *chartacea*. Semina *axibus filiformibus valvularum subsimplici serie inserta, pedicellata, punctata, omnino* Passifloræ.

Patria. Africa æquinoctialis.

1. S. *pubescens*, ramis tomentosis, foliis oblongo-ovatis basi obtusis: adultis pube rara conspersis, urceolo barbato.

Smeathmannia pubescens. *Solander l. c.*

Loc. Nat. Guinea, prope Sierra Leone, *Smeathman*, *Afzelius*.

2. S. *lævigata*, ramis glabris, foliis oblongis ovatisve basi acutis: adultis glaberrimis utrinque nitidis, urceolo imberbi inciso.

Smeathmannia lævigata. *Soland. l. c.*

Loc. Nat. Guinea, prope Sierra Leone, *Smeathman*, *Afzelius*, *Purdie*.

3. S. *media*, ramis glabris, foliis obovato-oblongis basi obtusis: adultis utrinque glabris subopacis.

Loc. Nat. Guinea, prope Sierra Leone, *Smeathman*.

Forsan varietas *S. lævigatæ*.

The affinity of *Smeathmannia* to *Paropsia* of M. du Petit Thouars will probably be admitted without hesitation; and its exact agreement in fruit in every important point, both with this genus and with *Modecca*, seems to leave no doubt of its belonging to *Passifloreæ*, with which it agrees in habit even better than *Paropsia*, and certainly much more nearly than *Malesherbia*, considered by M. de Jussieu (in *Flor. Peruv.* iii, *p.* xix) as belonging to the same family.

Smeathmannia differs then from the other genera of *Passifloreæ* solely in its greater number of stamina, which, however, may not be really indefinite; and an approach to this structure is already known to exist in an unpublished genus (*Thompsonia*) discovered in Madagascar by Mr. Thompson, of which the habit is entirely that of *Deidamia*, and whose stamina are equal in number to the divisions of both series of the perianthium.

But from *Smeathmannia* the transition is easy to *Ryania*, which differs chiefly in its still greater number of stamina, in the want of petals or inner series of perianthium, in the single style being only slightly divided, and in the form of its placentæ.

And *Ryania*, although it has a superior ovarium, may even be supposed to be related to *Asteranthos* and *Belvisia*, if the fruit of these two genera should prove to be unilocular with several parietal placentæ.

which is very doubtful, however, and can only be determined by an examination of the fruit, it may also be compared with *Rafflesia*. At first sight this singular genus seems to resemble our plant in several respects, particularly in the manner of insertion of its sessile flower into the branch, in the bracteæ surrounding the ovarium, the confluence and dilatation of its filaments, and in the existence of a double corona. But some of these points are obviously unimportant; and the comparison between the corona of the great flower and the double corolla of *Belvisia* will probably be considered paradoxical.[1]

It seems unnecessary to compare *Rafflesia* with *Cucurbitaceæ*, to which it could only be considered as approaching, if its affinity to *Aphyteia* should appear probable, and the relationship of that genus to *Cucurbitaceæ*, suggested chiefly by the structure of antheræ, were at the same time admitted.

223] The points of agreement between *Rafflesia* and *Sterculiaceæ* are the division and form of the coloured perianthium, the sessile antheræ terminating a column, and the separation of sexes.

[1] M. de Beauvois, in his account of *Napoleona* (*Flore d'Oware* ii, *p.* 32), has mentioned a genus allied to it, which has been since published by M. Desfontaines under the name of *Asteranthos*. These two genera are without doubt nearly related; and, even independent of the structure of fruit, which in both remains to be ascertained, possess sufficient characters to separate them from every known family, as M. de Jussieu is disposed to think; and certainly from *Symploceæ*, where M. Desfontaines has placed them.

In adopting the generic name proposed by M. Desvaux for *Napoleona*, this order may be called

BELVISEÆ.

Calyx monophyllus, limbo diviso, persistens. *Corolla?* monopetala, plicata, (multiloba vel indivisa; simplex v. duplex) decidua. *Stamina* vel definita v. indefinita; basi corollæ inserta. *Ovarium* inferum. *Stylus* 1. *Stigma* lobatum v. angulatum. *Pericarpium* baccatum, polyspermum.

Frutices (Africæ æquinoctialis; an etiam Brasiliæ?) *foliis alternis integerrimis exstipulatis, floribus axillaribus lateralibusve solitariis.*

BELVISIA, *Desvaux in Journal de Botanique appliq.* iv, *p.* 130.

Napoleona, *Palisot de Beauvois Flore d'Oware* ii, *p.* 29.

Calyx 5-*fidus*. *Corolla?* duplex; *exterior* indivisa; *interior* (e staminibus sterilibus connatis formata?) multifida. *Stamina: Filamenta* 5 dilatata biantherifera.

ASTERANTHOS, *Desfont. in Mem. du Mus.* vi, *p.* 9, *tab.* 3.

Calyx multidentatus. *Corolla?* simplex multiloba. *Stamina* indefinite numerosa distincta.

On these resemblances, however, I am not disposed to insist; and I am even persuaded that there is here no real affinity; though I confess I have no other objections to state to it than the valvular æstivation of the perianthium, and the absence both of the corona and of the annular elevations at the base of the column in *Sterculiaceæ*.

To conclude this part of my subject, I am inclined to think that *Rafflesia*, when its structure is completely known, will be found to approach either to *Asarinæ* or *Passifloreæ*; and that, from our present imperfect materials, notwithstanding the very slight affinity generally supposed to exist between these two orders, it cannot be absolutely determined to which of them it is most nearly allied.

The only question that remains to be examined respecting *Rafflesia* is, whether the flower with its enveloping bracteæ and reticulate base do not together form a complete plant parasitic on the root from which it springs?

That such was probably the case, occurred to me on [224
first inspecting the flower bud; the opinion being suggested not only by the direct origin of the flower from the root, but more particularly by the disposition, texture and colour of the bracteæ; in which it so nearly resembles certain plants known to be parasites, as *Cytinus*, *Cynomorium*, *Caldasia* of Mutis,[1] *Balanophora*, and *Sarcophyte*.

In this opinion I was confirmed on seeing the figure of the plant mentioned in Dr. Arnold's letter, as probably related to the Great Flower, though not more than three inches in diameter.

The plant in question, which had been found in Java by Dr. Horsfield several years before the discovery of *Rafflesia*

[1] In the Journal of Science, vol. iii. p. 127, from El Semanario del Nuevo Reyno de Granada, for 1810. To this genus belong *Cynomorium jamaicense*, and perhaps *cayanense* of Swartz, an unpublished species from Brazil, and some other plants of equinoctial America. Before the appearance of *Caldasia* in the Journal of Science, I was aware that these plants formed a genus very distinct from *Cynomorium* (Journal of Science, iii, p. 129), but I had not given it a name, which is still wanting, that of *Caldasia* having long been applied to a very different and well known genus.

The new name, however, may be left to M. Richard, who is about to publish, and who will no doubt illustrate with his usual accuracy, the plants formerly referred to *Cynomorium*, of one of the species of which (*C. cayanense*) he is himself the discoverer.

Arnoldi, only, however, in the unexpanded state, is represented in the figure referred to as springing from a horizontal root in the same manner as the Great Flower; like which also it is enveloped in numerous imbricate bracteæ, as having a perianthium of the same general appearance, with indications of a similar entire annular process or corona at the mouth of the tube, a pustular inner surface, and a central column terminated by numerous acute processes.
225] It is therefore unquestionably a second species of the same genus:[1] but the branch with leaves, which, though separately represented in the drawing, is considered as proceeding from the same root, appears to me, on an examination of the specimen figured, to belong to a species of *Vitis*: and on mentioning my supposition respecting the Great Flower to Dr. Horsfield, he informed me he had observed this second species of the genus also connected with leaves of a different kind, and which seemed likewise to be those of a *Vitis*.[2]

Even with all the evidence now produced, I confess I was inclined, on a more minute examination of the buds of *Rafflesia Arnoldi*, to give up the opinion of its being a parasite; on considering, first, the great regularity of the reticulate base, which, externally at least, seemed to be merely a dilatation of the bark of the root: secondly, the nearly imperceptible change of structure from the cortical part of the base to the bracteæ in contact with its upper elevated margin: thirdly, the remarkable change of direction and increased ramification of the vessels of the root at the point of dilatation; a modification of structure which must probably have taken place at a very early stage of

[1] This second species may be named *Rafflesia Horsfieldii*, from the very meritorious naturalist by whom it was discovered. At present, however, the two species are to be distinguished only by the great difference in the size of their flowers; those of the one being nearly three feet, of the other hardly three inches in diameter.

[2] Isert (in *Reise nach Guinea, p.* 283) mentions a plant observed by him in equinoctial Africa, parasitic on the roots of trees, consisting, according to the very slight notice he has given of it, almost entirely of a single flower of a red colour, which he refers to the Linnean class Icosandria, and compares in appearance, I suppose in the young state, to the half of a Pine-cone. It is not unlikely that this plant also may be really allied to *Rafflesia*, the smaller species of which it probably resembles in appearance.

its growth: and lastly, on finding these vessels in some cases penetrating the base of the column itself (*plate* 20 (22), *f*. 1).

But to judge of the validity of these objections, it became necessary to examine the nature of this connection in plants known to be parasitic on roots; in those especially, which [226
in several other respects resemble *Rafflesia*, as *Cytinus*, *Aphyteia*, *Cynomorium*, and *Balanophora*. On this subject I cannot find that a single observation has hitherto been made, at least with respect to the genera now mentioned. Sufficient materials, indeed, for such an investigation are hardly to be expected in collections, in which the parasite is most frequently separated from the root; and even when found in connection with it, is generally in a state too far advanced to afford the desired information. I consider myself fortunate, therefore, in having obtained specimens of several species where the union is preserved; and the result of the examination of these, though not completely satisfactory, has been to lead me back to my first opinion, namely, that the Great Flower is really a parasite, and that the root on which it is found probably belongs to a species of *Vitis*.

An account of some of the more remarkable of this class of parasitic plants, to which a few years ago I had paid particular attention, may hereafter form the subject of a separate communication. At present I shall confine myself to such general observations on the class as relate to the question respecting *Rafflesia*.

In the first place, plants parasitic on roots are chiefly distinguishable by the imperfect development of their leaves and the entire absence of green colour; an observation which, as applying to the whole tribe, was I believe originally made by Linnæus.[1] In both these points they agree with *Rafflesia*.

A second observation which may be made respecting them is, that their seeds are small, and their embryo not only minute, but apparently imperfectly developed; in some cases being absolutely undivided, and probably acoty-

[1] *Fungus Melitensis*, *p*. 3. *Amœn. Acad*. iv, *p*. 353.

ledonous, even in plants which, from their other characters, are referable to dicotyledonous, or at least to monocotyledonous families.

227 In these points the structure of *Rafflesia* remains to be ascertained. In the mean time, however, if it be considered as a parasite, and as likely to agree with the other plants of the tribe in the state of its embryo, it may be remarked, with reference to the question of its affinities, that such a structure would approximate it rather to *Asarinæ* than to *Passifloreæ*.

My principal and concluding observation relates to the modes of union between the stock and the parasite. These vary in the different genera and species of the tribe, which may be divided into such as are entirely dependent on the stock during the whole of their existence, and such as in their more advanced state produce roots of their own.

Among those that are in all stages absolutely parasitic, to which division *Rafflesia* would probably belong, very great differences also exist in the mode of connection. In some of those that I have examined, especially two species of *Balanophora*,[1] the nature of this connection is such, as can only be explained on the supposition that the germinating seed of the parasite excites a specific action in the stock the result of which is the formation of a structure, either wholly or in part, derived from the root, and adapted to the support and protection of the undeveloped parasite; analogous therefore to the production of galls by the puncture of insects.

On this supposition, the connection between the flower of *Rafflesia* and the root from which it springs, though considerably different from any that I have yet met with, may also be explained. But until either precisely the same kind of union shall have been observed in plants known to
228 be parasitic, or, which would be still more satisfactory, until the leaves and fructification belonging to the root to which *Rafflesia* is attached shall have been found, its being

[1] *Balanophora fungosa* of Forster, and *B. dioica*, an unpublished species, lately sent by Dr. Wallich from Nepaul, where it was discovered by Dr. Hamilton, and also found in Java by Dr. Horsfield.

a parasite, though highly probable, cannot be considered as absolutely ascertained.[1]

ADDITIONAL OBSERVATIONS.

Read November 21st, 1820.

SINCE my paper on *Rafflesia*, or the Great Flower of Sumatra, was read to the Society, further information respecting it has been received from Sir Stamford Raffles and Mr. Jack, which will form an important addition to my former account.

Sir Stamford, in a letter to Mr. Marsden, states the following particulars:

"I find the *Krûbût* or Great Flower to be much more general and more extensively known than I expected. In some districts it is simply called *Ambun Ambun*. It seems to spring from the horizontal roots of those immense Climbers, which are attached like cables to the largest trees in the forest. We have not yet met with the leaves. The fruit also is still a desideratum. It is said to be a many-seeded berry, the seeds being found in connection with the processes on the summit of the pistillum. I have had buds brought in from Manna, Sillibar, the interior of Bencoolen and Laye: and in two or three months we expect the full-blown flower. It takes three months from the first appearance of the bud to the full expansion of the flower; and the flower appears but once a year, at the conclusion of the rainy season."

The first communication from my friend Mr. Jack con- [229
sisted of a description of recent flower-buds, at that time regarded by him as hermaphrodite, but which he has since ascertained to be male. It is unnecessary to introduce this

[1] Annals of Philosophy for September 1820, p. 225.

description here, as it essentially agrees with that already given, and may also be considered as superseded by the important information contained in the following letter, which I have more recently received from the same accurate botanist.

BENCOOLEN, *June* 2, 1820.

"MY DEAR SIR,—Since I wrote you last I have ascertained several particulars respecting the Gigantic Flower of Sumatra, additional to those contained in the account forwarded by Sir Stamford Raffles to Mr. Marsden, and by him communicated to you, which it may be interesting to you to know.

"Numerous specimens, in every stage of growth, have been sent from various parts of the country, which have enabled me to ascertain and confirm every essential point. The first and most unexpected discovery is, that it has no stem of its own, but is parasitic on the roots and stems of a ligneous species of *Cissus* with ternate and quinate leaves: I have not ascertained the species.[1] It appears to take its origin in some crack or hollow of the stem, and soon shows itself in the form of a round knob, which, when cut through exhibits the infant flower enveloped in numerous bracteal sheaths, which successively open and wither away as the flower enlarges, until, at the time of full expansion, there are but a very few remaining, which have somewhat the appearance of a broken calyx. The flowers I find to be unisexual, which I did not before suspect, and consequently diœcious. The male I have already described. The female
230] differs very little in appearance from it, but totally wants the globular anthers, which are disposed in a circle round the lower side of the rim or margin of the central column of the male.

"In the centre of this column or pistillum in the female are perceived a number of fissures traversing its substance without order or regularity, and their surfaces are covered

[1] Mr. Jack has since determined it to be *Cissus angustifolia* of Roxburgh, *Fl. Ind.* i, *p.* 427.

with innumerable minute seeds. The flower rots away not long after expansion, and the seeds are mixed with the pulpy mass.

"The male and female flowers can be distinguished by a section not only when mature, but at every stage of their progress. I have made drawings of every essential part, which I hope soon to be able to send home, together with a further account than I have yet had leisure to make.

"I remain, &c.,

"WILLIAM JACK."

The two principal desiderata respecting *Rafflesia*, namely the satisfactory proof of its being a parasite, and the discovery of the female flower, are now therefore supplied.

Additional information, however, on several points is still wanting to complete the history of this extraordinary plant.

Thus, it would be interesting, by a careful examination of the buds in every stage, to trace the changes produced in the root by the action of the parasite, and especially to ascertain the early state of the reticulate base, which I have ventured to consider as a production of an intermediate nature, partly derived from the root itself, and which I suppose will be found to exist before the bracteæ become visible.

Further details are also wanting respecting the circumstance of its being found both on the roots and stems of the *Cissus* or *Vitis*,[1] no instance being, I believe, at present, [231 known of parasites on roots, which likewise originate from other parts of the plant.

Many important particulars remain to be ascertained respecting the *Pistillum*.

From Mr. Jack's account it appears that the seeds are found in the substance of the column; in other words, that the ovarium is superior. But as I have formerly remarked, that in the male flower the same internal structure seems to be continued below the apparent base of the column, it is

[1] As these two genera differ from each other merely in number of parts, I have formerly proposed to unite them under the name of *Vitis*. (*Tuckey's Congo*, *p.* 465. *Antè*, *p.* 151.)

possible that in the female the production of seeds may extend to an equal depth; the ovarium would then become essentially inferior, as far at least as regards the question of the affinity of the plant. This point would be determined by a description of the unimpregnated ovarium, a knowledge of whose structure is also wanting to enable us to understand the nature of the ripe fruit, and especially the origin and direction of the fissures, on the surfaces of which the seeds are produced.

It is desirable likewise to have a more particular description of the *Stigma*, to which Mr. Jack seems to refer both the corniculate processes of the disk, and the undivided limb of the column. These parts in the male flower have no evident papulose or secreting surface; for the hispid tips of the processes can hardly be regarded as such. But it is not likely that in the female flower they are equally destitute of this, which is the ordinary surface of a stigma; and it appears to me more probable that such a surface should be confined to a definite portion, probably the tips, of the corniculate processes, than that it should extend over every part of the apex of the column.

Whatever may be the fact, my conjecture respecting these processes being possibly imperfect stamina is completely set aside; though it is still difficult to connect their number and arrangement with the supposed structure of ovarium.

232] Until these points are ascertained, and the seeds have been examined, the question of the affinities of the genus will probably remain undetermined. In the mean time it may be remarked, that as far as the structure of the fruit of *Rafflesia* is yet understood, it may be considered as in some degree confirming the proposed association of the genus with *Asarinæ*; especially with *Cytinus*, in which the ovarium is unilocular, with numerous parietal placentæ extending nearly to the centre of the cavity, and having their surfaces covered with minute ovula.

From the appearance of the ripe fruit of *Aphyteia*, a similar structure may be supposed to exist also in that genus, of which, however, the unimpregnated ovarium has not been examined. But these two genera are parasitic on roots, and have also their stigmata remarkably developed; and although *Rafflesia* probably differs from both of them in having a superior ovarium, I have endeavoured to show that this difference alone would not form an insuperable objection to their affinity.

EXPLANATION OF THE PLATES RELATING TO RAFFLESIA ARNOLDI.

Plate 13 (XV.)

The expanded Flower reduced to somewhat less than $\frac{1}{3}$ of its natural size; the scale given on the plate being too long by nearly $\frac{1}{7}$.

Plate 14 (XVI).

A Flower-bud covered with its bracteæ, of the natural size.

Plate 15 (XVII). [233

The underside of the same Bud; to show the root, the reticulate base with the circular elevation in which it terminates, and the origin of the outer bracteæ. Natural size.

Plate 16 (XVIII).

Flower-bud, of which the bracteæ, whose insertions are shown, are removed. Natural size.

Plate 17 (XIX).

A different view of the Bud in the same state, to show the æstivation and veins of the segments of the perianthium. Natural size.

Plate 18 (XX).

Fig. 1. A vertical section of the Bud deprived of its bracteæ: exhibiting the principal vessels of the column and perianthium, and the structure of the root, especially the change in the direction, increased ramification and termination of its vessels at the base of the parasite. Natural size.

Fig. 2. One half of the vertically-divided perianthium of the same Bud, in which the internal surface of the tube, corona and segments is shown. Natural size.

Plate 19 (XXI).

Fig. 1. A Flower-bud, its bracteæ and perianthium being removed, to show the column with the two annular processes at its base. Natural size.

Fig. 2. A portion (about $\frac{1}{5}$) of the column, of which part of the limb is removed, to show the cavities of the neck, into which the antheræ are received. Natural size.

Fig. 3. The portion of the Limb removed from fig. 2, with its antheræ immersed in their proper cavities. Natural size.

234] Fig. 4. An Anthera, magnified three diameters, as are figures 5, 6, 7, and 8.

Fig. 5. A transverse section of the same above the middle.

Fig. 6. A transverse section of the same below the middle.

Figs. 7, 8. Vertical sections of the same.

Fig. 9. Pollen, magnified 200 diameters.

Plate 20 (XXII).

Fig. 1. A vertical section of part of the base of the smaller Flower-bud, showing the vessels of the root, some of which appear to penetrate the substance of the parasite. Natural size.

Figs. 2, 3. Portions of the column of the expanded Flower, nearly corresponding with those of the Bud, in *Pl.* 19 (21), *f.* 2 and 3. Natural size.

Fig. 4. Anthera of the expanded Flower, magnified 3 diameters, as are figures 5 and 6.

Fig. 5. Transverse section of the same below the middle.

Fig. 6. Vertical section of the same.

Fig. 7. Pollen of the expanded Flower, magnified 200 diameters.

Fig. 8. A transverse section of the Root, magnified 3 diameters.

ON THE

FEMALE FLOWER AND FRUIT

OF

RAFFLESIA ARNOLDI

AND ON

HYDNORA AFRICANA.

BY

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1844.

ON THE FEMALE FLOWER AND FRUIT OF RAFFLESIA ARNOLDI, &c.

READ JUNE 17TH, 1834.

THE principal object of the present communication is to complete, as far as my materials enable me, the history of *Rafflesia Arnoldi*, the male flower of which is described and figured in the thirteenth volume of the Society's Transactions.

The specimens from which this additional information has been obtained, as well as those formerly described, were received from the late Sir Stamford Raffles; and for the drawings so beautifully representing their structure, I am indebted to the same distinguished botanical painter and naturalist, who obligingly supplied those already published.

In my former essay some observations were made on the affinities of *Rafflesia*, a subject on which I could not then speak with much confidence. From such knowledge as I possessed, however, I ventured to state that this genus appeared to be most nearly allied to *Asarinæ*, and especially to *Cytinus*, on the one hand, and on the other to *Aphyteia* or *Hydnora*, an equally remarkable parasite of South Africa, but the structure of which was at that time very imperfectly understood.

An examination of complete specimens of *Hydnora africana* has confirmed this view; and as there are points in its structure which seem to throw some light on one of the most difficult questions respecting *Rafflesia,* I have included an account of this genus in the present paper.

The accompanying drawings of *Hydnora africana*, which so admirably display its structure, were kindly made from these specimens by my lamented friend and fellow-traveller Mr. Ferdinand Bauer, when he revisited England in 1824; they were probably the last drawings he ever made of an
222] equally interesting and difficult botanical subject, and I consider them his best.[1]

Since the publication of my former memoir, much light has been thrown on the structure and economy of *Rafflesia*, chiefly by Dr. Blume, who in his 'Flora Javæ' has given a very full history of a nearly related species, his *Rafflesia Patma*, as well as of *Brugmansia*, a parasite of similar economy, very distinct as a genus, but evidently belonging to the same natural family. Before, however, noticing more particularly what has been done by others, I shall resume the subject where I left it at the conclusion of my former memoir, in adverting to those points which I then regarded as the principal desiderata in the botanical history of this extraordinary plant.

The first of these related to the reticulate base, which I ventured to consider a production of an intermediate kind, or rather as one derived from the stock or root of the Vine,

[1] Since this paper was read, the Linnean Society have had to lament the loss of Francis Bauer, who died in 1841 at the advanced age of eighty-three. Like his brother Ferdinand, he continued, till within a short time of his death, to take the same interest in those scientific investigations which formed the constant occupation and the chief pleasure of a long life.

The figures of *Rafflesia* and *Hydnora*, which so admirably illustrate, and form the more valuable part of this communication, are among the best specimens of the unrivalled talent of the two brothers Francis and Ferdinand Bauer, who, as botanical painters, equally united the minute accuracy of the naturalist with the skill of the artist.

To this brief note I may be permitted to add how fortunate I consider myself in having so long enjoyed the friendship and so often been indebted for the important assistance of these two distinguished men, whose merits in the branch of art which they cultivated have never been equalled, and to both of whom the illustrations of the present paper, so happily connected, may form an appropriate monument, the work of their own hands.

but excited and determined in its form and nature by the specific stimulus of the parasite. I expected, therefore, to find it existing in the form of a covering to the bracteæ in the early state, as in *Cytinus*. This point has been fully confirmed, and is well shown in Mr. Bauer's drawings of the very young buds.[1] From the same figures it appears that the parasite is occasionally found on the stems of the Vine, as Dr. Jack had stated, but which seemed to me to require confirmation.

Of the structure of the female flower of *Rafflesia* I [223 judged entirely from Dr. Jack's account in his letter published in my former essay; and respecting this structure several important points, which even his subsequent description in the 'Malayan Miscellany' did not supply, were regarded as undetermined.

Whether the ovarium is wholly distinct from the calyx or cohering with it at the base, was the first of these points which required further examination. The specimens now prove it to be chiefly superior or free in the flowering state, and wholly so in the ripe fruit.

The internal structure of the ovarium, especially the origin and arrangement of the numerous ovuliferous surfaces or placentæ, I considered one of the principal desiderata. Dr. Jack's account of these placentæ, which, as far as it extends, is essentially correct, is confirmed by Dr. Blume's description and figures of *Rafflesia Patma*, as well as by the more complete drawings which accompany the present paper. The important question, however, namely the analogy of this apparently singular arrangement with ordinary structure, may be regarded as still in some degree obscure.

The transverse section of the ovarium presenting an indefinite number of cavities irregular in form, having no apparent order, and over the whole of whose surfaces the ovula are inserted, is hardly reconcileable to the generally received notions of the type of the female organ; and as

[1] That the whole of this covering belongs to the stock, is proved by its containing those raphides or acicular crystals which are so abundant in the root of the *Vitis* or *Cissus*, and which are altogether wanting in the parasite.

these cavities exist to the same extent and with similar irregularity from centre to circumference, they may with equal probability be considered as originating from the axis or from the parietes of the ovarium. The vertical section too, if viewed without reference to the external development of the top of the column, exhibits a structure equally anomalous. If, however, the corniculate processes terminating the disc of the column be regarded as styles, which is surely the most obvious and not an improbable view, their arrangement would lead to the supposition that the ovarium is composed of several concentric circular series of simple pistilla, each having its proper placenta, bearing ovula over its whole surface. But the structure is so much obscured by the complete confluence of the supposed component parts, that this view might not at once present itself. It is readily suggested, however, by the seemingly analogous structure of *Hydnora*, in which the cylindrical placentæ, whose number is considerable and apparently indefinite, are all pendulous from the top of the cavity, neither cohering
224] with its sides or base, wholly distinct from each other, and uniformly and densely covered with ovula.

But although this is the most obvious view suggested by *Hydnora*, a more careful examination, especially as to the relation of stigmata to placentæ, leads to a very different notion of the composition of the ovarium in that genus: for as the placentæ correspond with, and may be said to be continuations of the subdivisions of the stigmata, and as these stigmata appear to be three in number, each with numerous subdivisions diverging from the circumference towards the centre of the ovarium, and each of these subdivisions bearing one or more placentæ pendulous from its internal surface, the ovarium of *Hydnora* may be regarded as composed of three confluent pistilla, having placentæ really parietal, but only produced at the top of the cavity; the sides of which, however, exhibit no indication whatever of composition.

Between this most remarkable structure of *Hydnora* and that of *Cytinus* there is some, though not perhaps a very obvious analogy, each of the strictly parietal placentæ in the latter being subdivided into distinct lobes, as in many *Orchideæ*, a family which *Cytinus* also resembles in the structure of the seed, and probably in the mode of impregnation, though so widely different in almost every other respect.

It would certainly be difficult to reduce *Rafflesia* to the view here taken of the formation of the compound ovarium in these two genera; and it may therefore, perhaps, be said, that although the structure of *Hydnora*, in one important particular, suggests or confirms the more probable notion of the composition of ovarium in *Rafflesia*, as already stated,[1] it is in other respects very distinct.

Another point, which in my former paper I considered [225]
doubtful, namely the seat or limit of the stigmata, is not even now satisfactorily established; for the slender processes forming the hispid tips of the supposed styles, which have so much the appearance of the ultimate divisions of stigma, are merely hairs of a very simple structure, and exactly resembling those found in other parts of the column;

[1] My confidence in this hypothesis respecting *Rafflesia* is greatly lessened on considering the structure of the female flower of a lately discovered species of the genus, namely, *Rafflesia Cumingii* or *Manilluna*, in which the style-like processes terminating the column are much fewer in number, and so arranged as to form a single circular series of about ten, not very distant from the limb, with only from one to three processes within it, which are placed near the centre, while the irregular cavities in the ovarium are evidently much more numerous, and in arrangement have no apparent relation to that of the supposed styles, there being as great complexity in the centre as towards the circumference. These relations between styles and ovarial cavities seem, according to the figures of *Rafflesia Patma*, to be reversed in that species, its styles being apparently more numerous than the cavities of the ovarium; and as even in *Rafflesia Arnoldi* their correspondence is far from obvious, it would seem that the number and arrangement of these processes afford no satisfactory evidence of the composition of the ovarium in any known species of the genus. But if the placentation of *Rafflesia Arnoldi* and *Cumingii*, notwithstanding the objections stated in the text (p. 404), be considered parietal, as Blume has described it in *R. Patma*, and as from his figures it seems actually to be in *Brugmansia*, there would still be no means of determining the exact degree of composition of ovarium in *Rafflesia*; for in no species of the genus is there the slightest indication afforded by the arrangement of cavities or ramification of the assumed placentæ, to mark any definite number of component parts. Similar objections apply with equal force to the adoption of that opinion which regards placentation as in all cases central or derived from the axis.

In conclusion, therefore, it may perhaps be said that *Rafflesia*, in the structure both of ovarium and antheræ, is not obviously reconcileable to any hypothesis hitherto proposed to account either for the origin or for a common type of the sexual organs of Phænogamous plants.

though in several of the specimens examined they were greatly altered in appearance, from a coating of mucous matter taken up and again deposited by the spirit in which the specimens were preserved.[1] A slight difference, indeed, seems to exist between the tissue of the apices of the styles and the other parts of their surface; hardly sufficient, however, to prove it to be stigma, though this is no doubt the probable seat of that organ.

The next point of importance in the female flower of *Rafflesia* is the structure and gradual development of the ovula. These, in the earliest state observed, consist of merely conical or subcylindrical papillæ, having a perfectly smooth surface as well as uniform internal substance.

The first perceptible change taking place in the papilla is a slight contraction at its summit, the upper minute contracted apex being the rudiment of the nucleus. Immediately below this contracted portion a dilatation is soon observable, which, gradually enlarging and becoming slightly hollowed, forms a cup in which the nucleus, also proportionally increased in size, is partly immersed. This cup, the rudiment of the future integument, continues gradually to enlarge, until it completely covers and extends considerably beyond the nucleus, but without cohering with it. If a transverse section is made near the slightly depressed
226] apex of this integument, an extremely minute perforation or capillary channel, extending to the free apex of the included nucleus, may be observed.

This account of the gradual development of the ovulum of *Rafflesia*, I believe, is in every essential point applicable to Phænogamous plants generally, except that here one coat only is developed. It is, however, in some important points different from the description given by M. Mirbel, who considers the nucleus in its earliest state as included in the integuments, which in the next stage open and dilate so as to leave it entirely exposed; they then, as he supposes, remain quiescent until the nucleus has considerably enlarged,

[1] See Mr. Bauer's representation of the hairs in this state, TAB. 22 (XXIII), figs. 3, 4, 5, 6, and 7.

when they again become active and increase in size until they once more completely cover it.

While the development, as I have here described it, of the nucleus and its integument in *Rafflesia* is going on, another change is at the same time gradually taking place, namely, at first a slight bending, which at last ends in a complete inversion, in the direction of the nucleus and its integument in regard to the placenta, with which, in this advanced stage, the perforated apex of the latter is nearly or absolutely in contact.

In this change of direction, the ovulum of *Rafflesia* resembles that of the far greater part of Phænogamous plants: the change, however, is effected in a way which is much less common, the curvature in *Rafflesia* taking place solely in the upper part of the funiculus, the direction of the inverted ovulum being parallel with, but distinct from, the portion below the curvature; whereas in Phænogamous plants generally, the curvature is produced in that part of the funiculus which is connate with the testa or outer integument. For this difference, a reason, perhaps, may be assigned; the integument which generally forms the testa or outer coat being in *Rafflesia* entirely wanting, or only indicated by the remarkable dilatation of the apex of the funiculus.[1]

In the more essential points of structure, the ovula of *Hydnora* and *Cytinus* agree with that of *Rafflesia*. They differ, however, in both these genera in retaining their original direction.

In *Hydnora* I have ascertained the perforation of the single integument and the position of the included nucleus, [227
but the very earliest stages I have not yet distinctly seen; while in *Cytinus*, in addition to the coat analogous to that of *Rafflesia* and *Hydnora*, a two-lobed or bipartite membrane is observable.

Of these three genera, I have hitherto observed the pollen

[1] The earlier production of the inner of the two coats generally present in the ovula of Phænogamous plants, and the absence of the outer in this and several other cases, will probably be considered a valid objection to the terminology of M. Mirbel.

or mucous tubes only in *Cytinus*, in which they pass along the surfaces of a definite number of cylindrical cords existing in the style until they reach the cavity of the ovarium, when they follow the direction of the placentæ and become mixed with the ovula, to which I have not yet, however, found them actually attached.[1]

The structure of the pericarpium and the ripe seed of *Rafflesia* have been satisfactorily ascertained from the examination of a single fruit found among the numerous flower-buds in various states which were received from Sumatra by Sir Stamford Raffles long after his return to England. In this fruit, which is very accurately represented of the natural size in Mr. Bauer's figure, the column, deprived entirely of its style-like processes, had become a compact fleshy mass, having deep fissures on its surface dividing it into nearly square lobes, somewhat resembling the surface of the dilated base of *Testudinaria*, and within, like the ovarium, exhibiting irregular cavities, whose surfaces were thickly covered with minute seeds.

These seeds, which are also beautifully shown in Mr. Bauer's figures, differ but little in form from the ovula of the expanded but unimpregnated flower; they are considerably larger, however, and the apex of the funiculus is still more dilated. From their great hardness, as well as from their internal structure, they appear to be quite ripe; and it is worthy of remark, that of the many thousands contained in the fruit, the very considerable portion seen were of uniform size and appearance.

The testa or outer integument, which is evidently that existing in the unimpregnated ovarium, is of such hardness and thickness that it may be termed a nut; it is of a chestnut colour, its surface regularly reticulate and deeply pitted, a depression occupying the centre of each areola.

The inner integument is a thin light-coloured membrane,
228] very slightly areolated, and of uniform surface. Within

[1] In a few cases where the supposed pollen-tubes were present I found them applied to the apices of the enlarged ovula. In some instances I have met with only a very loose tissue, consisting of elongated cells mixed with mucus, forming cords descending from the stigmata, and reaching to, but not extending beyond, the origin of the placentæ.

this the nucleus, of similar form and dimensions, seems to be more firmly attached at its upper extremity to the coat by a short and very slender funiculus.

The nucleus separated from its coat has an areolated surface, and at first appears to be entirely composed of a loose and uniform cellular tissue. But on a more careful examination this substance is found to contain another cellular body, of nearly cylindrical form, adhering with some firmness to the upper extremity of the including cellular mass, whose vertical axis it occupies for nearly three fourths of its length.

This inner body, which I regard as the *embryo*, consists of large cells, disposed nearly, but not with absolute regularity, in two longitudinal series, and so transparent, that it may be safely affirmed that there is no included body nor any perceptible difference in the contents of any of the component cells.

This account of the embryo differs in some respects from Mr. Bauer's representation of it, especially as to the point of attachment, and in the distinct appearance and transparency of cells.[1]

The seed of *Hydnora* in many essential points resembles that of *Rafflesia*. Its nucleus consists of a dense albumen, the cells of which are so disposed as to exhibit, when slightly magnified, a kind of radiation in whatever direction it is cut. This albumen is much denser than that of *Rafflesia*, the greater density arising, perhaps, from the unusual thickness of the walls of each cell, its cavity bearing so small a proportion to the supposed external dimensions of the cell as to give it the appearance of a nucleus or more opaque central body.[2]

Enclosed in the albumen a perfectly spherical embryo is

[1] I have therefore added to TAB. 23 (XXV), a circumscribed figure, marked R. Br., in which I have endeavoured to represent (but not very successfully) the structure as I have seen it.

[2] But these supposed cells with thickened walls, admitting them to have been originally distinct, are in the ripe seed nearly or entirely obliterated, so that the substance of the cartilaginous albumen consists of a uniform, semi-transparent mass, in which the more opaque nuclei or cells, containing minute granular matter, are, as it were, immersed.

found, consisting entirely of a more minute and much less dense cellular tissue. On the surface of this embryo I have observed no point marking original attachment, nor any
229] indication of a channel connecting it with the surface of the albumen, in the centre of which it is seated.

In *Cytinus*, in which I believe I have at length found ripe fruits, the seeds are extremely minute, and generally retain at their base the bipartite membrane more distinctly observable in the unimpregnated ovulum. To this membrane the name of arillus may be given; but it may also, and, perhaps, with greater probability, be considered the imperfect production of the testa or outer membrane.

The seed itself is elliptical, with a slight inequality at top indicating the depression or perforation observable in the ovulum. The single integument of the seed is easily separable from the nucleus, and by moderate pressure splits longitudinally and with great regularity into two equal portions; in texture it is a crustaceous membrane, indistinctly reticulate, the areolæ, when very highly magnified, appearing to be minutely dotted with a semi-opaque centre.

The nucleus, corresponding exactly in size and form with the integument, has its surface also reticulate, but the areolæ are not dotted; and it appears, as far as I can ascertain in so minute a body, to consist of a uniform cellular tissue, very exactly resembling the nucleus of an Orchideous plant.

The result of the comparison now made, and which might be extended to other points of structure of *Rafflesia*, *Brugmansia*, *Hydnora* and *Cytinus*, seems to be, that these four genera, notwithstanding several important differences, form a natural family to which the name of RAFFLESIACEÆ may be given; and that this family is again divisible into three tribes or sections:

The first *Rafflesieæ*, consisting of *Rafflesia* and *Brugmansia*, is distinguishable by the ovarium being either in part or wholly superior to the origin of the calyx, in its composition or internal structure, in the placentation and direction of the ovula, in the structure of the seed and in that of the antheræ.

The second section, *Hydnoreæ*, formed of *Hydnora* alone, is characterised by its completely adherent ovarium, singularly divided stigmata, the peculiar origin and structure of its pendulous placentæ, its embryo enclosed and seated in the centre of a dense albumen, and by the arrangement and structure of its antheræ.

In the third section, or *Cytineæ*, the placentæ are parietal, the ovarium is connate with the calyx, and the cellular [230 undivided embryo forms the whole mass of the seed, or is apparently destitute of albumen.[1]

That this third section is nearly related to *Asarinæ* seems to me unquestionable; if, therefore, its affinity to *Hydnora* and *Rafflesia* be admitted, the place of this singular family would be nearly established.

That *Rafflesia*, *Hydnora* and *Cytinus* do not essentially differ from many of the more perfectly developed Phænogamous plants in their vascular structure, I have satisfactorily ascertained, and there is no sufficient reason to doubt that the same observation may be extended to *Brugmansia*.

In my former paper, in treating of the composition of the

[1] To the third section of *Rafflesiaceæ*, *Apodanthes* and *Pilostyles* may perhaps be referred. These genera indeed agree with *Cytinus* in their unilocular ovarium with parietal placentation, in their cellular undivided embryo forming the whole mass of the seed, and in their adherent or semi-adherent ovarium, whose cavity in *Pilostyles* extends even below the insertion of the bracteæ. The existence of petals, however, in both, and especially in *Apodanthes*, will probably be considered as an objection of some weight to their absolute union with *Cytineæ;* and there is even an important difference in their placentation, the ovula being produced equally over the whole surface of the ovarial cavity, while in *Cytinus* the placentæ are distinct, definite in number, and subdivided into numerous lobes, nearly as in *Orchideæ*.

Whether *Apodanthes* and *Pilostyles* are to be included in the same genus, as Professor Endlicher (in Gen. p. 76) first conjectured, and as Mr. Gardner has more recently (in Hooker Ic., new ser. vol. iii, tab. 644) endeavoured to prove though not improbable, must, I think, remain somewhat doubtful so long as we are unacquainted with the male flower of *Apodanthes*. In the mean time this genus may be distinguished from *Pilostyles* by the singular insertion of its petals, which also differ remarkably in texture from the quadrifid persistent calyx, and by the two bracteæ of the flower being seated below the origin of an angular ovarial cavity, and which, after the falling off of the parasite, remain attached to the stock.

vascular bundles existing in various parts of *Rafflesia*, I too hastily assumed the absence of spiral vessels, the expression used evidently implying that I had satisfied myself of their non-existence in the fasciculi or bundles examined; instead of which I should only have stated that I had not been able to find them.

The absence of spiral vessels has since been affirmed by Dr. Blume with respect to his *Rhizantheæ*, consisting of *Rafflesia* and *Brugmansia;* and still more recently by Messrs. Endlicher and Lindley, who, overlooking probably the very positive statement of Dr. von Martius respecting *Langsdorfia*, have equally denied the existence of spiral vessels in *Balanophoreæ*; and partly, perhaps chiefly, determined by this supposed conformity and peculiarity of structure, have referred *Rafflesiaceæ* and *Balanophoreæ* to the same natural class.

231] I have in the first place to correct my own error respecting *Rafflesia*, in various parts of the female flower of which I have found spiral vessels of the ordinary structure, consisting of a single, easily unrolled fibre; and on re-examining the same specimen of the male flower respecting which my former assertion was made, I found these vessels equally distinct. Professor Meyer has already stated their existence in the procumbent stems or rhizomata of *Hydnora triceps;* in which I have also found them in *Hydnora africana*, as well as in other parts of the same species; and in *Cytinus* they are still more obvious.

I may also add, that wherever I had specimens of *Balanophoreæ* in a fit state for minute examination, I have never failed to find spiral vessels in various parts of their tissue, particularly in *Cynomorium coccineum* and *Helosis guianensis*.[1]

[1] Although in *Rafflesiaceæ* and in the genera at present referred to *Balanophoreæ* spiral vessels undoubtedly exist, in the greater number, indeed, sparingly, but in some cases in hardly reduced proportion, it may still perhaps be alleged, by those botanists who have proposed to unite both families into one natural class, that the vascular system of all these parasites is uniform and more simple than that of the far greater part of Phænogamous plants; that the spiral or slight modifications of it is the only form of vessel hitherto observed in any of them; and that the large tubes or vessels, with frequent contractions, corresponding imperfect diaphragms, and variously marked surface, which have

I may hereafter have an opportunity of entering fully [232] into the question whether *Rafflesiaceæ* and *Balanophoreæ*

received several names, as vasa porosa, punctata, vasiform cellular tissue, dotted ducts, &c., and which are so conspicuous in the majority of arborescent Phænogamous plants, have never been observed in any part strictly belonging to these parasites. But even admitting the non-existence of the large vessels here referred to, their absence will hardly be regarded as a sufficient reason for the union into one class of the two families in question, especially when it is considered—

First. That conformity in vascular structure, even when accompanied by peculiarity of tissue, does not always indicate, much less determine, botanical affinity. This is strikingly exemplified in *Coniferæ* and *Winteraneæ*, two families which, though so nearly agreeing in the uniformity and peculiarity of their vessels, and in both of which the large tubes referred to are wanting, yet differ so widely from each other in their organs of reproduction and in their leaves, that they may be regarded as placed at opposite extremities of the scale of *Dicotyledones*.

Secondly. That uniformity of vascular structure is not always found in strictly natural families. Thus many *tropical woody climbers* exhibit remarkable peculiarities of vascular arrangement not existing in the greater part of the families to which they respectively belong, but which peculiarities appear to have no influence whatever in modifying their reproductive organs.

Thus also in *Myzodendron*[1] the whole woody tissue consists of vasa scalariformia, a peculiar structure, and very different from that of all the other genera belonging to *Loranthaceæ*, to which this genus has been referred, and to which, though it does not absolutely belong, it is nearly related. Even this peculiar structure of the stems of *Myzodendron* admits of considerable modifications in the different species of the genus, which is strikingly exemplified in comparing the loose vascular tissue with large and singularly constructed medullary rays of *M. brachystachyum* and *quadriflorum* with the more minute vessels and extremely narrow rays of *M. punctulatum*.

I may also notice that in *Tillandsia usneoides*, as well as in the nearly related species of that genus, the capillary stems are destitute even of spiral vessels, though in *Bromeliaceæ* generally the ordinary vascular system is found.

Whatever may be the state of vessels in the fully developed parasites belonging to *Rafflesiaceæ*, it appears to me that at least *Rafflesia* in its very early

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[1] *Myzodendron* of Banks and Solander, from μυζέω or μύζω *sugo*, and δένδρον, has been changed to *Misodendron* by De Candolle and all following systematic writers; no doubt merely from a mistake as to the intended derivation. *Myzodendron*, hitherto referred to *Loranthaceæ*, to which it is certainly closely allied, especially through *Antidaphne* of Pœppig, appears to me to have characters sufficient to distinguish it as, at least, a suborder or tribe (*Myzodendreæ*), namely, the structure of its ovarium, in which it approaches to *Santalaceæ*, having three ovula suspended from the apex of a central placenta, only one of which ripens; the entire absence of floral envelope in the male; the singular feathery appendages of the female flower and fruit compensating in the dispersion and subsequent adhesion of its seeds, which are destitute of that viscidity existing in those of the parasitic *Loranthaceæ*; and lastly, the embryo being undivided, with its dilated and exserted radicle enclosed in a semitransparent covering, a continuation of the membrane lining the cavity of the albumen in which the embryo is lodged.

233] form merely different orders of the same natural class, in giving an account of a new and remarkable genus of the latter family.[1]

At present I shall only remark, that the sole remaining character employed to unite these two families and supposed to distinguish them from all others, namely, the simple or

stages is entirely cellular, and that this continues to be the case not only until that mutual adaptation of parasite and stock which enables the former to complete its development has taken place, but until the first indications of its future structure have become perceptible. It may also be remarked, that even after the formation of vessels in the parasite is obvious, the direct union between *Rafflesia* and the *Vitis* continues to be chiefly if not entirely cellular, the connection consisting in a slight mutual penetration or indentation of the two substances, whose cells are easily distinguishable.

I may here advert to one of the most difficult points in the economy of *Rafflesiaceæ*, namely, by what means their minute embryos, which are at the same time of an extremely loose texture, are enabled to penetrate through the bark of the plants on which they vegetate, so as to account for such appearances as those exhibited in the nascent *Rafflesia Arnoldi* represented in Tab. 25 (XXVI), A, in which I have been unable to trace any perceptible communication with the surface, and where the parasite seems rather to grow out of than into the stock.

Connected with this point a question may also arise, whether the earliest effort of the seed after its deposition in the proper nidus, by whatever means this is effected, may not consist in the formation of a cellular tissue extending laterally under the bark of the stock and capable of producing the fully developed parasite.

This question might not occur in regard to *Rafflesia* and *Brugmansia*, in both of which the individual plants are in general sufficiently distant on the root of the *Vitis* to make it probable that each developed parasite is produced from a distinct seed. But in *Pilostyles*, and even *Cytinus*, where they are closely approximated, their possible origin from one common basis or thallus is more readily suggested, especially on considering that in the former genus, which is diœcious, each group of parasites is generally, perhaps always, exclusively of one sex; and that these groups, often of great density, not unfrequently surround completely the branch of the stock. But although this view did occur to me as not very improbable, and as tending to remove some of the apparent difficulties, I have never been able to trace any substance decidedly distinct from the proper tissue of the stock; there are, however, some appearances favouring the hypothesis in both genera, especially in *Pilostyles*, but which require careful examination in the living plants.

[1] This genus, which was first found by Francis Masson, is the *Mystropetalon* of Mr. Harvey (in South Afr. Gen. p. 418), who has described two species, from both of which Masson's plant is perhaps distinct.

I may here advert to a note at p. 225 of my former memoir (in Linn. Soc. Trans. vol. xiii), [*Antè, p.* 390] in which I thought it not improbable that a parasite briefly noticed by Isert (in Reise nach Guinea, p. 283) might be related to *Rafflesia*. I have now, however, reason to believe that Isert's plant is the *Thonningia sanguinea* of Vahl (in Act. Soc. Hist. Nat. Hafn. t. vi, p. 124, t. 6, and Schumacher, Guineische Plant. p. 431), a genus nearly related to, if really distinct from *Balanophora*.

acotyledonous embryo, exists equally in *Orchideæ*. And if it be employed along with those characters connected with their peculiar economy, namely, the imperfect development of leaves, the want of stomata and absence of green colour, the class cannot be limited to *Rafflesiaceæ* and *Balanophoreæ,* for an embryo of exactly the same kind exists in *Orobanche,* and other, perhaps all other, genera parasitic on roots, a remark which I made, though not with sufficient precision, in my former essay.[1] But such a classification, though founded on seemingly very important technical characters, would hardly be received in a strictly natural arrangement, and it seems to me quite as paradoxical to approximate two such genera as *Rafflesia* and *Balanophora.*

RAFFLESIA ARNOLDI.

Rafflesia Arnoldi, *R. B. in Linn. Soc. Transact.* vol. xiii, p. 201, tabs. 15—22 (*Antè, p.* 374, *tabs.* 13—20) Mas.
Rafflesia Titan, *Jack in Malayan Miscell., Append. to* vol. i.

DESC. PLANTA FEMINEA masculæ omninò similis insertione, bracteis et perianthio. [234

Columna quæ figura, stylis disci et limbo elevato indiviso apicis, necnon annulo duplici baseos cum mascula per singula puncta convenit; ab eadem differt *externè* rudimentis solum minutis papillæformibus polline destitutis antherarum, et loco cavitatum antheris maris respondentium sulci tantum lineares angusti nec profundi: *internè* ovario processibus indefinitè numerosis irregulariter confluentibus in cavitatibus labyrinthi speciem formantibus diviso.

Ovula numerosissima parietibus cavitatum ovarii sine ordine sparsa, primò nucleo papilliformi sessili nudo, mox basi attenuato in funiculum rectum, apice incrassatum primordium annulare integumenti simplicis quod sensim auctum demum nucleum omninò includit apice perforato, funi-

[1] *Antè, p.* 391-2.

culoque simul elongato extra medium arctè recurvato et incrassato.

Pericarpium, bracteis, calyce, apiceque patelliformi styligero columnæ delapsis, denudatum, omninò superum vel liberum, subovatum carnosum crassum altè rimosum indehiscens, cavitatibus sicut in ovario indefinitè numerosis inordinatis amorphis polyspermis.

Semina pedicellata, funiculi dimidio *inferiore* cylindraceo cellulari molli pallido: *superiore* maximè incrassato arctè recurvato subovato castaneo lacunoso solido duro. *Semen ipsum* ovatum vix diametro apicis dilatati funiculi, castaneum altè lacunosum.

Integumentum exterius crasso-crustaceum subnucamentaceum; *interius* membranaceum pallidum lacunis exterioris leviter impressum.

Albumen magnitudine integumenti interioris laxè cellulosum aqueo-pallidum.

Embryo e cellulis subduplici serie ordinatis iis albuminis majoribus constans, ex apice albuminis ortus, ejusque dimidio longior.

HYDNORA AFRICANA.

Hydnora africana, *Thunb. in Act. Holm.* (1775), vol. xxxvi, p. 69, tab. 2. *E. Meyer in Nov. Act. Acad. Cæsar. Nat. Curios.* vol. xvi, par. 2, p. 775, tab. 58.

Planta Aphyteja, *Resp. Achar. cum. tab.* (1776). *Amœn. Acad.* vol. viii, p. 310.

Aphyteia Hydnora, *Harv. Gen. South Afr.* p. 299.

Loc. Nat. Africa Australis parasitica in radicibus Euphorbiæ succulentæ cujusdam secundum Thunberg et Drege; et quandoque Cotyledonis orbiculatæ auct. D. Mundt *in Harvey, South Afr. Gen.* p. 299. Nuperrimè etiam in Africa boreali detecta, fid. sp. asserv. in Museo Parisiensi.

Desc. Primordia sunt Caules e dilatata radice plantæ sustinentis orti, humifusi v. sæpius semisepulti, angulati (4-5-6-goni) digitum crassi simplices v. sæpius ramosi, solidi angulis tuberculatis, tuberculis approximatis obtusis, apice sæpe rimoso, quasi dehiscenti sed nunquam fibras exse- [235 renti; intra corticem strato paulo laxiore magisque colorato, centro densiore e cellulis præsertim conflato et fasciculis tenuibus parcis vasorum instructo.

E tuberculo plurimum aucto exsertus est *Flos* erectus basi in pedunculum abbreviatum intùs vasculosum sensim paulo angustatus, penitus ebracteatus.

Perianthium monophyllum, tubulosum, subinfundibuliforme, carnosum, extùs (uti pedunculus) rimis plurimis superficialibus in areolis subrotundis plus minus angulatis squamas primo intuitu quodammodo referentibus divisum et quasi leprosum. *Tubus* intus glaberrimus sed sæpe transversim subrugosus. *Limbus* tubum subæquans tripartitus (rarissimè 4-partitus) æqualis, æstivatione induplicato-valvata; laciniis primum latere hiantibus, apicibus diutius cohærentibus demum distinctis, modicè patentibus ovalibus oblongisve obtusiusculis, marginibus veris latè et obliquè induplicatis majorem partem disci apicemque omninò occultantibus extùs ramentis numerosis subulatis conspersis marginalibusque elongatis ciliatis; singulis disco lævi e majore parte tecto *pulvinulo* adnato oblongo carnoso, sæpè longitudinaliter striato, apice marginibus laciniarum ibi coalitis occultato acutiusculo, basi obtusa subcordata.

Columna staminea infra medium tubi orta, brevissima, annulum efformans altè trilobum, lobis laciniis limbi oppositis rotundatis obtusis. *Antheris* indefinitè numerosis, connectivo communi crasso carnoso penitus adnatis, parallelo-approximatis, elongato-linearibus, bicruribus, crure altero plurimarum postico altero antico, nonnullis quasi pressione reliquarum et præcipuè iis ad ortum loborum columnæ sitis abbreviatis sæpiùs in dorso, rariùs in ventre lobi obviis; omnibus primum bilocularibus sed sulco unico longitudinali dehiscentibus.

Pollen simplex sphæroideum læve.

Ovarium totum adherens, parietibus cavitatis lævibus.

Stigma discum apicis ovarii occupans, sessile depressum trilobum; lobis iis annuli staminei et laciniis limbi perianthii oppositis; singulis striis linearibus numerosis, e peripheria cordata lobi centrum versus plus minus divergentibus, respondentibus totidem lamellis planis arctè approximatis sed ad cavitatem ovarii usque distinctis, ibique manifestiùs separatis et placentiferis.

Placentæ indefinitè numerosæ, una pluresve e superficie interiore lamellæ singulæ stigmatis ortæ, ideoque omnes ex apice ovarii pendulæ, cylindraceæ, dimidium cavitatis, cujus parietes læves omninò steriles, superantes, undique ovulis densè tectæ.

Ovula primum sessilia papillæformia uniformia, dein subcylindracea, brevè pedicellata, apice obtuso depresso, v. perforato v. membrana semitransparente tecto, nucleo incluso manifesto.

Pericarpium perianthio toto supero et annulo stamineo delapsis denudatum, stigmate persistenti apice clausum, sphæroideum magnitudine pomi minoris, areolis squamas
236] æmulantibus inæquale quasi leprosum, carnosum crassum indehiscens, cavitate placentis undique seminiferis densè repleta.

Semina subglobosa, pedicello brevi quandoque subnullo insidentia.

Integumentum exterius crasso-membranaceum subpulposum areolatum cellulis minutè granulatis: *interius* albumini arctè adherens.

Albumen densum, subcartilagineum, aqueo-pallidum, per lentem modicè augentem structura quasi radiata, sed magis auctum constare videtur substantia densa semitransparenti alba nec in cellulas manifestè divisa, sed undique farcta corpusculis celluliformibus figura variis, in serie extima majoribus oblongo-obovatis, reliquis minoribus vix symmetricè positis, omnibus semiopacis e membrana materia minutè granulosa repleta formatis.

Substantia densa Albuminis uniformis forsan e cellulis parietibus incrassatis et obliteratis, singulis nucleo (corpusculo) semiòpaco fœtis.

Embryo in centro albuminis parvus subglobosus aqueopallidus e cellulis numerosis parvis mollibus, materia minutè granulosa repletis, ab albumine facilè separabilis, et absque ulla manifesta communicatione cum ejusdem peripheria vel ope suspensorii, v. canalis intermedio.

EXPLANATION OF THE PLATES.

RAFFLESIA ARNOLDI.

TAB. 21 (XXII).

Fig. 1. A female flower-bud, with the roots of the *Vitis* (or *Cissus*) vertically divided, which shows the numerous irregular cavities of the ovarium chiefly, if not entirely, above the insertion of bracteæ and calyx, and the vascular lines continued from the walls of the cavities through the upper solid part of the column into the axes of the style-like processes:—natural size.

Fig. 2. A female flower-bud in the same stage of development, the bracteæ and calyx entirely removed, to show its outward resemblance to the male flower-bud (figured in Linn. Trans. vol. xiii, TAB. XXI) (*Antè, t.* 19):—natural size.

TAB. 22 (XXIII).

Fig. 1. A small segment of the column, of which part of the elevated undivided limb is removed, to show the narrow furrows of the sides of the column corresponding in number with the rudiments of antheræ, seen in

Fig. 2, which is the portion of the limb removed from fig. 1:—natural size. [237

Fig. 3. The upper half of one of the styles of the disc, with its terminating hairs:—magnified 10 diameters.

Fig. 4. A portion of fig. 3, somewhat more highly magnified (20 diameters), vertically divided.

Figs. 5, 6, and 7. Some of the hairs still more highly magnified, which, according to Mr. Bauer, have a secreting surface seen in fig. 7, and which in figs. 5 and 6 is covered with the secretion, consisting of spherical particles enveloped in mucus at fig. 8:—magnified 100 diameters (but see observations respecting them in page 225). (*Antè, p.* 405.)

Figs. 9 and 10. Longitudinal and transverse sections of a style:—magnified 50 diameters.

Fig. 11. A transverse section of half the ovarium, to show the numerous irregularly ramified cavities, and the arrangement of vascular cords belonging to the bracteæ and calyx:—natural size.

Fig. 12. A small portion of the ovarium, with the ovula covering the surface of the cavities, and the vascular lines passing through the axes of the parietes:—magnified 20 diameters.

Figs. 13—18. Ovula in various stages (the earliest observed are not represented):—magnified 100 diameters.

TAB. 23 (XXIV).

Fig. 1. A ripe pericarpium, of the natural size, the calyx, bracteæ and apex of the column being deciduous.

Fig. 2. The same divided vertically, and showing the thickness of the densely-fleshy and deeply-furrowed covering, and also that the whole of the ovarial cavity is above the insertion of bracteæ and calyx.

TAB. 24 (XXV).

Fig. 1. A small portion of the wall of two adjoining cavities, the surfaces covered with numerous seeds, all of equal size:—magnified 20 diameters.

Fig. 2. A seed with its funiculus, of which the lower erect portion is filiform, the recurved upper half being of the same texture, colour and surface with the seed, which it somewhat exceeds in thickness:—magnified 100 diameters.

Fig. 3. The same divided longitudinally, to show the structure of the seed (according to Mr. Bauer), and that the enlarged apex of the funiculus is solid: —magnified 100 diameters.

Fig. 4. The nucleus of the seed taken out of its thick nut-like outer covering:—magnified 100 diameters.

Fig. 5. The same nucleus, whose membranous coat is separated by pressure,
[238] to show the albumen:—magnified 100 diameters.

Fig. 6. The denuded loosely-cellular albumen.

Fig. 7. A portion of the albumen, exhibiting the embryo, its surface and lateral origin, according to Mr. Bauer:—magnified 100 diameters.

Fig. R. Br. is a longitudinal section of the albumen, exhibiting R. Brown's view of the origin, form, and surface of the embryo.

TAB. 25 (XXVI).

Fig. 1. A branch of the *Vitis*, on which are four very young buds of *Rafflesia Arnoldi*:—natural size. Of these,

a. (not separately figured) is merely a very slight swelling, caused by the nascent parasite, but before its parts are distinguishable.

A. (also separately figured, vertically divided and moderately magnified), the youngest parasite whose parts are distinguishable, deeply seated, entirely enclosed, and before its cortical covering corresponds with it in form.

B. (in like manner separately figured, divided and magnified), in which the parasite is entirely enclosed in its reticular covering.

C. In which the reticular covering has burst, vertically divided and magnified.

HYDNORA AFRICANA.

TAB. 26 (XXVII).

Fig. 1. A flower of *Hydnora africana*, with its very short base.

Fig. 2. The same longitudinally divided:—both of the natural size.

Tab. 27 (XXVIII).

Fig. 1. Transverse section of a part of the tube of the perianthium, to show the three-lobed columna staminea:—moderately magnified.

Fig. 2. The inner surface of one of the three lobes of the column or antheral annulus.

Fig. 3. Outer surface of the same:—both magnified in the same degree with fig. 1.

Fig. 4. Vertical section of a portion of one of the lobes of the columna staminea, to show the thickness and texture of the common connective.

Fig. 5. Transverse section of the same, which shows the original bilocularity of each anthera:—both more highly magnified.

Fig. 6. Grains of pollen, still more highly magnified.

Fig. 7. Transverse section of the flower, to show the form and surface of [239 the stigma (of which the three primary divisions are opposite to the lobes of the columna staminea):—magnified in the same degree with fig. 1.

Fig. 8. A portion of the stigma, which shows its composition.

Fig. 9. A transverse section about the middle of the same:—both magnified somewhat more than figs. 2 and 3.

Fig. 10. A vertical section of the stigma, showing that the divisions of its surface extend quite through to the cavity of the ovarium, separating it into an equal number of lamellæ, from the inner terminations of which the placentæ are pendulous:—more highly magnified than the preceding figures.

Fig. 11. A small portion of the same, still more highly magnified.

Fig. 12. A transverse section, more highly magnified than fig. 11, with its densely crowded ovula arising from every part of its surface.

Fig. 13. Three ovula more highly magnified than fig. 12, to show the pedicellus or attenuated base and depressed or perforated apex.

Tab. 28 (XXIX).

A ripe fruit (fig. 1), with the stock (the root of the supposed *Euphorbia*, fig. 3) and the decumbent angular branched stems of the parasite, from the thickened trunk of which the ripe fruit originates at fig. 2, and from a branch of which a very young flower-bud proceeds:—natural size.

Tab. 29 (XXX).

Fig. 1. The same ripe fruit vertically divided, with the prostrate thickened stem of the parasite and the root of the supposed *Euphorbia*, whose woody fibres and vessels appear to penetrate deeply into the substance of the thickened stem:—natural size.

Fig. 2. A portion of the fruit transversely divided.

Fig. 3. A transverse section of one of the placentæ, with the ripe seeds:—slightly magnified.

Fig. 4. Two seeds, more highly magnified than fig. 3.

Fig. 5. A seed, magnified in the same degree as fig. 4, and vertically divided, which exhibits the albumen more distinctly radiating than I have ever found it.

Fig. 6. A seed deprived of its outer coat.

Fig. 7. The same transversely divided, which, as well as fig. 5, shows the central globular embryo.

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SUPPLEMENT.

To render the account of *Rafflesia Arnoldi* more complete, I shall add the distinguishing characters of the order, tribes, genera and species of *Rafflesiaceæ* with which I am acquainted. These characters, which form the chief part of the present supplement, as well as the notes to the original communication, have been written since November last.

The paper itself is printed as it was read in June 1834, a very few slight alterations, and those chiefly verbal, excepted.[1]

[1] The following brief abstract was published in the Philosophical Magazine for July, 1834:—

"LINNEAN SOCIETY.

"June 17.—A paper was read 'On the Female Flower and Fruit of *Rafflesia*, with Observations on its Affinities, and on the Structure of *Hydnora*.' By Robert Brown, Esq., V.P.L.S.

"The author's principal object in this paper is to complete his account of *Rafflesia Arnoldi*, the male flower of which he described in a former communication, published in the 13th volume of the Society's Transactions; and, in connection with the question of its place in a natural arrangement, he introduces a more detailed description and figures of *Hydnora africana*, than have hitherto been given. The drawings of *Rafflesia* which accompany the paper are by Francis Bauer, Esq., and those of *Hydnora* by the late Mr. Ferdinand Bauer.

"From a comparison of *Rafflesia* with *Hydnora* and *Cytinus*, he is confirmed in the opinion expressed in his former paper, but founded on less satisfactory evidence, that these three genera (to which *Brugmansia* of Blume is now to be added), notwithstanding several remarkable peculiarities in each, may all be referred to the same natural family; and this family, named by him *Rafflesiaceæ*, he continues to regard as being most nearly allied to *Asarinæ*.

"He does not, however, admit an arrangement lately proposed by M. Endlicher, and adopted by Mr. Lindley, by whom these genera are included in the same natural class with *Balanophoreæ* of Richard; an approximation founded on their agreement in the structure of embryo, and on the assumed absence of spiral vessels. On this subject he remarks, that in having a homogeneous or acotyledonous embryo, they essentially accord, not only with many other plants, parasitical on roots, which it has never been proposed to unite with them, as *Orobanche*, &c., but also with *Orchideæ*, their association with which would be still more paradoxical. And with respect to the supposed peculiarity in their vascular structure, he states that he has found spiral vessels not only in *Rafflesia* (in which he had formerly denied their existence), and in *Hydnora* and *Cytinus*, but likewise in all the *Balanophoreæ* examined by him, particularly *Cynomcrium* and *Helosis*, as Dr. von Martius had long since done in *Langsdorfia*, and Professor Meyer very recently in *Hydnora*.

"In his observations on the ovulum of *Rafflesia*, he gives a view of its early

I have also to state, that an extensive and highly important essay, entitled, "An Attempt to analyse *Rhizantheæ,*" by Mr. William Griffith, has been read during the present season before the Linnean Society, of which an abstract is given in the Proceedings. From this essay I have here introduced the character of *Sapria*, a new genus belonging to *Rafflesiaceæ;* and have ventured to propose an alteration of the trivial name from *Himalayana* to *Griffithii,* in honour of the discoverer of this interesting addition to the tribe *Rafflesieæ,* whose species, with one exception, have names similarly derived.

RAFFLESIACEÆ.

CHAR. DIFF. ORD. *Perianthium* monophyllum regulare.

Corolla nulla.

Stamina: Antheræ numerosæ, simplici serie.

Ovarium: placentis pluribus polyspermis, ovulis orthotropis (sed in quibusdam recurvatione apicis, penitus vel partim, liberi funiculi quasi anatropis).

Pericarpium indehiscens polyspermum.

Embryo indivisus (cum v. absque albumine).

Parasiticæ *radicibus rariusve in ramis plantarum dicotyledonearum.*

stages of development, and which he extends to Phænogamous plants generally, in some respects different from that taken by M. Mirbel, who considers the nucleus of the ovulum, in its earliest state, as inclosed in its coats, which gradually open until they have attained their maximum of expansion, when they again contract around the nucleus, and, at the same time, by elongating, completely inclose it. Mr. Brown, on the other hand, regards the earliest stage of the nucleus as merely a contraction taking place in the apex of a pre-existing papilla, whose surface, as well as substance, is originally uniform, and that its coats are of subsequent formation, each coat consisting, at first, merely of an annular thickening at the base of the nucleus, which, by gradual elongation, it entirely covers before impregnation takes place.

"But this mode of development of the ovulum, he remarks, though very general, is not without exception; for in many, perhaps in all, *Asclepiadeæ* and *Apocineæ,* the ovulum continues a uniform cellular tissue, exhibiting no distinction of parts until after the application of the pollen tube to a definite part of its surface, when an internal separation or included nucleus first becomes visible."—See a translation of this abstract in *Annal. des Sc. Nat* ser. 2de, tom. i, p. 369.

Obs. Huic ordini appendendæ *Apodanthes* et *Pilostyles*, quæ a Rafflesiaceis Corolla tetrapetala et Antheris 2-3-seriatis diversæ; necnon quod in caule aut ramis solùm nec unquam in radicibus parasiticæ: attamen pluribus notis *Cytineis* conveniunt.

212] RAFFLESIEÆ.

Char. Diff. Trib. *Perianthium* 5-10-fidum.

Antheræ sub apice dilatato columnæ simplici serie adnatæ, distinctæ, poro unico v. duplici dehiscentes.

Ovarium placentis confluentibus v. distinctis undique ovuliferis.

Pericarpium (semiadherens v. liberum) carnosum.

Semina recurvata funiculo apice dilatato.

Embryo albumine inclusus axilis, albumine brevior.

Parasiticæ *in radicibus specierum* Vitis *v.* Cissi. Flos *subsessilis, bracteis imbricatis venosis.*

Rafflesia, *R. Br.*

Char. Diff. Gen. *Perianthium* 5-fidum, æstivatione imbricata, corona faucis annulari indivisa.

Columna genitalium apice dilatato patelliformi: disco processibus (stylis?) numerosis styliformibus!; limbo elevato indiviso.

Antheræ multicellulosæ, poro unico dehiscentes.

Rafflesia (Patma) hermaphrodita, antheris viginti pluribus, stylis indefinitè numerosis confertis, perianthii tubo intus lævi (diametro floris sesquipedali-bipedali).

Rafflesia Patma, *Blume, Flor. Jav.* p. 8, tabb. 1-3.

Loc. Nat. Crescit in umbrosis Insulæ parvæ *Nusa Kambangan*, Javæ ab austro vicinæ. *Blume.*

R. (Arnoldi) dioica, antheris viginti pluribus, stylis indefinitè numerosis confertis, annulo baseos columnæ duplici, perianthii tubo intus ramentaceo (diametro floris bi-tripedali).

Rafflesia Arnoldi, *R. Br. in Linn. Soc. Trans.* vol. xiii, p. 207. (*Antè, p.* 374).

Loc. Nat. In sylvis umbrosis Sumatræ, anno 1818 detexit b. J. Arnold, M. D.

R. (Horsfieldii) dioica? stylis indefinitè numerosis: centralibus confertis (diametro floris semipedali).

Loc. Nat. Java, D. Horsfield, qui Alabastra solum detexit et depingi curavit.

Obs. Species dubia a sequente diversa numero et ordinatione stylorum (fid. ic. ined. D. Horsfield).

R. (Cumingii) dioica, antheris 10-12, stylis antheras [243 numero vix superantibus abbreviatis: exterioribus (sæpius 10) simplici serie; interioribus (1-3) invicem subæquidistantibus, annulo baseos columnæ unico, perianthii tubo intus ramentaceo (diametro floris semipedali).

Rafflesia Manillana, *Teschem. in Boston Journ. Nat. Hist.* vol. iv, p. 63, tab. 6, *mas.*

Loc. Nat. In Samar, Insula Philippinarum; ubi primum legit *D. Cuming*, v. s. et in sp. vin. asserv.

Desc. Planta dioica *R. Arnoldi* multoties minor, diametro floris expansi sexpollicari, cæterum ante expansionem *externè* similis ut ovum ovo, indusio e cortice *Vitis* aut *Cissi* formato rugoso sed vix reticulato; *internè* convenit corona faucis indivisa tubo intus ramentaceo: differt annulo baseos columnæ unico (exteriore *R. Arnoldi* deficiente), antheris maris paucioribus (10-12), stylis utriusque sexus vix antheras numero superantibus, haud confertis sed subsimplici serie circulari propiùs limbo quam centro dispositis, cum nonnullis (1-3) centralibus invicem distinctis et ferè æquidistantibus, omnibus abbreviatis crassitie dimidium longitudinis subæquante, apice pilis brevibus acutis rigidulis barbato: femina absque antherarum rudimentis: ovarii cavitatibus stylos manifestè superantibus et tam numerosis in centro ac versus peripheriam ut in *R. Arnoldi*.

Obs. I. The trivial name *Manillana,* given to this species by Mr. Teschemacher, who has described and figured the male flower, can hardly be retained for a plant not known to grow in Luzon, of which Manilla is the capital, but in the island of Samar, where it was first found by Mr. Hugh Cuming. I have named it, therefore, in honour of the discoverer,—a change which is not likely to be objected to, as Mr. Teschemacher (*loc. cit.*) expresses his readiness to adopt any name Mr. Cuming may wish it to retain.

Obs. II. In the general tissue of this species each cell has an extremely small, round, opake nucleus. In a transverse section of the column both of the male and female flower, the central part appears to be somewhat more solid; and each of the cells, of which it seems to be entirely formed, contains a large nucleus, easily separable, of a somewhat oval shape, and apparently consisting of a membrane including minute granular matter, which renders it opake. In the surrounding somewhat looser substance of the column, there seems to be an oval cell within each outer or mother cell, occupying the greater part of its cavity, with less granular matter, and having frequently a minute round nucleus. The parietes of the placentæ have in each simple
244] cell a small nucleus like that of the general tissue and of the outer portion of the column.

Sapria, *Griffith in Proceed. Linn. Soc.* p. 217.

Char. Diff. Gen. *Flores* dioici. *Perianthium* 10-fidum! duplici serie imbricatum, corona faucis indivisa.

Columna apice dilatato concavo e centro conum indivisum exserenti.

Antheræ sub apice dilatato columnæ, simplici serie adnatæ, 2-3-cellulosæ, poro unico dehiscentes.

Ovarium inferum, placentis indefinitè numerosis (parietalibus, ovulis anatropis, *Griffith*).

Sapria Griffithii.

Sapria Himalayana, *Griffith, loc. cit.*

Loc. Nat. In radicibus *Vitis* v. *Cissi* cujusdam in sylvis umbrosis Montium Mishmee jugi Himalayani, anno 1836 detexit *D. Griffith.*

Brugmansia, *Blume, Flor. Jav.*

Char. Diff. Gen. *Flores* hermaphroditi.

Perianthium 5-fidum, laciniis bi-trifidis, æstivatione valvata apicibus arctè inflexis.

Columna supernè dilatata apice excavato indiviso.

Antheræ sub apice dilatato simplici serie adnatæ, poro duplici dehiscentes!

Ovarium adherens, placentis indefinitè numerosis (parietalibus, *Blume*).

Brugmansia Zippelii, *Blume, Flor. Javæ,* p. 15, tabb. 3-6.

Loc. Nat. In provinciâ Buitenzorg Javæ occidentalis, primus reperit Hortulanus Zippel. *Blume, loc. cit.*

HYDNOREÆ.

Char. Trib. *Perianthium* trifidum, æstivatione valvata.

Stamina tubo perianthii inserta.

Antheræ numerosæ, longitudinaliter dehiscentes, connatæ in *annulum* trilobum cujus lobi perianthii laciniis oppositi.

Ovarium inferum: *Stigma* sessile depressum trilobum, lobis singulis formatis e lamellis pluribus appositis ad ovarii cavitatem usque distinctis ibique placentiferis! *Placentæ* ab apice ovarii (stigmatis lamellis) pendulæ, subcylindraceæ, undique ovulis numerosissimis orthotropis tectæ.

Pericarpium calvum, carnosum, cavitate placentis undique seminiferis pleno.

Semina: Embryo globosus in centro! albuminis cartilaginei.

Hydnora, *Thunb.* [245

Char. Gen. idem ac tribus.

Hydnora (africana) hermaphrodita, perianthii laciniis latè induplicatis margine (angulo induplicationis) ciliatis apicibus demùm liberis, antheris bicruribus aversis (crure altero postico altero antico).

Hydnora africana, *Thunb. in Act. Holm.* vol. xxxvi, p. 69, tab. 2.

Loc. Nat. In Africâ australi primum detexit *Thunberg.*

H. (triceps) hermaphrodita, perianthii laciniis supernè dilatatis connatisque infernè hiantibus margine nudis, antheris omninò posticis.

Hydnora triceps, *Meyer in Nov. Act. Acad. Nat. Curios.* vol. xvi, par. 2, p. 779.

Loc. Nat. In Africâ australi. *D. Drege.*

H. (americana) dioica, perianthii laciniis liberis nudis: marginibus induplicatis angustissimis, antheris posticis.

Loc. Nat. Exemplar unicum in Herb. D. Hooker in Americâ australi lectum vidi.

CYTINEÆ.

Char. Diff. Trib. *Flores* diclines. *Perianthium* 4-8-fidum, æstivatione imbricata.

Mas. *Antheræ* in apice columnæ simplici serie, definitæ, biloculares loculis parallelo-appositis longitudinaliter dehiscentibus.

Fem. *Ovarium* totum adherens uniloculare, placentis parietalibus definitis (8-16) distinctis, per paria approximatis, lobatis. *Stylus* 1. *Stigma* radiato-lobatum. *Embryo* exalbuminosus, indivisus, homogeneus.

Cytinus, *Linn.*

Char. Gen. id. ac tribus.

Cytinus (Hypocistis) spica androgyna, perianthio quadrifido: laciniis extus tenuissimè pubescentibus.

Cytinus Hypocistis, *Linn.*

Thyrsine, *Gledit. verm. Abhand.* i, p. 199, tab. 2.
Loc. Nat. Europa australis et Africa borealis.

C. (DIOICUS) spicis dioicis paucifloris, floribus bibracte- 216
atis pedunculatis, perianthio sexfido: laciniis extus hispidulis.
Cytinus dioicus, *Juss. in Annal. du Mus.* xii, p. 443. *Hook. Ic.* vol. iv, tab. 336.
Phelypæa sanguinea, *Thunb. Nov. Gen.* pars 5ta, p. 93.
Aphyteia multiceps, *Burch. Trav.* vol. i, p. 213, fid. exempl. in herb. auctoris visi.
Loc. Nat. Africa australis.

C. (AMERICANUS) spicis dioicis multifloris, floribus sessilibus absque bracteis lateralibus, perianthio octofido patentissimo.
Loc. Nat. America æquinoctialis. *D. Barclay,* v. exemplaria mas. pl. in sp. vin. asserv.
OBS. Mascula planta solum visa. *Spicæ* densæ. *Perianthia* sessilia sæpius octo-quandoque novem-fida, laciniis patentissimis. *Columna* staminea teres. *Antheræ* 8-9, biloculares posticæ, loculis appositis longitudinaliter dehiscentibus, connectivis basi connatis extra medium distinctis singulisque in cuspidem subulatam productis. *Pollen* simplex. Nulla vestigia ovarii.

APODANTHEÆ.

CHAR. TRIB. *Flores* dioici. *Perianthium* 4-fidum v. 4-partitum, æstivatione imbricatum persistens.
Corolla 4-petala! decidua.
MAS. *Antheræ* infra apicem dilatatum indivisum columnæ bi-triseriatæ! sessiles uniloculares.
FEM. *Ovarium* adherens, uniloculare, ovulis orthotropis, per totam superficiem cavitatis sparsis. *Stigma* capitatum.
Pericarpium baccatum, inferum v. semisuperum.
Embryo exalbuminosus, indivisus, homogeneus.
Parasiticæ *in caulibus et ramis* (*nunquam in radicibus*) *plantarum dicotyledonearum.*

APODANTHES, *Poiteau.*

CHAR. GEN. *Perianthium* monophyllum 4-fidum, bibracteatum.

Petala ipso ovario (altius quam perianthium quod textura diversum) inserta.

MAS. . . . . . .

FEM. *Ovarium* semisuperum.

Pericarpium carnosum, cavitate tetragona.

Semina: testa nucamentacea lacunosa (funiculo nucleum æquante v. superante).

247] APODANTHES CASEARIÆ, *Poiteau in Annal. des Sc. Nat.* iii, p. 422, tab. 26, fig. 1.

Loc. Nat. Guiana gallica, in caulibus Caseariæ spec. macrophyllæ, *Vahl*, proximæ. *Poiteau*, v. in sp. vin. asserv. in Mus. Paris.

PILOSTYLES, *Guillemin.*

Frostia, *Bert. ined. et Endl. gen.* n. 725.

CHAR. GEN. *Perianthium* 4-partitum, superum.

Petala textura ferè perianthii et bractearum.

Ovarium cavitate infra insertionem bractearum superiorum producta.

Pericarpium cavitate absque angulis.

PILOSTYLES (BERTERII) bracteis sepalisque ovato-oblongis margine nudis, stigmate papuloso apice depresso-umbilicato!

Pilostyles Berterii, *Guillem. in Annal. Sc. Nat.* ser. 2, vol. ii, p. 21, tab. 1.

Apodanthes Berterii, *Gardn. in Hook. Ic.* new ser. vol. iii, tab. 655, A.

Loc. Nat. Chili, *Bertero* et *Bridges*, in Adesmiis parasitica, v. s.

P. (BLANCHETII) bracteis sepalisque subrotundis margin ciliatis! stigmate apice convexo.

Apodanthes Blanchetii, *Gardn. loc. cit.* B.

Loc. Nat. Brasilia, *Blanchet*, in Bauhiniæ sp. parasitica, v. s.

Obs. Mas hujusce v. maxime affinis specici vidi in Museo Vindobonensi a. b. *Pohl* in Brasiliâ lecta, in ramis Bauhiniæ cujusdam parasitica.

P. (Calliandræ) bracteis sepalisque ovatis margine nudis, stigmate ovato-conico apice convexo.

Apodanthes Calliandræ, *Gardn. in Hook. Ic.* new ser. vol. iii, tab. 644.

Loc. Nat. In provinciâ Goyaz Brasiliæ, in caulibus Calliandræ sp. *D. Gardner*, v. s.

CHARACTER AND DESCRIPTION

OF

KINGIA;

A NEW GENUS OF PLANTS

FOUND ON THE

SOUTH-WEST COAST OF NEW HOLLAND.

WITH OBSERVATIONS

ON THE

STRUCTURE OF ITS UNIMPREGNATED OVULUM, AND ON THE FEMALE FLOWER OF CYCADEÆ AND CONIFERÆ.

BY

R. BROWN, Esq., F.R.S.L. & E., F.L.S.

[*Reprinted from the 'Narrative of a Survey of the Intertropical and Western Coasts of Australia performed between the years* 1818 *and* 1822. *By Captain Philip P. King, R.N., F.R.S., F.L.S.' Vol. II, pp.* 534—565.]

LONDON.

1827.

CHARACTER AND DESCRIPTION [534

OF

KINGIA, &c.

(Read before the Linnean Society of London, Nov. 1 and 15, 1825.)

In the Botanical Appendix to the *Voyage to Terra Australis,* I have mentioned a plant of very remarkable appearance, observed in the year 1801, near the shores of King George the Third's Sound, in Mr. Westall's view of which, published in Captain Flinders' Narrative, it is introduced.

The plant in question was then found with only the imperfect remains of fructification: I judged of its affinities, therefore, merely from its habit, and as in this respect it entirely agrees with Xanthorrhœa, included the short notice given of it in my remarks on Asphodeleæ, to which that genus was referred.[1] Mr. Cunningham, the botanist attached to Captain King's voyages, who examined the plant in the same place of growth, in February, 1818, and in December, 1821, was not more fortunate than myself. Captain King, however, in his last visit to King George's Sound, in November, 1822, observed it with ripe seeds: and at length Mr. William Baxter, whose attention I had particularly directed to this plant, found it on the shores of the same port in 1823, both in flower and fruit. To this zealous collector, and to his liberal employer, Mr. Henchman, I am indebted for complete specimens of its fructifi- [535

[1] *Flinders' Voy.* vol. ii, *p.* 576. (*Antè, p.* 51.)

cation, which enable me to establish it as a genus distinct from any yet described.

To this new genus I have given the name of my friend Captain King, who, during his important surveys of the Coasts of New Holland, formed valuable collections in several departments of Natural History, and on all occasions gave every assistance in his power to Mr. Cunningham, the indefatigable botanist who accompanied him. The name is also intended as a mark of respect to the memory of the late Captain Philip Gidley King, who, as Governor of New South Wales, materially forwarded the objects of Captain Flinders' voyage; and to whose friendship Mr. Ferdinand Bauer and myself were indebted for important assistance in our pursuits while we remained in that colony.

KINGIA.

Ord. Nat. *Junceæ* prope Dasypogon, Calectasiam et Xerotem.

Char. Gen. *Perianthium* sexpartitum, regulare, glumaceum, persistens. *Stamina* sex, fere hypogyna: *Antheris* basi affixis. *Ovarium* triloculare, loculis monospermis; *ovulis* adscendentibus. *Stylus* 1. *Stigma* tridentatum. *Pericarpium* exsuccum, indehiscens, monospermum, perianthio scarioso cinctum.

Planta *facie* Xanthorrhœæ elatioris. Caudex *arborescens cicatricibus basibusve foliorum exasperatus?* Folia *caudicem terminantia confertissima longissima, figura et dispositione* Xanthorrhœæ. Pedunculi *numerosi foliis breviores, bracteis vaginantibus imbricatis tecti, floriferi terminales erecti, mox, caudice parum elongato foliisque novellis productis, laterales, et divaricati vel deflexi, terminati capitulo denso globoso floribus tribracteatis.*

Kingia *Australis.* Tab. C.[1]

Desc. *Caudex* arborescens erectus simplicissimus cylin-

[1] See note at p. 187.

draceus, 6—18-pedes altus, crassitie femoris. *Folia* caudicem terminantia numerosissima patula, apicibus ar- [536
cuato-recurvis, lorea, solida, ancipitia apice teretiusculo, novella undique tecta pilis adpressis strictis acutis lævibus, angulis lateralibus et ventrali retrorsum scabris. *Pedunculi* numerosi teretes 8—12-pollicares crassitie digiti, vaginis integris brevibus imbricatis hinc in foliolum subulatum productis tecti. *Capitulum* globosum, floridum magnitudine pruni minoris, fructiferum pomum parvum æquans. *Flores* undique densè imbricati, tribracteati, sessiles. *Bractea exterior* lanceolata brevè acuminata planiuscula erecta, extus villosa intus glabra, post lapsum fructus persistens: *duæ laterales* angusto-naviculares, acutissimæ, carina lateribusque villosis, longitudine fere exterioris, simul cum perianthio fructifero, separatim tamen, dilabentibus. *Perianthium* sexpartitum regulare subæquale glumaceum: *foliola* lanceolata acutissima disco nervoso nervis immersis simplicissimis, antica et postica plana, lateralia complicata lateribus inæqualibus, omnia basi subangustata, extus longitudinaliter sed extra medium præcipue villosa, intus glaberrima, æstivatione imbricata. *Stamina* sex subæqualia, æstivatione stricta filamentis sensim elongantibus: *Filamenta* fere hypogyna ipsis basibus foliolorum perianthii quibus opposita leviter adhærentia, filiformia glabra teretia: *Antheræ* stantes, ante dehiscentiam lineares obtusæ filamento paulo latiores, defloratæ subulatæ vix crassitie filamenti, loculis parallelo-contiguis connectivo dorsali angusto adnatis, axi ventrali longitudinaliter dehiscentibus, lobulis baseos brevibus acutis subadnatis: *Pollen* simplex brevè ovale læve. *Pistillum: Ovarium* sessile disco nullo squamulisve cinctum, lanceolatum trigono-anceps villosum, triloculare, loculis monospermis. *Ovula* erecta fundo anguli interioris loculi paulo supra basin suam inserta, obovata lenticulari-compressa, aptera: *Testa* in ipsa basi acutiusculâ foramine minuto perforata: *Membrana interna* respectu testæ inversa, hujusce nempe apici lata basi inserta, ovata apice angustato aperto foramen testæ obturante: *Nucleus* cavitati membranæ conformis, ejusdem basi insertus, cæterum liber, pulposus solidus, apice acu-

tiusculo lævi aperturam membranæ internæ attingente. *Stylus* trigonus strictus, infra villosus, dimidio superiore glabro, altitudine staminum, iisdem paulo præcocior, exsertus nempe dum illa adhuc inclusa. *Stigmata* tria brevis-
537] sima acuta denticuliformia. *Pericarpium* exsuccum, indehiscens, villosum, basi styli aristatum, perianthio scarioso et filamentis emarcidis cinctum, abortione monospermum. *Semen* turgidum obovatum retusum, integumento (testâ) simplici membranaceo aqueo-pallido, hinc (intus) fere a basi acutiuscula, *raphe* fusca verticem retusum attingente ibique in *chalazam* parvam concolorem ampliata. *Albumen* semini conforme densè carnosum album. *Embryo* monocotyledoneus, aqueo-pallidus subglobosus, extremitate inferiore (radiculari) acuta, in ipsa basi seminis situs, semiimmersus, nec albumine omnino inclusus.

Tab. C. fig. 1. Kingiæ Australis pedunculus capitulo florido terminatus; fig. 2, capitulum fructiferum; 3, sectio transversalis pedunculi; 4, folium: hæ magnitudine naturali, sequentes omnes plus minus auctæ sunt; 5, flos; 6, stamen: 7, anthera antice et; 8, eadem postice visa; 9, pistillum; 10, ovarii sectio transversalis; 11, ejusdem portio longitudinaliter secta exhibens ovulum adscendens cavitatem loculi replens; 12, ovulum ita longitudinaliter sectum ut membrana interna solummodo ejusque insertio in apice cavitatis testæ visa sit; 13, ovuli sectio longitudinalis profundius ducta exhibens membranam internam et nucleum ex ejusdem basi ortum; 14, bracteæ capituli fructiferi; 15, pericarpium perianthio filamentisque persistentibus cinctum; 16, pericarpium perianthio avulso filamentorum basibus relictis; 17, semen.

Obs. I.—It remains to be ascertained, whether in this genus a resin is secreted by the bases of the lower leaves, as in Xanthorrhœa; and whether, which is probable, it agrees also, in the internal structure of its stem with that genus. In Xanthorrhœa the direction of fibres or vessels of the caudex seems at first sight to resemble in some degree the dicotyledonous arrangement, but in reality much more nearly approaches to that of Dracæna Draco, allowance being made for the greater number, and extreme narrowness of leaves, to which all the radiating [538 vessels belong.[1]

Obs. II.—I have placed Kingia in the natural order Junceæ along with Dasypogon, Calectasia and Xerotes, genera peculiar to New Holland, and of which the two former have hitherto been observed only, along with it, on the shores of King George's Sound.

The striking resemblance of Kingia, in caudex and leaves, to Xanthorrhœa, cannot fail to suggest its affinity to that genus also. Although this affinity is not confirmed by a minute comparison of the parts of fructification, a sufficient agreement is still manifest to strengthen the doubts formerly expressed of the importance of those characters by which I attempted to define certain families, of the great class Liliaceæ.

In addition, however, to the difference in texture of the outer coat of the seed, and in those other points, on which I then chiefly depended in distinguishing Junceæ from Asphodeleæ, a more important character in Junceæ exists in the position of the embryo, whose radicle points always to the base of the seed, the external umbilicus being placed in the axis of the inner or ventral surface, either immediately above the base as in Kingia, or towards the middle, as in Xerotes.

Obs. III.—*On the structure of the* Unimpregnated Ovulum *in Phænogamous Plants.* [539

The description which I have given of the Ovulum of Kingia, though essentially different from the accounts hitherto published of that organ before fecundation, in

[1] My knowledge of this remarkable structure of Xanthorrhœa is chiefly derived from specimens of the caudex of one of the larger species of the genus, brought from Port Jackson, and deposited in the collection at the Jardin du Roi of Paris by M. Gaudichaud, the very intelligent botanist who was attached to Captain De Freycinet's voyage.

reality agrees with its ordinary structure in Phænogamous plants.

I shall endeavour to establish these two points; namely, the agreement of this description with the usual structure of the Ovulum, and its essential difference from the accounts of other observers, as briefly as possible at present; intending hereafter to treat the subject at greater length, and also with other views.

I have formerly more than once[1] adverted to the structure of the Ovulum, chiefly as to the indications it affords, even before fecundation, of the place and direction of the future Embryo. These remarks, however, which were certainly very brief, seem entirely to have escaped the notice of those authors who have since written on the same subject.

In the Botanical Appendix to the Account of Captain Flinders' Voyage, published in 1814, the following decription of the Ovulum of *Cephalotus follicularis* is given "Ovulum erectum, intra testam membranaceam continens sacculum pendulum, magnitudine cavitatis testæ," and in reference to this description, I have in the same place remarked that, from "the structure of the Ovulum, even in the unimpregnated state, I entertain no doubt that the radicle of the Embryo points to the umbilicus."[2]

My attention had been first directed to this subject in 1809, in consequence of the opinion I had then formed
540] of the function of the Chalaza in seeds;[3] and some time before the publication of the observation now quoted, I had ascertained that in Phænogamous plants the unimpregnated Ovulum very generally consisted of two concentric membranes or coats, enclosing a Nucleus of a pulpy cellular texture. I had observed also that the inner coat had no connection either with the outer or with the nucleus, except at its origin; and that with relation to the outer coat it was generally inverted, while it always agreed in direction with the nucleus. And,

[1] *Flinders' Voy.* ii, p. 601 (*Antè, p.* 77), and *Linn. Soc. Transac.* xii. p. 136.
[2] *Flinders' Voy.* loc. cit.
[3] *Linn. Soc. Transac.* x, p. 35.

lastly, that at the apex of the nucleus the radicle of the future Embryo would constantly be found.

On these grounds my opinion respecting the Embryo of Cephalotus was formed. In describing the ovulum in this genus, I employed, indeed, the less correct term, "sacculus," which, however, sufficiently expressed the appearance of the included body in the specimens examined, and served to denote my uncertainty in this case as to the presence of the inner membrane.

I was at that time also aware of the existence, in several plants, of a foramen in the coats of the Ovulum, always distinct from, and in some cases diametrically opposite to, the external umbilicus, and which I had in no instance found cohering either directly with the parietes of the Ovarium, or with any process derived from them. But, as I was then unable to detect this foramen in many of the plants which I had examined, I did not attach sufficient importance to it; and in judging of the direction of the Embryo, entirely depended on ascertaining the apex of the nucleus, either directly by dissection, or indirectly from the vascular cord of the outer membrane; the termination of this cord affording a sure indication of the origin of the inner membrane, and consequently of the base of the nucleus, the position of whose apex is therefore readily de- [541
termined.

In this state of my knowledge the subject was taken up in 1818, by my lamented friend the late Mr. Thomas Smith, who, eminently qualified for an investigation where minute accuracy and great experience in microscopical observation were necessary, succeeded in ascertaining the very general existence of the foramen in the membranes of the Ovulum. But as the foramina in these membranes invariably correspond both with each other and with the apex of the nucleus, a test of the direction of the future Embryo was consequently found nearly as universal, and more obvious than that which I had previously employed.

To determine in what degree this account of the vegetable Ovulum differs from those hitherto given, and in some measure, that its corectness may be judged of, I shall proceed to state the various observations that have been actually made, and the opinions that have been formed on the subject as briefly as I am able, taking them in chronological order.

In 1672, Grew[1] describes in the outer coat of the seeds of many Leguminous plants a small foramen, placed opposite to the radicle of the Embryo, which, he adds, is "not a hole casually made, or by the breaking off of the stalk," but formed for purposes afterwards stated to be the aeration of the Embryo, and facilitating the passage of its radicle in germination. It appears that he did not consider this foramen in the testa as always present, the functions which he ascribes to it being performed in cases where it is not found, either, according to him, by the hilum itself, or in hard fruits, by an aperture in the stone or shell.

542] In another part of his work[2] he describes and figures, in the early state of the Ovulum, two coats, of which the outer is the testa; the other, his "middle membrane," is evidently what I have termed nucleus, whose origin in the Ovulum of the Apricot he has distinctly represented and described.

Malpighi, in 1675,[3] gives the same account of the early state of the Ovulum; his "secundinæ externæ" being the testa, and his chorion the nucleus. He has not, however, distinguished, though he appears to have seen, the foramen of Grew, from the fenestra and fenestella, and these, to which he assigns the same functions, are merely his terms for the hilum.

In 1694, Camerarius, in his admirable essay on the sexes of plants,[4] proposes, as queries merely, various modes in which either the entire grains of pollen, or their particles after bursting may be supposed to reach and act upon the unimpregnated Ovula, which he had himself carefully observed. With his usual candour, however, he acknowledges his obligation on this subject to Malpighi, to whose more detailed account of them he refers.

[1] *Anatomy of Veget. begun* p. 3. *Anat. of Plants*, p. 2.

[2] *Anat. of Plants*, p. 210, tab. 80.

[3] *Anatome Plant.* p. 75, et 80.

[4] *Rudolphi Jacobi Camerarii de sexu plantarum epistola*, p. 8. 46, et seq.

Mr. Samuel Morland, in 1703,[1] in extending Leeuwenhoek's hypothesis of generation to plants, assumes the existence of an aperture in the Ovulum, through which it is impregnated. It appears, indeed, that he had not actually observed this aperture before fecundation, but inferred its existence generally and at that period, from having, as he says, "discovered in the seeds of beans, peas, and Phaseoli, just under one end of what we call the eye, a manifest perforation, which leads directly to the seminal [513
plant," and by which he supposes the embryo to have entered. This perforation is evidently the foramen discovered in the seeds of Leguminous plants by Grew, of whose observations respecting it he takes no notice, though he quotes him in another part of his subject.

In 1704, Etienne François Geoffroy,[2] and in 1711, his brother Claude Joseph Geoffroy,[3] in support of the same hypothesis, state the general existence of an aperture in the unimpregnated vegetable Ovulum. It is not, however, probable that these authors had really seen this aperture in the early state of the Ovulum in any case, but rather that they had merely advanced from the observation of Grew, and the conjecture founded on it by Morland, whose hypothesis they adopt without acknowledgment, to the unqualified assertion of its existence, in all cases. For it is to be remarked, that they take no notice of what had previously been observed or asserted on the more important parts of their subject, while several passages are evidently copied, and the whole account of the original state and development of the Ovulum is literally translated from Camerarius's Essay. Nor does the younger Geoffroy mention the earlier publication of his brother, from which his own memoir is in great part manifestly derived.

In 1718, Vaillant,[4] who rejects the vermicular hypothesis of generation, supposes the influence of the Pollen to consist in an aura, conveyed by the tracheæ of the style to the

[1] *Philosoph. Transact.* vol. xxiii, n. 287, p. 1474.

[2] *Quæstio Medica an Hominis primordia Vermis?* in auctoris *Tractatu de Materia Medica*, tom. i. p. 123.

[3] *Mem. de l'Acad. des Sc. de Paris*, 1711, p. 210.

[4] *Discours sur la Structure des Fleurs*, p. 20.

ovula, which it enters, if I rightly understand him, by the
544] funiculus umbilicalis: at the same time he seems to admit the existence of the aperture in the coat.

In 1745, Needham,[1] and in 1770, Gleichen,[2] adopt the hypothesis of Morland, somewhat modified, however, as they consider the particles in the grains of Pollen, not the grains themselves, to be the embryos, and that they enter the ovula by the umbilical cord.

Adanson, in 1763,[3] states the Embryo to exist before fecundation, and that it receives its first excitement from a vapour or aura proceeding from the Pollen, conveyed to it through the tracheæ of the style, and entering the Ovulum by the umbilical cord.

Spallanzani,[1] who appears to have carefully examined the unimpregnated Ovula of a considerable variety of plants, found it in general to be a homogeneous, spongy, or gelatinous body; but in two Cucurbitaceæ to consist of a nucleus surrounded by three coats. Of these coats he rightly supposes the outermost to be merely the epidermis of the middle membrane or testa. Of the relative direction of the testa and inner coat in the two plants in question he takes no notice, nor does he in any case mention an aperture in the Ovulum.

Gærtner, who, in the preface to his celebrated work, displays great erudition in every branch of his subject, can hardly, however, be considered an original observer in this part. He describes the unimpregnated Ovulum as a pulpy homogeneous globule, whose epidermis, then scarcely distinguishable, separates in a more advanced stage, and becomes the testa of the seed, the inner membrane of which is
545] entirely the product of fecundation.[5] He asserts also that the Embryo constantly appears at that point of the ovulum where the ultimate branches of the umbilical vessels perforate the inner membrane; and therefore mistakes the apex for the base of the nucleus.

[1] *New Microscopical Discoveries*, p. 60.
[2] *Observ. Microscop.* p. 45, *et* 61, § cxviii.
[3] *Fam. des Plant.* tom. i, p. 121.
[4] *Fisica Anim. e Veget.* tom. iii, p. 309—332.
[5] *Gært. de Fruct. et Sem.* i, p. 57, 59, *et* 61.

In 1806 Mons. Turpin[1] published a memoir on the organ by which the fecundating fluid is introduced into the vegetable ovulum. The substance of this memoir is, that in all Phænogamous plants fecundation takes place through a cord or fasciculus of vessels entering the outer coat of the ovulum, at a point distinct from, but, at the period of impregnation, closely approximated to the umbilicus ; and to the cicatrix of this cord, which itself is soon obliterated, he gives the name of Micropyle : that the ovulum has two coats each having its proper umbilicus, or, as he terms it, omphalode; that these coats in general correspond in direction; that more rarely the inner membrane is, with relation to the outer, inverted; and that towards the origin of the inner membrane the radicle of the embryo uniformly points.

It is singular that a botanist, so ingenious and experienced as M. Turpin, should, on this subject, instead of appealing in every case to the unimpregnated ovulum, have apparently contented himself with an examination of the ripe seed. Hence, however, he has formed an erroneous opinion of the nature and origin, and in some plants of the situation, of the micropyle itself, and hence also he has in all cases mistaken the apex for the base of the nucleus.

A minute examination of the early state of the ovulum does not seem to have entered into the plan of the late celebrated M. Richard, when in 1808 he published his valuable and original *Analyse du Fruit.* The ovulum has, [546
according to him, but one covering, which in the ripe seed he calls episperm. He considers the centre of the hilum as the base, and the chalaza, where it exists, as the natural apex of the seed.

M. Mirbel, in 1815, though admitting the existence of the foramen or micropyle of the testa,[2] describes the ovulum as receiving by the hilum both nourishing and fecundating vessels,[3] and as consisting of a uniform parenchyma, in which the embryo appears at first a minute point, gradually converting more or less of the surrounding tissue into its

[1] *Annal. du Mus. d'Hist. Nat.* vii, p. 199.
[2] *Elém. de Physiol. Vég. et de Bot.* tom. i, p. 49.
[3] *Id.* tom. i, p. 314.

own substance; the coats and albumen of the seed being formed of that portion which remains.[1]

In the same year, M. Auguste de Saint Hiliare[2] shows that the micropyle is not always approximated to the umbilicus; that in some plants it is situated at the opposite extremity of the ovulum, and that in all cases it corresponds with the radicle of the embryo. This excellent botanist, at the same time, adopts M. Turpin's opinion, that the micropyle is the cicatrix of a vascular cord, and even gives instances of its connection with the parietes of the ovarium; mistaking, as I believe, contact, which in some plants unquestionably takes place, and in one family, namely, Plumbagineæ, in a very remarkable manner, but only after a certain peried, for original cohesion, or organic connection, which I have not met with in any case.

In 1815 also appeared the masterly dissertation of Professor Ludolf Christian Treviranus, on the development of
547] the vegetable Embryo,[3] in which he describes the ovulum before fecundation as having two coats; but of these, his inner coat is evidently the middle membrane of Grew, the chorion of Malpighi, or what I have termed nucleus.

In 1822, Mons. Dutrochet, unacquainted, as it would seem, with the dissertation of Professor Treviranus, published his observations on the same subject.[4] In what regards the structure of the ovulum, he essentially agrees with that author, and has equally overlooked the inner membrane.

It is remarkable that neither of these observers should have noticed the foramen in the testa. And as they do not even mention the well-known essays of MM. Turpin and Auguste de St. Hilaire on the micropyle, it may be presumed that they were not disposed to adopt the statements of these authors respecting it.

Professor Link, in his *Philosophia Botanica*, published in 1824, adopts the account given by Treviranus, of the

[1] *Id.* loc. cit.
[2] *Mém. du Mus. d'Hist. Nat.* ii, p. 270, *et seq.*
[3] *Entwick. des Embryo im Pflanzen-Ey.*
[4] *Mém. du Mus. d'Hist. Nat.* tom. viii, p. 241, *et seq.*

coats of the ovulum before impregnation;[1] and of M. Turpin, as to the situation of the micropyle, and its being the cicatrix of a vascular cord. Yet he seems not to admit the function ascribed to it, and asserts that it is in many cases wanting.[2]

The account which I have given of the structure of the vegetable ovulum differs essentially from all those now quoted, and I am not acquainted with any other observations of importance respecting it.

Of the authors referred to, it may be remarked, that those who have most particularly attended to the ovulum externally, have not always examined it at a sufficiently [518
early period, and have confined themselves to its surface: that those who have most minutely examined its internal structure, have trusted too much to sections merely, and have neglected its appearance externally: and that those who have not at all examined it in the early stage have given the most correct account of its surface. This account was founded on a very limited observation of ripe seeds, generalized and extended to the unimpregnated ovulum, in connexion with an hypothesis then very commonly received: but this hypothesis being soon after abandoned, their statement respecting the ovulum was rejected along with it.

In the ovulum of Kingia, the inner membrane, with relation to the external umbilicus, is inverted; and this, as I have already observed, though in direct opposition to M. Turpin's account, is the usual structure of the organ. There are, however, several families in each of the two primary divisions of phænogamous plants, in which the inner membrane, and consequently the nucleus, agrees in direction with the testa. In such cases the external umbilicus alone affords a certain indication of the position of the future embryo.

It is an obvious consequence of what has been already stated, that the radicle of the embryo can never point directly to the external umbilicus or hilum, though this is

[1] *Elém. Philos. Bot.* p. 338. [2] *Id.* p. 340.

said to be generally the case by the most celebrated carpologists.

Another observation may be made, less obviously a consequence of the structure described, but equally at variance with many of the published accounts and figures of seeds, namely, that the radicle is never absolutely enclosed in the albumen; but, in the recent state, is either immediately in contact with the inner membrane of the seed, or this contact is established by means of a process generally very
549] short, but sometimes of great length, and which indeed in all cases may be regarded as an elongation of its own substance. From this rule I have found one apparent deviation, but in a case altogether so peculiar, that it can hardly be considered as setting it aside.

It is necessary to observe, that I am acquainted with exceptions to the structure of the ovulum as I have here described it. In Compositæ its coats seem to be imperforated, and hardly separable, either from each other or from the nucleus. In this family, therefore, the direction of the embryo can only be judged of from the vessels of the testa.[1] And in Lemna I have found an apparent inversion of the embryo with relation to the apex of the nucleus. In this genus, however, such other peculiarities of structure and economy exist, that, paradoxical as the assertion may seem, I consider the exception rather as confirming than lessening the importance of the character.

It may perhaps be unnecessary to remark, that the raphe, or vascular cord of the outer coat, almost universally belongs to that side of the ovulum which is next the placenta. But it is at least deserving of notice, that the very few apparent exceptions to this rule evidently tend to confirm it. The most remarkable of these exceptions occur in those species of Euonymus, which, contrary to the usual structure of the genus and family they belong to, have pendulous ovula; and, as I have long since noticed, in the perfect ovula only of Abelia.[2] In these, and in the other cases in which the raphe is on the outer side, or that most remote

[1] *Linn. Soc. Transact.* xii, p. 136. [2] Abel's *China*, p. 377.

from the placenta, the ovula are in reality resupinate; an economy apparently essential to their development.

The distinct origins and different directions of the nourishing vessels and channel through which fecunda- [550 tion took place in the ovulum, may still be seen in many of those ripe seeds that are winged, and either present their margins to the placenta, as in Proteaceæ, or have the plane of the wing at right angles to it, as in several Liliaceæ. These organs are visible also in some of those seeds that have their testa produced at both ends beyond the inner membrane, as Nepenthes; a structure which proves the outer coat of scobiform seeds, as they are called, to be really testa, and not arillus, as it has often been termed.

The importance of distinguishing between the membranes of the unimpregnated ovulum and those of the ripe seed, must be sufficiently evident from what has been already stated. But this distinction has been necessarily neglected by two classes of observers. The first consisting of those, among whom are several of the most eminent carpologists, who have regarded the coats of the seed as products of fecundation. The second, of those authors who, professing to give an account of the ovulum itself, have made their observations chiefly, or entirely, on the ripe seed, the coats of which they must consequently have supposed to be formed before impregnation.

The consideration of the *arillus*, which is of rare occurrence, is never complete, and whose development takes place chiefly after fecundation, might here, perhaps, be entirely omitted. It is, however, worthy of remark, that in the early stage of the ovulum, this envelope is in general hardly visible even in those cases where, as in Hibbertia volubilis, it attains the greatest size in the ripe seed; nor does it in any case, with which I am acquainted, cover the foramen of the testa until after fecundation.

The *testa*, or outer coat of the seed, is very generally formed by the outer membrane of the ovulum; and in most cases where the nucleus is inverted, which is the more [551 usual structure, its origin may be satisfactorily determined; either by the hilum being more or less lateral, while the

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foramen is terminal; or more obviously, and with greater certainty, where the *raphe* is visible, this vascular cord uniformly belonging to the outer membrane of the ovulum. The *chalaza*, properly so called, though merely the termination of the raphe, affords a less certain character, for in many plants it is hardly visible on the inner surface of the testa, but is intimately united with the areola of insertion of the inner membrane or of the nucleus, to one or other of which it then seems entirely to belong. In those cases where the testa agrees in direction with the nucleus, I am not acquainted with any character by which it can be absolutely distinguished from the inner membrane in the ripe seed; but as a few plants are already known, in which the outer membrane is originally incomplete, its entire absence, even before fecundation, is conceivable; and some possible cases of such a structure will be mentioned hereafter.

There are several cases known, some of which I have formerly noticed,[1] of the complete obliteration of the testa in the ripe seed; and on the other hand it appears to constitute the greater part of the substance of the bulb-like seeds of many Liliaceæ, where it no doubt performs also the function of albumen, from which, however, it is readily distinguished by its vascularity.[2] But the most remarkable deviation from the usual structure and economy of the outer membrane of the ovulum, both in its earliest stage and in the ripe fruit, that I have yet met with, occurs in Banksia and Dryandra. In these two genera I have ascertained that the inner membrane of the ovulum, before fecundation,
552] is entirely exposed, the outer membrane being even then open its whole length; and that the outer membranes of the two collateral ovula, which are originally distinct, cohere in a more advanced stage by their corresponding surfaces, and together constitute the anomalous dissepiment of the capsule; the inner membrane of the ovulum consequently forming the outer coat of the seed.

The *inner membrane* of the ovulum, however, in general

[1] *Linn. Soc. Transact.* xii, p. 149. (*Antè*, *p.* 364.) [2] Ibid.

appears to be of greater importance as connected with fecundation, than as affording protection to the nucleus at a more advanced period. For in many cases, before impregnation, its perforated apex projects beyond the aperture of the testa, and in some plants puts on the appearance of an obtuse, or even dilated stigma; while in the ripe seed it is often either entirely obliterated, or exists only as a thin film, which might readily be mistaken for the epidermis of a third membrane then frequently observable.

This *third coat* is formed by the proper membrane or cuticle of the Nucleus, from whose substance in the unimpregnated ovulum it is never, I believe, separable, and at that period is very rarely visible. In the ripe seed it is distinguishable from the inner membrane only by its apex, which is never perforated, is generally acute and more deeply coloured, or even sphacelated.

The membrane of the nucleus usually constitutes the innermost coat of the seed. But in a few plants an additional coat, apparently originating in the inner membrane of Grew, the vesicula colliquamenti or amnios of Malpighi, also exists.

In general the Amnios, after fecundation, gradually enlarges, till at length it displaces or absorbs the whole substance of the nucleus, containing in the ripe seed both the embryo and albumen, where the latter continues to exist. In such cases, however, its proper membrane is commonly [553 obliterated, and its place supplied either by that of the nucleus, by the inner membrane of the ovulum, or, where both these are evanescent, by the testa itself.

In other cases the albumen is formed by a deposition of granular matter in the cells of the nucleus. In some of these cases the membrane of the amnios seems to be persistent, forming even in the ripe seed a proper coat for the embryo, the original attachment of whose radicle to the apex of this coat may also continue. This, at least, seems to me the most probable explanation of the structure of true Nymphæaceæ, namely, Nuphar, Nymphæa, Euryale, Hydropeltis, and Cabomba, notwithstanding their very remarkable germination, as observed and figured in Nymphæa and Nuphar by Tittmann.[1]

In support of this explanation, which differs from all those yet given, I may here advert to an observation published many years ago, though it seems to have escaped every author who has since written on the subject, namely, that before the maturity of the seed in Nymphæaceæ, the sacculus contains along with the embryo a (pulpy or semi-fluid) substance, which I then called Vitellus, applying at that time this name to every body interposed between the albumen and embryo.[2] The opinion receives some confirmation also from the existence of an extremely fine filament, hitherto overlooked, which, originating from the centre of the lower surface of the sacculus, and passing through the hollow axis of the Albumen, probably connects this coat of the Embryo in an early stage with the base of the nucleus.

554] The same explanation of structure applies to the seeds of Piperaceæ and Saururus; and other instances occur of the persistence either of the membrane or of the substance of the amnios in the ripe seed.

It may be concluded from the whole account which I have given of the structure of the ovulum, that the more important changes consequent to real, or even to spurious fecundation, must take place within the nucleus; and that the albumen, properly so called, may be formed either by a deposition or secretion of granular matter in the utriculi of the amnios, or in those of the nucleus itself, or lastly, that two substances having these distinct origins, and very different textures, may coexist in the ripe seed, as is probably the case in Scitamineæ.

On the subject of the ovulum, as contained in an ovarium, I shall at present make but one other remark, which forms a necessary introduction to the observations that follow.

[1] *Keimung der Pflanzen*, p. 19 et 27, tab. 3 et 4.
[2] *Prodr. Flor. Nov. Holl.* i, p. 306.

On the Structure of the Female Flower in CYCADEÆ *and* CONIFERÆ.

That the apex of the nucleus is the point of the ovulum where impregnation takes place, is at least highly probable, both from the constancy in the appearance of the embryo at that point, and from the very general inversion of the nucleus; for by this inversion its apex is brought nearly, or absolutely, into contact with that part of the parietes of the ovarium, by which the influence of the pollen may be supposed to be communicated. In several of those families of plants, however, in which the nucleus is not inverted, and the placentæ are polyspermous, as Cistineæ,[1] it is difficult to comprehend in what manner this influence can [555
reach its apex externally, except on the supposition, not hastily to be admitted, of an impregnating aura filling the cavity of the ovarium; or by the complete separation of the fecundating tubes from the placentæ, which, however, in such cases I have never been able to detect.

It would entirely remove the doubts that may exist respecting the point of impregnation, if cases could be produced where the ovarium was either altogether wanting, or so imperfectly formed, that the ovulum itself became directly exposed to the action of the pollen, or its fovilla; its apex, as well as the orifice of its immediate covering, being modified and developed to adapt them to this economy.

But such, I believe, is the real explanation of the structure of Cycadeæ, of Coniferæ, of Ephedra, and even of Gnetum, of which Thoa of Aublet is a species.

To this view the most formidable objection would be removed, were it admitted, in conformity with the preceding observations, that the apex of the nucleus, or supposed

[1] This structure of ovulum, indicated by that of the seed, as characterising and defining the limits of Cistineæ (namely, Cistus, Helianthemum, Hudsonia, and Lechea), I communicated to Dr. Hooker, by whom it is noticed in his *Flora Scotica* (p. 284), published in 1821; where, however, an observation is added respecting Gærtner's description of Cistus and Helianthemum, for which I am not accountable.

point of impregnation, has no organic connection with the parietes of the ovarium, In support of it, also, as far as regards the direct action of the pollen on the ovulum, numerous instances of analogous economy in the animal kingdom may be adduced.

The similarity of the female flower in Cycadeæ and Coniferæ to the ovulum of other phænogamous plants, as I have described it, is indeed sufficiently obvious to render the opinion here advanced not altogether improbable. But the
556] proof of its correctness must chiefly rest on a resemblance, in every essential point, being established, between the inner body in the supposed female flower in these tribes, and the nucleus of the ovulum in ordinary structures; not only in the early stage, but also in the whole series of changes consequent to fecundation. Now, as far as I have yet examined, there is nearly a complete agreement in all these respects. I am not entirely satisfied, however, with the observations I have hitherto been able to make on a subject naturally difficult, and to which I have not till lately attended with my present view.

The facts most likely to be produced as arguments against this view of the structure of Coniferæ, are the unequal and apparently secreting surface of the apex of the supposed nucleus in most cases; its occasional projection beyond the orifice of the outer coat; its cohesion with that coat by a considerable portion of its surface, and the not unfrequent division of the orifice of the coat. Yet most of these peculiarities of structure might perhaps be adduced in support of the opinion advanced, being apparent adaptations to the supposed economy.

There is one fact that will hardly be brought forward as an objection, and which yet seems to me to present a difficulty, to this opinion; namely, the greater simplicity in Cycadeæ, and in the principal part of Coniferæ, of the supposed ovulum which consists of a nucleus and one coat only, compared with the organ as generally existing when enclosed in an ovarium. The want of uniformity in this respect may even be stated as another difficulty, for in some genera of Coniferæ the ovulum appears to be complete.

In Ephedra, indeed, where the nucleus is provided with two envelopes, the outer may, perhaps, be supposed rather analogous to the calyx, or involucrum of the male flower, than as belonging to the ovulum; but in Gnetum, [557 where three envelopes exist, two of these may, with great probability, be regarded as coats of the nucleus; while in Podocarpus and Dacrydium, the outer cupula, as I formerly termed it,[1] may also, perhaps, be viewed as the testa of the ovulum. To this view, as far as relates to Dacrydium, the longitudinal fissure of the outer coat in the early stage, and its state in the ripe fruit, in which it forms only a partial covering, may be objected.[2] But these objections are, in a great measure, removed by the analogous structure already described in Banksia and Dryandra.

The plurality of embryos sometimes occurring in Coniferæ, and which, in Cycadeæ, seems even to be the natural structure, may also, perhaps, be supposed to form an objection to the present opinion, though to me it appears rather an argument in its favour.

Upon the whole, the objections to which the view here taken of the structure of these two families is still liable, seem to me, as far as I am aware of them, much less important than those that may be brought against the other opinions that have been advanced, and still divide botanists on this subject.

According to the earliest of these opinions, the female flower of Cycadeæ and Coniferæ is a monospermous pistillum, having no proper floral envelope.

To this structure, however, Pinus itself was long considered by many botanists as presenting an exception.

Linnæus has expressed himself so obscurely in the natural character which he has given of this genus, that I find it difficult to determine what his opinion of its structure really was. I am inclined, however, to believe it to have been [558 much nearer the truth than is generally supposed; judging of it from a comparison of his essential with his artificial

[1] *Flinders' Voy.* vol. ii, p. 573 (*antè, p.* 47). [2] *Id.* loc. cit.

generic character, and from an observation recorded in his *Prælectiones*, published by Giseke.[1]

But the first clear account that I have met with, of the real structure of Pinus, as far as regards the direction, or base and apex of the female flowers, is given, in 1767, by Trew, who describes them in the following manner:—"Singula semina vel potius germina stigmati tanquam organo feminino gaudent,"[2] and his figure of the female flower of the Larch, in which the stigmata project beyond the base of the scale, removes all doubt respecting his meaning.

In 1789, M. de Jussieu, in the character of his genus Abies,[3] gives a similar account of structure, though somewhat less clearly as well as less decidedly expressed. In the observations that follow, he suggests, as not improbable, a very different view, founded on the supposed analogy with Araucaria, whose structure was then misunderstood; namely, that the inner scale of the female amentum is a bilocular ovarium, of which the outer scale is the style. But this, according to Sir James Smith,[4] was also Linnæus's opinion; and it is the view adopted in Mr. Lambert's splendid monograph of the genus published in 1803.

In the same year in which Mr. Lambert's work appeared, Schkuhr[5] describes, and very distinctly figures, the female flower of Pinus, exactly as it was understood by Trew, whose opinion was probably unknown to him.

559] In 1807 a memoir on this subject, by Mr. Salisbury, was published,[6] in which an account of structure is given, in no important particular different from that of Trew and Schkuhr, with whose observations he appears to have been unacquainted.

M. Mirbel, in 1809,[7] held the same opinion, both with respect to Pinus and to the whole natural family. But in 1812, in conjunction with M. Schoubert,[8] he proposed a

[1] *Prælect. in Ord. Nat.* p. 589.
[2] *Nov. Act. Acad. Nat. Curios.* iii, p. 453, tab. 13, fig. 23.
[3] *Gen. Pl.* p. 414.
[4] Rees's *Cyclop. art. Pinus.*
[5] *Botan. Handb.* iii, p. 276, tab. 308.
[6] *Linn. Soc. Transact.* viii, p. 308.
[7] *Ann. du Mus. d'Hist. Nat.* tom. xv, p. 473.
[8] *Nouv. Bulletin des Sc.* tom. iii, pp. 73, 85, *et* 121.

very different view of the structure of Cycadeæ and Coniferæ, stating, that in their female flowers there is not only a minute cohering perianthium present, but an external additional envelope, to which he has given the name of cupula.

In 1814 I adopted this view, as far at least as regards the manner of impregnation, and stated some facts in support of it.[1] But, on reconsidering the subject in connection with what I had ascertained respecting the vegetable ovulum, I soon after altogether abandoned this opinion, without, however, venturing explicitly to state that now advanced, and which had then suggested itself.[2]

It is well known that the late M. Richard had prepared a very valuable memoir on these two families of plants; and he appears, from some observations lately published by his son, M. Achille Richard,[3] to have formed an opinion respecting their structure somewhat different from that of M. Mirbel, whose cupula is, according to him, the perianthium, more or less cohering with the included pistillum. He was probably led to this view on ascertaining, which I had also done, that the common account of the structure of [560
Ephedra was incorrect,[4] its supposed style being in reality the elongated tubular apex of a membranous envelope, and the included body being evidently analogous to that in other genera of Coniferæ.

To the earliest of the opinions here quoted, that which considers the female flower of Coniferæ and Cycadeæ as a naked pistillum, there are two principal objections. The first of these arises from the perforation of the pistillum, and the exposure of that point of the ovulum where the embryo is formed to the direct action of the pollen; the second from the too great simplicity of structure of the supposed ovulum, which I have shown accords better with that of the nucleus as existing in ordinary cases.

To the opinions of MM. Richard and Mirbel, the first

[1] *Flinders' Voy.* ii, 572 (*antè, p.* 46).

[2] *Tuckey's Congo,* p. 451 (*antè, p.* 138), *et Linn. Soc. Transact.* vol. xiii, p. 213 (*antè, p.* 380, *note*).

[3] *Dict. Class. d'Hist. Nat.* tom. iv, p. 395, *et* tom. v, p. 216.

[4] *Id.* tom. vi, p. 208.

objection does not apply, but the second acquires such additional weight, as to render those opinions much less probable, it seems to me, than that which I have endeavoured to support.

In supposing the correctness of this opinion to be admitted, a question connected with it, and of some importance, would still remain, namely, whether in Cycadeæ and Coniferæ the ovula are produced on an ovarium of reduced functions and altered appearance, or on a rachis or receptacle. In other words, in employing the language of an hypothesis, which, with some alterations, I have elsewhere attempted to explain and defend, respecting the formation of the sexual organs in Phænogamous plants,[1] whether the ovula in these two families originate in a modified leaf, or proceed directly from the stem.

561] Were I to adopt the former supposition, or that best agreeing with the hypothesis in question, I should certainly apply it, in the first place, to Cycas, in which the female spadix bears so striking a resemblance to a partially altered frond or leaf, producing marginal ovula in one part, and in another being divided into segments, in some cases nearly resembling those of the ordinary frond.

But the analogy of the female spadix of Cycas to that of Zamia is sufficiently obvious; and from the spadix of Zamia to the fruit-bearing squama of Coniferæ, strictly so called, namely, of Agathis or Dammara, Cunninghamia, Pinus, and even Araucaria, the transition is not difficult. This view is applicable, though less manifestly, also to Cupressinæ; and might even be extended to Podocarpus and Dacrydium. But the structure of these two genera admits likewise of another explanation, to which I have already adverted.

If, however, the ovula in Cycadeæ and Coniferæ be really produced on the surface of an ovarium, it might, perhaps, though not necessarily, be expected that their male flowers should differ from those of all other phænogamous plants, and in this difference exhibit some analogy to the

[1] *Linn. Soc. Transact.* vol. xiii, p. 211 (*antè, p.* 378).

structure of the female flower. But in Cycadeæ, at least, and especially in Zamia, the resemblance between the male and female spadices is so great, that if the female be analogous to an ovarium, the partial male spadix must be considered as a single anthera, producing on its surface either naked grains of pollen, or pollen subdivided into masses, each furnished with its proper membrane.

Both these views may at present, perhaps, appear equally paradoxical; yet the former was entertained by Linnæus, who expresses himself on the subject in the following terms, "Pulvis floridus in Cycade minime pro Antheris agnoscendus est sed pro nudo polline, quod unusquisque qui un- [562
quam pollen antherarum in plantis examinavit fatebitur."[1] That this opinion, so confidently held by Linnæus, was never adopted by any other botanist, seems in part to have arisen from his having extended it to dorsiferous Ferns. Limited to Cycadeæ, however, it does not appear to me so very improbable as to deserve to be rejected without examination. It receives, at least, some support from the separation, in several cases, especially in the American Zamiæ, of the grains into two distinct, and sometimes nearly marginal, masses, representing, as it may be supposed, the lobes of an anthera; and also from their approximation in definite numbers, generally in fours, analogous to the quaternary union of the grains of pollen, not unfrequent in the antheræ of several other families of plants. The great size of the supposed grains of pollen, with the thickening and regular bursting of their membrane, may be said to be circumstances obviously connected with their production and persistence on the surface of an anthera, distant from the female flower; and with this economy, a corresponding enlargement of the contained particles or fovilla might also be expected. On examining these particles, however, I find them not only equal in size to the grains of pollen of many antheræ, but being elliptical and marked on one side with a longitudinal furrow, they have that form which is one of the most common in the simple pollen of phænogamous plants. To suppose, therefore, merely on the grounds already stated,

[1] *Mém. de l'Acad. des Scien. de Paris*, 1775, p. 518.

that these particles are analogous to the fovilla, and the containing organs to the grains of pollen in antheræ of the usual structure, would be entirely gratuitous. It is, at the same time, deserving of remark, that were this view
563] adopted on more satisfactory grounds, a corresponding development might then be said to exist in the essential parts of the male and female organs. The increased development in the ovulum would not consist so much in the unusual form and thickening of the coat, a part of secondary importance, and whose nature is disputed, as in the state of the nucleus of the seed, respecting which there is no difference of opinion; and where the plurality of embryos, or at least the existence and regular arrangement of the cells in which they are formed, is the uniform structure in the family.

The second view suggested, in which the anthera in Cycadeæ is considered as producing on its surface an indefinite number of pollen masses, each enclosed in its proper membrane, would derive its only support from a few remote analogies; as from those antheræ, whose loculi are subdivided into a definite, or more rarely an indefinite, number of cells, and especially from the structure of the stamina of Viscum album.

I may remark, that the opinion of M. Richard,[1] who considers these grains, or masses, as unilocular antheræ, each of which constitutes a male flower, seems to be attended with nearly equal difficulties.

The analogy between the male and female organs in Coniferæ, the existence of an open ovarium being assumed, is at first sight more apparent than in Cycadeæ. In Coniferæ, however, the pollen is certainly not naked, but is enclosed in a membrane similar to the lobe of an ordinary anthera. And in those genera in which each squama of the amentum produces two marginal lobes only, as Pinus, Podocarpus, Dacrydium, Salisburia, and Phyllocladus, it nearly resembles the more general form of the antheræ
564] in other Phænogamous plants. But the difficulty occurs in those genera which have an increased number of lobes

[1] *Dict. Class. d'Hist. Nat.* tom. v. p. 216.

on each squama, as Agathis and Araucaria, where their number is considerable and apparently indefinite, and more particularly still in Cunninghamia, or Belis,[1] in which the lobes, though only three in number, agree in this respect, as well as in insertion and direction, with the ovula. The supposition, that in such cases all the lobes of each squama are cells of one and the same anthera, receives but little support either from the origin and arrangement of the lobes themselves, or from the structure of other phænogamous plants: the only cases of apparent, though doubtful, analogy that I can at present recollect occurring in Aphyteia, and perhaps in some Cucurbitaceæ.

That part of my subject, therefore, which relates to the analogy between the male and female flowers in Cycadeæ and Coniferæ, I consider the least satisfactory, both in regard to the immediate question of the existence of an anomalous ovarium in these families, and to the hypothesis repeatedly referred to, of the origin of the sexual organs of all phænogamous plants.

In concluding this digression, I have to express my regret that it should have so far exceeded the limits [565
proper for its introduction into the present work. In giving an account, however, of the genus of plants to which it is annexed, I had to describe a structure, of whose nature and importance it was necessary I should show myself aware; and circumstances have occurred while I was engaged in preparing this account, which determined me to enter much more fully into the subject than I had originally intended.

1 In communicating specimens of this plant to the late M. Richard, for his intended monograph of Coniferæ, I added some remarks on its structure, agreeing with those here made. I at the same time requested that, if he objected to Mr. Salisbury's Belis as liable to be confounded with Bellis, the genus might be named Cunninghamia, to commemorate the merits of *Mr. James Cunningham*, an excellent observer in his time, by whom this plant was discovered; and in honour of *Mr. Allan Cunningham*, the very deserving botanist who accompanied Mr. Oxley in his first expedition into the interior of New South Wales, and Captain King in all his voyages of survey of the Coasts of New Holland.

A

BRIEF ACCOUNT

OF

MICROSCOPICAL OBSERVATIONS

Made in the Months of June, July, and August, 1827,

ON THE PARTICLES CONTAINED IN THE POLLEN OF PLANTS;

AND

ON THE GENERAL EXISTENCE OF ACTIVE MOLECULES

IN ORGANIC AND INORGANIC BODIES.

BY

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[*Not Published.*]

MICROSCOPICAL OBSERVATIONS.

THE observations, of which it is my intention to give a summary in the following pages, have all been made with a simple microscope, and indeed with one and the same lens, the focal length of which is about $\frac{1}{32}$nd of an inch.[1]

The examination of the unimpregnated vegetable Ovulum, an account of which was published early in 1826,[2] led me to attend more minutely than I had before done to the structure of the Pollen, and to inquire into its mode of action on the Pistillum in Phænogamous plants.

In the Essay referred to, it was shown that the apex of the nucleus of the Ovulum, the point which is universally the seat of the future Embryo, was very generally brought into contact with the terminations of the probable channels of fecundation; these being either the surface of the placenta, the extremity of the descending processes of the style,

[1] This double convex lens, which has been several years in my possession, I obtained from Mr. Bancks, optician, in the Strand. After I had made considerable progress in the inquiry, I explained the nature of my subject to Mr. Dollond, who obligingly made for me a simple pocket microscope, having very delicate adjustment, and furnished with excellent lenses, two of which are of much higher power than that above mentioned. To these I have often had recourse, and with great advantage, in investigating several minute points. But to give greater consistency to my statements, and to bring the subject as much as possible within the reach of general observation, I continued to employ throughout the whole of the inquiry the same lens with which it was commenced.

[2] In the Botanical Appendix to Captain King's Voyages to Australia, vol. ii, p. 534, *et seq.* (*antè p.* 435).

or more rarely, a part of the surface of the umbilical cord. It also appeared, however, from some of the facts noticed in the same Essay, that there were cases in which the Particles contained in the grains of pollen could hardly be conveyed
4] to that point of the ovulum through the vessels or cellular tissue of the ovarium; and the knowledge of these cases, as well as of the structure and economy of the antheræ in Asclepiadeæ, had led me to doubt the correctness of observations made by Stiles and Gleichen upwards of sixty years ago, as well as of some very recent statements, respecting the mode of action of the pollen in the process of impregnation.

It was not until late in the autumn of 1826 that I could attend to this subject; and the season was too far advanced to enable me to pursue the investigation. Finding, however, in one of the few plants then examined, the figure of the particles contained in the grains of pollen clearly discernible, and that figure not spherical but oblong, I expected, with some confidence, to meet with plants in other respects more favorable to the inquiry, in which these particles, from peculiarity of form, might be traced through their whole course: and thus, perhaps, the question determined whether they in any case reach the apex of the ovulum, or whether their direct action is limited to other parts of the female organ.

My inquiry on this point was commenced in June 1827, and the first plant examined proved in some respects remarkably well adapted to the object in view.

This plant was *Clarckia pulchella*, of which the grains of pollen, taken from antheræ full grown, but before bursting, were filled with particles or granules of unusually large size, varying from nearly $\frac{1}{4000}$th to about $\frac{1}{5000}$th of an inch in length, and of a figure between cylindrical and oblong, perhaps slightly flattened, and having rounded and equal extremities. While examining the form of these particles immersed in water, I observed many of them very evidently in motion; their motion consisting not only of a change of place in the fluid, manifested by alterations in their relative positions, but also not unfrequently of a change of form in

the particle itself; a contraction or curvature taking place repeatedly about the middle of one side, accompanied by a corresponding swelling or convexity on the opposite side of the particle. In a few instances the particle was seen to turn on its longer axis. These motions were such as to satisfy me, after frequently repeated observation, that they arose neither from currents in the fluid, nor from its [5
gradual evaporation, but belonged to the particle itself.

Grains of pollen of the same plant taken from antheræ immediately after bursting, contained similar subcylindrical particles, in reduced numbers, however, and mixed with other particles, at least as numerous, of much smaller size, apparently spherical, and in rapid oscillatory motion.

These smaller particles, or Molecules as I shall term them, when first seen, I considered to be some of the cylindrical particles swimming vertically in the fluid. But frequent and careful examination lessened my confidence in this supposition; and on continuing to observe them until the water had entirely evaporated, both the cylindrical particles and spherical molecules were found on the stage of the microscope.

In extending my observations to many other plants of the same natural family, namely *Onagrariæ*, the same general form and similar motions of particles were ascertained to exist, especially in the various species of Œnothera, which I examined. I found also in their grains of pollen taken from the antheræ immediately after bursting, a manifest reduction in the proportion of the cylindrical or oblong particles, and a corresponding increase in that of the molecules, in a less remarkable degree, however, than in Clarckia.

This appearance, or rather the great increase in the number of the molecules, and the reduction in that of the cylindrical particles, before the grain of pollen could possibly have come in contact with the stigma,—were perplexing circumstances in this stage of the inquiry, and certainly not favorable to the supposition of the cylindrical particles acting directly on the ovulum; an opinion which I was inclined to adopt when I first saw them in motion. These circumstances, however, induced me to multiply my observations, and I accordingly examined numerous species of many of the more important and remarkable families of the two great primary divisions of Phænogamous plants.

In all these plants particles were found, which in the different families or genera, varied in form from oblong to spherical, having manifest motions similar to those already described; except that the change of form in the oval and
6] oblong particles was generally less obvious than in Onagrariæ, and in the spherical particle was in no degree observable.[1] In a great proportion of these plants I also remarked the same reduction of the larger particles, and a corresponding increase in the molecules after the bursting of the antheræ: the molecule, of apparently uniform size and form, being then always present; and in some cases, indeed, no other particles were observed, either in this or in any earlier stage of the secreting organ.

In many plants belonging to several different families, but especially to Gramineæ, the membrane of the grain of pollen is so transparent that the motion of the larger particles within the entire grain was distinctly visible; and it was manifest also at the more transparent angles, and in some cases even in the body of the grain in Onagrariæ.

In *Asclepiadeæ*, strictly so called, the mass of pollen filling each cell of the anthera is in no stage separable into distinct grains; but within, its tesselated or cellular membrane is filled with spherical particles, commonly of two sizes. Both these kinds of particles when immersed in water are generally seen in vivid motion; but the apparent motions of the larger particle might in these cases perhaps be caused by the rapid oscillation of the more numerous molecules. The mass of pollen in this tribe of plants never bursts, but merely connects itself by a determinate point, which is not unfrequently semitransparent, to a process of nearly similar consistence, derived from the gland of the corresponding angle of the stigma.

[1] In *Lolium perenne*, however, which I have more recently examined, though the particle was oval and of smaller size than in Onagrariæ, this change of form was at least as remarkable, consisting in an equal contraction in the middle of each side, so as to divide it into two nearly orbicular portions.

In *Periploceæ*, and in a few *Apocineæ*, the pollen, which in these plants is separable into compound grains filled with spherical moving particles, is applied to processes of the stigma, analogous to those of Asclepiadeæ. A similar economy exists in *Orchideæ*, in which the pollen masses are always, at least in the early stage, granular; the grains, whether simple or compound, containing minute, nearly spherical particles, but the whole mass being, with [7 very few exceptions, connected by a determinate point of its surface with the stigma, or a glandular process of that organ.

Having found motion in the particles of the pollen of all the living plants which I had examined, I was led next to inquire whether this property continued after the death of the plant, and for what length of time it was retained.

In plants, either dried or immersed in spirit for a few days only, the particles of pollen of both kinds were found in motion equally evident with that observed in the living plant; specimens of several plants, some of which had been dried and preserved in an herbarium for upwards of twenty years, and others not less than a century, still exhibited the molecules or smaller spherical particles in considerable numbers, and in evident motion, along with a few of the larger particles, whose motions were much less manifest, and in some cases not observable.[1]

In this stage of the investigation having found, as I believed, a peculiar character in the motions of the particles of pollen in water, it occurred to me to appeal to this peculiarity as a test in certain families of Cryptogamous plants, namely, Mosses, and the genus Equisetum,

[1] While this sheet was passing through the press I have examined the pollen of several flowers which have been immersed in weak spirit about eleven months, particularly of *Viola tricolor*, *Zizania aquatica*, and *Zea Mays*; and in all these plants the peculiar particles of the pollen, which are oval or short oblong, though somewhat reduced in number, retain their form perfectly, and exhibit evident motion, though I think not so vivid as in those belonging to the living plant. In *Viola tricolor*, in which, as well as in other species of the same natural section of the genus, the pollen has a very remarkable form, the grain on immersion in nitric acid still discharged its contents by its four angles, though with less force than in the recent plant.

in which the existence of sexual organs had not been universally admitted.

In the supposed stamina of both these families, namely, in the cylindrical antheræ or pollen of Mosses, and on the surface of the four spathulate bodies surrounding the naked ovulum, as it may be considered, of Equisetum, I found minute spherical particles, apparently of the same size with the molecule described in Onagrariæ, and having equally
8] vivid motion on immersion in water; and this motion was still observable in specimens both of Mosses and of Equiseta, which had been dried upwards of one hundred years.

The very unexpected fact of seeming vitality retained by these minute particles so long after the death of the plant would not perhaps have materially lessened my confidence in the supposed peculiarity. But I at the same time observed, that on bruising the ovula or seeds of Equisetum, which at first happened accidentally, I so greatly increased the number of moving particles, that the source of the added quantity could not be doubted. I found also that on bruising first the floral leaves of Mosses, and then all other parts of those plants, that I readily obtained similar particles, not in equal quantity indeed, but equally in motion. My supposed test of the male organ was therefore necessarily abandoned.

Reflecting on all the facts with which I had now become acquainted, I was disposed to believe that the minute spherical particles or Molecules of apparently uniform size, first seen in the advanced state of the pollen of Onagrariæ, and most other Phænogamous plants,—then in the antheræ of Mosses and on the surface of the bodies regarded as the stamina of Equisetum,—and lastly in bruised portions of other parts of the same plants, were in reality the supposed constituent or elementary Molecules of organic bodies, first so considered by Buffon and Needham, then by Wrisberg with greater precision, soon after and still more particularly by Müller, and, very recently, by Dr. Milne Edwards, who has revived the doctrine and supported it with much interesting detail. I now therefore expected to find these molecules in all organic bodies: and accordingly on examining the various animal and vegetable tissues, whether living or dead, they were always found to exist; and merely by bruising these substances in water, I never failed to disengage the molecules in sufficient numbers to ascertain their apparent identity in size, form, and motion, with the smaller particles of the grains of pollen.

I examined also various products of organic bodies, particularly the gum resins, and substances of vegetable origin, extending my inquiry even to pit-coal; and in all these [9
bodies Molecules were found in abundance. I remark here also, partly as a caution to those who may hereafter engage in the same inquiry, that the dust or soot deposited on all bodies in such quantity, especially in London, is entirely composed of these molecules.

One of the substances examined, was a specimen of fossil wood, found in Wiltshire oolite, in a state to burn with flame; and as I found these molecules abundantly, and in motion in this specimen, I supposed that their existence, though in smaller quantity, might be ascertained in mineralized vegetable remains. With this view a minute portion of silicified wood, which exhibited the structure of Coniferæ, was bruised, and spherical particles, or molecules in all respects like those so frequently mentioned, were readily obtained from it; in such quantity, however, that the whole substance of the petrifaction seemed to be formed of them. But hence I inferred that these molecules were not limited to organic bodies, nor even to their products.

To establish the correctness of the inference, and to ascertain to what extent the molecules existed in mineral bodies, became the next object of inquiry. The first substance examined was a minute fragment of window-glass, from which, when merely bruised on the stage of the microscope, I readily and copiously obtained molecules agreeing in size, form, and motion with those which I had already seen.

I then proceeded to examine, and with similar results, such minerals as I either had at hand or could readily obtain, including several of the simple earths and metals, with many of their combinations.

Rocks of all ages, including those in which organic remains have never been found, yielded the molecules in abundance. Their existence was ascertained in each of the constituent minerals of granite, a fragment of the Sphinx being one of the specimens examined.

To mention all the mineral substances in which I have found these molecules, would be tedious; and I shall confine myself in this summary to an enumeration of a few of the most remarkable. These were both of aqueous and igneous origin, as travertine, stalactites, lava, obsidian,
10] pumice, volcanic ashes, and meteorites from various localities.[1] Of metals I may mention manganese, nickel, plumbago, bismuth, antimony, and arsenic. In a word, in every mineral which I could reduce to a powder, sufficiently fine to be temporarily suspended in water, I found these molecules more or less copiously; and in some cases, more particularly in siliceous crystals, the whole body submitted to examination appeared to be composed of them.

In many of the substances examined, especially those of a fibrous structure, as asbestus, actinolite, tremolite, zeolite, and even steatite, along with the spherical molecules, other corpuscles were found, like short fibres somewhat moniliform, whose transverse diameter appeared not to exceed that of the molecule, of which they seemed to be primary combinations. These fibrils, when of such length as to be probably composed of not more than four or five molecules, and still more evidently when formed of two or three only, were generally in motion, as least as vivid as that of the simple molecule itself; and which from the fibril often changing its position in the fluid, and from its occasional bending, might be said to be somewhat vermicular.

In other bodies which did not exhibit these fibrils, oval particles of a size about equal to two molecules, and which were also conjectured to be primary combinations of these, were not unfrequently met with, and in motion generally more vivid than that of the simple molecule; their motion consisting in turning usually on their longer axis, and then

[1] I have since found the molecules in the sand-tubes, formed by lightning, from Drig in Cumberland.

often appearing to be flattened. Such oval particles were found to be numerous and extremely active in white arsenic.

As mineral bodies which had been fused contained the moving molecules as abundantly as those of alluvial deposits, I was desirous of ascertaining whether the mobility of the particles existing in organic bodies was in any degree affected by the application of intense heat to the containing substance. With this view small portions of wood, both living and dead, linen, paper, cotton, wool, silk, hair, and muscular fibres, were exposed to the flame of a candle or burned in platina forceps, heated by the blowpipe ; and in all these bodies so heated, quenched in water, and immediately submitted to examination, the molecules were found, and in as evident motion as those obtained from the same substances before burning.

In some of the vegetable bodies burned in this manner, in addition to the simple molecules, primary combinations of these were observed, consisting of fibrils having transverse contractions, corresponding in number, as I conjectured, with that of the molecules composing them ; and those fibrils, when not consisting of a greater number than four or five molecules, exhibited motion resembling in kind and vivacity that of the mineral fibrils already described, while longer fibrils of the same apparent diameter were at rest.

The substance found to yield these active fibrils in the largest proportion and in the most vivid motion was the mucous coat interposed between the skin and muscles of the haddock, especially after coagulation by heat.

The fine powder produced on the under surface of the fronds of several Ferns, particularly of *Acrostichum calomelanos*, and the species nearly related to it, was found to be entirely composed of simple molecules and their primary fibre-like compounds, both of them being evidently in motion.

There are three points of great importance which I was anxious to ascertain respecting these molecules, namely, their form, whether they are of uniform size, and their absolute magnitude. I am not, however, entirely satisfied with what I have been able to determine on any of these points.

As to form, I have stated the molecule to be spherical, and this I have done with some confidence; the apparent exceptions which occurred admitting, as it seems to me, of being explained by supposing such particles to be compounds. This supposition in some of the cases is indeed hardly reconcileable with their apparent size, and requires for its support the further admission that, in combination, the figure of the molecule may be altered. In the particles formerly considered as primary combinations of molecules, a certain change of form must also be allowed; and even the simple molecule itself has sometimes appeared to me when in motion to have been slightly modified in this respect.

12] My manner of estimating the absolute magnitude and uniformity in size of the molecules, found in the various bodies submitted to examination, was by placing them on a micrometer divided to five thousandths of an inch, the lines of which were very distinct; or more rarely on one divided to ten thousandths, with fainter lines, not readily visible without the application of plumbago, as employed by Dr. Wollaston, but which in my subject was inadmissible.

The results so obtained can only be regarded as approximations, on which, perhaps, for an obvious reason, much reliance will not be placed. From the number and degree of accordance of my observations, however, I am upon the whole disposed to believe the simple molecule to be of uniform size, though as existing in various substances and examined in circumstances more or less favorable, it is necessary to state that its diameter appeared to vary from $\frac{1}{15,000}$th to $\frac{1}{20,000}$th of an inch.[1]

I shall not at present enter into additional details, nor

[1] While this sheet was passing through the press, Mr. Dollond, at my request, obligingly examined the supposed pollen of *Equisetum virgatum* with his compound achromatic microscope, having in its focus a glass divided into 10,000ths of an inch, upon which the object was placed; and although the greater number of particles or molecules seen were about 1-20,000th, yet the smallest did not exceed 1-30,000th of an inch.

shall I hazard any conjectures whatever respecting these molecules, which appear to be of such general existence in inorganic as well as in organic bodies; and it is only further necessary to mention the principal substances from which I have not been able to obtain them. These are oil, resin, wax and sulphur, such of the metals as I could not reduce to that minute state of division necessary for their separation, and finally, bodies soluble in water.

In returning to the subject with which my investigation commenced, and which was indeed the only object I originally had in view, I had still to examine into the probable mode of action of the larger or peculiar particles of the pollen, which, though in many cases diminished in number before the grain could possibly have been applied to the stigma, and particularly in Clarckia, the plant first examined, were yet in many other plants found in less diminished propor- [13
tion, and might in nearly all cases be supposed to exist in sufficient quantity to form the essential agents in the process of fecundation.

I was now therefore to inquire, whether their action was confined to the external organ, or whether it were possible to follow them to the nucleus of the ovulum itself. My endeavours, however, to trace them through the tissue of the style in plants well suited for this investigation, both from the size and form of the particles, and the development of the female parts, particularly Onagrariæ, was not attended with success; and neither in this nor in any other tribe examined, have I ever been able to find them in any part of the female organ except the stigma. Even in those families in which I have supposed the ovulum to be naked, namely, Cycadeæ and Coniferæ, I am inclined to think that the direct action of these particles, or of the pollen containing them, is exerted rather on the orifice of the proper membrane than on the apex of the included nucleus; an opinion which is in part founded on the partial withering confined to one side of the orifice of that membrane in the larch,—an appearance which I have remarked for several years.

To observers not aware of the existence of the elementary active molecules, so easily separated by pressure from all vegetable tissues, and which are disengaged and become more or less manifest in the incipient decay of semitransparent parts, it would not be difficult to trace granules through the whole length of the style : and as these granules are not always visible in the early and entire state of the organ, they would naturally be supposed to be derived from the pollen, in those cases at least in which its contained particles are not remarkably different in size and form from the molecule.

It is necessary also to observe that in many, perhaps I might say in most plants, in addition to the molecules separable from the stigma and style before the application of the pollen, other granules of greater size are obtained by pressure, which in some cases closely resemble the particles of the pollen in the same plants, and in a few cases even exceed them in size: these particles may be considered as
14] primary combinations of the molecules, analogous to those already noticed in mineral bodies and in various organic tissues.

From the account formerly given of Asclepiadeæ, Periploceæ, and Orchideæ, and particularly from what was observed of Asclepiadeæ, it is difficult to imagine, in this family at least, that there can be an actual transmission of particles from the mass of pollen, which does not burst, through the processes of the stigma; and even in these processes I have never been able to observe them, though they are in general sufficiently transparent to show the particles were they present. But if this be a correct statement of the structure of the sexual organs in Asclepiadeæ, the question respecting this family would no longer be, whether the particles in the pollen were transmitted through the stigma and style to the ovula, but rather whether even actual contact of these particles with the surface of the stigma were necessary to impregnation.

Finally, it may be remarked that those cases already adverted to, in which the apex of the nucleus of the ovulum, the supposed point of impregnation, is never brought into contact with the probable channels of fecundation, are more unfavorable to the opinion of the transmission of the particles of the pollen to the ovulum, than to that which considers the direct action of these particles as confined to the external parts of the female organ.

The observations, of which I have now given a brief account, were made in the months of June, July, and August, 1827. Those relating merely to the form and motion of the peculiar particles of the pollen were stated, and several of the objects shown, during these months, to many of my friends, particularly to Messrs. Bauer and Bicheno, Dr. Bostock, Dr. Fitton, Mr. E. Forster, Dr. Henderson, Sir Everard Home, Captain Home, Dr. Horsfield, Mr. Kœnig, M. Lagasca, Mr. Lindley, Dr. Maton, Mr. Menzies, Dr. Prout, Mr. Renouard, Dr. Roget, Mr. Stokes, and Dr. Wollaston; and the general existence of the active molecules in inorganic as well as organic bodies, their apparent indestructibility by heat, and several of the facts respecting the primary combinations of the molecules were communicated to Dr. Wollaston and Mr. Stokes in the last week of August.

None of these gentlemen are here appealed to for the [15
correctness of any of the statements made; my sole object in citing them being to prove from the period and general extent of the communication, that my observations were made within the dates given in the title of the present summary.

The facts ascertained respecting the motion of the particles of the pollen were never considered by me as wholly original; this motion having, as I knew, been obscurely seen by Needham, and distinctly by Gleichen, who not only observed the motion of the particles in water after the bursting of the pollen, but in several cases marked their change of place within the entire grain. He has not, however, given any satisfactory account either of the forms or of the motions of these particles, and in some cases appears to have confounded them with the elementary molecule, whose existence he was not aware of.

Before I engaged in the inquiry in 1827, I was acquainted only with the abstract given by M. Adolphe

Brongniart himself, of a very elaborate and valuable memoir, entitled "*Recherches sur la Génération et le Développement de l'Embryon dans les Végétaux Phanérogames,*" which he had then read before the Academy of Sciences of Paris, and has since published in the *Annales des Sciences Naturelles.*

Neither in the abstract referred to, nor in the body of the memoir which M. Brongniart has with great candour given in its original state, are there any observations, appearing of importance even to the author himself, on the motion or form of the particles; and the attempt to trace these particles to the ovulum with so imperfect a knowledge of their distinguishing characters could hardly be expected to prove satisfactory. Late in the autumn of 1827, however, M. Brongniart having at his command a microscope constructed by Amici, the celebrated professor of Modena, he was enabled to ascertain many important facts on both these points, the result of which he has given in the notes annexed to his memoir. On the general accuracy of his observations on the motions, form, and size of the granules, as he terms the particles, I place great reliance. But in attempting to trace these particles through their whole course, he has overlooked two points of the greatest importance in the investigation.

16] For, in the first place, he was evidently unacquainted with the fact that the active spherical molecules generally exist in the grain of pollen along with its proper particles; nor does it appear from any part of his memoir that he was aware of the existence of molecules having spontaneous or inherent motion and distinct from the peculiar particles of the pollen, though he has doubtless seen them, and in some cases, as it seems to me, described them as those particles.

Secondly, he has been satisfied with the external appearance of the parts in coming to his conclusion, that no particles capable of motion exist in the style or stigma before impregnation.

That both simple molecules and larger particles of different form, and equally capable of motion, do exist in these parts, before the application of the pollen to the stigma can possibly take place, in many of the plants submitted by him to examination, may easily be ascertained; particularly in *Antirrhinum majus*, of which he has given a figure in a more advanced state, representing these molecules or particles, which he supposes to have been derived from the grains of pollen, adhering to the stigma.

There are some other points respecting the grains of pollen and their contained particles in which I also differ from M. Brongniart, namely, in his supposition that the particles are not formed in the grain itself, but in the cavity of the anthera; in his assertion respecting the presence of pores on the surface of the grain in its early state, through which the particles formed in the anthera pass into its cavity; and lastly, on the existence of a membrane forming the coat of his boyau or mass of cylindrical form ejected from the grain of pollen.

I reserve, however, my observations on these and several other topics connected with the subject of the present inquiry for the more detailed account, which it is my intention to give.

July 30*th*, 1828.

ADDITIONAL REMARKS ON ACTIVE MOLECULES.

By ROBERT BROWN, F.R.S.

About twelve months ago I printed an account of Microscopical Observations made in the summer of 1827, on the Particles contained in the Pollen of Plants; and on the general Existence of active Molecules in Organic and Inorganic Bodies.

In the present Supplement to that account my objects are, to explain and modify a few of its statements, to advert to some of the remarks that have been made, either on the correctness or originality of the observations, and to the causes that have been considered sufficient for the explanation of the phenomena.

In the first place, I have to notice an erroneous assertion of more than one writer, namely, that I have stated the active Molecules to be animated. This mistake has probably arisen from my having communicated the facts in the same order in which they occurred, accompanied by the views which presented themselves in the different stages of the investigation; and in one case, from my having adopted the language, in referring to the opinion, of another inquirer into the first branch of the subject.

2] Although I endeavoured strictly to confine myself to the statement of the facts observed, yet in speaking of the active Molecules, I have not been able, in all cases, to avoid the introduction of hypothesis; for such is the supposition that the equally active particles of greater size, and frequently of very different form, are primary compounds of these Molecules,—a supposition which, though professedly conjectural, I regret having so much insisted on, especially as it may seem connected with the opinion of the absolute identity of the Molecules, from whatever source derived.

On this latter subject, the only two points that I endeavoured to ascertain were their size and figure: and although I was, upon the whole, inclined to think that in these respects the Molecules were similar from whatever substances obtained, yet the evidence then adduced in support of the supposition was far from satisfactory; and I may add, that I am still less satisfied now that such is the fact. But even had the uniformity of the Molecules in those two points been absolutely established, it did not necessarily follow, nor have I anywhere stated, as has been imputed to me, that they also agreed in all their other properties and functions.

I have remarked that certain substances, namely, sulphur, resin, and wax, did not yield active particles, which, however, proceeded merely from defective manipulation; for I have since readily obtained them from all these bodies: at the same time I ought to notice that their existence in sulphur was previously mentioned to me by my friend Mr. Lister.

In prosecuting the inquiry subsequent to the publication of my Observations, I have chiefly employed the simple microscope mentioned in the Pamphlet as having been made for me by Mr. Dollond, and of which the three lenses that I have generally used, are of a 40th, 60th, and 70th of an inch focus.

Many of the observations have been repeated and confirmed with other simple microscopes having lenses of similar powers, and also with the best achromatic compound microscopes, either in my own possession or belonging to my friends.

The result of the inquiry at present essentially agrees with that which may be collected from my printed account, [3
and may be here briefly stated in the following terms; namely,

That extremely minute particles of solid matter, whether obtained from organic or inorganic substances, when suspended in pure water, or in some other aqueous fluids, exhibit motions for which I am unable to account, and which from their irregularity and seeming independence resemble in a remarkable degree the less rapid motions of some of the simplest animalcules of infusions. That the smallest moving particles observed, and which I have termed Active Molecules, appear to be spherical, or nearly so, and to be between 1-20,000dth and 1-30,000dth of an inch in diameter; and that other particles of considerably greater and various size, and either of similar or of very different figure, also present analogous motions in like circumstances.

I have formerly stated my belief that these motions of the particles neither arose from currents in the fluid containing them, nor depended on that intestine motion which may be supposed to accompany its evaporation.

These causes of motion, however, either singly or combined with others,—as, the attractions and repulsions among the particles themselves, their unstable equilibrium in the fluid in which they are suspended, their hygrometrical or capillary action, and in some cases the disengagement of volatile matter, or of minute air bubbles,—have been considered by several writers as sufficiently accounting for the appearances. Some of the alleged causes here stated, with others which I have considered it unnecessary to mention, are not likely to be overlooked or to deceive observers of any experience in microscopical researches; and the insufficiency of the most important of those enumerated may, I think, be satisfactorily shown by means of a very simple experiment.

This experiment consists in reducing the drop of water containing the particles to microscopic minuteness, and prolonging its existence by immersing it in a transparent fluid of inferior specific gravity, with which it is not miscible, and in which evaporation is extremely slow. If to almond-oil, which is a fluid having these properties, a considerably
4] smaller proportion of water, duly impregnated with particles, be added, and the two fluids shaken or triturated together, drops of water of various sizes, from 1-50th to 1-2000dth of an inch in diameter, will be immediately produced. Of these, the most minute necessarily contain but few particles, and some may be occasionally observed with one particle only. In this manner minute drops, which if exposed to the air would be dissipated in less than a minute, may be retained for more than an hour. But in all the drops thus formed and protected, the motion of the particles takes place with undiminished activity, while the principal causes assigned for that motion, namely, evaporation, and their mutual attraction and repulsion, are either materially reduced or absolutely null.

It may here be remarked, that those currents from centre to circumference, at first hardly perceptible, then more obvious, and at last very rapid, which constantly exist in drops exposed to the air, and disturb or entirely overcome the proper motion of the particles, are wholly prevented in drops of small size immersed in oil,—a fact which, however, is only apparent in those drops that are flattened, in consequence of being nearly or absolutely in contact with the stage of the microscope.

That the motion of the particles is not produced by any cause acting on the surface of the drop, may be proved by an inversion of the experiment; for by mixing a very small proportion of oil with the water containing the particles, microscopic drops of oil of extreme minuteness, some of them not exceeding in size the particles themselves, will be found on the surface of the drop of water, and nearly or altogether at rest; while the particles in the centre or towards the bottom of the drop continue to move with their usual degree of activity.

By means of the contrivance now described for reducing the size and prolonging the existence of the drops containing the particles, which, simple as it is, did not till very lately occur to me, a greater command of the subject is obtained, sufficient perhaps to enable us to ascertain the real cause of the motions in question.

Of the few experiments which I have made since this manner of observing was adopted, some appear to me so curious, that I do not venture to state them until they are verified by frequent and careful repetition.

I shall conclude these supplementary remarks to my former Observations, by noticing the degree in which I consider those observations to have been anticipated.

That molecular was sometimes confounded with animalcular motion by several of the earlier microscopical observers, appears extremely probable from various passages in the writings of Leeuwenhoek, as well as from a very interesting Paper by Stephen Gray, published in the 19th volume of the Philosophical Transactions.

Needham also, and Buffon, with whom the hypothesis of organic particles originated, seem to have not unfrequently fallen into the same mistake. And I am inclined to believe that Spallanzani, notwithstanding one of his statements respecting them, has under the head of *Anima-*

letti d'ultimo ordine included the active Molecules as well as true Animalcules.

I may next mention that Gleichen, the discoverer of the motions of the Particles of the Pollen, also observed similar motions in the particles of the ovulum of Zea Mays.

Wrisberg and Müller, who adopted in part Buffon's hypothesis, state the globules, of which they suppose all organic bodies formed, to be capable of motion; and Müller distinguishes these moving organic globules from real Animalcules, with which, he adds, they have been confounded by some very respectable observers.

In 1814 Dr. James Drummond, of Belfast, published in the 7th volume of the Transactions of the Royal Society of Edinburgh, a very valuable Paper, entitled "On certain Appearances observed in the Dissection of the Eyes of Fishes."

In this Essay, which I regret I was entirely unacquainted with when I printed the account of my Observations, the author gives an account of the very remarkable motions of the spicula which form the silvery part of the choroid coat of the eyes of fishes.

These spicula were examined with a simple microscope, and
6] as opaque objects, a strong light being thrown upon the drop of water in which they were suspended. The appearances are minutely described, and very ingenious reasoning employed to show that, to account for the motions, the least improbable conjecture is to suppose the spicula animated.

As these bodies were seen by reflected and not by transmitted light, a very correct idea of their actual motions could hardly be obtained; and with the low magnifying powers necessarily employed with the instrument and in the manner described, the more minute nearly spherical particles or active Molecules which, when higher powers were used, I have always found in abundance along with the spicula, entirely escaped observation.

Dr. Drummond's researches were strictly limited to the spicula of the eyes and scales of fishes; and as he does not appear to have suspected that particles having analogous motions might exist in other organized bodies, and far less in inorganic matter, I consider myself anticipated by this acute observer only to the same extent as by Gleichen, and in a much less degree than by Müller, whose statements have been already alluded to.

All the observers now mentioned have confined themselves to the examination of the particles of organic bodies. In 1819, however, Mr. Bywater, of Liverpool, published an account of Microscopical Observations, in which it is stated that not only organic tissues, but also inorganic substances, consist of what he terms animated or irritable particles.

A second edition of this Essay appeared in 1828, probably altered in some points, but it may be supposed agreeing essentially in its statements with the edition of 1819, which I have never seen, and of the existence of which I was ignorant when I published my pamphlet.

From the edition of 1828, which I have but lately met with, it appears that Mr. Bywater employed a compound microscope of the construction called Culpepper's, that the object was examined in a bright sunshine, and the light from the mirror thrown so obliquely on the stage as to give a blue colour to the infusion.

The first experiment I here subjoin in his own words. [7

"A small portion of flour must be placed on a slip of glass, and mixed with a drop of water, then instantly applied to the microscope; and if stirred and viewed by a bright sun, as already described, it will appear evidently filled with innumerable small linear bodies, writhing and twisting about with extreme activity."

Similar bodies, and equally in motion, were obtained from animal and vegetable tissues, from vegetable mould, from sandstone after being made red hot, from coal, ashes, and other inorganic bodies.

I believe that in thus stating the manner in which Mr. Bywater's experiments were conducted, I have enabled microscopical observers to judge of the extent and kind of optical illusion to which he was liable, and of which he does not seem to have been aware. I have only to add, that it is not here a question of priority; for if his observations are to be depended on, mine must be entirely set aside.

July 28th, 1829.

OBSERVATIONS

ON THE

ORGANS AND MODE OF FECUNDATION

IN

ORCHIDEÆ AND ASCLEPIADEÆ.

BY

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ON THE

ORGANS AND MODE OF FECUNDATION

IN

ORCHIDEÆ AND ASCLEPIADEÆ.

READ NOVEMBER 1ST AND 15TH, 1831.[1]

IN the Essay now submitted to the Society, my principal object is to give an account of some observations, made chiefly in the course of the present year, on the structure and economy of the sexual organs in Orchideæ and Asclepiadeæ,—the two families of phænogamous plants which have hitherto presented the most important objections to the prevailing theories of vegetable fecundation.

But before entering on this account, it is necessary to notice the various opinions that have been held respecting the mode of impregnation in both families: and in concluding the subject of Orchideæ, I shall advert to a few other points of structure in that natural order.

[1] [This portion of the Memoir was originally printed for private distribution in October, 1831. The additions made to it when reprinted in the 'Linnean Transactions,' consist chiefly of the references to the authors quoted, of three notes at pp. 495, 496 and 497, and of the plates and their explanations. The alterations are merely verbal, with the exception of a passage at pp. 522-4, beneath which I have appended the corresponding passage of the first impression in a note.—EDIT.]

ORCHIDEÆ.

The authors whose opinions or conjectures on the mode of impregnation in Orchideæ I have to notice, may be divided into such as have considered the direct application of the pollen to the stigma as necessary: and those who,—from certain peculiarities in the structure and relative position of the sexual organs in this family,—have regarded the direct contact of these parts as in many cases difficult
686] or altogether improbable, and have consequently had recourse to other explanations of the function.

In 1760, Haller, the earliest writer of the first class, in describing his Epipactis, states that the antheræ or pollen masses, after leaving the cells in which they are originally inclosed, are retained by the process called by him sustentaculum, the rostellum of Richard, from which they readily fall upon the stigma.[1] He adds, that both in this genus and in Orchis the stigma communicates by a fovea or channel with the ovarium.

But as in 1742 he correctly describes the stigma of Orchis,[2] and in his account of Epipactis[3] notices also the gland derived, as he says, from the sustentaculum, and which is introduced between and connects the pollen masses, his opinion on the subject, though not expressed, is distinctly implied even at that period; or as indeed it may be said to have been so early as 1736,[4] when he first described the channel communicating with the ovarium, and considered it as being in the place of a style.

In 1763, Adanson[5] states that the pollen masses are projected on the stigma, of which his description is at least as satisfactory as that of some very recent writers on the subject. He also describes the flower of an Orchideous plant as being monandrous, with a bilocular anthera, containing pollen which coheres in masses (a view of structure

[1] *Orchid. class. constitut. in Act. Helvet.* iv, p. 100.
[2] *Hall. Enum.* p. 262. [3] *Id.* p. 274.
[4] *Meth. stud. bot.* p. 21. [5] *Fam. des Plant.* ii, p. 69.

first entertained, but not published, by Bernard de Jussieu);[1] and he correctly marks the relation both of the stamen and placentæ of the ovarium to the divisions of the perianthium.

In 1777, Curtis, in the Flora Londinensis in his figure and account of *Ophrys apifera*, correctly delineates and describes the pollen masses, called by him antheræ, the [657
glands at their base inclosed in distinct cuculli or bursiculæ, and the stigma, with the surface of which he represents the masses as coming in contact.

In his second volume, the two lateral adnate lobes of the stigma, and the auriculæ of the column of *Orchis mascula*, are distinctly shown; and these auriculæ, now generally denominated rudimentary stamina, are also delineated in some other species of Orchis afterwards figured in the same work.

In 1793, Christian Konrad Sprengel[2] asserts that the pollen masses are applied directly to the secreting or viscid surface on the front of the column, in other words to the stigma, and that insects are generally the agents in this operation.

In 1799, J. K. Wachter[3] supports the same opinion, as far as regards the necessity of direct contact of the pollen masses with the female organ; and this observer was the first who succeeded in artificially impregnating an Orchideous plant, by applying the pollen to the stigma of *Habenaria bifolia*.

In 1799 also, or beginning of 1800, Schkuhr[4] takes the same view of the subject, and states that the pollen masses, which resist the action of common moisture, are readily dissolved by the viscid fluid of the stigma.

In 1800 Swartz,[5] in adopting the same opinion, notices various ways in which the application of the pollen may be effected in the different tribes of this family, repeats the statement of Schkuhr on the solvent power of the stigma, and in *Bletia Tankervilliæ* describes ducts

[1] *Juss. gen. pl.* p. 66.
[2] *Entd. Geheim.* p. 401.
[3] *Römer, Archiv.* ii, p. 209.
[4] *Handbuch* iii, p. 192.
[5] *Act. Holm.* 1800, p. 134.

which convey the absorbed fluid from that organ to the ovarium.

In 1804, Salisbury[1] asserts that he had succeeded in
[658] impregnating many species belonging to different tribes of Orchideæ, by applying the pollen masses to the stigma, whose channel communicating with the cavity of the ovarium, and first noticed by Haller, he also describes.

In 1827, Professor L. C. Treviranus[2] published an account of several experiments made by him in 1824, which satisfactorily prove that impregnation in this family may be effected by the direct application of the pollen to the stigma.

About the end of 1830 a letter from Professor Amici[3] to M. Mirbel was published, in which that distinguished microscopical observer asserts that in many phænogamous plants the pollen tubes, or *boyaux*, penetrate through the style into the cavity of the ovarium, and are applied directly to the ovula.

In this important communication Orchideæ are not mentioned, but M. Adolphe Brongniart in a note states that he himself has seen the production of *boyaux* or pollen tubes even in this family; that here, however, as well as in all the other tribes in which he had examined these tubes, he found them to terminate in the tissue of the stigma.

Of the second class of authors the earliest is Linnæus,[4] who, in 1764, not satisfied either with his own or any other description then given of the stigma, inquires whether the influence of the pollen may not be communicated internally to the ovarium.

In 1770, Schmidel,[5] in an account which he gives of a species of Epipactis, describes and figures the upper lip of the stigma, the rostellum of Richard, with its gland both before and after the bursting of the anthera; and as he

[1] *Linn. Soc. Transact.* vii, p. 29. [2] *Zeitschrift f. Physiol.* ii, p. 225.
[3] *Annal. des Sc. Nat.* xxi, p. 329.
[4] *Prælect. in Ord. Nat. ed. Giseke,* p. 182.
[5] *Gesn. Op. Bot. hist. plant.* fasc. ii, p. 15, tab. 19.

denominates that part, before the pollen masses are [689
attached to it, "stigma virgineum," it may be considered as belonging to the same class.

Koelreuter, the next writer in point of time, and whose essay was published before Linnæus's query appeared, states, in 1775,[1] that the pollen masses, which he denominates naked antheræ, impart their fecundating matter to the surface of the cells of the true anthera, regarded by him consequently as stigma, and that through this surface it is absorbed and conveyed to the ovarium.

In 1787, Dr. Jonathan Stokes[2] conjectures that in Orchideæ, as well as in Asclepiadeæ, the male influence, or principle of arrangement, as it is termed by John Hunter, may be conveyed to the embryo without the intervention of air: a repetition certainly of Linnæus's conjecture, with which, however, as it was not published till 1791, he could not have been acquainted.

In 1791, Batsch[3] states that in Orchis and Ophrys,—and his observation may be extended at least to all Satyrinæ or Ophrydeæ,—the only way in which the mass of pollen can act on the ovarium, is by the retrogradation of the impregnating power through the pedunculus or caudicula of the pollen mass to the gland beneath it, which he is disposed to refer rather to the stigma than to the anthera.

The late Professor Richard, in 1802,[4] expressly says that fecundation is operated in Orchideæ and Asclepiadeæ without a change of place in the stamina; his opinion therefore must be considered identical with that of Batsch, and extended to the whole order.

It might perhaps be inferred from the description which I gave of Orchideæ in a work published in 1810,[5] that my opinion respecting the mode of impregnation agreed with [690
that of Batsch and Richard, though it is not there actually expressed, nor indeed very clearly in another publication of nearly the same date,[6] in which I had adverted to this

1 *Act. Phys. Palat.* iii, p. 55.
2 *With. Bot. Arrang.* 2nd ed. ii, p. 964.
3 *Botanische Bemerk.* i, p. 3.
4 *Dict. de Botan. par Bulliard*, ed. 2, p. 56.
5 *Prodr. Flor. Nov. Holl.* i, p. 310.
6 *Linn. Soc. Transact.* x, p. 19.

family. But I have since on several occasions more explicitly stated that opinion, which, until lately, I always considered the most probable hypothesis on the subject. At the same time its probability in this family appeared to me somewhat less than in Asclepiadeæ. For in Orchideæ a secreting surface in the female organ, apparently destined to act on the pollen without the intervention of any other part, is manifest; and some direct evidence of the fact existed, though not then considered satisfactory. In Asclepiadeæ, however, I entertained hardly any doubt on the subject; the only apparently secreting surface of the stigma in that family being occupied by the supposed conductors of the male influence, and no evidence whatever, with which I was acquainted, existing of its action through any other channel.

In 1816 or 1818 I received from the late celebrated Aubert du Petit Thouars some printed sheets of an intended work on Orchideæ, which, with a few alterations, was completed and published in 1822.[1]

From the unfinished work, as well as that which was afterwards published, it appears that this ingenious botanist considered the glutinous substance connecting the grains or lobules of pollen as the "aura seminalis" or fecundating matter; that the elastic pedicel of the pollen mass, existing in part of the family, but according to him not formed before expansion, consists of this gluten; and that in the expanded flower the gluten which has escaped from the pollen is, in all cases, in communication with the stigma.

He describes the stigma as forming on the surface of
691] the column a glutinous disk, from which a central thread or cord of the same nature is continued through the style to the cavity of the ovarium, where it divides into three branches, and that each of these is again subdivided into two. The six branches thus formed, are closely applied to the parietes of the ovarium, run down on each side of the corresponding placenta to its base, each giving off nume-

[1] *Hist. des Orchid.* p. 14.

rous ramuli, which spread themselves among the ovula, and separate them into irregular groups.

Hence, according to this author, a communication is established between the anthera and the ovula, which he adds are impregnated through their surface, and not, as he supposes to be the case in other families, through their funiculus or point of attachment to the placenta.

The remarkable account of the stigma here quoted, though coming from so distinguished and original an observer, and one who had particularly studied this family of plants, seems either to have been entirely overlooked, or in some degree discredited by more recent writers, none of whom, as far as I can find, have even alluded to it. And I confess it entirely escaped me until after I had made the observations which will be stated in the present essay, and which confirm its accuracy as to the existence and course of the parietal cords, though not as to their nature and origin.

In 1824 Professor Link[1] expresses his opinion that the rostellum of Richard is without doubt the true stigma.

In 1829 Mr. Lindley,[2] who for several years has particularly studied and has lately published part of a valuable systematic work on Orchideous Plants, states that in this family impregnation takes effect by absorption from the pollen masses through their gland into the stigmatic channel.

In 1830, in his Introduction to the Natural System of Botany, the same statement is repeated; and in this [692] work it also appears that he regards the glands to which the pollen masses become attached in Ophrydeæ as derived from the stamen, and not belonging to the stigma,[3] as in 1810 I had described them. It would even appear, from a passage in his systematic work[4] published in the same

[1] *Philos. Bot.* p. 298. [2] *Synops. Brit. Flor.* p. 256.

[3] "The pollen is not less curious. Now we have it in separate grains, as in other plants, but cohering to a mesh-work of cellular tissue, which is collected into a sort of central elastic strap; now the granules cohere in small angular indefinite masses, and the central elastic strap becomes more apparent, has a glandular extremity, which is often reclined in a peculiar pouch especially destined for its protection."—*Introduct. to Nat. Syst. of Bot.* p. 263.

[4] *Gen. and Sp. of Orchid.* Part I, p. 3.

year, that he considers the analogous glands, existing in most other tribes of Orchideæ, as equally belonging to the stamen: in his "Introduction," however, he refers them to the stigma in all cases except in Ophrydeæ.

Towards the end of 1830 the first part of Mr. Francis Bauer's Illustrations of Orchideous Plants edited by Mr. Lindley, was published.

From this work, of the importance and beauty of which it is impossible to speak too highly, it may be collected that Mr. Bauer's opinion or theory of impregnation in Orchideæ does not materially differ from that of Batsch, Richard, and other more recent writers. From one of the figures it appears that this theory had occurred to him as early as 1792; and in another figure, bearing the same date, he has accurately represented the structure of the grains of pollen in a plant belonging to Ophrydeæ, a structure which I had not ascertained in that tribe till 1806. Although Mr. Bauer's theory is essentially the same as that of Batsch and Richard, yet there are some points in which it may be considered peculiar; and chiefly in his supposing impregnation to take effect long before the ex-
693] pansion of the flower, at a time when the sexual organs are so placed with relation to each other that the fecundating matter, believed by him to pass from the pollen mass through its caudicula, where that part exists, to the gland attached to it, may be readily communicated to the stigma, with which the gland is then either in absolute contact or closely approximated. The more important points of this account may be extended to nearly the whole order, but is strictly applicable only to Satyrinæ or Ophrydeæ, a tribe in which Mr. Bauer seems, with Mr. Lindley, to consider the glands as belonging to the stamen and not to the stigma.[1] In those genera of this tribe in which the glands

[1] In the second part of Mr. Bauer's Illustrations, which has appeared since this paper was read, the explanation of Tab. 3, fig. 6, is corrected in the following manner:

"*For* 6. A pollen mass with its caudicula and gland taken out of the anther;

"*Read* 6. A pollen mass with its caudicula and the internal socket of the stigmatic gland."

It is evident, indeed, in the second part of the Illustrations, from figs. 8, 9, 11, and 12, of Tab. 12, representing details of *Satyrium pustulatum*, and the are included in a pouch or bursicula, he describes and figures perforations in the back of the pouch, through which the fecundating matter is communicated from the glands to the stigma; and one of the figures is intended to represent a gland in the act of parting with the fecundating matter.

It is impossible to judge correctly of Mr. Bauer's theory until all the proofs and arguments in its favour are adduced. I may observe, however, that those already published are by no means satisfactory to me.

For, in the first place, in the very early stage in which, [694
according to this theory, impregnation is supposed to be effected, it appears to me that the pollen is not in a state to impart its fecundating matter, nor the stigma to receive it; and it may be added, though this is of less weight, that the ovula have neither acquired the usual degree of development, nor that position which they afterwards take, and which gives the apex of the nucleus or point of impregnation the proper direction, with regard to the supposed impregnating surface.

Secondly, in the figure which may be said to exhibit a demonstration of the correctness of the theory,—in that, namely, representing the gland in the act of parting with the fecundating matter,—the magnifying power employed (which is only fifteen times) is surely insufficient for the establishment of a fact of this kind; while the disengagement of minute granules, which no doubt often takes place when the gland is immersed in water, may readily be accounted for in another way.[1]

drawings of which were made in 1800, that Mr. Bauer must, from that time at least, have correctly understood the origin of the glands in Ophrydeæ. There is nothing, however, in any of the figures in Tab. 3 of the first part at variance with their explanations, from which I judged of his opinion. It may therefore be concluded that Mr. Bauer had not examined these explanations before their publication.

[1] This second observation ought not now to be taken into account, as in the second part of Mr. Bauer's Illustrations the following correction occurs respecting the figure alluded to (Tab. 3. fig. 8).

"This is in some measure an ideal figure to represent in what way the fecundating matter is supposed to leave the caudicula and stigmatic gland; for this reason there has been no attention paid to preserving a proportion between the pollen mass and the fecundating matter."

I may here, however, remark, that it was evidently not my intention, in the

Thirdly, I have never been able to find those perforations, represented by Mr. Bauer, in the bursiculæ of Orchis and Ophrys, and the existence of which in these genera is essential to his hypothesis.

And, lastly, the appearance of the stigma in *Bletia Tan-*
695] *kervilliæ*, after impregnation, as he believes, according to my view of the subject would rather prove that it was in a state capable of acting upon, but had not yet received the fecundating matter from, the anthera.

In thus venturing to differ from so accurate and experienced an observer as Mr. Bauer on a subject which he has for many years minutely studied and so beautifully illustrated, I am well aware how great a risk I incur of being myself found in error.

I am very desirous, however, that the perusal of this sketch of the various statements that have appeared on the question of impregnation, with the greater part of which he is at present probably unacquainted, should induce him to re-examine the facts and arguments by which his own opinion on this subject is supported. He will thus either succeed in establishing his theory on more satisfactory grounds, or, if the examination should prove unfavourable, he will, I am persuaded, from his well-known candour, as readily abandon it.

The notice here given of the opinions of botanists on impregnation in Orchideæ brings the subject down to the spring of the present year, when from circumstances, which I may hereafter have occasion to advert to, my attention was directed to this family of plants, the particular study of which I had for a long time discontinued.

In reviewing notes respecting them, made many years ago, I found some points merely hinted at, or imperfectly made out, which seemed deserving of further examination; and in the course of these inquiries, other observations of at least equal importance suggested themselves.

observation in question, to throw any doubt on the correctness of Mr. Bauer's figure, being aware that very minute granular matter, separating from the gland when immersed in water, is actually visible with a lens of about half an inch focus. I objected to it only as a satisfactory proof of the theory referred to.

I now proceed to state, in some cases briefly, in others at greater length, the results of this investigation.

The first question that occupied me was, the relation which the lateral and generally rudimentary stamina bear 696
to the other parts of the flower.

Into this subject I had in part entered in my Observations on Apostasia, published by Dr. Wallich in his 'Plantæ Asiaticæ Rariores,'[1] and had then considered it probable that in all cases these Stamina, in whatever state of development they were found, belonged to a different series from the middle and usually fertile stamen; in other words, were placed opposite to the two lateral divisions of the inner series of the perianthium. In 1810, however, when I first advanced my hypothesis of the true nature of these processes of the column, I supposed, though the opinion was not then expressed, that they formed the complement of the outer series of stamina; a view which has been since very generally adopted, especially by Dr. Von Martius, who has given it in a stenographic formula, and by Mr. Lindley, who has exhibited the relative position of parts in this family in a diagram.[2] A careful examination of the structure of the column in various tribes of the order, chiefly by means of transverse sections, has fully confirmed the opinion I entertained when treating of Apostasia; and more particularly established the fact in Cypripedium, in which these lateral stamina are perfectly developed.

On the hypothesis of rudimentary stamina I may remark, that it presented itself to me some time before the publication of the Prodromus Floræ Novæ Hollandiæ; and my belief is, that until the appearance of that work this view had not been taken by any other observer in England. Mr. Bauer at least, in a recent conversation on the subject, readily admitted, with his usual candour, that although acquainted with a case of accidental development, the general view had not occurred to him until stated by me.

In my mind it arose from contrasting the structure of 697
Cypripedium with those genera of New Holland Orchideæ —Diuris, Prasophyllum, and others—in which the lateral

[1] Vol. i, p. 74. [2] *Introduct. to Nat. Syst.* p. 264.

processes or appendages of the column are so remarkably developed; and I afterwards, in searching for additional confirmations of the hypothesis, believed I had found such in the more minute lateral auriculæ of the column present in most Ophrydeæ.

These auriculæ, however, though they might serve to confirm, would hardly have suggested the hypothesis, at the period especially of which I speak. They had indeed until then been altogether overlooked, except by Malpighi,[1] by Curtis in his Flora Londinensis, perhaps in Walcott's Flora Britannica, and by Mr. Bauer, whom they were not likely to escape.

In my recent observations on Apostasia, referred to, I noticed a singular monstrosity of *Habenaria bifolia*, which, if such deviations from ordinary structure are always to be trusted, would throw great doubt on the hypothesis being applicable to these auriculæ of Ophrydeæ. For in this case, in which three antheræ are formed, auriculæ not only exist on the middle or ordinary stamen, but one is also found on the upper side of each of the lateral antheræ, which are here opposite to two divisions of the outer series of the perianthium. I have lately met with another instance of a similar monstrosity equally unfavourable; and I may add that this doubt is still further strengthened by my not being able to find vascular cords connected with these auriculæ in the only plants of Ophrydeæ in which I have carefully examined, with this object, the structure of the column, namely, *Orchis Morio*, *mascula*, and *latifolia*.

I do not indeed regard the absence of vessels as a complete proof of these auriculæ not being rudimentary stamina. But I may remark, that in the other tribes of Orchideæ, in
698] many of whose genera analogous processes are found, and in which tribes alone cases of their complete development have hitherto been observed, vessels not only generally exist in these processes, but may be traced to their expected origins, namely, into those cords which also supply the inner lateral divisions of the perianthium.

Although not necessarily connected with my subject, I

[1] *Op. Om.* tab. 25, fig. 142.

may here advert to the remarkable monstrosity in the flowers of an *Ophrys* described and figured by M. His[1] upwards of two years before the appearance of my Prodromus. This account I did not meet with till after that part of the volume relating to Orchideæ was printed; and I have here only to observe respecting it, that neither the monstrosity itself, consisting of the conversion into stamina of the three inner divisions of the perianthium, nor the author's speculation founded on it, has any connection with my opinion which relates to the processes of the column.

M. His's paper, however, and the remarkable structure of *Epistephium* of M. Kunth, have together given rise to a third hypothesis, whose author, M. Achille Richard,[2] considers an Orchideous flower as generally deprived of the outer series of the perianthium, which is present only in Epistephium. He consequently regards the existing inner series of perianthium, or that to which the labellum belongs, as formed of metamorphosed stamina.

This hypothesis, although apparently sanctioned by the structure of Scitamineæ, I consider untenable; the external additional part in Epistephium, which I have examined, appearing to me rather analogous to the calyculus in some Santalaceæ, in a few Proteaceæ, and perhaps to that of Loranthaceæ.

With reference to the support the hypothesis may [699
derive from the monstrosity described by M. His, I may add that I have met with more than one case of similar conversion into stamina of the inner series of the perianthium, or at least of its two lateral divisions, with a manifest tendency to the same change in the labellum: and in one of these cases, namely *Neottia picta*, in addition to the conversion of the two lateral divisions of the perianthium, the lateral processes of the column were also completely developed.

The next point examined was the composition of the Stigma with the relation of its lobes or divisions to the other parts of the flower, and especially to the supposed compo-

[1] *Journal de Physique*, lxv. (1807), p. 241.
[2] *Mém. de la Soc. d'Hist. Nat. de Paris*, iv, p. 16.

nent parts of the ovarium. On this subject very little information is to be obtained from the writings of botanists, most of whom have contented themselves with describing the stigma as a disk, a fovea glutinosa, a secreting surface, or viscid space in front of the column. The late celebrated Richard, however, who adverts to the occasional existence of two lateral processes of his gynizus, may be supposed to have had more correct notions of its composition: and it may also be observed, that in Curtis's plate of *Ophrys apifera* already referred to, and still more distinctly in Mr. Bauer's figure of *Orchis mascula*, the two lateral lobes are represented as distinct, corresponding very exactly with Haller's description, in 1742, of the stigma in this genus.

The result of my examination of this point satisfied me that Orchideæ have in reality three stigmata, generally more or less confluent, but in some cases manifestly distinct, and two of which are in several instances even furnished with styles of considerable length.

These stigmata are placed opposite to the three outer divisions of the perianthium, and consequently terminate the axes of the supposed component parts of the ovarium, always regarded by me as made up of three simple ovaria
700] united by their ovuliferous margins; a structure in which the ordinary relation of stigmata to placentæ is that here found.

In Mr. Bauer's 'Illustrations' already referred to, a very different account is given of the composition of the ovarium, which is there said to be formed of six pieces.

This view of its composition seems to be founded on the existence of six vascular cords, on the apparent interruptions in the cellular tissue, and on the singular dehiscence of the capsule. But the mere number of vascular cords, which, being destined to supply all parts of the flower, may be said rather to indicate the divisions of the perianthium than those of the ovarium, cannot be considered as affording an argument of much importance, and, if it were, would equally apply to many other families having trilocular ovaria, as Irideæ; while the interruptions or inequalities of cellular tissue may be viewed as only the preparation for that dehiscence which, though very remarkable in this order, is in a great degree analogous to that taking place in most Cruciferæ, in several Leguminosæ, and in other families of plants. It may also be objected to Mr. Bauer's view of the composition of ovarium, that the arrangement of the parietal placentæ, which on this hypothesis would occupy the axes of the three alternate component parts, is contrary to every analogy; while the position of the stigmata, if my account should prove to be correct, affords evidence nearly conclusive of the ovarium being formed of only three parts.

In those genera of Orchideæ in which the lateral stamina are perfect, and the middle stamen without anthera, namely, Cypripedium and Apostasia, all these lobes or divisions of stigma are equally developed, are of nearly similar form and texture, and, as I have proved by direct experiment in Cypripedium, are all equally capable of performing the proper function of the organ.

In most other cases the anterior lobe, or that placed [701
opposite to the perfect stamen, and deriving its vessels from the same cord, manifestly differs both in form and texture from the other two. To this anterior, or upper lobe, as it generally becomes in the expanded flower, the glands always belong to which the pollen masses become attached, but from which they are in all cases originally distinct, as may be proved even in Ophrydeæ.

According to my view, therefore, of the mode of impregnation, its office is essentially different from that of the two lateral lobes or stigmata, which in various degrees of development are always present, and in all cases, when the ovarium is perfect, are capable of performing their proper function.

The greatest development of these lateral stigmata takes place in the tribe of Satyrinæ or Ophrydeæ, as in many species of *Habenaria*, those especially which are found near or within the tropics; and still more remarkably in *Bonatea speciosa*, a plant hardly indeed distinguishable from the same extensive genus.

It would seem that in *Bonatea* the extraordinary development and complete separation of these lateral stigmata,

have effectually concealed their true nature; and accordingly they have uniformly been considered as forming parts or appendages of the labellum, with which indeed their bases cohere. That they are really stigmata, however, I have proved by a careful examination of the tissue of their secreting surface, by the action of the pollen artificially applied to this tissue, by the descent of its tubes, hereafter to be described, along the upper surface of the styles which is destitute of epidermis, and by the consequent enlargement of the ovarium. *Diplomeris* of Mr. Don,[1] which may also be regarded as a species of Habenaria, is another example of nearly the same kind; and the
702] description of stigma which, in 1813, I introduced into the character of *Satyrium*,[2] implies an analogous development in that genus.

On the relative position of stamina and stigmata in the column of an Orchideous plant, it may be remarked that there is hardly an instance of a perfectly developed stamen and stigma placed opposite to each other, and consequently deriving their vessels from the same cord.

For, in the ordinary structure of the family in which only one perfect stamen is produced, the corresponding stigma loses entirely or in great part its proper function, which it recovers, so to speak, in those cases where this stamen becomes imperfect, or is destitute of an anthera: and hence, perhaps, it may be said that to obtain in any case the complete devolopment of the lateral stamina, and, what is of greater importance, to ensure in all cases the perfection of the lateral stigmata, these organs are never placed opposite, but uniformly alternate with each other.

The general conformation of the ovarium, with regard to the number and relative position of the parietal placentæ, and the arrangement of their numerous ovula, has long been well understood. But the early structure and evolution of the unimpregnated ovulum have not yet, as far as I know, been in any degree attended to.

In its gradual development, the ovulum exhibits a series

[1] *Prodr. Flor. Nepal.* p. 26.
[2] *Ait. Hort. Kew.* ed. 2, vol. v, p. 196.

of changes nearly agreeing with those which M. Mirbel[1] has described and illustrated as taking place in other families.

In the earliest state in which I have examined the ovulum in Orchideæ, it consists merely of a minute papilla projecting from the pulpy surface of the placenta. In the [703
next stage the annular rudiment of the future testa is visible at the base of the papilliform nucleus. The subsequent changes, namely, the enlargement of the testa, the production of a funiculus, which is never vascular, and the curvature or inversion of the whole ovulum, so as to approximate the apex of its nucleus to the surface of the placenta, take place in different genera at different periods with relation to the development of the other parts of the flower. In general when the flower expands, the ovulum will be found in a state and direction proper for receiving the male influence. But in several cases, as in Cypripedium and Epipactis, genera which in many other respects are nearly allied, the ovulum has not completed its inversion, nor is the nucleus entirely covered by its testa until long after expansion, and even after the pollen has been acted on by the stigma, and its tubes have penetrated into the cavity of the ovarium.

The tissue of the perfect stigmata in Orchideæ does not materially differ from that of many other families. In the early state the utriculi composing it are densely approximated, having no fluid interposed. In the more advanced but unimpregnated state, these utriculi enlarge, and are separated from each other by a copious and generally viscid secretion. The channel of the style, or stigma, whose parietes are similarly composed, undergoes the same changes. Both these states are represented in one of Mr. Bauer's plates, who however considers the more advanced stage as subsequent to impregnation.

In the advanced but still unimpregnated state of the ovarium, the upper portions, which are in continuation with the axes of the three placentæ, but do not produce

Annal. des Sc. Nat. xvii, p. 302;—and in *Mém. de l'Acad. des Sc. de l'Instit.* ix, p. 212.

ovula, are of a texture somewhat different from that of the greater part of the cavity, but still more obviously different from that of the cavity of the style, being neither apparently
704] secreting nor consisting of similar utriculi. A narrow line of like surfaee is found extending on each side of every placenta nearly as far as it is ovuliferous. The three lines occupying the upper part of the axes, and the six lines marginal to the three placentæ, may, for a reason which will hereafter appear, be called the conducting surfaces of the ovarium.

The female organ, as now described, is in a proper state to be acted upon by the pollen applied to the stigma, and for the transmission of the fecundating matter into the cavity of the ovarium, in a manner and form which I shall presently attempt to explain.

In reflecting on the whole evidence existing in favour of the direct application of the pollen mass to the stigma, and especially on the recent experiments of Professor Treviranus,[1] I could no longer doubt that in this manner impregnation was actually effected in Orchideæ; and the sole difficulty in my mind to its being the only way arose from adverting to a circumstance that must have been remarked by every one who has particularly attended to this family, either in Europe or in tropical regions; namely, that all the capsules of a dense spike are not unfrequently ripened: a fact which at first seems hardly reconcilable with this mode of fecundation, at least on the supposition that the pollen mass is applied to the stigma by insects.

Without going fully into the question at present, I shall here only remark, that in several such cases I have satisfied myself, by actual examination of the stigmata belonging to capsules taken at many different heights in the spike, that pollen, by whatever means, had actually been applied to them.[2]

[1] *Zeitschrift f. Physiol.* ii, p. 225.

[2] It may also be observed, that the same difficulty applies to many other cases of dense inflorescence, as to the female spikes or strobili of Coniferæ, Zamia, and Zea; in all of which the symmetry of the ripe fruit is generally perfect, although partial failures of impregnation might be at least equally expected.

Believing, therefore, this is to be the only mode in [705
which impregnation is effected, I proceeded to examine the immediate changes produced by the application of the pollen masses to the stigma.

From numerous observations and experiments made with this view, chiefly in Satyrinæ or Ophrydeæ, and Arethuseæ, not however confined to these tribes, it was ascertained that the grains of pollen, soon after being applied to the stigma, either in the entire mass or separately, produce tubes or *boyaux* analogous to those first observed in one case by Professor Amici,[1] and afterwards in numerous others, and in many families, by M. Adolphe Brongniart.[2]

In Orchideæ one tube only is emitted from the absolutely simple grain, while the number of tubes generally corresponds with that of the divisions or cells of the compound grain. These tubes are of extreme tenuity, their diameter being generally less than 1-2000th of an inch, and they acquire a great length, even while adhering to the grains producing them. From these, however, they separate generally while still involved in the secretion and mixed with the utriculi of the stigma; and I have never observed an instance of a tube with its grain attached to it lower than the tissue of the stigma. In form they are perfectly cylindrical, or of equal diameter, neither dilated at the apex nor sensibly contracted in any part of their course. I have never found them either branched or jointed; but have frequently observed apparent interruptions in the tube, probably caused by partial coagulations of the contained fluid. Even in their earliest stage, while in length hardly equal to the diameter of the grain, I have not been able to observe them to contain distinct granules in employing a magnifying power of 150. With a [706
power of 300 or 400 indeed, extremely minute and very transparent granular matter may be detected; but such granules are very different from those which have been supposed to belong to the grains of pollen.

As an entire pollen mass is usually applied to the surface

Atti della Soc. Ital. xix, par. 2, p. 254. *Annal. des Sc. Nat.* ii, p. 66.
Annal. des Sc. Nat. xii, p. 34.

of the stigma, and as a great proportion of the mass so applied is acted upon by the fluid in which it is immersed, the tubes produced are generally very numerous, and together form a cord which passes through the channel of the stigma or style.

On reaching the cavity of the ovarium this cord regularly divides into three parts, the divisions being closely applied to those short upper portions of the axes of the valves which are not placentiferous; and at the point where the placenta commences each cord again divides into two branches. These six cords descend along the conducting surfaces already described when speaking of the unimpregnated ovarium, and generally extend as far as the placentæ themselves, with which they are thus placed nearly but perhaps not absolutely in contact.

The cords now described, both general and partial, seem to me to be entirely composed of pollen tubes, certainly without any mixture of the utriculi of the stigma, or, as far as I can ascertain, of the tissue of the conducting surfaces.

In two cases, namely *Ophrys apifera* and *Cypripedium spectabile*, I at one time believed I had seen tubes going off laterally from the partial cords towards the placentæ and mixing with the ovula; but I am not at present entirely satisfied with the exactness of these observations, and I have never been able to detect similar ramifications in any other case.[1]

That the existence of these tubes in the cavity of the ovarium is essential to fecundation in Orchideæ, can hardly be questioned. But the manner in which they operate on, 707] or whether they come actually in contact with, the ovula, are points which still remain undetermined.

I am aware that Professor Amici,[2] who discovered in several plants the remarkable fact of the penetration of the pollen tubes into the cavity of the ovarium, and who regards this economy as being very general, likewise believes that in all cases a pollen tube comes in contact with an

[1] See Additional Observations.
[2] *Annal. des Sc. Nat.* xxi, p. 329.

ovulum. M. Du Petit Thouars also, in his account already quoted of these cords, supposed by him to belong to the stigma of Orchideæ, describes their ultimate ramifications as mixing with the ovula.

I do not however consider myself so far advanced as these observers in this very important point;[1] and what I shall have to adduce on the subject of Asclepiadeæ, makes me hesitate still more to adopt their statements.

I may also remark that in Orchideæ the six cords are to be met with even in the ripe capsule, in which, allowance being made for the effect of pressure, they are not materially reduced in size; and the statement by M. Du Petit Thouars, of the lateral branches separating the ovula into irregular groups, is certainly not altogether correct; these groups being equally distinct before the existence of the cords.

With regard to the question of the origin of the pollen tubes, several arguments might be adduced in favour of M. Brongniart's opinion; which is, that they belong to the inner membrane of the grain, the intimate cohesion of the two membranes being assumed in most cases, and the no less intimate union of the constituent parts of compound grains in some others. That an inner membrane does occasionally exist is manifest in the pollen of several Coniferæ, in which the outer coat regularly bursts and is deciduous; and it will hereafter appear, that the structure in Asclepiadeæ confirms the correctness of this view.

But whatever opinion may be entertained as to the [70] origin of the tube, it can hardly be questioned that its production or growth is a vital action excited in the grain by the application of an external stimulus. The appropriate and most powerful stimulus to this action is no doubt contact, at the proper period, with the secretion or surface of the stigma of the same species. Many facts, however, and among others the existence of hybrid plants, prove that this is not the only stimulus capable of producing the effect; and in Orchideæ I have found that the action in

[1] See Additional Observations.

the pollen of one species may be excited by the stigma of another belonging to a very different tribe.

The elongation of the tubes, so remarkable in this family, and their separation from the grain long before their growth is completed, render it probable that they derive nourishment either from the particles contained in the grain, or from the conducting surfaces with which they are in contact.

The first visible effect of the action of the pollen on the stigma is the enlargement of the ovarium, which, in cases where it was reversed by torsion in the flowering state, generally untwists and resumes its original position.

Of the changes produced in the ovulum consequent to impregnation, the first consists in its enlargement merely; and in the few cases where the nucleus is at this period still partially exposed, it becomes completely covered by the testa, the original apex, but now the lower extremity of which continues open. The next change consists in the disappearance of the nucleus, probably from its acquiring greater transparency, and becoming confluent with the substance of the testa. Soon after, or perhaps simultaneously with, the disappearance of the original nucleus, and while the enlargement of the whole ovulum is gradually proceeding, a minute opaque round speck, generally seated about the middle of the testa, becomes visible. The
709] opaque speck is the commencement of the future embryo. At this period, or until the opaque corpuscle or nucleus has acquired more than half the size it attains in the ripe seed, a thread may be traced from its apex very nearly to the open end of the testa, or as it may be supposed, to the apex of the original nucleus of the unimpregnated ovulum.

This thread consists of a simple series of short cells, in one of which, in a single instance only however, I observed a circulation of very minute granular matter; and in several cases I have been able to distinguish in these cells that granular areola so frequently existing in the cells of Orchideous plants, and to which I shall have occasion hereafter to advert.

The lowermost joint or cell of this thread is probably the original state of what afterwards, from enlargement and deposition of granular matter, becomes the opaque speck or rudiment of the future embryo.

The only appreciable changes taking place in this opaque rudiment of the embryo are its gradual increase in size, and at length its manifest cellular structure.

In the ripe state it forms an ovate or nearly spherical body, consisting, as far as I have been able to ascertain, of a uniform cellular tissue covered by a very thin membrane, the base of which does not exhibit any indication of original attachment at that point; while at the apex the remains of the lower shrivelled joints of the cellular thread are still frequently visible.

This cellular body may be supposed to constitute the Embryo, which would therefore be without albumen, and whose germinating point, judging from analogy, would be its apex, or that extremity where the cellular thread is found; and consequently that corresponding with the apex of the nucleus in the unimpregnated ovulum.

The description here given of the undivided embryo in Orchideous plants as forming the whole body of the nucleus, [710
and consequently being destitute of albumen, agrees with the account first I believe published by M. du Petit Thouars,[1] and very soon after by the late excellent Richard.[2]

The only other remark I have to make on the fructification of this family, is, that the seed itself, as well as its funiculus, is entirely without vessels, and that the funiculus, which in the ripe seed is inserted into the testa close to one side of its open base, can hardly be traced beyond that point.

I shall conclude my observations on Orchideæ with a notice of some points of their general structure, which chiefly relate to the cellular tissue.

In each cell of the epidermis of a great part of this family, especially of those with membranaceous leaves, a single circular areola, generally somewhat more opaque than the membrane of the cell, is observable. This areola, which is more or less distinctly granular, is slightly convex,

[1] *Hist. des Orchid.* p. 19. [2] *Mém. du Mus. d'Hist. Nat.* iv, p. 41.

and although it seems to be on the surface is in reality covered by the outer lamina of the cell. There is no regularity as to its place in the cell; it is not unfrequently however central or nearly so.

As only one areola belongs to each cell, and as in many cases where it exists in the common cells of the epidermis it is also visible in the cutaneous glands or stomata, and in these is always double,—one being on each side of the limb,—it is highly probable that the cutaneous gland is in all cases composed of two cells of peculiar form, the line of union being the longitudinal axis of the disk or pore.

This areola, or nucleus of the cell as perhaps it might be termed, is not confined to the epidermis, being also found not only in the pubescence of the surface, particularly when [illegible] jointed, as in Cypripedium, but in many cases in the parenchyma or internal cells of the tissue, especially when these are free from the deposition of granular matter.

In the compressed cells of the epidermis the nucleus is in a corresponding degree flattened; but in the internal tissue it is often nearly spherical, more or less firmly adhering to one of the walls, and projecting into the cavity of the cell. In this state it may not unfrequently be found in the substance of the column, and in that of the perianthium.

The nucleus is manifest also in the tissue of the stigma, where, in accordance with the compression of the utriculi, it has an intermediate form, being neither so much flattened as in the epidermis, nor so convex as it is in the internal tissue of the column.

I may here remark, that I am acquainted with one case of apparent exception to the nucleus being solitary in each utriculus or cell, namely in *Bletia Tankervilliæ*.

In the utriculi of the stigma of this plant I have generally, though not always, found a second areola apparently on the surface, and composed of much larger granules than the ordinary nucleus, which is formed of very minute granular matter, and seems to be deep seated.

Mr. Bauer has represented the tissue of the stigma in this species of Bletia, both before and as he believes after impregnation; and in the latter state the utriculi are marked with from one to three areolæ of similar appearance.

The nucleus may even be supposed to exist in the pollen of this family. In the early stages of its formation at least a minute areola is often visible in the simple grain, and in each of the constituent parts or cells of the compound grain. But these areolæ may perhaps rather be considered as merely the points of production of the tubes.

This nucleus of the cell is not confined to Orchideæ, [712]
but is equally manifest in many other Monocotyledonous families; and I have even found it, hitherto however in very few cases, in the epidermis of Dicotyledonous plants; though in this primary division it may perhaps be said to exist in the early stages of development of the pollen. Among Monocotyledones the orders in which it is most remarkable are Liliaceæ, Hemerocallideæ, Asphodeleæ, Irideæ, and Commelineæ.

In some plants belonging to this last-mentioned family, especially in *Tradescantia virginica* and several nearly related species, it is uncommonly distinct, not only in the epidermis and in the jointed hairs of the filaments,[1] but in

[1] The jointed hair of the filament in this genus forms one of the most interesting microscopic objects with which I am acquainted, and that in three different ways:

1st. Its surface is marked with extremely fine longitudinal parallel equidistant lines or striæ, whose intervals are equal from about 1-15,000th to 1-20,000th of an inch. It might therefore in some cases be conveniently employed as a micrometer.

2ndly. The nucleus of the joint or cell is very distinct as well as regular in form, and by pressure is easily separated entire from the joint. It then appears to be exactly round, nearly lenticular, and its granular matter is either held together by a coagulated pulp not visibly granular,—or, which may be considered equally probable, by an enveloping membrane. The analogy of this nucleus to that existing in the various stages of development of the cells in which the grains of pollen are formed in the same species, is sufficiently obvious.

3rdly. In the joint when immersed in water, being at the same time freed from air, and consequently made more transparent, a circulation of very minute granular matter is visible to a lens magnifying from 300 to 400 times. This motion of the granular fluid is seldom in one uniform circle, but frequently in several apparently independent threads or currents: and these currents, though often exactly longitudinal and consequently in the direction of the striæ of the membrane, are not unfrequently observed forming various angles with these striæ. The smallest of the threads or streamlets appear to consist of a

713] the tissue of stigma, in the cells of the ovulum even before impregnation, and in all the stages of formation of the grains of pollen, the evolution of which is so remarkable in those species of Tradescantia.[1]

The few indications of the presence of this nucleus, or areola, that I have hitherto met with in the publications of botanists, are chiefly in some figures of epidermis, in the recent works of Meyen and Purkinje, and in one case in M. Adolphe Brongniart's memoir on the structure of leaves. But so little importance seems to be attached to it, that the appearance is not always referred to in the explanations of the figures in which it is represented. Mr. Bauer, however, who has also figured it in the utriculi of the stigma of *Bletia Tankervilliæ,* has more particularly noticed it, and seems to consider it as only visible after impregnation.

714] The second point of structure in Orchideæ to which I shall at present more briefly advert, is the frequent exist-

single series of particles. The course of these currents seems often in some degree affected by the nucleus, towards or from which many of them occasionally tend or appear to proceed. They can hardly, however, be said to be impeded by the nucleus, for they are occasionally observed passing between its surface and that of the cell; a proof that this body does not adhere to both sides of the cavity, and also that the number and various directions of the currents cannot be owing to partial obstructions arising from the unequal compression of the cell.

[1] In the very early stage of the flower-bud of *Tradescantia virginica,* while the antheræ are yet colourless, their loculi are filled with minute lenticular grains, having a transparent flat limb, with a slightly convex and minutely granular semi-opaque disk. This disk is the nucleus of the cell, which probably loses its membrane or limb, and, gradually enlarging, forms in the next stage a grain also lenticular, and which is marked either with only one transparent line dividing it into two equal parts, or with two lines crossing at right angles, and dividing it into four equal parts. In each of the quadrants a small nucleus is visible; and even where one transparent line only is distinguishable, two nuclei may frequently be found in each semicircular division. These nuclei may be readily extracted from the containing grain by pressure, and after separation retain their original form.

In the next stage examined, the greater number of grains consisted of the semicircular divisions already noticed, which had naturally separated, and now contained only one nucleus, which had greatly increased in size.

In the succeeding state the grain apparently consisted of the nucleus of the former stage considerably enlarged, having a regular oval form, a somewhat granular surface, and originally a small nucleus. This oval grain continuing to increase in size, and in the thickness and opacity of its membrane, acquires a pale yellow colour, and is now the perfect grain of pollen.

ence, particularly in the parasitical tribes, of fibrous or spirally striated cells in the parenchyma, especially of the leaves, but also in the white covering of the radical fibres.

In the leaves, they are either short spirally striated cells whose longer diameter is at right angles to the surface, as in *Stelis* and *Pleurothallis*, and whose fibres or striæ are connected by a broader membrane; or, being greatly elongated and running in the direction of the leaf, resemble compound spiral vessels of enormous diameter, and consisting entirely of the spiral fibres with no visible connecting membrane: the real spiral vessels in the same species being, as they generally are in the family, very slender and simple. In the white covering of the radical fibres the shorter striated cell is met with in many genera, especially I think in Oncidium and Epidendrum, in one species of which they have been remarked and figured by Meyen.[1]

My concluding observation on Orchideæ relates to the very general existence and great abundance, in this family, of Raphides or acicular crystals in almost every part of the cellular tissue.

In each cell where they exist these crystals are arranged in a single fasciculus, which is generally of a square form.

The individual crystals,—which are parallel to each other,—are cylindrical, with no apparent angles, and have short and equally pointed extremities.

The abundance of these fasciculi of crystals in the cellular tissue of the auriculæ of the column or supposed lateral stamina in Orphydeæ, is very remarkable, giving these processes externally a granular appearance, which has been [715
noticed though its cause seems to have been overlooked.

In the recent work of Meyen,[2] also, some examples of these crystals in Orchideæ are given.

[1] *Phytotomie*, tab. 11, f. 1 and 2. [2] *Phytotomie*.

ASCLEPIADEÆ.

The various statements and conjectures on the structure and functions of the sexual organs in this family were collected, and published in 1811, by the late Baron Jacquin, in a separate volume, entitled, 'Genitalia Asclepiadearum Controversa.'

To this work, up to the period when it appeared, I may refer for a complete history, and to the tenth volume of the Linnean Society's Transactions, along with the first of the Wernerian Natural History Society's Memoirs, published somewhat earlier, for a slight sketch, of the subject.

I shall here therefore only notice such statements as Jacquin has either omitted or imperfectly given, and continue the history to the present time.

In 1763, Adanson correctly describes the stamina in Asclepias as having their filaments united into a tube surrounding the ovaria, their antheræ bilocular and cohering with the base of the stigma, and the pollen of each cell forming a mass composed of confluent grains as in Orchideæ. He is also correct in considering the pentagonal body as the stigma; but he has entirely overlooked its glands and processes, nor does he say anything respecting the manner in which the pollen masses act upon or communicate their fecundating matter to it.

In 1779, Gleichen,[1] although he expressly says that in young flower-buds the pollen masses are distinct from those glands of the pentagonal central body to which they
716] afterwards are attached, yet considers both masses and glands as equally belonging to the anthera, the mass being the receptacle of the pollen. He further states that before the masses unite with the glands they are removed from the cells in which they were lodged, and are found firmly implanted by their sharp edge into the wall of the tube which surrounds the ovaria; that in this state a white

[1] *Microscop. Entd.* p. 73, et seq.

viscid substance hangs to them, which, when highly magnified, appears to consist of very slender tubes containing minute globules; and these tubes with their contents he considers as constituting the early preparation for the formation of pollen. He also asserts that the tops of the styles are not originally connected with the pentagonal body to which the glands belong—the stigma of Adanson, Jacquin, and others; and that therefore the true stigmata are those extremities of the styles on which, he adds, vesicles and threads are observable. And lastly, he supposes that impregnation, which he says is of rare occurrence in this family, does not usually take place until those stigmata have penetrated through the substance of the pentagonal body, and are on a level with its apex; at the same time he is disposed to believe that insects may occasionally assist in this function, by carrying the fecundating matter directly to the stigmata, if I understand him, even before they enter the pentagonal body. His conclusion therefore is, that in Asclepiadeæ impregnation may be effected in two different ways.

This description, in several respects so paradoxical, and of which Jacquin has overlooked some of the most important parts, is too remarkable to be here either omitted or abridged. It is not indeed strictly correct in more than two points, namely, in the pollen masses being originally distinct from the glands, and in the masses, when found implanted in the membrane surrounding the ovarium, having minute tubes filled with granular matter [717
hanging to them. The remaining statements, however, though essentially erroneous, are so far founded in fact, that had Gleichen either opened or rather dilated the opening which must have existed in the pollen mass when these tubes were found hanging to it, and more carefully attended to the state of the other parts of the flower when the mass was seen implanted in the tube, he must necessarily have obtained a correct view of the whole structure, and consequently have greatly advanced—by at least half a century—not only our knowledge of this particular family, but also the general subject of vegetable impregnation.

In 1793, Christian Konrad Sprengel, who adopts the opinion of Jacquin both with respect to the pollen masses and pentagonal stigma, further states, that this stigma has a secreting upper surface or apex, and is formed of two united bodies, each of which conveys to its corresponding ovarium the fecundating matter, consisting of the oily fluid which exudes from the surface of the pollen mass. He also considers insects as here essentially necessary in impregnation, which they effect by extracting, in a manner particularly described, the pollen masses from the cells, and applying them to the apex of the stigma. And lastly, as extraordinary activity of the insect is necessary, or at least advantageous in the performance of this operation, that activity is, according to him, produced by the intoxicating secretion of the nectaria.[1]

In 1809, an essay on Asclepiadeæ was published in the first volume of the Memoirs of the Wernerian Natural History Society, in which one of my principal objects was to establish the opinion, more or less conjectural, of Adanson,
718] Richard, Jussieu, and Schreber, respecting the structure of the stamina and stigma. With this view I appealed to the remarkable fact, that in the early state of the flower-bud the pollen masses are absolutely distinct from the glands and processes of the stigma, to which they in a more advanced stage become attached. This proof of the real origin of parts I then believed to be entirely new. It has, however, been already seen that the fact was noticed by Gleichen, and it will presently appear that it was also well known to another original observer.

In the essay referred to, I had not very minutely examined the texture of the pollen mass, and in true Asclepiadeæ I had failed in ascertaining its real internal structure; not having been then aware of the existence of the included grains of pollen, but believing, until very lately, that the mass in its most advanced state consisted of one

[1] It may here be remarked, that the prevailing form of inflorescence in Asclepiadeæ is well adapted to this economy; for the insect so readily passes from one corolla to another, that it not unfrequently visits every flower of the umbel.

undivided cavity, filled with minute granular matter mixed with an oily fluid; and hence concluded that the fecundating matter was conveyed from the mass through the arm and gland to the stigma.

In the month of April last I saw, for the first time, drawings of several Asclepiadeæ made between 1805 and 1813 by Mr. Bauer, who, aware of the interest I took in this subject, with his accustomed liberality and kindness, offered me any part of them for publication.

Among these drawings, exceeding perhaps in beauty and in the completeness of the details all the other productions with which I am acquainted even of this incomparable artist, an extensive series, exhibiting the gradual development of the parts of the flower in *Asclepias curassavica*, were the most important.

In this series, made in 1805, and commencing when the pollen is just separable in a pulpy mass from its cell, the glands of the undivided stigma being still invisible, the fact of the distinct origins of these parts is very satis- [719
factorily shown, in accordance with my observations in the essay referred to.[1]

But in these drawings Mr. Bauer has gone further than I did, having also represented the internal structure of the pollen mass as cellular; each cell in the flower-bud just before expansion being filled with a grain of pollen, marked with lines indicating its quaternary composition; while in the expanded flower this grain is exhibited as shrivelled, having discharged its contents, which consist of a mixture of an oily fluid and minute granules. From this, the concluding stage of the series, it may be inferred that Mr. Bauer's opinion respecting the mode of impregnation in Asclepiadeæ agrees with that which I had adopted, and

[1] In a flower-bud much earlier than the commencement of Mr. Bauer's series I have found the pistilla to consist merely of two distinct very short semicylindrical bodies, the rudiments no doubt of the future stigma.

In this stage also the antheræ are flat, nearly orbicular or ovate, greenish, rather thick and opaque, but petal-like, with no inequality of surface, or any other appearance of the future cells, which in a somewhat more advanced stage are indicated by two less opaque areolæ, and at the same time the two semicylindrical bodies unite to form the stigma. (Pl. 36, figs. 7—11.)

which, though probably originating with Richard in 1799,[1] and briefly stated by him in 1802,[2] was first distinctly expressed as a conjecture in 1789 by M. de Jussieu.

In 1817, Mr. Stephen Elliott states that he observed, in his *Podostigma*[3]—a genus nearly allied to Asclepias—a fibre or cord extending through the centre of the corpuscular pedicel or attenuated base of the stigma, and communicating from the anthera to the ovarium. He adds, that Dr. Macbride has since seen it in some species of Asclepias.

There can be no doubt that the cord here noticed is of the same nature with that which Gleichen has described in a different state, and of which I shall presently have occasion to speak.

720] In 1824, Professor Link,[4] while he admits the distinct origins of the pollen masses and glands or corpuscula seated on the angles of the stigma, yet considers both these parts as equally belonging to the anthera. In this respect his opinion is identical with that of Gleichen. The pollen mass, he adds, is composed either of a cellular tissue, or manifestly of grains of pollen: the former part of the description being no doubt meant to apply to true Asclepiadeæ, the latter to Periploceæ.

Professor L. C. Treviranus, in 1827,[5] published some observations on this family, in which his account of the structure of the pollen differs in several points from that exhibited in Mr. Bauer's drawings, which he states he had seen three years before this publication.

In *Asclepias curassavica*, the species more particularly examined by Treviranus, he describes the pollen mass as filled with compressed, nearly round but obtusely angular, colourless, simple grains, containing minute granules; the pressure of the external grains, or those in contact with the general covering, giving it the appearance of being cellular.

In speaking of the mode of impregnation, he says, that the pollen mass, at the time when its connection is esta-

[1] *Encycl. Botan.* i, p. 212.
[2] *Bulliard, Dict. de Bot.* ed. 2, p. 56.
[3] *Bot. of Carol. and Georg.* i, p. 327.
[4] *Phil. Bot.* p. 300.
[5] *Zeitsch. f. Physiol.* ii, p. 230.

blished with the process or arm of the gland, which is then very viscid, undergoes manifest changes, from being ventricose and opaque becoming flat, hard, and transparent. These changes he thinks are probably owing to the extraction of its fecundating matter by the process through which it passes to the glands, and by them to the angles of the stigma, whence it may be easily communicated to the styles and ovaria. His opinion, therefore, in every respect agrees with that which originated with Richard and Jussieu, and which I had adopted.

The celebrated traveller and naturalist, Dr. Ehrenberg, in 1829,[1] has given a very interesting account of the [72]
structure of the pollen masses in Asclepiadeæ, from observations commenced in 1825, and others made in 1828.

In this account he describes the pollen mass as consisting of a proper membrane bursting in a regular manner, the cavity being not cellular but undivided and filled with grains of pollen, each grain having a cauda or cylindrical tube often of great length, and all these tubes being directed towards the point or line of dehiscence. This appendage or cauda he considers analogous to the *boyau* of Amici and Brongniart differing however in its forming an essential part of the grain in Asclepiadeæ; whereas in other families the application of an external stimulus is necessary for its production.

He is entirely silent as to the manner in which these caudate grains communicate with or act upon the stigma; and does not in any case remark,—what must, I think, have been the fact, at least in several of the plants in which this structure was observed, and especially in those with pendulous pollen,—that the mass examined was no longer in the cell of the anthera, but had been removed and probably applied to some part of the stigma.

In the month of July last I examined several species of Asclepias, with reference to Mr. Bauer's drawings and Dr. Ehrenberg's account of the pollen;—the first object, there-

[1] *Linnæa* iv, p. 94.

therefore, was to ascertain the structure of the pollen mass.

[1] Although on this subject my earliest observations essentially agreed with Mr. Bauer's figures of the mass, which represent it as having a subdivided cavity with a grain of pollen in each cell; yet a further examination had led me to adopt the opinion of Treviranus and Ehrenberg, who describe its cavity as being undivided and filled with distinct grains.

722] I was confirmed in this opinion on considering the state of the mass after the production of the pollen tubes; for it appeared very improbable that the cells, unless they were of extreme tenuity, could be either suddenly removed or sufficiently ruptured to admit of the passage of the tubes from its more distant parts to the point or line of dehiscence.

The appearance, however, occasionally met with, of lacerated membranes proceeding, as it seemed, from the

[1] [In the original impression, printed for distribution in October, 1831, the passage from this point down to the paragraph on p. 524 commencing "On the 16th of July," stood as follows. This was replaced in the 'Linnean Transactions' by that which is given in the text.—Edit.]

"My earliest observations on this subject, made on several species of *Asclepias*, seemed to prove that the mass is cellular, nearly as Mr. Bauer has represented it. But on a further examination I was convinced that it can be termed cellular only in the early stages, in consequence of the state of the grains of pollen which then certainly cohere; while in the more advanced, and especially in the mature state, it is no longer really cellular, the grains being now distinct from each other; sections of the mass, however, whether transverse or longitudinal, still exhibit a cellular appearance.

"These grains, when in this their perfectly developed state, are colourless, nearly round, but slightly and obtusely angular, probably from mutual pressure, much compressed, with an undivided cavity, and no indication of their being composed of four or any other number of united cells. Their membrane is transparent, and has no appearance of being made up of two united coats, and the cavity is filled and rendered opaque by spherical granules of nearly uniform size, with occasionally a few oily particles. In this state no appearance or indication of the tubes or appendages described by Dr. Ehrenberg was found.

"The general covering of the mass, which is of a deep yellow colour and very distinctly areolated, the meshes being angular, and in size as well as in form nearly corresponding with the included grains, may perhaps be considered as the outermost series of cells, whose laminæ are closely applied to each other, as in the epidermis, and their cavity consequently obliterated. They thus form a coat of considerable thickness, necessary for the protection of the grains of pollen, in a mass which is destined to be removed from its original place by an insect, and applied by this agent to a distant part of the same or of a different flower."

margins of the areolæ of the inner surface of the mass, added to the facts which had originally led me to adopt Mr. Bauer's view, determined me to re-examine the subject.

The result of this examination, made on specimens of *Asclepias phytolaccoides* and *purpurascens*, but especially the former, proved that the mass in these species is really cellular in all stages, as Mr. Bauer has represented it in *A. curassavica*, and that in the advanced flower-bud, as in the expanded flower, the cells may be seen, though not without difficulty, after their grains are removed.

The pollen mass in several species of Asclepias, particularly in *Asclepias phytolaccoides*[1] (and in *A. curassavica*, as figured by Mr. Bauer), consists of cells disposed in three series parallel to its sides, the middle series being often more or less interrupted.

The cells of the outer layer of each side have their opposite walls very unequal both in colour and thickness. The outer wall of each of these cells, which is formed by one of the areolæ of the surface, is of a deep yellow colour, nearly opaque, and of such thickness as to prevent external bursting; the inner is of a paler yellow, semi-transparent, and so much thinner as to determine internal rupture, which in these cells, after the production of the tubes, seems to take place without regularity, and to such an extent, that after the removal of the grain the remains of the inner wall are [723
not very readily distinguishable.

Sections of the mass, indeed, both transverse and longitudinal, exhibit an appearance of cellularity; but there is here a source of fallacy, unless the contained grains are also visible in the section; and the best proof of its being cellular is derived from the state of the central or middle series after the bursting of the mass.

The cells of this central layer are of equal thickness throughout, and on the production of the tubes burst in a definite manner towards the convex edge of the mass, and at the same time generally separate from each other. They continue, however, to inclose the grain, or, as it may be

[1] Tab. 35, fig. 8.

considered, the inner membrane of the grain of pollen, whose outer membrane is formed by the cell itself; and the tenacity of this outer membrane is such that it may easily be removed from the inner without further apparent rupture.

These central grains, thus covered by their respective cells, may readily be distinguished, by their pale yellow colour and a certain degree of opacity, from the naked grains or inner membranes, which, like their tubes, are entirely colourless, and transparent.[1]

In Asclepiadeæ, therefore, it may be said that the greatest development of the pollen grain exists; namely a grain having an undivided cavity, whose membranes are entirely distinct, and the pollen tubes of which seem to possess the highest degree of vitality yet met with.

In the perfectly developed state of the pollen mass, the grain, considered as distinct from its outer membrane or containing cell, is nearly round, but slightly and obtusely angular, much compressed, with an undivided cavity, and exhibiting no indication of its being composed of four or
724] any other number of united cells. Its membrane is transparent and colourless, made up of two united coats, and the cavity is filled with spherical granules of nearly uniform size, among which a few oily particles are occasionally observable.[2] In this state no appearance or indication of the tubes or appendages described by Dr. Ehrenberg is found.

On the 16th of July, in repeating my examination of *Asclepias purpurascens*,[3] I observed in several flowers one or more pollen masses removed from their usual place, namely the cell of the anthera, and no longer fixed by the descending arm to the gland of the stigma, but immersed in one of the fissures formed by the projecting alæ of the antheræ, and in most cases separated from the gland, a small portion of the arm or process, generally that only below its flexure, remaining attached to the mass.[4]

[1] Tab. 35, fig. 9.
[2] Tab. 34, fig. 6; and tab. 56, figs. 3 and 13.
[3] Tab. 34.
[4] Tab. 35, figs. 2, 3, 4, and 7.

In the cases now described, the mass, which in general is entirely concealed by the alæ, was so placed in the fissure, that its inner or more convex edge was in contact with the outer wall of the tube formed by the united filaments, and the gibbous part of the edge closely pressed to that point where this tube is joined to the base of the corresponding angle of the stigma.[1]

These masses, at the point of contact, in most cases adhered firmly to the tube or base of the stigma, and on being separated, a white cord or fasciculus of extremely slender threads or tubes, issuing from the gibbous part of the edge, which had then regularly burst, came into view.

On laying open the pollen mass,—which in this state was easily done, by first dilating the aperture that gave issue to the cord,—each of the tubes composing it was found to proceed from a grain of pollen. These grains retained nearly their original form, but were become more transparent, and had generally lost a great portion of their granules; and these granules were not often to be found even in the tube, especially after it had acquired considerable [725
length.[2]

Almost every grain in the mass had produced its tube, and the tubes were directed from all parts of it towards the point of dehiscence. In this state the mass had become more convex from the increased bulk of its contents.

The tube so produced from each grain of pollen cannot be said to be emitted from it, but is manifestly an elongation of its membrane. These tubes are transparent, cylindrical, about 1-2000th of an inch in diameter, neither branched nor jointed, with no apparent interruption in their cavity, and when of great length, which they often attain, are frequently without granular matter.

I next proceeded to examine the course of the cord, which in most cases,—and indeed in all where the mass had remained a sufficient length of time in the fissure,—had opened a passage for itself through the membrane, or rather had separated the upper edge of this membrane from

[1] Tab. 34, fig 7.

[2] Tab. 35, figs. 7 and 10; and tab. 34, fig. 12.

the base of the stigma, to which it was before united. Having effected this separation, it was found to proceed along the surface of the base of the stigma in a line exactly opposite to the glands seated on the apex of the same bevelled angle. The cord having passed along the surface of the attenuated base of the stigma until it arrives at its articulation with the two styles, then inclines towards the inner side of the apex of the style nearest to it, and actually introduces itself, wholly or in part, into the hollow of the apex, which in this stage is in some degree exposed.[1] But as the partial separation of the styles from the stigma, then taking place, is not always sufficient for the free admission of the whole cord, a few of the tubes not unfrequently become bent, in some cases even zigzag, doubtless
726] in consequence of the obstacles opposed to them; and such tubes very seldom enter the style, but along with others hang down externally below the joint. This introduction of part of the tubes into the apex of the style is soon followed by a manifest enlargement of the ovarium, and of the style itself, which, in *Asclepias purpurascens*, then exhibits a discoloured blackish line, visible even on the surface of its inner side. On opening the cavity or body of the style in this stage, a fasciculus of tubes was constantly seen passing down the centre, which was originally pulpy, and the walls of the cavity formed by the passage of these tubes were always found indurated and blackened, having every appearance of being absolutely killed.

I have never been able hitherto to follow these tubes further than the commencement of the placenta, where they really appear to terminate.[2] I have not at least yet succeeded in tracing any of them either on the surface or in the substance of the placenta, though with this object I have examined it not only in its first degree of enlargement, but also in some of its more advanced stages.

The same series of appearances, with very slight modifications only, were observed in all the species of Asclepias (not indeed more than seven in number) which I had

[1] Tab. 34, figs. 7—9; and tab. 35, figs. 4 and 10.
[2] Tab. 34, figs. 10 and 11; and tab. 35, figs. 5 and 6.

opportunities of examining during the summer. For in those species in which the pollen mass was not found transferred from its original position to the fissure, and in contact with the base of the style, no doubt by means of insects, it was not difficult to place it there; and in doing so I never failed to obtain the same results.

I now turned my attention to the base of the stigma, expecting to find there such a modification of surface as might serve to account for the rupture and production of the tubes in the mass brought in contact with it. I have, however, in no case been able to observe the slightest [727
appearance of secretion, or any difference whatever in texture, between that part and the general surface of the stigma.

The bursting of the mass in Asclepias is uniformly on the more rounded edge; and this, it may be observed, is the inner edge or margin of the mass, with reference to the cell of the anthera in which it is formed; and I may further remark, that in the only case in which I have hitherto observed dehiscence in an erect pollen mass, namely, in *Hoya carnosa*, it also takes place along the inner margin.

In Asclepias the bursting always commences at the most prominent point of the convex edge, and to this part it is generally confined: it is sometimes, however, found extending through the greater part of its length.

On carefully examining the convex edge, and more particularly its most prominent portion, I have not been able to observe in it any change or peculiarity of texture, or even any obvious difference in the form of the meshes of the reticulated surface. Notwithstanding this apparent want of secretion in the base of the stigma, and of difference of texture in the covering of the mass of pollen at the point where it comes in contact with that organ, it must still be supposed that there is some peculiarity both in the surface of the stigma and in the prominent edge of the mass, on which the effects in question depend.

These effects are indeed very remarkable; the stimulus here supposed to be derived from the surface of the stigma,

and applied to the prominent point of the convex edge of the pollen mass, producing its appropriate action not only in those cells or grains of pollen in immediate contact with that point, but generally in every grain in the mass. But as there are no visible conductors of this stimulus within the mass, it must either be supposed to be propagated from one cell to another, or conveyed from the prominent [728
point of the edge to every other part of the surface of the covering itself.

To ascertain whether contact of the convex edge of the pollen mass with this point of the stigma was absolutely necessary for the rupture of the mass and the production of tubes, I in the first place introduced a mass into the fissure, but with its convex edge outwards. In this position no change whatever took place.

I next removed one of the glands of the angles of the stigma, and applied the convex edge of a mass to the surface thus exposed, which even in this stage—to facilitate the removal of the gland by insects—continues to secrete. In this case, dehiscence and protrusion of pollen tubes did follow, more slowly, however, and less completely, than when brought in contact with the non-secreting base.

On applying the pollen mass of one species of Asclepias to the base of the stigma of another, the usual changes generally took place; but still, as it seemed, less perfectly, and only after a longer interval.

Pollen masses of *Asclepias purpurascens* being applied to the stigma of *Epipactis palustris*, and immersed in its viscid secretion, the dehiscence, contrary to expectation, not only took place, but even more speedily than usual, that is within twenty-four hours. Some of the grains were also found discharged from the mass unchanged, while others, both discharged and still inclosed, had begun to produce tubes.

The greater number of these observations were also made with *A. phytolaccoides*, which, on account of the greater size of its flower, I at first preferred. I found, however, with reference to such experiments, an objection to employing this species, arising from the great excitability,

so to speak, of its mass, which in some cases produced its tubes merely on continued immersion in water. I even found that in this species, in the gradual decay of the [729
flower, where the parts remain soft, the rupture and protrusion of tubes took place while the mass was still in its original position, immersed in the cell of its anthera.[1] The tubes produced in this situation often acquire a great length, but coming, immediately on their protrusion from the mass, in contact with the membrane of the anthera, their course is necessarily altered; and in their new direction, which is generally upwards, they not unfrequently arrive at the top of the cell, or even extend beyond it.

In addition to the several species of Asclepias already referred to, *Cynanchum* (*Vincetoxicum*) *nigrum* is the only plant of this family in which I have observed the whole of the appearances; namely, the rupture of the mass, the production and protrusion of the pollen tubes, their union into a cord, with the course and entrance of this cord into the cavity of the style.

The present essay, therefore, as far as regards this family, might with greater propriety have been entitled, "On the mode of impregnation in the genus Asclepias." It seems, however, allowable to conclude, that in all the genera having pendulous pollen masses, the same economy, slightly modified perhaps in some cases, is likely to be found. But among those with erect pollen masses, there are several in which more considerable differences may be expected. Of this section of the family I have hitherto had the opportunity of submitting only one plant to careful examination, namely, *Hoya carnosa;* and even here my observations are incomplete.

In *Hoya carnosa* I have never found the pollen tubes produced, or masses ruptured, while remaining in their original position; but I have succeeded in producing these effects by bringing them in contact with certain parts of the corona.

The rupture and protrusion of pollen tubes, then, take

[1] Tab. 35, fig. 11.

730] place through the whole length of the inner edge of the mass, which, as in all the genuine species of Hoya, is truncated and pellucid.[1] But I have not yet been able so to place the mass as to produce a cord of tubes communicating with the stigma, nor can I at present conjecture how this is to be effected.

I shall conclude with some observations equally relating to both the families that have been treated of.

It is in the first place deserving of remark, that while Asclepiadeæ and Orchideæ so widely differ in almost every other respect, there should yet be an obvious analogy between them in those points in which they are distinguished from all other Phænogamous plants.

It is unnecessary here to state the numerous and important differences existing between these two families: but it may be of some interest to make a few remarks on their points of agreement or analogy.

These are chiefly two: The first being the presence of
731] an apparently additional part, not met with in other families; the second, the cohesion of the grains of pollen, and their application in masses to the female organ.

With regard to the first peculiarity it may be observed, that there is no real addition made to the number of organs in either family, and that in both families the apparent

[1] In the tubes of *Hoya carnosa* I have been able to confirm Professor Amici's observation with respect to circulation taking place in the *boyaux* of the grains of pollen. In this case the membrane being very transparent, and the granules, before the tube has acquired any considerable length, not being so numerous as to obscure the view of the opposite currents, they were very distinctly seen.

I have also observed circulation in the pollen tubes in a few other cases; especially in *Tradescantia virginica*, in which, while the tube was still very short, the circle partly existing in the tube was completed in the body of the grain. The circular current in grains of pollen before the production of the tube may likewise, in some cases, but not very readily, be distinguished, as in *Lolium perenne*.

It might perhaps be supposed that the molecular motion, which in a former essay I stated I had seen within the body of the grain of pollen, might have been merely an imperfect view of the circulation of granules, and such I am inclined to think it really was in *Lolium perenne*.

I have, however, also very distinctly seen within the membrane of the grain of pollen in some species of Asclepias, vivid oscillatory motion of granules without any appearance of circulation.

addition consists in a modification or production of the stigma; the modified part of which loses the proper function of that organ.

This production of the stigma,—which is generally present, and wanting only in certain Orchideæ, where its place is sometimes supplied by an analogous modification of the male organ,—though differing very remarkably in appearance in the two families, agrees in being originally distinct from the pollen masses, and in the advanced stage becoming firmly attached to them; in adhering but slightly to the point of its formation after the attachment to the pollen takes place; and in being so constructed as to be readily removed by insects from its original position along with the pollen masses.

As to the second point of agreement; namely, the cohesion of the grains of pollen into masses of considerable size, and the application of these masses to the stigma,—it is obviously connected with that which might perhaps be termed a third peculiarity; the apparent necessity for an unusual number of pollen tubes which are to act in concert; in the one family to penetrate to and regularly arrange themselves in the cavity of the ovarium;[1] in the other to open a communication with the stigma, and then to pass along a non-secreting surface, until they arrive at a distant point, where they are to be introduced into the cavity or body of the style.

With respect to the agency of Insects in fecundation in those two orders, there can be no doubt that it is very frequently employed in Orchideæ; at the same time there are evidently cases in that family in which, from the relative [732
position of the organs, the interposition of these agents is not always required. But in those Asclepiadeæ at least that have been fully examined, the absolute necessity for their assistance is manifest.

Two questions still remain.

The first regards the proof of the actual penetration of the pollen tubes into the cavity of the ovarium in both families.

[1] See Additional Observations.

In Asclepiadeæ I shall only observe, that I consider the evidence complete; but in Orchideæ it may be admitted that it is not altogether so satisfactory. Of the descent of pollen tubes through the cavity of the stigma in Orchideæ, the evidence appears to me unquestionable. With respect, however, to the origin of the cords formed of similar tubes, so numerous and so regularly arranged in the cavity of the ovarium, and which are in contact with surfaces not altogether incapable of secretion, it might perhaps be alleged, either that they wholly originate from the supposed conducting surfaces, or that they consist of a mixture derived from both sources.

That mucous threads, or capillary tubes, in most respects similar to pollen tubes, and certainly altogether belonging to the style, exist in some plants, there is no doubt; and such I have observed in Didymocarpus, Ipomopsis, and in Allamanda, before the application of the pollen to the stigma. I am still, however, of opinion, that those found in the cavity of the ovarium in Orchideæ are really derived from the pollen;[1] an opinion which receives some confirmation from the manifest descent of the pollen tubes in the style in many other families, as in several Scrophularinæ, Cistineæ, Viola, and Tradescantia.

The second question is, Whether the granules originally filling the grain of pollen, and which may often be found in the tubes, especially in their nascent state, both in these and in many other families, are the essential agents in the
733] process of fecundation; the tubes being merely the channels conveying them to the organ or surface on which they are destined to act.

The arguments which might be adduced in favour of this, the generally received opinion, would probably be the variety in the form and size of the granules in different plants, with their great uniformity in these respects in the same species, added to the difficulty of conceiving in what manner the tubes themselves can operate. On the other hand, their great diminution in number, or even total disappearance, in Asclepiadeæ and Orchideæ, long before the

[1] See Additional Observations.

tubes have finished their growth, would afford an argument of some weight at least against their essential importance in any case; and it may be added, that in Asclepiadeæ there appears to be no other source of nourishment for the tube until it has penetrated into the style, than these granules. Nor is it necessary to suppose that the tubes themselves act directly, it being even probable that they also contain a fluid or granular matter much more minute than that originally filling the cavity of the grain.[1]

Our knowledge indeed appears to me not yet sufficient to warrant even conjectures as to the form of the immediate agent derived from the male organ, or the manner of its application to the ovulum in the production of that series of changes constituting fecundation. I may, however, be allowed to observe, that at present, with respect to this function, we are at least as far advanced in these two families, hitherto considered so obscure, as we are in any other tribe of Phænogamous plants: and I even venture to add, that in investigating the obscure subject of generation, additional light is perhaps more likely to be derived from a further minute and patient examination of the structure and action of the sexual organs in Asclepiadeæ and Orchideæ, than from that of any other department either of the vegetable or animal kingdom.

[1] See Additional Observations.

734] EXPLANATION OF THE PLATES.

Tab. 30 (34). Asclepias purpurascens.

Fig. 1. A branch in flower:—natural size.

Fig. 2. An expanded flower, of which two of the foliola coronæ and one of the antheræ are removed:—moderately magnified.

Fig. 3. A front or inner view of an anthera, to show the extent of bursting, particularly with relation to the pollen mass, of which the greater part is included in the non-dehiscent portion:—magnified as fig. 2.

Fig. 4. A pollen mass, more highly magnified, separated from its gland and arm, and divided transversely, to show its cellular structure (first discovered in *Asclepias curassavica* in 1805 by Mr. Bauer), with grains of pollen, their granules, and some drops of an oily fluid.

Fig. 5. A pollen mass entire, with a small portion of the arm adhering to its apex:—magnified as fig. 4.

Fig. 6. A transverse section of a pollen mass, still more highly magnified, in one of the cells of which is seen the single grain (or inner membrane), also separately exhibited to show that it is simple and slightly angular.

Fig. 7. The pistillum with pollen masses, that have burst and protruded their tubes, applied to the base of the stigma, the glands and their arms being removed. The cords formed by the pollen tubes have passed along the corresponding sides of the conical base of the stigma, and have reached the tops of the styles.

Fig. 8. A longitudinal section (more highly magnified) of the conical base of the Stigma with the two styles, to show more distinctly the course of the pollen tubes.

735] Fig. 9. A pollen mass after bursting, with its cord formed of the pollen tubes, entering the apex of the style, which is there lacerated.

Fig. 10. The two Ovaria with their styles, one being somewhat enlarged in consequence of impregnation, and opened longitudinally; exhibiting pollen tubes extending from the apex of the style to the commencement of the placenta.

Fig. 11. The same two ovaria and styles, both opened, to show that in one (the left), which is somewhat smaller, no pollen tubes are contained; the other (the right), which is impregnated, shows the tubes reaching the ovula, but not extending further.

Fig. 12. Two grains of pollen (or rather grains deprived of their outer membranes), with portions of their tubes and contained spheroidal granules; proving that the tubes are extensions of this (the inner) membrane;—very highly magnified.

TAB. 31 (35). ASCLEPIAS PHYTOLACCOIDES.

Fig. 1. An expanded flower (magnified), from which two of the foliola coronæ and one anthera have been removed.

Fig. 2. The complete Pistillum, and on one side two of the antheræ, the membrane formed by the united filaments being cut off a little below the stigma; on the other side, a naked pollen mass applied to the stigma, with its gland and arm adhering.

Fig. 3. A longitudinal section of fig. 2, to show on the left side a pollen mass, with a small portion only of the arm adhering, applied to the base of the stigma, and which, having burst, shows the protrusion of the cord formed by the pollen tubes.

Fig. 4. A longitudinal section of one half of the Stigma and the corres- [736
ponding style transversely cut near the base, showing more distinctly the position of the pollen mass with the protrusion and course of the tubes.

Fig. 5. The Style of fig. 4, laid open lengthways, exhibiting within its cavity and beyond it the pollen tubes reaching the apex of the placenta, a reflected portion of which, with three of its ovula, is also shown.

Fig. 6. An impregnated Pistillum, of which the style is laid open longitudinally, and the placenta, thickly covered with ovula, exposed, to show the descent and course of the pollen tubes.

Fig. 7. A Pollen mass, to the apex of which the base of the arm adheres, with pollen tubes protruding from the point of dehiscence:—more highly magnified.

Fig. 8. A transverse section of a Pollen mass, showing an arrangement of the cells somewhat different from that of *A. purpurascens*, there being here a middle irregular series, the cells of which in some cases appear to separate and cover the grains after the production of the tubes.

Fig. 9. Two grains of pollen with portions of their tubes, very highly magnified, the grain to the left having its outer covering or membrane, which is removed from the grain to the right, and shown separately further to the left.

Fig. 10. A Pollen mass which has burst and protruded its tubes, exhibited as entering the cavity of the style, which is laid open to show the commencement of their descent.

Fig. 11. Two Pollen masses (with their arms and gland), which have burst and protruded their tubes while still inclosed in the cells of the antheræ; [737
this happening in *A. phytolaccoides* in that particular kind of decay mentioned in p. 529 of the text.

TAB. 32 (36).

Fig. 1. Two Pollen masses of *Asclepias purpurascens* with protruded tubes; the only instance met with in which both cords are introduced into the same style.

Fig. 2. A grain of pollen, of the same species, with a portion of its tube; the unusual form probably caused by the pressure of other grains and their tubes.

Fig. 3. A grain of pollen of *Asclepias purpurascens* containing numerous minute granules and two larger drops or globules of an oily fluid.

Figs. 4, 5, & 6. Various combinations of pollen masses of *Asclepias purpurascens*. In these it is supposed that the insect having removed and applied to the stigma some of the masses, has extracted, by means of the arms still adhering to it, other masses with their glands and arms.

A combination of the same kind, different from and more remarkable than any of these, but perhaps not very accurately represented, is given, in his *Microscop. Entdeck.*, tab. 36, fig. 8, by Gleichen, who appears (op. cit. p. 81) to have also met with other combinations, without suspecting in any case the real cause of such apparently anomalous structures.

Fig. 7. A flower bud of *Asclepias curassavica* in the earliest stage in which I was able to distinguish its parts; the unopened corolla in its place with one of the sepala, the other four being exhibited separately:—highly magnified.

738] Fig. 8. The Corolla of fig. 7, opened and in part removed, to show the state of the contained organs; the figure exhibiting two petals hardly cohering at base; within these, two distinct petal-like bodies, alternating with them, and which are the antheræ; and two other smaller bodies, which are the pistilla as yet unconnected.

Fig. 9. An Anthera taken from fig. 8, and more highly magnified, to show that in this early stage it is entirely petal-like, there being no indication of the two cells, of which the first appearance in a somewhat more advanced stage is given at Fig. 10.

Fig. 11. A Petal of fig. 8, more highly magnified.

Fig. 12. The Pistilla of fig. 8, as yet distinct, scarcely at all angular, and with no manifest cavities; so that these two bodies may be regarded as chiefly or entirely the component parts of the stigma.

Fig. 13. Two Grains of pollen taken from the pollen mass of the expanded flower of *Asclepias curassavica*.

ADDITIONAL OBSERVATIONS ON THE MODE OF FECUNDATION IN ORCHIDEÆ. [739]

Read June 5th, 1832.

THE following additions to the Paper which was communicated to the Society in November last, on the Sexual Organs and Mode of Fecundation in Orchideæ and Asclepiadeæ, relate entirely to the former family.

In the essay itself I had ascertained from the examination of a considerable number of species belonging to different tribes of Orchideæ, that in the expanded flower of this family, however long it had remained in that state, no appearance whatever existed of those tubes which form the mucous cords, either in the tissue of the stigma or in the cavity of the ovarium, anterior to the application of the pollen to the stigma; and that in all cases where pollen had been applied to that organ and enlargement of the ovarium had followed, the mucous cords were to be found.

From these facts I had concluded that the tubes forming the cords were entirely and directly produced from the grains of pollen; and hence I accounted for the cohesion of the pollen into masses, and its frequent application in that state to the stigma.

Some cases, however, in which a few lobules or even grains of pollen only were observed on the stigmata of impregnated flowers, had led me to express myself doubtfully on this point. And since my paper was read, I have had opportunities of making several observations and experiments which prove that the application of a very small portion of a pollen mass to the stigma is sufficient for the production of mucous cords of the ordinary size in the cavity of the ovarium.

My observations on this point and on the gradual pro- [740]
duction and descent of these cords have been made chiefly on *Bonatea speciosa*, perhaps the most favourable subject for such experiments in the whole family.

My first observation on Bonatea related to the probability of a single insect impregnating several or even many flowers with one and the same mass of pollen.

To effect this, it is only necessary that the viscidity of the retinaculum or gland with which the pollen mass becomes inseparably connected, and by means of which the mass is removed from its cell and adheres to the insect, should exceed that of the surface of the stigma, and that the viscidity of the stigma should be sufficient to overcome the mutual cohesion of the lobules composing the mass.

These different degrees of viscidity are very manifest in *Bonatea speciosa,* in which, imitating the supposed action of the insect, I have succeeded in impregnating most of the flowers of the spike with a single pollen mass. I believe they exist also in the greater number of Ophrydeæ, as well as in many Neotteæ and Arethuseæ.

But even in Ophrydeæ they are not universally met with, a very remarkable exception existing, I believe, in the whole genus Ophrys, in which the resemblance of the flower to an insect is so striking, and in which also the retinacula, whose viscidity hardly equals that of the stigma, are included and protected by concave processes of the upper lip of that organ.

It may also be remarked, that in the genus Ophrys impregnation is frequently accomplished without the aid of insects, and in general the whole pollen mass is found adhering to the impregnated stigma. Hence it may be conjectured, that the remarkable forms of the flowers in this genus are intended to deter not to attract insects,
741] whose assistance seems to be unnecessary, and the action of which, from the diminished vicidity of the retinaculum, might be injurious. On this subject I will also hazard another remark, that the insect forms in Orchideous flowers, resemble those of the insects belonging to the native country of the plants.

The next object I had in view was to determine the first appearance and progress of the mucous tubes.

My observations on the *origin* of these tubes are not altogether satisfactory.

It appeared, however, in Bonatea, which was also the plant most particularly examined, that they first become visible soon, but not immediately, after the production of the pollen tubes from the lobules or grains of the mass applied to the stigma; and that their earliest appearance is in the tissue of the stigma, in the immediate vicinity of the pollen tubes, from which they are with difficulty distinguishable, and only by their being less manifestly or not at all granular in their surface or contents, and in general having those interruptions in their cavity, which I have termed coagula, and which I have never yet met with in tubes actually adhering to the grain of pollen.

But even these characters, in themselves so minute, might be supposed to depend on a difference in the state of the contents of the pollen tube, after it has quitted the grain producing it. It is possible therefore that the mucous cords may be entirely derived from the pollen, not however by mere elongation of the original pollen tubes, but by an increase in their number, in a manner which I do not attempt to explain.

The only other mode in which these tubes are likely to be generated, is by the action of the pollen tubes on the coagulable fluid, so copiously produced in the stigma at the only period when impregnation is possible.

The obscurity respecting the origin of these mucous tubes does not, however, extend to their gradual in- [742
crease and progress, both of which may be absolutely ascertained.

In Bonatea they are, in the first stage of their production, confined to the stigma, with the proper tissue of which they are more or less mixed. Soon after they may be found on the anterior protected surface of the style, at first in small numbers; but gradually increasing, they form a mucous cord of considerable size, in which very few or none of the utriculi of the stigma are observable. This cord, which is originally limited to the style, begins, though sometimes not until several days have elapsed, to appear in the cavity of the ovarium, where it divides and subdivides in the manner I have described in my paper, its descent being gradual until the cords nearly equal the length of the placenta, to which they are parallel and approximated.

That these cords are not in any degree derived from those portions of the walls of the cavity of the ovarium, to which they are closely applied, and which I have termed the conducting surfaces, is manifest from the identity in state of those surfaces before and after the production of the cords.

In Bonatea the first evidence of the action of the pollen consists in the withering of the stigma; a similar decay of the greater part of the style soon follows, and the enlargement of the ovarium generally begins before the withering of the style is completed. When the enlargement of the ovarium is considerable, and the mucous cords are fully[1] formed in its cavity, a corresponding enlargement of the ovula takes place, and the nucleus becomes first visible.

I have no satisfactory observations in Bonatea respecting any tubes going off from these cords and mixing with the ovula; but in *Orchis Morio* I have repeatedly and very clearly observed them scattered in every part of the surface of the placenta, and in not a few cases have been able to
743] trace them into the aperture of the ovulum, to which they adhere with considerable firmness.[2]

At what period they reach the foramen of the testa, whether before or immediately after the first faint appearance of the nucleus, I have not yet been able to determine. That the tubes thus traced to the foramen of the ovulum are of the same nature as those which I have called mucous tubes, and not those directly produced by the pollen, is proved by their exact agreement with the former in every respect, except in their being remarkably and irregularly flexuose, apparently from the numerous obstacles they have to overcome after leaving the cords and beginning to mix with the ovula; for in the cords themselves, where the

[1] ["Carefully" in the original—an obvious error of the press.—Edit.]

[2] Since these additional observations were read, I have found in several other Orchideæ, especially *Habenaria viridis* and *Ophrys apifera*, tubes scattered over the surface of the placenta, and not unfrequently inserted, in like manner, into the apertures of ovula.

course of the tubes is not at all impeded, they are very nearly or altogether straight.

The two most important facts stated in the present communication are; *first*, the production of tubes not directly emitted from the grains of pollen, but apparently generated by them; and, *secondly*, the introduction of one or sometimes more than one of those tubes into the foramen of the ovulum, the point corresponding with the radicle of the future embryo.

The principal points remaining to be examined, and which we may hope, by careful investigation, to ascertain, are the precise state of the ovulum at the moment of its contact with the tube, and the immediate changes consequent to that contact.

Supplementary Note. [744

Since the paper on Fecundation in Orchideæ and Asclepiadeæ was read before the Society, and a Pamphlet containing all its more important statements was distributed in the beginning of November, 1831,[1] two essays have appeared on the same subject. The first on both families by M. Adolphe Brongniart, in the numbers of the *Annales des Sciences Naturelles* for October and November, 1831, but which were not published until January and February, 1832; the second, by Dr. Ehrenberg, on Asclepiadeæ alone, in the Transactions of the Royal Academy of Sciences of Berlin, before which it was read in November, 1831.

M. Brongniart's statements respecting Orchideæ to a great extent agree with those of my essay. They differ, however, in the following important points:

1st, He does not seem to be aware of the operation of insects in the fecundation of this family.

2ndly, He considers the mucous cords in the cavity of the ovarium (first seen by M. du Petit Thouars, with whose observations he seems to be entirely unacquainted),

[1] I may also refer to an excellent abstract of the Paper which appeared on the 1st of December, 1831, in the Philos. Mag. and Annals of Philosophy.

as a continuation of the tissue of the stigma and style, and as existing before the application of the pollen to the female organ.

And 3rdly, He supposes that the male influence reaches the ovula in Orchideæ before the inversion of the nucleus; an opinion founded, as it seems, on his observations on Epipactis, in which, as well as in some other genera of the order, this is the state of the ovulum in the expanded flower.

In ASCLEPIADEÆ M. Brongniart's observations, made chiefly in *Asclepias amœna* and *Gomphocarpus fruticosa*, accord with my statements as far as relates to the applica-
745] tion of the more convex edge of the pollen mass to the base of the stigma, its consequent dehiscence, the protrusion of the pollen tubes, and their penetration into the cavity of the style.

The chief differences are,

1st, His not even suspecting the agency of insects in the fecundation of this family, and particularly in the plants examined by him, in which I have regarded their assistance as absolutely necessary.

2ndly, In his assuming that the pollen mass in these two genera of Asclepiadeæ is ruptured, and comes in contact with the base of the stigma without leaving the cell of the anthera.

3rdly, His conjecturing that the secretion visible in the expanded flower on the angles of the stigma after removing the glands, is absorbed by the glands and conveyed through their arms or processes to the pollen mass, which it excites to the production of pollen tubes.

Dr. Ehrenberg, on the subject of Asclepiadeæ, repeats, with some slight modifications, his former statements quoted in my paper, and illustrates them by figures. In addition, he suspects that the pollen masses (which with Professor Link he regards as the true anthera, and the cells in which they are lodged as processes of the perigonium), are not originally distinct from the glands of the stigma, regarded by him as the filaments of his supposed anthera.

The central pentangular body he considers as the stigma, but he has no observations on the mode in which the pollen is applied to it.

And lastly, His original statement respecting the grains of pollen is so far modified, that he now believes them to be in the early stages without tubes or *boyaux*, which, according to him, make their appearance at the period of impregnation.

SUPPLEMENTARY OBSERVATIONS

ON THE

FECUNDATION

OF

ORCHIDEÆ AND ASCLEPIADEÆ.

BY

ROBERT BROWN.

[*Reprinted from a separate publication for distribution.*]

LONDON.

1833.

SUPPLEMENTARY OBSERVATIONS, &c. [a]

ORCHIDEÆ.

In the observations appended to my Paper on these two Natural Families, printed in the 16th Volume of the 'Linnean Society's Transactions,' and which relate entirely to Orchideæ, it is stated, that in several species of Ophrydeæ the Tubes, produced either directly from the grains of Pollen, or in consequence of their application to the Stigma, were found spread over the surface of the Placentæ, and not unfrequently inserted into the aperture of the Ovula. The correctness of this statement I have confirmed, during the present season, by numerous observations, not only on the same, but also on several other species. Another remarkable appearance observed in some of these species, especially in *Orchis ustulata, fusca, Morio*, and in *Ophrys apifera*, and which indeed I had before met with, but neglected to mention in my Paper, consists in the elongation and protrusion of the jointed or cellular filament connecting the upper extremity of the Embryo with that of the original nucleus (the Tercine of M. Mirbel).

The Filament so protruded often equals the whole Ovulum in length, and its elongation seems to depend not only on the enlargement of each of the cells or joints, of which the included thread consists, but also on the production of additional joints.

As, however, the Pollen tube is found applied to the aperture of the Ovulum uniformly before either the Embryo or its thread is distinguishable, and as I have never observed the protruded thread of the Ovulum until after the secondary nucleus or Embryo, of which it is a continuation, becomes visible, I consider it as a production subsequent to impregnation.

It is possible, therefore, that the nearly similar tubes which have been observed terminating, as it is supposed, the nucleus of the unimpregnated Ovulum in a few other Families, may in some of these cases be of like origin.

2] To the observations formerly made on the general structure of Orchideæ, I have here to add,—

1st, That the cells of the testa of the ripe seed are frequently spirally striated, though these cells in the Ovulum before and even for some time after impregnation are absolutely without striæ.

2nd, The Fibrillæ constituting the pubescence frequently produced, and in some cases entirely covering the surface of the aërial roots, as they have been called, of the parasitical portion of the Order, are very remarkable.

These Fibrillæ, which I have examined both in dried and recent specimens of several species, but more particularly in the living state in *Renanthera coccinea*, are simple tubular hairs without joints, and whose apices, by which they adhere when attached to other bodies, are either of the same diameter, or somewhat dilated; and then, as in Renanthera, often more or less lobed.

In their natural state they exhibit, in most cases, hardly any indication of spiral structure; but the membrane, of which they entirely consist, is sufficiently elastic to admit of being extended, and at the same time unrolled, to about twice the length of the Tube. They then form a broad ribbon of equal width throughout, and spirally twisted from right to left,—a direction opposite to that which generally obtains in spiral vessels. It is possible that this may not be the direction of the spire in all cases; it is manifest, however, very generally, if not universally, in Renanthera.

The existence of spiral tubes produced on the surface is probably of very rare occurrence; and among Phænogamous plants I have hitherto met with it only in the hairs of the inner surface of the Corolla of some species of Ceropegia, in the wool enveloping the spines in several species of Mammillaria and Melocactus, and in the Coma of the seed of an Apocyneous plant from Brazil: for the spiral vessels in the seeds of Collomiæ, first observed by Mr. Lindley, and described by him as external, are seated between the two membranes of the testa, as I have long since described those of Casuarina. They differ, however, in direction; being in Collomia transverse or perpendicular, while in Casuarina they are longitudinal, or parallel to the membranes.

ASCLEPIADEÆ.

With regard to this Family, it was remarked, both in the Pamphlet which was distributed in the beginning of November, 1831, and in my Paper in the 'Transactions of the Linnean Society,' published in 1833, that I had never been able to find the Pollen tubes descending lower than the commencement of the ovuliferous portion of the Placenta. But as this was far from satisfactory, especially after the further course of the analogous Tubes in Orchideæ had been ascertained, I determined to re-examine the subject.

For this purpose *Asclepias phytolaccoides* was selected; and on the 12th of the present month I succeeded in tracing the Pollen tubes in that species, not only over the whole ovuliferous surface of the Placenta, but also going off to the Ovula, to a definite point of each of which a single Tube was found in many cases attached.

These observations I have now so frequently repeated, and always with results so exactly similar, that I have great confidence in the correctness of the following statement:

In the newly expanded flower, the Ovulum in *Asclepias phytolaccoides* is nearly obovate, and is compressed in the same direction as the ripe seed, but in a much less degree: its umbilical cord is inserted on the axis of the inner or ventral side, about one fourth from the apex, and a process proceeding from it is continued, though not very distinctly, to the opposite or lower extremity. On the upper and broader end of the Ovulum a deep groove is observable, commencing at its inner margin, which is nearly in contact with the Placenta, and extending through its whole breadth, and somewhat obliquely downwards, so as to terminate at the same height on the outer side of the Ovulum with the upper edge of the ventral umbilical cord. This groove, or that point of it to which the Pollen tube is attached, occupies the place of the Foramen so generally found in the unimpregnated ovulum of Phænogamous plants. In *Asclepias phytolaccoides*, however, and I believe the observation may be extended to every species of the genus, there is certainly no perforation, nor at this period are the coats and nucleus of the Ovulum separable or even distinguishable; and the same apparent simplicity of structure is found even in its earlier stages.

Soon after the Pollen tubes enter the cavity of the Ovarium, even before the Corolla falls off, they may be found spread over the whole ovuliferous surface of the Placenta, which then often becomes of a light brown colour, but never dark brown or black, like the upper non-ovuliferous portion. From the surface of the Placenta the Tubes go off, one to each Ovulum, along the depressed apex of which the Tube passes till it reaches the outer extremity of the groove, where it is invariably inserted. To this point the Tube adheres so firmly, that I am inclined to think it actually penetrates, to some depth at least into the substance of the Ovulum; a fact, however, which I have not yet absolutely ascertained.

Soon after the insertion of the Pollen tube, a change takes place in the appearance of the Ovulum, an internal body or nucleus becoming visible, with the upper attenuated extremity of which the point of insertion accurately corresponds.

The Pollen tube, when thus inserted into the Ovulum, is not always absolutely destitute of granules; in some cases containing a few, which in size and form seem to be identical with those that completely fill it in its nascent state.

But as such granules, at the period of insertion, are either very few in number, or apparently altogether wanting, I am still inclined to consider them rather as furnishing the nourishment of the Tube than as being the essential agents in fecundation; the really active particles in this function being probably much more minute.

These supplementary observations may be concluded with the remark, that although the descent of Tubes derived from the Pollen into the cavity of the Ovarium, and their insertion into that point of the Ovulum where the Radicle of the future Embryo is seated, has been absolutely ascertained in several species of Orchideæ and in one of Asclepiadeæ, and probably will be found in the whole of these two extensive families, yet it does not follow that this descent and insertion of Tubes should be expected to extend to all Phænogamous plants; for among these some structures of the female organ exist, which hardly admit of this œconomy.

LONDON; *July* 31*st*, 1833.

ON THE

RELATIVE POSITION

OF THE

DIVISIONS OF STIGMA

AND

PARIETAL PLACENTÆ

IN THE

COMPOUND OVARIUM OF PLANTS.

BY

ROBERT BROWN, F.R. & L.S.

[*Reprinted from* '*Plantæ Javanicæ Rariores.*' *Part II*, *pp.* 107-112.]

LONDON.

1840.

ON THE DIVISIONS OF STIGMA,[1] &c. 107

To estimate correctly the importance of the relation between the divisions of the Stigma and the parietal placentæ of the compound ovarium, namely, whether when agreeing 108
in number they are placed opposite to or alternate with each other, it is necessary to take into consideration the theoretical view which appears the most probable of the origin or formation of a simple ovarium, and that of the stigma belonging to it, as well as the various kinds and degrees of confluence by which the real nature of both organs, but especially the latter, is so often obscured.

It is at present, I believe, universally agreed to consider a polyspermous legumen as that state of the simple ovarium, which best exemplifies the hypothetical view of the formation of this organ generally adopted; namely, that it consists of the modification of a leaf folded inwards and united by its margins, which in most cases are the only parts of the organ producing ovula; or, at least, where this power of production is not absolutely confined to the margins, it generally commences with or includes them.

The exceptions to the structure as here stated are of two kinds:—

First. Where the whole internal surface of the carpel is equally ovuliferous, which is the case in a few families of very small extent, as *Butomeæ*, *Nymphæaceæ*, and *Lardizabaleæ*.

[1] [Extracted from Mr. Brown's account of *Cyrtandreæ*, given in the second part of Dr. Horsfield's 'Plantæ Javanicæ Rariores,' published in 1840. Separate copies of this note were distributed in December, 1839.—*Edit. Ann. Nat. Hist.*]

Secondly. Where the production of ovula is limited to the external angle of the cell or axis of the leaf supposed to form the carpel.

A case of this kind is found in a portion of one of those families in which the whole surface is generally ovuliferous, namely, in *Hydropeltideæ*, which I have always regarded as merely a section of *Nymphæaceæ*;[1] and from the nature of these differences in placentation, which are more apparent than real, an argument might even be adduced in favour of that opinion.

A placenta apparently limited to the outer angle of the cell also occurs in the greater number of species of *Mesembryanthemum*. As this structure, however, is certainly not without exception in that very natural genus, several species, among which are *Mesembryanthemum crystallinum*, *cordifolium*, *papulosum* and *nodiflorum*, having the placenta confined to the internal angle of the cell or margins of the carpel; and as in some of those species in which the outer angle is placentiferous, the production of ovula is not confined to it, but extends to the lower half of the inner angle;—this apparent deviation from ordinary structure may perhaps be explained by assuming cohesion of the inflected portion of the carpel with the wall of the cell;—an hypothesis, in some degree supported by the fact, that in several species the termination of the assumed inflected portion is free and not ovuliferous.

But whatever opinion may be adopted as to the relation of this seemingly anomalous to the ordinary structure, it cannot, as M. Fenzl proposes,[2] be employed as the essential character of a distinct natural family limited to the Linnæan genus *Mesembryanthemum*.

The placenta then of a simple ovarium in its usual state, according to this view, is necessarily double; though by the complete suppression of ovula in one of its two component parts, and their diminished production in the other, the ovarium is not unfrequently reduced to a single ovulum. That such is the origin of the single ovulum is at least

[1] Gen. Rem. in Flinders's Voy. vol. ii, Append. p. 598. (*Anté p.* 74.)
[2] Annal. des Wien. Mus. vol. i, p. 349.

manifest in a monstrosity of *Tropæolum majus*, in which the stamina are converted into pistilla; but the complete action being impeded by the presence of the regular trilocular pistillum, and the two marginal cords of each open ovarium remaining distinct, the origin of the ovulum from one only of these cords is satisfactorily shown.

An ovarium with two or a greater number of cells, whose placentæ project into the cavities more or less from their inner angles, is an organ, the composition of which is sufficiently obvious.

But a compound ovarium may be differently constructed; and, first, instead of each simple organ forming a complete cell by the union of its own margins or adjoining portions of its surface, the corresponding margins or adjoining portions of surface of the proximate component parts may unite together so as to form a parietal placenta, often apparently simple, but in reality double in all cases. This view of the composition of a unilocular ovarium having two or more parietal placentæ is also very generally received. But exceptions, supposed to prevail in whole families, in which the disk and not the margins are placentiferous, have lately been assumed by Professor Lindley, *Orchideæ* and *Orobancheæ* being the examples of this structure to which he more particularly refers.

The accurate determination of this question appears to me of great importance to the theoretical botanist, but the subject will be most advantageously discussed after treating of the origin and modifications of stigmata.

An ovarium less manifestly compound is that in which the centre of the cavity is occupied by a placenta entirely unconnected with its sides; the supposed inflected portions of each component organ, according to the view here adopted, being removed, or reabsorbed so completely in a very [109
early stage of its development as to leave no trace of their existence either on the walls of the cavity or on the surface of the central placenta, which may either be polyspermous, or produce only a smaller and definite number of ovula having a relation to its supposed component parts, or, lastly, in some cases be reduced to a single ovulum.

These are the principal modifications of the compound ovarium when forming a simple series; but it is necessary to observe that both surfaces of the inflected and included portions of the carpels are not unfrequently equally productive of ovula, a structure which is manifest in many *Cyrtandraceæ*, especially *Cyrtandra*, although in several other genera of the same family the production is confined to the inner or upper surface of the margin. In other cases the polyspermous ovuliferous portion or placenta is connected with the inner angle of the cell by a single point only, which may proceed either from the apex or base of the cavity. This modification of structure, though in some families hardly of generic importance, seems to me to assist in explaining the apparently anomalous structures of *Hydnora*, *Rafflesia*, and *Brugmansia*.

On the subject of the origin and type of Stigma, my first observation is, that the style where present can only be regarded as a mere attenuation, in many cases very gradual, of the whole body of the ovarium. Hence the idea naturally suggests itself, that the inner margins of the carpel, which in the lower part are generally ovuliferous, in the upper part perform the different, though in some degree analogous, function of stigma. As the function, however, of this organ implies its being external, and as in different families, genera, and even species, it has to adapt itself to
110] various arrangements of parts destined to act upon it, corresponding modifications of form and position become necessary; hence it is frequently confined to the apex, and very often, especially in the compound ovarium with united styles, appears to be absolutely terminal.

In such cases, as it must always include and be closely approximated to the vascular cord of the axis, it has by some botanists been considered as actually derived from it, which it is, however, only in the same manner as the marginal placentæ are derived from the axis of the carpel. But according to the notion now advanced, each simple pistillum or carpel has necessarily two stigmata, which are to be regarded, not as terminal, but lateral.

That the stigma is always lateral may be inferred from its being obviously so in many cases; and in one genus at least, *Tasmannia*, it extends nearly the whole length of the ovarium, so as to be commensurate with and placed exactly opposite to the internal polyspermous placenta.

That the stigma is always double appears probable from those cases in which it is either completely developed, as in the greater part of *Gramineæ* where the ovarium is simple; in the compound ovarium in *Urena;* and from those in which the development, though less complete, is still sufficiently obvious, as in many *Euphorbiaceæ* and in several *Irideæ.* This degree of development, however, is comparatively rare, confluence between the two stigmata of each carpel being the more usual structure; and in the compound pistillum a greater degree of confluence often takes place in the stigmata than in the placentæ;—a fact, which in all such cases is obviously connected with adaptation of surface to the more complete performance of function.

Another difference frequently occurs between the mode of confluence of placentæ and stigmata, namely, that in the compound but unilocular ovarium, while the placentæ of the adjoining carpels are united, the stigmata of each carpel are generally confluent. But this rule admits of exceptions, as in *Parnassia*, in many *Cruciferæ*, and in *Papaveraceæ*; in all these cases the stigmata as well as placentæ of the adjoining carpels are confluent, a structure satisfactorily proved in *Cruciferæ* by several cases of monstrosity, in which the stamina are transformed into pistilla; and in *Papaveraceæ* by a series of modifications of structure as well as by a like transformation of stamina.

A similar confluence of stigmata in the compound multilocular pericarpium is of much rarer occurrence; it is found, however, in the majority of *Irideæ*, in which the three stigmata alternate with the cells, and consequently with the placentæ of the trilocular ovarium. That this is the correct view of the composition of the stigmata in *Irideæ* is at least probable from their occasional deep division, and more particularly still from the bifid petal-like styles or stigmata which are opposite to the cells of the ovarium in other genera of the same family, as in *Iris* and *Moræa*. In both these arrangements the adaptation to the performance of function is equally manifest.

If the correctness of these observations be admitted, it follows that characters dependent on the various modifications of stigmata are of less value, both in a systematic point of view as determining the limits of families, and theoretically in ascertaining the true composition of organs, than those derived from the analogous differences in the ovaria or placentæ.

In those cases in which the nature of the composition of the ovarium is doubtful, it may, in the first place, be remarked, that wherever in the compound unilocular pistillum the placentæ are double or two-lobed, it is more probable that such placentæ are derived from two adjoining carpels, and are consequently marginal or submarginal, than that they occupy the disc of one and the same carpel; this being entirely the appearance in many cases where the marginal origin of placentæ is admitted; while in the greater part of those in which the disc is known to be ovuliferous, the ovula are never collected in two distinct masses, being generally scattered equally over the surface.

But the double placentæ are manifest in *Orchideæ*, the principal family in which Mr. Lindley considers the ovula as occupying the disc and not the margins. In this family also the alternation of stigmata with placentæ is that relation which is most usual in compound unilocular ovaria, where the apparent number of stigmata and placentæ is equal; and that in *Orchideæ* each apparent stigma is formed by the confluence of the two stigmata of one and the same carpel, is proved by tracing to their origins their vascular cords, which are found to coalesce with those of the three outer foliola of the perianthium.

This view of the composition of the ovarium in *Orchideæ* is confirmed by finding that it agrees with the ordinary arrangement in monocotyledonous plants; namely, the opposition of the double parietal placentæ to the three inner divisions of perianthium[1], while in *Apostasia* the three placentæ of the trilocular ovarium are opposite to the three outer

[1] Denham, Trav. in Afr. Append. p. 243. (*Anté, p.* 300.)

divisions; and it is further strengthened on considering what takes place in *Scitamineæ*, where the same agreement is found both in the placentæ of the trilocular ovarium, which in this family is the ordinary structure, and in the unilocular, which is the exception.

I am aware that the agreement of *Orchideæ* with the usual relation of parts in Monocotyledones is not admitted by M. Achille Richard, nor by Mr. Lindley, who has adopted his hypothesis respecting the structure of the flower in this family. According to M. Richard, the outer series of perianthium is generally wanting, being found only in one genus, *Epistephium*: the three outer divisions actually existing in the whole order, according to this view, become petals, and the three inner divisions sterile petaloid stamina.

I have some years ago[1] stated several objections to this hypothesis; at present I shall advert to one of those only, considering it as conclusive; namely, the position of the two lateral stamina, which are generally rudimentary, but in some cases perfectly developed, in this family. In several species of *Cypripedium*, which is one of these cases of perfect development, I had then ascertained, by means of numerous transverse sections made at various heights in the column and at its base, that their vascular cords united with those of the two lateral inner divisions of the flower, while that of the third, generally the only perfect stamen, is manifestly opposite to the anterior division of the outer series. The position of stamina, therefore, so far from being regular, as the hypothesis in question considers it, is absolutely without example, two of the inner series being opposite to two of the supposed outer series of stamina.

A very different view respecting the formation of the ovarium in *Orchideæ* is that first advanced by Mr. Bauer and adopted by Mr. Lindley, namely, that it consists of six carpels, of which three, placed opposite to the outer series of perianthium or sepals, are sterile; the remaining three, opposite to the inner series, or petals, being fertile, and bearing their placentæ on their axes or disks.

The chief argument in support of this view is no doubt

[1] Linn. Soc. Trans. vol. xvi, p. 698. (*Antè, p.* 501.)

derived from the very remarkable dehiscence of the capsule into six valves. But I have elsewhere pointed out cases where an analogous dehiscence occurs, in which, however, a similar composition has never been supposed to exist: and if the presence of six vascular cords in sections of the ovarium be likewise adduced in favour of the opinion, I may add that I have in the same place remarked that these vascular bundles belong not to the ovarium only, but also to the perianthium and stamina, and are equally observable in other families with adherent ovarium, as *Irideæ,* in which a similar composition has never been inferred.

With regard to the second family, in which Mr. Lindley believes the disk of the carpel to be ovuliferous, namely, *Orobancheæ*, I find no other argument advanced in support of this view than that derived from the bursting of the capsule into two lateral valves; but an opinion founded on dehiscence only may be said to be a mere begging of the question; division through the axis of carpels, especially in the families related to *Orobancheæ,* being nearly as common as separation of their margins. In this family also, as in *Orchideæ,* the placentæ are double, an argument in favour of their submarginal origin: and although, whether the carpels be regarded as lateral, or anterior and posterior, the placentæ are not strictly marginal, yet there are other families where a similar position of placentæ is found, but in which the structure assumed in this hypothesis has never been suspected. As to the supposed affinity of *Orobancheæ* with *Gentianeæ*, which might be adduced in support of this view, as far as it is founded on the assumed agreement of the two orders in the lateral position of their carpels, the argument, even if correct, would hardly be conclusive; for in *Gentianeæ* there is at least one genus having quadrifid and another with quinquefid flowers, in which the carpels are
112] not lateral, but anterior and posterior, as I believe them to be in *Orobancheæ;* nor has it ever been supposed that in *Gentianeæ* the disk or axis is ovuliferous.

In the account now given of the modifications of ovarium and stigma, I have, in conformity with the ordinary language of botanists, employed the term *confluence,* by which, however, is not to be understood the union or cohesion of parts originally distinct, for in the great majority of cases the separation or complete development of these parts from the original cellular and pulpy state has never taken place. But with this explanation the word may still be retained, unless connate should be considered less exceptionable.

I have also assumed that ovula belong to the transformed leaf or carpel, and are not derived from processes of the axis united with it, as several eminent botanists have lately supposed. That the placentæ and ovula really belong to the carpel alone is at least manifest in all cases where stamina are changed into pistilla. To such monstrosities I have long since referred in my earliest observations on the type of the female organ in phænogamous plants,[1] and since more particularly in my paper on *Rafflesia*:[2] the most remarkable instances alluded to in illustration of this point being *Sempervivum tectorum*, *Salix oleifolia*, and *Cochlearia armoracia*, in all of which every gradation between the perfect state of the anthera and its transformation into a complete pistillum is occasionally found.

[1] In Linn. Soc. Trans., vol. xii, p. 89.

[2] Ibid. vol. xiii, p. 212, note. (*Antè, p.* 379.)

ON THE

PLURALITY AND DEVELOPMENT

OF THE

EMBRYOS

IN THE

SEEDS OF CONIFERÆ.

BY

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ON THE PLURALITY, &c.[1]

The following short paper on a subject which I intend to treat at greater length, contains a few facts of sufficient interest perhaps to admit of its being received as a communication to the present meeting.

In my observations on the structure of the female flower

[1] Read before the British Association at Edinburgh in August 1834, and published in the Annales des Sciences Naturelles for October 1843. The following abstract was given in the "Report of the Fourth Meeting of the British Association," 1835, pp. 596-7:—"The earliest observations of the author on this subject were made in the summer of 1826, soon after the publication of his remarks on the female flower of *Cycadeæ* and *Coniferæ*. He then found that in several *Coniferæ*, namely, *Pinus Strobus*, *Abies excelsa*, and the common Larch, the plurality of embryos in the impregnated ovulum was equally constant, and their arrangement in the albumen as regular as in *Cycadeæ;* and similar observations made during the present summer on several other species, especially *Pinus sylvestris* and *P. Pinaster*, render it highly probable that the same structure exists in the whole family. The first change which takes place in the impregnated ovulum of the *Coniferæ* examined, is the production or separation of a solid body within the original nucleus. In this inner body, or albumen, several subcylindrical corpuscula, of a somewhat different colour and consistence from the mass of the albumen, seated near its apex and arranged in a circular series, soon become visible. In each of these corpuscula, which are from three to six in number, a single thread or funiculus, consisting of several, generally of four, elongated cells or vessels, with or without transverse septa, originates. The funiculi are not unfrequently ramified, each branch or division terminating in a minute rudiment of an embryo. But as the lateral branches of the funiculi usually consist of a single elongated cell or vessel, while the principal or terminal branch is generally formed of more than one, embryos in *Coniferæ* may originate either in one or in several cells, even in the same funiculus. A similar ramification in the funiculi of the *Cycas circinalis* has been observed by the author. Instances of the occasional introduction of more than one embryo in the seeds of the several plants belonging to other families have long been known, but their constant plurality and regular arrangement have hitherto only been observed in *Cycadeæ* and *Coniferæ*."

in *Cycadeæ* and *Coniferæ*, published in 1826,[1] I endeavoured to prove that in these two families of plants the ovulum was in no stage inclosed in an ovarium, but was exposed directly to the action of the pollen.

In support of this opinion, which has since been generally, though I believe not universally adopted, the exact resemblance between the organ until then termed ovarium in these two families, and the ovulum in other phænogamous plants, was particularly insisted on; and I at the same time referred, though with less confidence, to their agreement in the more important changes consequent to fecundation.

I noticed also the singular fact of the constant plurality of embryos in the impregnated ovula of *Cycadeæ*, and the not unfrequent occurrence of a similar structure in *Coniferæ*. In continuing this investigation, in the course of the same summer in which the essay referred to appeared, it seemed probable, from the examination of several species of the Linnæan genus *Pinus*, namely, *Pinus Abies, Strobus* and *Larix*, that the plurality and regular arrangement of embryos were as constant in *Coniferæ* as in *Cycadeæ;* for in all the species of *Pinus* here referred to, the preparation for the production of several embryos was equally manifest, and the points or areolæ of production were in like manner disposed in a single circular series at the upper extremity of the amnios.

From these observations, which I have since confirmed in the same and also in other species of *Pinus*, an additional and important point of resemblance is established between
369] *Cycadeæ* and *Coniferæ;* and it is worthy of remark, that while the female organ in these two families exists in a simpler form than in other phænogamous plants, the normal state of the impregnated ovulum is much more complex, and might even be considered as compound, or made up of the essential parts of several confluent ovula.

On considering the well-known œconomy of several *Coniferæ*, and especially of the genus *Pinus*, as at present limited, namely, in their requiring (at least) two seasons to ripen their cones, it occurred to me that these plants, from

[1] In the Appendix to Capt. King's Voyage. [*Antè, p.* 453.]

the extreme slowness in the process of maturation, conjoined with the considerable size of their seeds, and also from the striking peculiarity already noticed, were probably the best adapted for an investigation into the origin and successive changes of the vegetable embryo.

With this view chiefly I commenced in the present summer (1834) a series of observations, intending to follow them up from the period when the enlargement of the impregnated cone begins to take place, to its complete maturity at the end of the second or beginning of the third year.

Pinus sylvestris was selected for this purpose, corresponding observations being also made on other species, particularly *Pinaster* and *Strobus;* and although the investigation is necessarily incomplete, the facts already ascertained appear to me of sufficient importance to be submitted to physiological botanists.

In an essay on the organs and mode of fecundation in *Orchideæ* and *Asclepiadeæ*, published in 1831, I have given some account of the earliest changes observable in the impregnated ovulum of the former family; and in noticing the jointed thread, or single series of cells by which the embryo is suspended, I remarked that the terminating cell or joint of this thread is probably the original state of what afterwards, from enlargement, subdivision of its cavity, and deposition of granular matter in its cells, becomes the more manifest rudiment of the future embryo.

I had not indeed actually seen this joint in its supposed earliest state; the following observations on *Pinus*, however, will perhaps be considered as giving additional probability to the conjecture.

But before entering on my account of the origin and development of the embryo in *Pinus*, I shall state briefly the still earlier changes consequent to impregnation that take place in this genus; not only with the view of rendering the account of the embryo itself more readily intelligible, but also in confirmation of the opinion formerly advanced on the nature of the female organ in *Coniferæ* and *Cycadeæ*.

The first and most evident change observable is the production or separation of a distinct body within the nucleus of the ovulum, which, before impregnation, is a solid uniform substance.

370] In this stage the upper extremity of the included body, or amnios, is slightly concave, and has a more or less rough or unequal surface; the inequality being in consequence of the laceration of the cellular tissue, by which it was in its early stage attached to the apex of the original nucleus, or rather to a short cylindrical process arising from it and corresponding in size and form with this concave upper extremity, from which it separates when the amnios has attained its full size.

On this concave upper extremity of the amnios a few minute points of a deeper colour, and disposed in a single circular series, are sometimes observable; in general, however, they are hardly to be distinguished.

Below the concave apex the amnios itself is slightly transparent for about one fourth of its length, the remaining portion being entirely opake.

On dividing the whole longitudinally it is found to consist of a pulpy cellular substance, in which no definite cavity is originally observable; the upper transparent portion is, however, of a looser texture, and on the included embryos becoming manifest, a cavity irregular both in figure and extent is formed in its centre.

But before the embryos themselves or their funiculi become manifest, the areolæ, or portions of the substance destined for their production, are visible.

These areolæ, as I observed them in the common larch in May, 1827, are from three to five in number, of nearly cylindrical form, arranged in a circular or elliptical series, and are seated near the apex, with which they probably communicate by the similarly arranged points of its surface already noticed.

In the amnios of *Pinus sylvestris*, as observed in June and July last, the corresponding parts were found considerably more advanced. In the specimens then examined, the remains of the embryoniferous areolæ, from four to six in number, were still visible, but consisting of conical membranes of a brown colour, presenting their acute apices towards the surface, and at the base seeming to pass gradually into the lighter-coloured pulpy substance of which the mass of the amnios consists.

Corresponding and nearly approximated to each of these conical membranes, a filament, generally of great length, and either entirely simple or giving off a few lateral branches, was found. This filament or funiculus consisted generally of four series of elongated transparent cells or vessels, usually adhering together with firmness, but in some cases readily separable without laceration; and in one of the species examined, *Pinus Pinaster*, the transverse septa of the funiculus were either very obscure or altogether wanting.

The upper extremity of each funiculus was in all cases [371
manifestly thickened and of a depressed spheroidal form; and in each of the four cells or vessels of which it consisted exhibited a small opake areola analogous to the nucleus of the cell, so frequently observable in the tissue of Monocotyledonous plants, and which also exists, though less commonly, in Dicotyledones.

A lacerated and extremely transparent membrane was generally found surrounding and adhering to the thickened origin or head of the funiculus.

In the earliest state examined of *Pinus Pinaster*, the funiculus was found equally transparent through its whole length, and having no appearance of subdivision or any other indication of embryo at its lower extremity. In a somewhat more advanced state of the same plant, as well as in the two other species observed, namely, *Pinus sylvestris* and *Strobus*, the lower extremity of the funiculus was subdivided into short cells, sometimes disposed in a double series, but more frequently with less regularity and in greater numbers, the lowest being in all cases the most minute and also the most opake, from the deposition of granular matter, which is nearly or entirely wanting in the upper part of the cord. This opake granular extremity of the funiculus is evidently the rudiment of an embryo. When the funiculus ramifies, each branch is generally terminated by a similar rudiment, and these lateral embryoniferous branches not unfrequently consist of a single vessel or cell, while the embryo of the trunk or principal branch is as generally derived from more than one.

That each of those opake bodies terminating the trunk and branches of the funiculi are really rudimentary embryos, is proved by tracing them from their absolutely simple state to that in which the divisions of the lower extremity become visible, and those again into the perfect cotyledons.

The results of this investigation in its present incomplete state are, 1st, that the plurality of rudimentary embryos in *Pinus* (and probably in other *Coniferæ*) is not only constant, but much greater than could well have been imagined independent of actual observation ; each impregnated ovulum not only containing several distinct funiculi, but each funiculus being capable of producing several embryos. In the ripe seed, however, it is a rare occurrence to find more than one of these embryos perfected.

2ndly. That an embryo in *Coniferæ* may originate in one or in more than one cell or vessel even in the same cord; and it also appears that the lower extremity of the funiculus, the seat of the future embryo, is originally in no respect different from the rest of its substance.

The greater part of the appearances now described are represented in the accompanying Plate.

372] *April* 20, 1844.

Postscript.—It is necessary to notice the recent publication of a very important memoir by MM. de Mirbel and Spach on the development of the embryo in *Coniferæ*.[1]

These excellent observers confirm the principal statements of the preceding essay, with the brief abstract of which only they were acquainted.

They have also extended the investigation to *Thuja* and *Taxus*, two genera which I had not examined, and in which, especially in the latter, the structure appears to be re-

[1] Annales des Sc. Nat. 2 série, November 1843.

markably modified; and they have ascertained some points in *Pinus* itself that I had overlooked.

In this memoir M. de Mirbel refers to his early observations on the structure of the seeds of *Cycas* which occur in an essay read before the Academy of Sciences in October 1810, and soon after published in the 'Annales du Muséum.'[1]

These observations and the figures illustrating them clearly prove M. de Mirbel's knowledge of the plurality of embryos in *Cycas* at that period. And in his recent memoir on *Coniferæ* he regards them as giving the earliest notice of that remarkable structure; stating also that my first publication on the same subject was in 1835.

But as the 'Prodromus Floræ Novæ Hollandiæ' was published before M. de Mirbel's essay in the 'Annales du Muséum,' which appears from his references to that work in the essay in question, he must have overlooked the following passages:—

"In Cycadi angulata puncta areæ depressæ apicis seminis totidem canalibus brevibus respondent gelatina homogenea primum repletis et membrana propria instructis, unico quantum observavimus embryonifero, quo augente reliqui mox obliterati sunt."—*Prodr.* p. 347.

"Structura huic omnino similis hactenus absque exemplo nec ulla analoga (nempe embryones plures in distinctis cavitatibus ejusdem albuminis) nisi in Cycadi et nonnunquam in Visco cognita sit."—*Prodr.* p. 307.

I may add, that this structure of *Cycas* was ascertained in living plants on the east and north coasts of New Holland in 1802 and 1803.

The earliest observer of the principal fact, however, was probably the late Aubert du Petit Thouars, who in a dissertation on the structure and affinities of *Cycas* published in 1804,[2] distinctly notices the points on the surface and the corresponding corpuscula within the apex of the albumen, into which corpuscula he hazards the conjecture that the grains [373
of pollen enter and become the future embryos. This, in

[1] Annales du Muséum d'Hist. Nat. tom. xvi, p. 252, tab. 20.
[2] Histoire des Végétaux des Iles d'Afrique, p. 9, tab. 2, *n*.

regard to *Cycas*, might be considered the revival of the general hypothesis advanced by Morland in 1703,[1] and some years afterwards adopted, but without acknowledgment, by C. J. Geoffroy,[2] and which seems to have entirely originated in the discovery by Grew of the existence of a foramen opposite to the radicle of the embryo in the ripe seeds of some Leguminous plants.[3]

But as M. du Petit Thouars had evidently no intention of extending his hypothesis beyond *Cycas* and probably *Zamia*, it can hardly be said to anticipate the general and ingeniously supported theory of Dr. Schleiden, respecting which physiological botanists are at present almost equally divided. On this theory it is not my intention at present to express an opinion; nor did the question of the mode of action of the pollen form any part of my object in the preceding essay. I shall only here remark, that according to the latest statements of Dr. Schleiden with which I am acquainted,[4] although he admits that his investigation is not in all points complete, he seems to have no doubt that his theory of the origin of the vegetable embryo in the pollen tube is applicable to *Coniferæ*. He has in the first place ascertained the existence of my areolæ or corpuscula, which he denominates large cells in the embryo-sac or albumen, in all the European genera of *Coniferæ*;[5] and in *Abies excelsa*, *Taxus baccata*, and *Juniperus Sabina*, he states that he has succeeded in preparing free the whole pollen tubes from the nucleary papillæ to the bottom of the corpuscula. But as (if my observations are correct, and they seem to be confirmed by those of M. de Mirbel) the corpuscula are not developed in *Pinus*, as the genus is at present limited, until the spring or even beginning of summer of the year after flowering, and if Dr. Schleiden's statement be also correct, the pollen must remain inactive for at least twelve months.

The quiescent state of pollen for so long a time is indeed

[1] Philosophical Transactions, vol. xxiii, part 2, n. 287, p. 1474.
[2] Mém. de l'Acad. des Sc. de Paris, 1711, p. 210.
[3] Anat. of Plants, p. 2. [4] Schleiden, Grund. der Bot. 2 Theil, p. 374.
[5] *Op. cit.* pp. 354 et 357.

not altogether improbable on considering the analogous œconomy in several tribes of insects, in some of which the male fluid remains inactive in the female for a still longer period;[1] and in plants, though for a much shorter period, I may refer to *Goodenoviæ*, in which the pollen is applied to the stigma a considerable time before that organ is sufficiently developed to act upon or transmit its influence.[2] But the supposed protracted state of inactivity in the pollen of *Pinus* does not necessarily lead to the adoption of Dr. [371]
Schleiden's theory. With respect to *Cycadeæ*, whatever opinion may be adopted as to the precise mode of action of the pollen in that family, it is certain that the mere enlargement of the fruit, the consolidation of albumen, and the complete formation of the corpuscula in its apex are wholly independent of male influence, as I have proved in cases where pollen could not have been applied, namely, in plants both of *Cycas* and *Zamia* (*Encephalartos*) producing female flowers in England at a time when male flowers were not known to exist in the country.

EXPLANATION OF PLATE 33 (VII).

Fig. 1. A scale of the cone of *Pinus sylvestris*, with its winged seeds, one of which is abortive: natural size.

N.B. The remaining figures are more or less magnified.

Fig. 2. An unripe seed, of which the testa, in this state cartilaginous, is cut open, partly removed and thrown back to show the included body, which is the half-ripe original nucleus with its sphacelated apex and the free portion of the inner coat, extending from the apex to about one third of the length of the nucleus, below which it is intimately connected with and inseparable from the outer coat.

Fig. 3. The amnios or albumen, with the coats opened and laid back.

a. The body of the albumen, with its slightly concave upper extremity: in this stage separated from *b*, the apex, which is conical above, below cylindrical, and which was suspended from the top of the original nucleus.

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[1] Herold. Entwickel. der Schmetterl. &c. 1815, et Siebold in Müller's Archiv, 1837, p. 392.

[2] Append. to Flinders's Austral. p. 561. [*Antè*, *p*. 33.]

Fig. 4. A plan rather than actual representation of a longitudinal section of any one seed examined, but the parts accurately copied from the calyptræform membranes, the funiculi or suspensors, and the nascent embryos of seeds of *Pinus sylvestris.* In this stage the funiculi are distinct from the calyptræform membranes within which they originated.

Fig. 5 is also a plan of the slightly concave apex of the amnios or albumen, with its semitransparent points or pores circularly arranged; in this species (*Pinus sylvestris*) seldom exceeding five, and not unfrequently being only four or even three.

Fig. 6. One of the funiculi or suspensors, with its dilated upper extremity, to which the lacerated remains of a thin transparent membrane adhere: the funiculus itself ramified, each of the two lateral branches consisting of a single elongated tube or cell terminating in a rudimentary embryo: the trunk of the funiculus composed of several (apparently four) tubes or cells terminated by a single embryo, which is already slightly divided, the divisions being the commencement of its cotyledons.

Figs. 7 & 8. Two other funiculi belonging to the same seed less advanced, but both ramified.

Fig. 9. A funiculus of *Pinus Pinaster* with its thickened head, in which the nuclei of its component elongated cells or tubes, and its adhering lacerated membrane are visible. The figure is given particularly to show that in this (the only one observed) there is no opake granular portion of the compound funiculus; in other words, no indication of a nascent embryo.

Fig. 10. A funiculus of *Pinus Abies*, Linn., with its rudimentary embryo and thickened head, still partly inclosed in the calyptræform membrane.

ON THE ORIGIN

AND

MODE OF PROPAGATION

OF THE

GULF-WEED.

BY

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ON THE

ORIGIN AND MODE OF PROPAGATION OF THE GULF-WEED.

Read before the Linnean Society, May 7, 1850.

Read a letter, dated May 19th, 1845, addressed by the President to Admiral Sir Francis Beaufort, for communication to Baron Alexander von Humboldt, "On the Origin and Mode of Propagation of the Gulf-weed." The letter is as follows:—

"My dear Captain Beaufort,—I am vexed to have kept Baron Humboldt's letter so long, and now in returning it, that it should be accompanied by so little satisfactory information on the only one of its queries with which I could have been supposed to deal, namely, that which relates to the origin and mode of propagation of the Gulf-weed.

"On this subject it appears that M. de Humboldt (in his Personal Narrative) first supported the more ancient notion, that the plant, originally fixed, was brought with the stream from the Gulf of Florida, and deposited in what Major Rennell calls the recipient of that stream. More recently, however, Baron Humboldt has adopted the opinion,[1] also held by several travellers, that the Gulf-weed originates and propagates itself where it is now found. To the adoption of this view it appears that he has been led chiefly by the

[1] Histoire de la Géographie du Nouveau Continent, vol. iii, p. 73, and Meyen, Reise, vol. i, p. 36-9.

observations of the late Dr. Meyen, who in the year 1830 passed through a considerable portion of the great band of
78] Gulf-weed, and who ascertained, as he states, from the examination of several thousand specimens, that it was uniformly destitute both of root and fructification; he concludes, therefore, that the plant propagates itself solely by lateral branches; he at the same time denies that it is brought from the Gulf of Florida, as, according to his own observation, it hardly exists in that part of the stream near the great band, though found in extensive masses to the westward. I have here to remark that, as far as relates to the absence of root and fructification, Meyen has only confirmed by actual observation what had been previously stated by several authors, particularly by Mr. Turner (in his 'Historia Fucorum,' vol. i, p. 103, published in 1808), and Agardh (in his 'Species Algarum,' p. 6, published in 1820). But Meyen materially weakens his own argument in stating that he considers the Gulf-weed (*Sargassum bacciferum* of Turner and Agardh), and the *Sargassum natans*, or *vulgare*, specifically distinguished from it by these authors, as one and the same species; adding, that he has observed among the Gulf-weed all the varieties of *Sargassum vulgare* described by Agardh; and finally, that on the coast of Brazil he has found what he regards as the Gulf-weed in fructification. Now, as *Sargassum natans* has been found fixed by a discoid base or root, in the same manner as the other species of the genus, and as according to Meyen the Gulf-weed has been found in fructification, the legitimate conclusion from his statements seems to be, that this plant is merely modified by the peculiar circumstances in which it has so long been placed. I am not, however, disposed to adopt Dr. Meyen's statement that he actually found the true *Sargassum natans*, much less all its supposed varieties, mixed with the Gulf-weed, having reason to believe that at the period of his voyage his practical knowledge of marine submersed Algæ was not sufficient to enable him accurately to distinguish species in that tribe. It is not yet known what other species of *Sargassum* are mixed with the Gulf-weed, what proportion they form of the great band, nor in what state, with respect

to root or fructification, they are found; though, in reference to the questions under discussion, accurate information on these points would be of considerable importance.

"That some mixture of other species probably exists may be inferred even from Dr. Meyen's statement, and indirectly from that of Lieut. Evans, who, in his communication published in Major Rennell's invaluable work on the Currents of the Atlantic, asserts that he found the Gulf-weed in fructification, which he compares with that of Ferns, a statement which would seem to prove merely that he had found along with the Gulf-weed a species of *Sargassum* with dotted leaves, the real fructification of the genus bearing no resemblance to that of Ferns, though to persons slightly acquainted with the subject the arranged dots on the leaves might readily suggest the comparison.

"With regard to the non-existence of roots in the Gulf-weed as a proof of specific distinction, it is to be observed that the genus *Sargassum*, now consisting of about sixty species, is one of the most natural and most readily distinguished of the family *Fucaceæ*, and that there is no reason to believe that any other species of the genus, even those most nearly related to, and some of which have been confounded with it, are originally destitute of roots; though some of them are not unfrequently found both in the fixed and in considerable masses in the floating state, retaining vitality and probably propagating themselves in the same manner (see Forskål, Fl. Ægypt.-Arab., p. 192, n. 52). It is true, indeed, that a *Sargassum*, in every other respect resembling Gulf-weed, has, I believe, not yet been found furnished either with roots or fructification, neither Sloane's nor Browne's evidence on this subject being satisfactory.[1] But the shores of the Gulf of Florida have yet not been sufficiently examined to enable us absolutely to decide that that is not the original source of the plant; and the differences

[1] See Sloane's Jam. i, p. 59. I have examined Sloane's specimens in his Herbarium; they belong to Gulf-weed in its ordinary form, and are alike destitute of root and fructification; hence they are probably those gathered by him in the Atlantic, and not those which he says grew on the rocks on the shores of Jamaica. Browne's assertion to the same effect is probably merely adopted from Sloane.

between the Gulf-weed and some other *Sargassa*, especially *S. natans*, are not such as to prove these two species to be permanently distinct. The most remarkable of these differences consists in the leaves of the Gulf-weed being uniformly destitute of those dots or areolæ so common in the genus *Sargassum*, and which are constantly present in *S. natans*. These dots, in their greatest degree of development, bear a striking resemblance to the perforations or apertures of the imbedded fructification in the genus. But as the receptacles of the fructification, as well as the vesicles, are manifestly metamorphosed leaves; and as the production of fructification is not adapted to the circumstances in which the Gulf-weed is placed, it is not wholly improbable, though this must be regarded as mere hypothesis, that the propagation by lateral branches, continued for ages, may be attended with the entire suppression of these dots.

"That the Gulf-weed of the great band is propagated
80] solely by lateral or axillary ramification, and that in this way it may have extended over the immense space it now occupies, is highly probable, and perhaps may be affirmed absolutely without involving the question of origin, which I consider as still doubtful.

"My conclusion, therefore, is somewhat different from that of Baron Humboldt, to whom I would beg of you to forward these observations, which will prove that I have not been inattentive to his wishes and to your own, though they will at the same time prove that I have had very little original information to communicate."

SOME ACCOUNT

OF

TRIPLOSPORITE,

AN

UNDESCRIBED FOSSIL FRUIT.

BY

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LONDON.

1851.

SOME ACCOUNT OF AN UNDESCRIBED FOSSIL FRUIT.

Read June 15th, 1847.

The following imperfect account of a singularly beautiful and instructive silicified Fossil has been hastily drawn up, to supply in some measure the possible want of any other memoir for the present Meeting.

The remarks which I am enabled to make, from detached memoranda, on so short a notice, will principally serve to explain the accompanying drawings, which I have carefully superintended, and which exhibit a very satisfactory microscopic analysis of its structure, and do great credit to the artistical talent of Mr. George Sowerby, jun.

The only specimen of this fossil known to exist was brought to London in 1843 by M. Roussell, an intelligent dealer in objects of natural history. His account of it was, that it had been in the possession of Baron Roget, an amateur collector in Paris, for about thirty years; that after his death it was brought to public sale with the rest of his collection, but no offer being made nearly equal to the sum he paid for it, which was 600 francs, it was bought in. It was purchased here from M. Roussell jointly by the British Museum, the Marquis of Northampton, and myself, for nearly £30. It seems to have entirely escaped the notice of the naturalists of Paris. Nothing else is known of its history, but from its obvious analogy in structure and in its mineral condition with *Lepidostrobus*, it may be conjectured to belong to the same geological formation.

The specimen is evidently the upper half of a Strobilus

very gradually tapering towards the top. As brought to England it was not quite two inches in length; but a transverse slice, probably of no great thickness, had been removed from it in Paris: the transverse diameter of the lower slices somewhat exceeded the length of the specimen;
[170] its surface, which was evidently waterworn, is marked with closely-approximated hexagonal areæ, of which the four lateral sides are nearly twice the length of the upper and lower: these hexagons, which are the waterworn terminations of the bracteæ of the Strobilus, becoming gradually smaller and less distinct towards the top.

A transverse section of the Strobilus exhibits a central axis, from which radii directly proceed, constantly thirteen in number, resembling, when perfect, the spokes of a wheel, but several of them being always more or less incomplete. These radii alternate with an equal number of oblong bodies, also radiating, of a lighter colour, and which are not directly connected with the axis: beyond these twenty-six radiating bodies a double series of somewhat rhomboidal areolæ exist. These appearances not readily indicating the actual structure in the transverse, are satisfactorily explained by the vertical section.

From the vertical section it appears that the Strobilus is formed of a central axis of small diameter compared with the parts proceeding from it, which consist,—

1. Of bracteæ densely approximated and much imbricated; the lower half of each of these stands at right angles to the axis, while the imbricating portion, of about equal length with the lower, and forming an obtuse angle with it, is gradually thickened upwards: these form the spokes and external rhomboidal areæ of the transverse section.

2. Of an equal number of oblong bodies of a lighter colour and more transparent, each of which is adnate and connected by cellular tissue with the upper surface of the supporting bractea. These bodies are sections of *Sporangia* filled with innumerable microscopic *sporules*, originally connected in threes (very rarely in fours), but ultimately separating, as shown in Tab. 35 (XXIV), fig. G.

From this triple composition or union of sporules, which differs from the constant quadruple union in tribes of existing plants, namely, *Ophioglosseæ* and *Lycopodiaceæ*, which, from other points of structure, may be supposed most nearly related to the fossil, I have called it *Triplosporite,* a name which expresses its fossil state, the class or primary division to which it belongs, and its supposed peculiarity of structure.

The structure of the *axis,* which is well preserved in the specimen, distinctly shows, in the arrangement of its *n* vascular bundles, a preparation for the supply of an equal number of bracteæ. These vascular fasciculi are nearly equidistant in a tissue of moderately elongated cells.

The vessels are exclusively scalariform, very closely resembling those of the recent Ferns and *Lycopodiaceæ* ; and among fossils, those of *Psarolites, Lepidodendron,* and its supposed fruit, *Lepidostrobus,* as well as several other fossil genera; namely, *Sigillaria, Stigmaria, Ulodendron, Halonia?* and *Diploxylon.*

The coat of the sporangium appears to be double; the outer layer being densely cellular and opake, the inner less dense, of a lighter colour, and formed of cells but slightly elongated.

On the lower or adnate side of the sporangium this inner layer seems to be continued, in some cases at least, in irregular processes to a considerable depth. I cannot, however, find that the sporules are actually formed in this tissue, but in another of somewhat different appearance and form, of which I have been only able to see the torn remains.

The minute granular bodies which accompany the sporules in the drawing Tab. 35 (XXIV), fig. G, are probably particles of the mother cells, and are neither uniform in size nor outline.

The whole specimen has suffered considerable decay or loss of substance, which is most obvious in the sporangia from their greater transparency, but equally exists in the opake bracteæ, in which radiating crystallization occupies the space of the removed cellular substance.

I cannot at present enter fully into the question of the affinities of *Tripolosporite.* I may remark, however, that in its scalariform vessels it agrees with all the fossil genera supposed to be Acotyledonous. In the structure of its sporangia and sporules it approaches most nearly, among recent tribes, to *Lycopodiaceæ,* and *Ophioglosseæ;* and among fossils, no doubt, to *Lepidostrobus,* and consequently to *Lepidodendron.*

The stem structure of *Lepidodendron,* known to me only in one species, *Lepidodendron Harcourtii,* offers no objection to this view, the vascular arrangement of the axis of its stem bearing a considerable resemblance to that of *Triplosporite.* To the argument derived from an agreement in structure between axis of stem and of strobilus I attach considerable importance, an equal agreement existing both in recent and fossil *Coniferæ.*

472] In conclusion I have to state, that very recently (since the drawings were completed, and as well as the specimens seen by such of my friends as were interested in fossil botany) Dr. Joseph Hooker has detected in the sporangia of a species referred to *Lepidostrobus* sporules, and those also united in threes. There are still, however, characters which appear to me sufficient to distinguish that genus from the fossil here described.

To the brief account here given of *Triplosporite* it is necessary to add a few remarks on some nearly-related fossils, chiefly *Lepidostrobi,* whose structure is now more completely known than it was when that account was submitted to the Society.

On the affinities of *Lepidostrobus* to existing structures, respecting which various opinions have been held, it is unnecessary here to advert to any other than that of M. Brongniart, which is now very generally adopted, namely, that *Lepidostrobus* is the fructification of *Lepidodendron,* and that the existing family most nearly related to *Lepidodendron* is *Lycopodiaceæ*. The same view is in great part adopted in my paper. But I hesitated in absolutely referring *Triplosporite* to *Lepidostrobus*, from the very imperfect knowledge then possessed of the structure of that genus. The specimens of *Lepidostrobus* examined by M. Brongniart were so incomplete, that they suggested to him an erroneous view of the relation of the supposed sporangium to its supporting bractea, and of the contents of the sporangium itself they afforded him no information whatever.

In concluding my account of *Triplosporite*, I noticed the then very recent discovery of spores in an admitted species of *Lepidostrobus* by Dr. Joseph Hooker, who, aware of the interest I took in everything relating to *Triplosporite*, the sections and drawings of which he had seen, communicated to me a section of the specimen in which spores had been observed, but which in other respects was so much altered by decomposition, that it afforded no satisfactory evidence of the mutual relation of the parts of the strobilus. The appearances, however, were such, that I hazarded the opinion of its being generically different from *Triplosporite*, an opinion strengthened by M. Brongniart's account of the origin of the sporangium.

Since the abstract of my paper was printed in the Pro- 473
ceedings of the Society, the second volume of the Memoirs of the Geological Survey of Great Britain has appeared, which contains an article entitled " Remarks on the Structure and Affinities of some *Lepidostrobi*." The principal object of Dr. Hooker, the author of this valuable essay, is from a careful examination of a number of specimens, all more or less incomplete, or in various degrees of decomposition and consequent displacement or absolute abstraction of parts, to ascertain the complete structure or common type of the genus *Lepidostrobus*; but the type so deduced is in every essential point manifestly exhibited, and in a much more satisfactory manner, by the single specimen of *Triplosporite*. This does not lessen the value of Dr. Hooker's discovery and investigation, but it gives rise to the question whether *Triplosporite*, which he has not at all referred to, and therefore probably considered as not belong-

ing to *Lepidostrobus*, be really distinct from that genus; and although there are still several points of difference remaining, namely, the form of the strobilus in *Triplosporite*, confirmed by a second specimen presently to be noticed, and in *Lepidostrobus* the more limited insertion of sporangium, and the very remarkable difference in the form of the unripe spores, hardly reconcilable with a similar origin to that described in *Triplosporite*, I am upon the whole inclined to reduce my fossil to *Lepidostrobus* until we are, from still more complete specimens of that genus, better able to judge of the value of these differences. The name *Triplosporites*, however, is already adopted, and a correct generic character given, in the second edition of Professor Unger's 'Genera et Species Plantarum Fossilium,' p. 270, published in 1850, who at the date of his preface in 1849 was not aware of Dr. Hooker's essay on *Lepidostrobus*, the character of which he has adopted entirely from M. Brongniart's account.

In October 1849 M. Brongniart showed me a fossil so closely resembling the *Triplosporite*, both in form and size, that at first sight I concluded it was the lower half of the same strobilus. On examination, however, it proved to be of somewhat greater diameter. It was nearly in the same mineral state, except that the crystallizations consequent on loss of substance were rather less numerous; it differed also in the central part of the axis being still more complete; in the bracteæ being more distant and of a slightly different
474] form : but the spores in composition, form, and apparently in size were identical. This specimen had then very recently been received from the Strasburg Museum, but nothing was known of its origin or history.

May 5, 1851.

EXPLANATION OF THE PLATES OF TRIPLOSPORITE.

Tab. 34 (XXIII).

The figures A, B, C, and D are of the natural size.

Fig. A. A portion of the surface of the Strobilus, showing the hexagonal areolæ.
Figs. B & C. Transverse sections, exhibiting different appearances of the bracteæ and sporangia.
Fig. D. A vertical section of fig. A.

The remaining figures, E, F, G and H, are all more or less magnified.

Fig. E. A transverse section of the axis.
Fig. F. A more highly magnified drawing of a portion of fig. E, to show the arrangement and proportion of the vascular and cellular tissues.
Fig. G. A horizontal section of a sporangium, made probably near its origin.
Fig. H. A portion of the outer wall of a sporangium or bractea.

Tab. 35 (XXIV).

All the figures magnified.

Fig. A. A vertical section of the axis, near, but not exactly in the centre, showing the ramifications of the central cord of the axis going to the circumference of the axis, and connected or supported by a loose cellular tissue at *a a*.
Fig. B. A small portion of the axis, from which proceeds a bractea cut vertically through its centre, showing its vascular cord, and bearing on its lower and horizontal half a vertical section of an adnate sporangium, of which the base is cellular, rising irregularly and without spores,—probably a rare occurrence.
Fig. C. A small portion of the axis, to show the scalariform vessels with [illegible] the slightly elongated surrounding cells.
Fig. D. A similar portion, from the central axis of the bractea of fig. B.
Fig. E. A similar portion, from the line of union between the bractea and sporangium of fig. B.
Fig. F. A small portion of a sporangium, sufficiently magnified to show the arrangement and composition of sporules.
Fig. G. Several sporules, both in their compound and simple state, still more highly magnified, with the minute granular matter which usually accompanies them.

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END OF VOL. I.

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