The Past and Present of the Cuttlefishes.

PART II.

THOSE who are acquainted with even the superficial details of the history and progress of the theory of evolution, amidst the critical warfare through which in the days of its youth it was fated to pass, will remember the somewhat famous controversy regarding the eyes of cuttlefishes and their relations with Vertebrate eyes, in which Mr. Darwin and Mr. St. George Mivart took part. The latter, insisting upon the likeness of the cuttlefish eye to the vertebrate eye, laid stress upon this likeness to enforce his argument that, as such likeness could not be 'due to inheritance from a common progenitor, it would be difficult if not impossible to explain such likeness as arising by the slow variation postulated by Darwin's theory of natural selection.' Mr. Mivart's words are clear

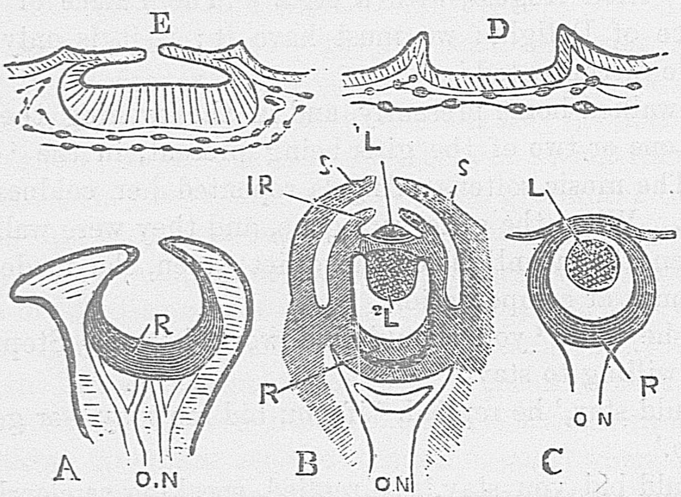

FIG. 3.[1]—*Development of the Cuttlefish Eye.*

A, Section of eye of Nautilus; B, of Two-gilled Cuttlefish; C, of a Snail; D and E, Early stages in formation of eye. References correspond in all the figures: L¹ L², lens; I R, iris; S S, cornea; R, retina; O N, optic nerve.

enough. Speaking of the presumed likeness between the eyes of vertebrates and cuttlefishes, he says, 'there can hardly be any hesitation in saying that for such an exact, prolonged, and correlated series of similar structures (sclerotic, retina, choroid, lens, &c., of the eye) to have been brought about in two independent instances by merely indefinite and minute accidental variations, is an improbability which amounts virtually to impossibility.' The primary difficulty, that of the development of the eye in any group by gradual and progressive modification, is, however, solved and obliterated by

[1] For Figs. 1, 2, see *Belgravia* for March.

the history of the individual development of any single eye in that group. Mr. Mivart's specific difficulty, that of the causes of the likeness between cuttlefish eyes and Vertebrate eyes, vanishes away when the progress of research demonstrates that the likeness in question is only apparent. For in truth there exists between these eyes just that amount of distinction and variation which the evolutionist would expect to find in products and structures of two varied and divergent twigs of the tree of descent. Darwin remarks, in reply to Mr. Mivart, that Hensen's memoir on the cuttlefish eye incontestably shows the difference between that organ and the eye of Vertebrata. The only likeness is that implied in vision of all kinds—a transparent organ, containing a lens 'for throwing an image at the back of a darkened chamber.' When the two eyes are carefully compared, the differences become prominent and apparent. Thus, as Mr. Lankester has shown, the eye of the cuttlefish begins its development as a pit (fig. 3, D) in the *epiblast* or outer layer of the embryo. Around this pit grows a fold which, as its edges meet in the middle line (E), shuts off the pit from the exterior. The epiblast lining the front of the pit or vesicle becomes the ciliary body and processes of the eye, whilst that lining the back of the vesicle gives origin to the retina (R). Then the pit becomes a closed sac, and a third layer (*mesoblast*) grows between the outer epiblast and its wall. The lens of the eye now forms in two pieces. The inner piece grows from the front wall of the pit or vesicle into its cavity, and ultimately the lens exhibits the characteristic double structure (B, L^1 L^2) of the adult cuttlefish eye. The iris (I R) grows outside the optic vesicle in front, in the shape of two folds, whilst external to the iris other two folds (S S) form the front chamber of the eye. This front chamber may or may not remain closed; usually it opens externally by a small aperture (fig. B) which persists in the middle of the cornea.

Thus there can be little hesitation in affirming that a study of the eyes of the cuttlefishes teaches two important lessons: Firstly, that their development adds another proof to the already overwhelming amount of testimony which supports the doctrine of evolution. In the course of its development the eye of one of the higher or two-gilled cuttlefishes (B) passes through stages which correspond with the permanent condition of the eye in the nautilus (A), in which there is neither lens, vitreous humour, nor cornea, the eye being merely a vesicle or sac (S) lined by the retina (R), and opening externally by a very small aperture. Just before the optic pit becomes closed (E), the permanent state of the nautilus eye is duly figured forth. Again, at a later stage, when the vesicle is closed (fig. C) and when the lens (L) projects into it, the condition of eye common in the adult gasteropod is imitated. The development of a single higher cuttlefish eye (B) is, in fact, a panorama of the evolution of molluscan eyes at large.

A second lesson taught us by the investigation of the organ of sight in cuttlefishes is that of hesitation in assuming or rejecting the genetic relationship of living forms, or in criticising the possibilities of evolution, until exact research has placed the determination of these relationships and of the ways of development within our grasp. Thus a study of the cuttlefish eye proves that, whatever its complexities, it represents the advanced and modified result of the development of lower molluscan eyes. Such a study also corrects erroneous notions of the genealogy of the animal world. The presumed relationship between vertebrate and cuttlefish eyes disappears at once under the light of Hensen's researches. As Darwin so well puts it, in speaking of the difference between these two eyes, 'the crystalline lens in the higher cuttlefish (fig. 3, B) consists of two parts (L^1, L^2), placed one behind the other like two lenses, both having a very different structure and disposition from what occurs in the Vertebrata. The retina is wholly different, with an actual inversion of the elemental parts, and with a large nervous ganglion included within the membranes of the eye.' Then, in further detailing the disappearance of the difficulties started by Mr. Mivart, Darwin says, 'It is of course open to any one to deny that the eye in either case (cephalopods or vertebrates) could have been developed through the action of natural selection of successive slight variations; but if this be admitted in the one case, it is clearly possible in the other; and fundamental differences of structure in the visual organs of two groups might have been anticipated, in accordance with this view of their manner of formation. As two men have sometimes independently hit on the same invention, so in the several foregoing cases it appears that natural selection, working for the good of each being, and taking advantage of all favourable variations, has produced similar organs, as far as function is concerned, in distinct organic beings, which owe none of their structure in common to inheritance from a common progenitor.'

The present history of the cuttlefishes may be concluded by the briefest possible reference to their distribution and classification. Over 2,000 species of cephalopods are known. But geology claims the vast majority, only 218 species being included in the ranks of living animals. The cuttlefishes are very widely distributed in existing seas. They occur in the far north; they are plentifully represented in the colder seas by the squids which form the bait of the Newfoundland cod-fishers; but in tropical regions they attain their greatest size and numerical strength. Their classification is both simple and natural. Their division into *Dibranchiates* ('two-gilled') and *Tetrabranchiates* ('four-gilled') is a method of arrangement which accurately reflects variations in their existing structure, as it correctly indicates the main lines of their geological and past history. Of four-gilled cuttlefishes there is but one living example—the pearly nautilus (fig. 4). Its special and distinctive peculiarities may be rapidly summed up in the statement that it has four gills, numerous arms (*c*), no suckers, no ink-sac, an incompletely tubular funnel (*f*), stalked eyes, and an external many-chambered shell, in the last formed and largest compartment (*e*) of which the body is lodged.

The absence of an ink-sac in the nautilus is a fact correlated with its bottom-living habits and with the absence of any need or

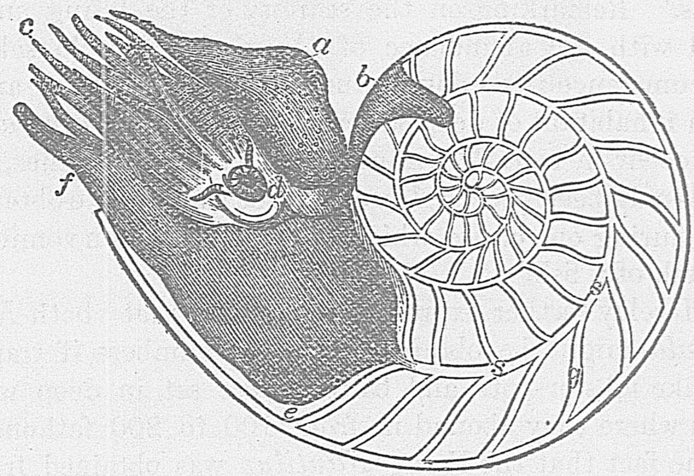

FIG. 4.—*Pearly Nautilus.*

requirement for the sudden concealment from enemies which the more active two-gilled forms demand. The many-chambered shell of the pearly nautilus exhibits a flat, symmetrical, spiral shape. Its many-chambered state is explained by the fact that as the animal grows it successively leaves the already formed chambers, and secretes a new chamber to accommodate the increasing size of body. Each new chamber is partitioned off from that last occupied by a shelly wall called a *septum* (*g*). Through the middle of the series of septa runs a tube named the *sipuncle* (*s*, *s*), whose function has been credited with being that of maintaining a low vitality in the disused chambers of the shell.

All other living cuttlefishes possess, on the contrary, two gills, never more than ten arms provided with suckers, an ink-sac, unstalked eyes, a completely tubular funnel, and an internal shell.

If, however, the nautilus represents in its solitary self the four-gilled cuttlefishes of to-day, it likewise, like 'the last of the Mohicans,' appears as the descendant of a long line of famous ancestors. In its distribution, the nautilus is limited to the southern seas. It is still the rarest of animals in our museums, although its shells are common enough. The scarcity of living nautili appears difficult to account for, when we find Dr. Bennett informing us that the natives of the New Hebrides dive for one species, and likewise capture it in fish-falls; the Fijians capturing *Nautilus Pompilius* with lobster-bait. Mr. Moseley tells us that the *Challenger* expedition obtained but a single specimen of the nautilus. It 'swam round and round a shallow tub in which it was placed, moving after the manner of all cephalopods—backwards, that is, with the shell foremost. It floated at the surface, with a small portion of the top of the shell just out of the water, as observed by Rumphius.' Remarking on the scarcity of the living animal, as compared with the abundance of the shells, Mr. Moseley says, 'The circumstance is no doubt due to the fact that the animal is mostly an inhabitant of deep water. The shells of *Spirula* (fig. 7) similarly occur in countless numbers on tropical beaches, yet the animal has only been procured two or three times. We obtained one specimen during our cruise, which had evidently been vomited from the stomach of a fish.'

Mr. Moseley further expresses his opinion that 'both *Nautilus* and *Spirula* might be obtained in some numbers if traps, constructed like lobster-pots, and baited, were set in deep water off the coasts where they abound in from 100 to 200 fathoms.' He adds, 'The fact that the living *Nautilus* was obtained from 320 fathoms shows that it occurs at great depths. It is probably a mistake to suppose that it ever comes to the surface voluntarily to swim about. It is probably only washed up by storms, when injured perhaps by the waves.'

It is thus the pearly nautilus floats under certain circumstances on the surface of the water. The argonaut (fig. 5), credited in poetry and fiction with this power, never floats on the surface, as was of old believed. It is simply a mundane cuttlefish, whose two expanded arms are never used as sails, after the popularly supposed fashion, but are employed solely to secrete and attach to the body the false shell (fig. 5, A) with which it is provided. Pope's advice—

> Learn of the little nautilus to sail,
> Spread the thin oar and catch the driving gale—

is thus utterly wasted; since his remarks apply to no cuttlefish whatever, and least of all to the argonaut, which, like its cephalopod neighbours, creeps along the sea-bed by aid of its sucker-provided arms, or shoots backwards in the sea by aid of the water-jets from its funnel.

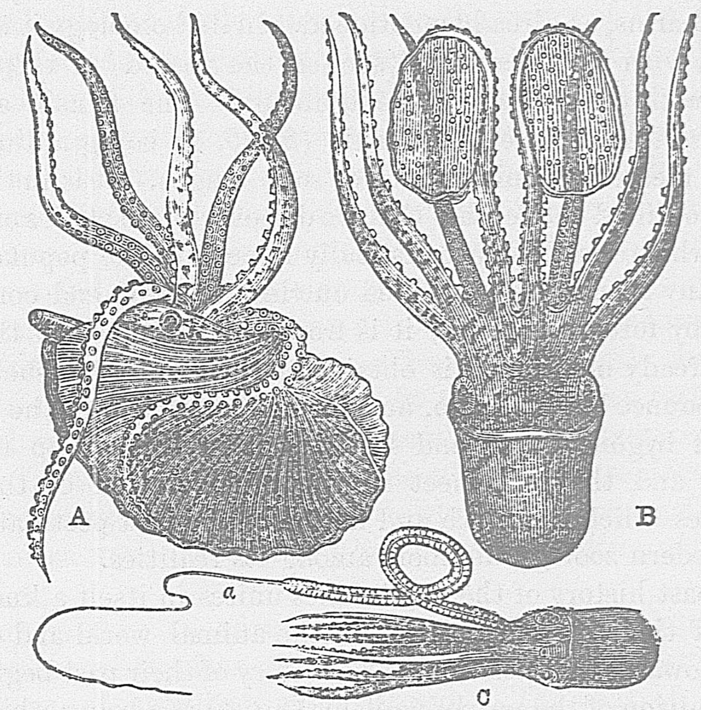

FIG. 5.—*Paper Nautilus.*
A, Female Argonaut showing shell, around which the two expanded arms are clasped; B, female removed from shell; C, the male Argonaut (shell-less).

Amongst the two hundred odd living two-gilled cuttlefishes, considerable diversity of external form may be seen; but the general type already described is at the same time closely adhered

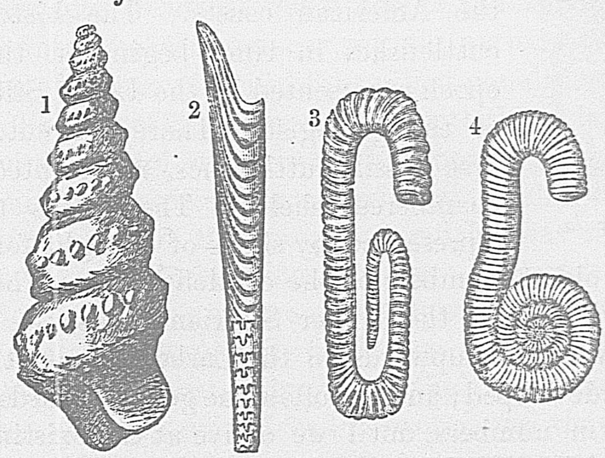

FIG. 6.—*Shells of Fossil Cuttlefishes.*
1, Turrilites; 2, Baculites; 3, Hamites; 4, Scaphites.

to; and save in the case of the paper nautilus or argonaut, in which the characteristic shape of body is concealed by the shell, the cuttlefish characters are readily apparent. The shell of the paper nautilus (fig. 5, A) is termed 'false' or 'pedal,' because it is not formed by the mantle, as all true shells are, but by the two expanded arms, as already mentioned. In its homology it therefore coincides with foot-secretions (such as the 'beard' of the mussel), and not with the shells of its neighbours. The female argonaut alone possesses a 'shell,' the male (fig. 5, C) being a diminutive creature, measuring only an inch or so in length. It is in the ranks of the two-gilled cuttlefishes that we discover those phases of cuttlefish life which most characteristically appeal to the popular mind. Thus, many species of two-gilled cuttles are eaten and considered dainties by foreign nations; it is from this group that the sepia colour already mentioned is obtained; their internal shells gave us the 'pounce' of long ago, and formed an article in the materia medica of bygone days; and lastly, it is in this group that the mythical and the real meet in the consideration of the giant cuttlefishes which the myth and fiction of the past postulated, and which modern zoology numbers among its realities.

The past history of the cuttlefishes unites in itself a knowledge at once of their present position in the animal world and of their progress towards that position. The history of their past begins with the recognition of the pearly nautilus (fig. 4) as a being which, as a four-gilled cuttlefish possessing an external many-chambered shell, stands alone in the world of life. It is the tribes of two-gilled cuttlefishes which people our ocean to-day, and which exhibit all the gradations of form and size, from the minute *Spirula* (fig. 7) to the great *Architeuthis* of the American coasts. The history of the cuttlefishes in time begins in the far-back epoch represented by the Lower Silurian rocks of the geologist. There are entombed the first fossil cuttlefishes, represented by their chambered shells. The genus *Orthoceras*, represented by shells of straight form, is thus amongst the oldest members of the cuttlefish race. The *Nautilus* genus itself begins in the Upper Silurian rocks; we may trace the well-known shells upwards to the Carboniferous strata where they are best developed; and we follow the genus onwards in time, as it decreases in numbers, until we arrive at the existing order of things, in which the solitary nautilus remains, as we have seen, to represent in itself the fulness of cephalopod life in the oceans of the past. The older or Palæozoic rocks reveal a literal wealth of these chambered shells, and therefore of the existence of the four-gilled cuttlefishes as the founders of the race. When we ascend to the

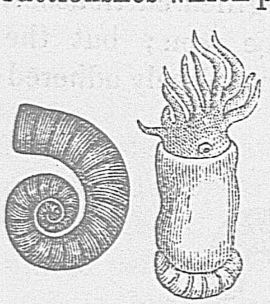

FIG. 7.—*Spirula.*

Mesozoic rocks (ranging from the Trias to the Chalk), we meet with new types of the chambered shells well-nigh unknown in the Palæozoic period. In the Mesozoic rocks appears the fulness of *Ammonite* life. Here we find shells named after the horns of the Egyptian god, Jupiter Ammon; these, instead of being tolerably plain like the *Nautilidæ*, exhibit beautifully sculptured outlines, and folded septa, or partitions, between the chambers of the shell. The shells allied to *Nautilus* and occurring in the Palæozoic formations differ from Nautilus chiefly in their varying degrees of curvature or straightness. *Lituites* is a curved form allied to *Nautilus*; whilst *Orthoceras* and *Gomphoceras* are groups representing the straightened forms. But in the Silurian period more complex forms appear, with elaborate and folded septa. These are the early Ammonites, such as *Goniatites* and *Bactrites*. In the Secondary rocks we find the still more complex true Ammonites themselves. Here the *lobes* and *saddles* of the shells, as the edges of the septa are named, are of the most elaborate patterns, whilst the shapes of shell are of the most varied character (*Baculites*, *Turrilites*, *Ammonites*, &c., fig. 6).

There is thus an advance and progression exhibited in the development of the four-gilled races which accords perfectly with the theory of evolution and descent. The seas of the Trias, Oolite, and Chalk periods must have literally swarmed with these striking forms of cephalopod life; but as the close of the Chalk period dawned, and as the Secondary age came to an end, the fulness of the Ammonite generations disappeared for ever. In the succeeding Tertiary period not a single ammonite of any kind occurs; the genus *Nautilus* remaining in the Tertiary period—as it survived into the Mesozoic or middle period—as the sole representative of a once plentiful four-gilled population.

If the history of the four-gilled cuttlefishes is thus plainly told as having its beginnings in the Palæozoic period, its maximum development in the Mesozoic period, and its lingering presence in the Tertiary period, the two-gilled cuttlefishes may be said to possess an equally interesting history. Compared with their four-gilled neighbours, the two-gilled forms are late comers upon creation's scene. Not a single fossil two-gilled form occurs in all the Palæozoic period extending from the Laurentian to the Permian rocks. If they existed in Palæozoic seas, they have at least left no trace of their presence. Their softness of body may perchance have contributed to their elimination from the oldest fossil records; but laying aside mere conjecture, we find the first fact of the past history of the two-gilled forms in the presence of the fossil shells of the extinct *Belemnites* in the Triassic rocks. The

Belemnites themselves disappear at the close of the Mesozoic period; but fossilised shells of species allied to our living Sepias occur in the Oolite; and the internal shells of squids are found in the Lias or lower Oolites. In the Tertiary rocks, Argonaut (fig. 5) shells occur in the Pliocene deposits; the Eocene rocks also give us sepia remains; and various other two-gilled fossils (*Beloptera*, &c.) are found in Eocene and Miocene formations.

Briefly summarised, then, we find that the chief details in the past history of the cuttlefishes are told when we are reminded that the four-gilled forms are by far the more ancient of the two groups; that they first appear in the Silurian rocks, whilst the two-gilled forms appear first in the Secondary rocks; and lastly, that the record of the one group is the converse of the other. For, the four-gilled species attained their maximum in the Primary and Secondary rocks, and have practically died out, leaving the pearly nautilus as their sole representative in existing seas. The two-gilled race, starting in the Secondary rocks, and leaving the extinct belemnites as a legacy to the past, have, on the other hand, flourished and progressed, and attain their maximum, both in size and numbers, in the existing seas and oceans of our globe.

What ideas concerning the origin and evolution of these animals may be legitimately deduced from the foregoing facts of their structure and distribution in time? In the answer to such a question, asked concerning any group of living beings, lies the culminating point of all biological science. That the cuttlefishes fall nominally into their place in the scale of being indicated by evolution, and that in their individual development, in the growth of their special organs, such as eye and ear, as well as in the general relations they bear to each other as living forms, they illustrate the results of progressive development, cannot for a moment be doubted. The further fact that the existing four-gilled nautilus, despite its lengthy ancestry, as regards its brain, its eye, its tentacles, and other features of its history, is a less specialised and lower form than the two-gilled cuttlefishes, clearly points to the evolution of the two-gilled from the four-gilled stock. The preponderance of the latter race in time, and its long and solitary representation of the class, as well as the relatively late appearance of the two-gilled species, are facts which collectively point to the two-gilled forms as derivatives of the older four-gilled race. The more active and structurally higher races of to-day, in other words, have sprung from the less specialised and lower cuttlefishes of the geological yesterday. No question, then, of the reality of progressive development, as a factor in evolving new species and groups of cuttlefishes from the confines of already formed species, can be entertained.

It is easy, moreover, to show from the researches of Würtenberger that even in one group—that of the ammonites themselves—the evidence of evolution is full and complete. The *Planulate* or 'ribbed' ammonites have, according to this author, given origin to the *Armata*, or spinous forms. The ribs of the one pass by gradual modification, well represented in the fossil shells, into the spines of the other. So closely are these species of ammonites connected that, as Würtenberger remarks, it is almost hopeless to define where one species ends and another begins. The modifications of form which connect one curious shape of shell with another of different shape and species are not sought in vain in palæontological records.

Turning more specifically to the shell in general, we may discover in the modifications of this single structure a clue to the entire evolution of the cuttlefish race. The 'shells' of the two-gilled cuttlefishes exist for the most part as horny 'pens' or as limy plates, secreted by the 'shell gland' of the mantle which forms the true shell of all molluscs. In considering the nature of the various shells of cephalopods, 'palæontology,' as Professor Ray Lankester puts it, 'crosses the path of embryology.' Starting with the shells which are certainly oldest in point of time, and therefore of development, we find in the Nautili and their neighbours, structures which represent fulness of shell-growth. It appears a long hypothetical journey from the well-developed shell of the nautilus-type to the limy plate or horny 'pen' shell of the squid. But the halting-places on the way diminish the apparent length of the journey, as they lessen the seeming irregularity of the path. The simple rudimentary shells of our two-gilled cuttlefishes, are to be regarded as the degenerate remains of structures fully developed in their ancestors. To this idea, their succession in time bears faithful witness; and to its correctness the connecting links, accessible to us, plainly testify.

Starting with the perfect four-gilled shells as ancestors of the imperfect pens and shells of living cuttlefishes, we may find in some such straight shell as that of *Orthoceras*—a type of shell persisting onwards to the Trias from the Silurian—as likely a form as any other to have evolved the newer races in part. We discover next in the extinct *Belemnites* of the Mesozoic rocks a first halting-place. Already we are in the domain of the two-gilled cuttles; for the belemnite was a kind of squid or calamary, and possessed the ten arms of its race. Evolved from some orthoceras-like or straightened nautiloid ancestor, the belemnite shell bears proof of its descent in its structure. Here we discover a chambered portion resembling the straight nautilus shell; and, combined with the chambers, is an anterior part, the *pro-ostracum*, and a posterior portion, the *guard*. Next in order in the list of connecting forms comes the little *Spirula*, in which an originally outside shell becomes enclosed by the mantle. The shell of Spirula (fig. 7), often termed the 'post-horn' shell from its shape, exhibits a spiral form; the coils lying in one plane, but not being in contact as are the whorls of the nautilus shell. The shell of Spirula is practically a belemnite shell, minus a *guard* and *pro-ostracum*. In Spirula, therefore, the transition from an external nautilus-like shell to an internal shell is clearly to be witnessed. In *Spirulirostra*, a fossil and extinct form found in the Tertiary rocks, we have a shell like that of Spirula, but possessing in addition a *guard* imitating that of the belemnites. Within the actual domain of the zoologist are the shells we discover in the existing Sepias. In these animals a limy plate represents the results of degenerative action consequent upon altered life and habits which no longer tend towards shell-perfection. The chambers of the originally outside shell of the spirula type, and the chambered part of the inside shell of the belemnite type, have together disappeared in the limy plate or 'cuttle-bone' of sepia and its allies—a rudiment of its chambered portion being indeed still recognisable in its so-called 'mucro,' and we have thus left to us in the sepia, merely the rudiments of the belemnite's 'chambers' and 'guard.' The horny 'pen' of the squid represents a still more modified structure on which the laws of development have operated, modifying and deleting the shell-rudiment until it remains merely as an interesting landmark in the evolution of its possessors.

Thus the history of the cuttlefish shell forms an important chapter in the biography of the race. The rudimental shells of the two-gilled cuttlefishes, like the teeth which never cut the gum in unborn whales, have a reference not to their present life, but to a former state of things. Contemplating the 'pen' or 'cuttle-bone' of a modern squid or sepia, our thoughts become moulded in mental continuity with the past. There rise to view before our mind's eye the ancient nautili and their sculptured kith and kin the ammonites, crowding the sea-beds of the far-back Mesozoic, and still more remote Palæozoic ages. Then, through the operation of the inevitable laws of organic progress and advance—making the ancient world then, as they constitute our world to-day, the theatre of continual change—we see the two-gilled stock arise in Secondary times from the four-gilled race. First there is seen the modification of shell. Concurrently with the decrease of shell comes increase of head-development and elaboration of nerve-centres, tending to make the new two-gilled form what we know it to be to-day—the wary, watchful organism, living in the waters above, and occupying a sphere of vital activity immeasurably superior to the dull existence passed by its four-gilled ancestors on the ocean bed. The shell degenerates more and more as the cuttlefish race rises on its own branch of the animal tree. Development in numbers succeeds individual advance. The cephalopod tribes of to-day dawn fuller and fuller as the Tertiary period progresses. Thus the fulness of cuttlefish life to-day, exhibited in all its strange weirdness, is interwoven, like the lines of human history itself, with the warp and woof of the past. And not the least important clue to the history of that past is found in the apparently insignificant 'shell' we have discussed; since in its mere degeneracy it leads us backwards in an instructive glance to those early times when the chief branches on life's tree had not reached their full fruition, and to the days when the world itself was young.

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