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INAUGURAL ADDRESS BY THE PRESIDENT,

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WHAT EVOLUTIONARY PROCESSES DO THE MOLLUSCA SHOW?

LADIES AND GENTLEMEN,—

My first duty—and it is also a great pleasure—on succeeding to this presidential chair, is naturally to tender you my sincere thanks for the great honour you have thus conferred upon me in selecting me for the position. When I call to mind the noted naturalists, some, alas! no longer with us, who have in the past filled the office of president with such ability and distinction, I feel that, while it is not for me to dispute the wisdom of your choice, a long interval in merit separates him, who now has the honour to address you, from his presidential forbears. Nevertheless, let me assure you that so far as the endeavour to do one's uttermost to advance the best interests of the Society is concerned, no breach of continuity shall be observable.

As some earnest of this I trust you will accept the fact, that at rather short notice, the mission of addressing you at this Annual Meeting has been taken up by myself. In the natural course of events my predecessor should have given us his swan-song.

Under these circumstances it seemed best to put before you the results of some recent cogitations on my part as to what evidences exist, if any, of progressive development in the Molluscan phylum. This naturally implies passing in review many well-known points and familiar facts; but though the beads may be old and the string not altogether new, the rethreading may perhaps prove interesting, and possibly even suggestive, to the members of this Society.

The extreme plasticity of the Mollusca naturally renders them both peculiarly susceptible and readily responsive to the operation of the two great factors that govern the lives of all animals, namely, the influence on them of their environment, and the necessity laid on one and all of procuring food. The Molluscan mode of life is, in fact, mainly governed by the combined action of these two controlling influences, and in turn becoming itself a potent factor, completes the cycle by reacting on the animal, which is thus impelled, so long as similar conditions hold, yet further along a given line of development.

Owing, however, to the paucity of stable elements to be acted on, continuous progress in any direction has, despite the antiquity of the race, been slow indeed. The total lack of anything like internal framework has militated against any such wonderful progress as exhibited in the Vertebrate kingdom; the very plasticity of the Mollusca has thwarted progressive development, as we understand the phrase, and they readily retrograde or branch off into bye-paths.

Hence the study of evolution in this group is an exceedingly complex one, offering, like a very tangled skein, so many clues to follow out that one is in doubt which thread to pursue first.

On the present occasion it will suffice to take certain leading features and organs, to summarize what is known concerning them, and to endeavour to ascertain how far, if at all, any definite conclusions can be based upon them.

It may fairly be conceded that the tidal zone was in all probability the cradle of the race, and that thence the various members gradually betook themselves, mostly to deeper and deeper water on the one hand, but also, though perhaps more tentatively and gradually, to fluviatile and terrestrial conditions on the other.

Now the first requirement of a soft-bodied animal, and especially of one considered by its fellows to be good eating, is protection. In early days, however, enemies were far fewer than now, and it was rather from the force of the elements that preservation was needed.

This first requirement is supplied by the shell, and all three types, univalve, bivalve, and multivalve, make their appearance early in the history of the race.

The last named, the Chitons, first occur in the Ordovician (*Priscochiton*). They are, however, a conservative race, and have not materially changed their form since those far-off days. Still, taking the Amphineura as a whole, the class shows a desire to disburden itself of its coat-of-mail. Through the successive genera of one branch of the Polyplacophora (*Acanthochites*, *Amicula*, *Cryptochiton*, and *Cryptoplax*) the component plates become wider and wider apart, and the whole animal more vermiform, while in the worm-like Aplacophora the shell has disappeared, though numerous calcareous spicules remain scattered over the mantle.

As regards the Gastropoda, when it is borne in mind that the embryonic shell is nautiloid and exogastric (and allowing for the gastropod peculiarity of spiral torsion, which is a deep-seated phenomenon, foreshadowed early in the cleavage of the egg-cell), the number and variety of forms assumed in the adult state is remarkable. Seeing that departures from this embryonic and therefore primitive type are pronounced, even in the earliest known gastropods, it is not possible to say how far environment or other forces may have played part in their development. Certain elongate forms like *Terebra* would seem a positive disadvantage to the animal, and still more so to the Hermit-crab, who, with mistaken notions of levity, occupies an empty example.

Nevertheless, certain broad characteristics are observable. Primarily among the inhabitants of a rough foreshore the massive strength of the shell is noticeable, the object being, of course, to withstand the battering action of the waves and hard substances like stones cast up by them.

To this end the conical form of the tests of *Patella* and *Fissurella* is admirably adapted, hence the recurrence of this particular shape in widely different molluscs. Thus it reappears in the Capulidæ, a family dating back in time as far as do the Docoglossa, the Hipponycidæ ; *Ancylus* and *Acroloxus*, which in swift running waters are liable, only in a lesser degree, to the same troubles as the marine surf dwellers ; and more strikingly still in those pulmonates (*Siphonaria* and *Gadinia*) that have reverted to the marine surf as a habitat. The patelloid shape is also approximated in the fresh-water genus *Septaria*, in which the operculum, being no longer in use, is reduced in size and buried in the substance of the foot. While a parallel instance, in a widely different animal, dwelling under similar conditions, is afforded by the familiar Barnacle.

The early spiral Rhipidoglossates seem mostly to have had stout shells ; certainly this is the case with the modern Neritidæ, Turbinidæ, Trochidæ, and their allies. Most of the members of these groups are furnished with thick opercula, which are not withdrawn far within the mouth of the shell. With the capacity on the part of the animal, however, for retreating further and further into the shell and so out of the more immediate reach of danger of violent injury, the operculum, always an incumbrance, tends to become less and less ponderous.

Other inter-tidal forms belonging to families higher in the molluscan scale have also, under the necessity of facing similar conditions, developed strong shells: such are *Littorina*, *Purpura*, *Nassa*, and among tropical forms *Pterocera*, *Turbinella*, and *Strombus*. The last-named, indeed, is the most difficult of all shells to break, resisting even the lusty application of a geological hammer.

When, however, the foreshore is quitted in favour of deeper water, where no surf ever breaks and where the sea-bottom is composed of soft sand, or silt, a ponderous shell ceases to be essential for protective purposes and becomes a positive disadvantage in locomotion. This drawback is further increased in the case of Gastropoda that are carnivorous, as the higher forms mostly are, for even the slow-moving bivalves on which they feed require greater activity to seek out and capture than a rooted plant. Hence the reduction in shell and operculum shown by the inhabitants of the laminarian as contrasted with those of the littoral zone.

The process continuing as specialization proceeds, the shell ever tends to decrease in size till it remains solely as a protector for the more vital organs, as in the Tectibranchs, or disappears altogether, as in the rhipidoglossate *Titiscania* and the Nudibranchs.

A similar reduction and disappearance take place among the pelagic forms. Light as *Ianthina* shells are, they are substantial compared to the glassy films carried by the Heteropoda and Pteropoda Thecosomata, while *Phyllirhoë* and the Pteropoda Gymnosomata have discarded all covering whatsoever.

The fresh-water Gastropoda, save those few that inhabit turbulent waters, have, as might be expected, thin shells; but though *Amphipeplea* and *Physa* tend to overflow their shells, an absolutely shell-less fresh-water gastropod remains to be discovered.

On land heavy shells are certainly at a discount, and though some such occur among the Auriculidæ, in certain species of *Strophocheilus*, in *Leucochroa* (where it serves as a protection against excessive heat), and many of the Cyclophoridæ, still, viewed broadly, the tendency, as might be expected, is to a lightening and diminution of the shell to the point of disappearance, and this more especially in the carnivorous and semi-carnivorous forms. In fact, nearly all the families of land-snails culminate with highly specialized representatives, in which the shell is not only extremely dwarfed, as in many well-known instances, but is reduced to an internal vestigeal plate, as in *Chlamydophorus* (Testacellidæ), *Limax* and allied genera (Limacidæ), *Metostracon* (Helicidæ), *Hyalimax* (Succineidæ ?), and *Athoracophorus*, or to mere granules, as in *Arion*, while it is totally wanting in *Trigonochlamys*, *Pseudomilax*, *Philomycus*, *Veronicella*, and *Oncidium*.

The Scaphopod shells do not assist in our present enquiry. The animals have not materially altered their habits, and the function of the shell is merely to protect the soft parts from the lateral pressure of the surrounding silt, and to that end the tubular form is most suited. The young shell in its very early stages is so deeply cleft as to be almost bivalve. Unfortunately some recent textbooks, professedly founding their information on the translation of Claus' great work, have overlooked the 'almost.' In the course of growth the apical portion of the Scaphopod shell is absorbed in proportion as the aperture is added to, consequently the apical slits in all adult shells, and the perforations in *Schizodentalium*, owe their existence to absorption, and are not due, as in certain Gastropoda, to the inclusion of quondam marginal slits.

Among the Pelecypoda the shore-frequenters of the older and, broadly speaking, less specialized types exhibit on the whole stouter and more convex shells than the later and more specialized ones. Especially stout are some that have, like *Tridacna* and *Hippopus*, to withstand the full beat of ocean waves; so, too, are those of the fossil reef-builders of the *Rudistes* group.

The most primitive form, *Nucula*, that has come down to us from palæozoic times is without siphons or byssus, but some species of its near ally, *Arca*, which boasts an equally long ancestry, have attained the faculty of mooring themselves by a byssus and so defying the waters. *Mytilus*, which also comes of a family having a long pedigree, has not a particularly stout test capable of resisting heavy blows, but it meets the waves with its outwardly directed, sharp, wedge-shaped shell and cleaves them instead; while it does not settle, or perhaps, to speak more accurately, does not establish, itself in spots where it would be liable to damage from stones thrown up by the sea.

Allusion may here be made to the great inequality of size the anterior and posterior portions of the body present in certain forms like *Mytilus*, and the disappearance *pari passu* of the anterior adductor muscle in proportion, as, by the increase of growth in the posterior portion of the body, it is brought more and more into line with the hinge and posterior adductor muscle, and consequently ceases to be needful.[1]

It is possible that in the case of *Mytilus* the predisposing cause may be due to the long-continued action of gravity operating on successive generations of suspended animals, aided perhaps by some other morphological influence. Whether a similar tendency to monomyarianism observable in forms that, like *Pecten*, *Ostrea*, etc., rest on their sides, may be attributable to a like cause is not clear, but it is at least remarkable that so many of the Monomyaria should be forms that assume a position out of the normal vertical.

Tridacna, so long a puzzle, and concerning which it was even held that the animal must have rotated in its shell, has been successfully shown by Mons. R. Anthony[2] to be simply a case of a monomyarian that has taken to live with its umbo downwards. All its anatomical features correspond closely in arrangement and position with those of *Mytilus*, only it occupies a relatively reverse position, and its huge plastic body tends by its own weight to spread out and consequently to form a shell that has its longer axis at right angles to that of the *Mytilus* shell.

To return, however, to the pelecypod shell. Most of the bivalves, as a matter of fact, do not live in exposed positions, but burrow more or less deeply into soft sand or silt. Here those that do not penetrate to any depth below the surface, and do not live in deep water beyond the reach of ground swells, are liable to considerable pressure from the shifting of the loose material that surrounds them. Hence these generally have acquired stout, more or less globular, shells, as in *Isocardia*, *Cardium*,[3] the Veneridæ, etc.

The disadvantage of this form of shell, of course, is the amount of muscular power required to force a passage with it down into the sand. A gauge of this may be seen in the huge scar of the retractor pedis muscle in the Veneridæ, that has generally been overlooked because it is situated at the back of the broad hinge-plate.

In proportion, however, as the bivalve seeks shelter from the strains of the shifting sand, either in quieter waters or by burrowing deeper, so the shell in response tends to become less heavy and solid, and to assume a flatter shape, permitting of more rapid passage down into the silt. This is seen in the later date forms, such as *Tellina*, *Psammobia*, and *Scrobicularia*. The habit of deeper burrowing is of necessity accompanied by an increase in the length of the siphons to ensure proper respiration, and this in turn results in the prolongation of the

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[1] This was first pointed out by Mr. B. Sharp, Proc. Acad. Philad., 1888, pp. 121–124, and first illustrated by specimens in the Index Hall of the Natural History Museum shortly afterwards.

[2] Comptes-rendus Acad. Sci. Paris, tom. cxxxviii (1904), pp. 296–298.

[3] It is interesting to note that the spines on the shell of the prickly species of *Cardium* are more pronounced on those dwelling in sand than on those individuals inhabiting muddy or silty sea-floors, the more shifting material exacting a better means of anchorage.

posterior portion of the test to house them, as well as the ultimate abandonment of the flattened form, till finally in the deepest burrowers, the Myidæ and Solenidæ, the closed shell is frankly abandoned, and the valves, which no longer cover the whole animal, function solely as fenders against lateral pressure from the surrounding silt.

Facility in penetration is probably likewise the accountable cause of the elongate shape of the rock-boring representatives of several families of Pelecypoda.

To the borers, rather than to the burrowers, should be referred *Fistulana* and *Brechites*, with their specialized shelly tubes, which are a secondary product quite distinct from the true shell. In the case of the former we have had proof of its drilling powers brought before this Society on more than one occasion.[1]

There are a few instances among the bivalves in which the shell becomes internal (i.e. invested by the mantle): *Chlamydoconcha*, which passes its life attached to the sheltered sides of rocks by its byssus; *Ephippodonta*,[2] which is commensal in the burrow of a species of prawn (*Axinus*); *Scioberetia*, which is a parasite in the ambulacral zones of an incubating echinoderm (*Tripylus*); and *Entovalva*, which is parasitic within *Synapta*. Semper has also recorded the occurrence in similar situation of another mollusc with internal shell, from the Philippines,[3] possibly belonging to the same genus as the last.

No instance of a shell-less pelecypod has as yet been recorded.

While, therefore, it is not so pronounced as in the case of the Gastropoda, there is still evidence of an increasing tendency in the Pelecypoda towards the reduction of the shell as one proceeds from the more primitive to the more specialized forms.

One feature in connection with the bivalve shell there is, that distinctly shows a tendency to simplification, and that is the progressive reduction of the number of teeth in the hinge. The oldest forms, such as many of the Palæoconcha of Neumayr, the more archaic living forms (Nuculidæ, Arcidæ, etc.), and the embryo shells of many higher forms (Ostreidæ, Pteriidæ, Philobryidæ, Mytilidæ, etc.), exhibit a more or less rectilinear hinge-line with numerous small teeth (Taxodont). In the yet more advanced forms (*Condylocardia* and *Scioberetia*) this stage, present in the early embryo, is succeeded by the series of folds (characteristic of the young stages of the higher Pelecypods) that subsequently divide off into cardinal and lateral teeth, thus linking the Taxodont with the Heterodont and Desmodont types of hinge. In these last groups the hinge-teeth progressively dwindle in number, till in the most specialized Septibranchs they are wanting altogether, as they are also, exceptionally, in other less advanced forms.

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[1] Proc. Malac. Soc., vol. v, pp. 258, 345; vi, p. 185; and as an exhibit at the meeting in December last.

[2] The anatomy of this genus formed the subject of one of the late Martin F. Woodward's earliest papers: Proc. Malac. Soc., vol. i, pp. 20–25. Examples were also exhibited at a recent meeting by Mr. Burne.

[3] Reisen im Archipel der Philippinen: Holothurien, p. 99.

In dealing with the Cephalopoda it is essential to take into account the past history of the race, since so many, especially of the shell-bearing forms, have long been extinct.

The modern representatives of the class[1] number close on 500 species, belonging to about 80 genera, of which total about half are referable to the genera *Polypus*, *Sepia*, and *Loligo*, while only five species, all belonging to the genus *Nautilus*, are possessed of an external shell.

The Nautiloidea,[2] which began in the Cambrian with seven straight-shelled species representing four genera, attained their maximum in the Silurian with about 230 species belonging to 20 different genera and subgenera. Since that epoch they have steadily diminished in numbers down to their minimum at the present day, while the surviving genus, *Nautilus*, only made its first appearance in the Trias, or, *sensu stricto*, the Tertiary. Nor did the vigorous offshoot of Ammonoidea that started in the Devonian and attained to a countless host of species, which from some monographs one might almost infer were referable to an equal number of genera, succeed in keeping up the number of testaceous Cephalopoda, for with the close of the Cretaceous period the whole group died out after experimenting in every type of shell-form in the effort to survive.

Nothing is at present known of the embryonic development of *Nautilus*, and we do not consequently know if the primitive, embryo shell differs in any respect from the adult, but the fact that the earliest Cephalopods had straight shells and that the line of development led through curved to coiled forms is suggestive, and raises the speculation whether the primitive gastropod shell may not also have been straight, and this phase in its development subsequently suppressed in its embryonic history.

Following up the scale of geological time, we meet with the first of the decapods (*Aulacoceras*, belonging to the family Belemnoteuthidæ) in the Trias. It is interesting to note that, in the same series, the earliest gastropod referable to the Tectibranchia, a species of *Bullinella*, is also recorded. So that we have a cephalopod with an internal shell comparing in time with a gastropod of a group that only subsequently in the chalk period achieved a partially internal shell (*Philine*).

The Myopsida or next higher tribe of Cephalopoda began in the Lias (*Geoteuthis* and *Beloteuthis*); while in the Cretaceous of Lebanon the oldest known octopod, *Palæoctopus Newboldi*, makes its appearance just as the Belemnites and Ammonites disappear from the scene.

So far as the shell is concerned, then, the Cephalopoda seem to have been yet more eager than the Gastropoda to jettison the encumbrance, and their predatory habits have obviously had much to do in hastening this consummation.

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[1] Cf. Hoyle: "Cat. Recent Cephalopoda" and "Supplement," Proc. Roy. Phys. Soc., Edinburgh, ix (1886), p. 207; xii (1897), p. 364.

[2] Foord: "Cat. Fossil Ceph. in Brit. Mus.," pt. ii, pp. xviii–xix. These and the following paragraphs have been kindly checked by Mr. G. C. Crick.

Turning next to the form of the animal itself, it cannot be said that any definite line of development is presented, unless, perhaps, in the case of the more specialized Gastropoda, where, with the discarding of the shell, the visceral hump tends to be smoothed down and distributed along the dorsal keel till the true slug-like form is attained. Even this seems to be due to the burrowing habit of the animal rather than indicative of any definite product of development.

The foot largely modifies in response to individual requirements, whether for locomotory or other purpose. The simple reptant foot becomes a strong sucker-like organ in the Docoglossa, *Haliotis*, and other rock-frequenting kinds. It assumes the snow-plough outline in *Natica*, *Sigaretus*, and other species that search about in loose surface sand for their bivalve prey. It is expanded and functions like a snow-shoe in those of the Bullidæ that frequent very soft ooze, while the widely extended pleuropodial[1] margins function as fins, enabling the animal to swim (*Hydatina*, *Gastropteron*, etc.). In the pteropods and other oceanic gastropods it is modified into a swimming organ, but in this connection it is interesting to note that, according to Tesch,[2] the fin of the heteropod is constituted by the extension of the columella muscle through the true foot and its fan-like expansion into the swimming organ.

In the Pelecypoda the primitive reptant foot of the Nuculidæ becomes a leaping organ in *Cardium* and *Trigonia*, and converted by successive stages into an efficient digging organ in the burrowers, while it is aborted in fixed forms.

The Cephalopod foot has made more definite progress. Beginning with the numerous series of weak tentacles in the *Nautilus*, and presumably also in the fossil predecessors and allies thereof, it culminates in the powerful eight-armed weapon of *Polypus*.

The alimentary system does not furnish any particular evidence with respect to our quest of the moment, although, taking the molluscan group as a whole, the radula, which is characteristic of the phylum, does.

Speaking broadly, the teeth in the older families are numerous and weak. There may be as many as 300 or more teeth in each transverse row in the Rhipidoglossa. Our late Secretary, Mr. Martin F. Woodward, in his careful and most excellent monograph on "The Anatomy of *Pleurotomaria Beyrichii*," discussed the question of the radula, and gave reasons[3] that will hardly be disputed for thinking it represents the most primitive type among all existing Gastropoda, and, further, that it was derived from one in which all the teeth in a transverse row were similar. In *Pleurotomaria*, although all the various specialized tooth areas merge into one another, five tracts on

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[1] The term 'parapodia' adopted by some authorities has already long been in use, in a very different sense, for quite other animals; nor does 'pteropodia,' proposed by von Jhering, seem quite appropriate. Garstang's alternative term, therefore, seems preferable.

[2] Siboga Expeditie, vol. li, p. 104.

[3] Quart. Journ. Micro. Sci., N.S., vol. xliv, p. 255.

either side of the median are distinguishable; but of these the first and second, and again the fourth and fifth, counting from the centre, show less differentiation from each other than from the third, so that three tracts on either side are really all that practically strike the eye. Now Troschel and others have laid considerable stress on the breaking up of the rhipidoglossate radula into three zones on either side and on the occasional replacement of a group of marginal laterals by a single large tooth, which generally retains sufficient traces of the individuals it replaces to suggest that it represents the fusion of a series. This is noticeable in *Addisonia*, *Cocculina*, the Neritidæ and Helicidæ among the Rhipidoglossa, and also in certain archi-tænioglossate Cyclophoridæ, the Solariidæ, and even in *Ovula*.[1] Hence it may be legitimately inferred that the tænioglossate radula, whose formula is 1 : 1 : 1 : 1 : 1 : 1 : 1, is derived from the rhipidoglossate by a fusion of the elements of the three original zones.

The docoglossate radula, judged from its modern representatives, the Patellidæ, is explicable on similar lines, for if the aborted median tooth, sometimes represented by a rudimentary plate, be allowed for, the remaining teeth form three series of pairs on either side.

A further fusion, or, what is more probable in this case, the suppression of the outer laterals, in the Rhachiglossa and more primitive of the Toxoglossa gives rise to the 1 : 1 : 1, the typical radula of these forms; and a further abortion of the laterals to the single median tooth left in *Harpa*, *Marginella*, and most of the Volutidæ. In the Cones, on the other hand, it is the median tooth that is abolished, leaving the double row of barbed laterals.

What, then, is to be said of such exceptions as occur in *Ianthina* and *Scala* and others? Simply that either individual requirements have necessitated a return to the more primitive form of radula, or that their ancestry goes further back in geological time than suspected. Fossils doubtfully referred to the latter occur in the Silurian and Devonian, but *Ianthina* extends, so far as at present known, only back to the Middle Tertiaries.

The Opisthobranchia offer every variety of radula in their ranks, from the uniform multiserial to the single row of median teeth in *Elysia*, and much further research will be necessary ere a solution of this diversity is found.

The Pulmonata present considerable variation in the composition of the radula. The Auriculidæ, pronounced by Pelseneer[2] to be the most primitive of the group, have also a primitive type of radula, but geologically date only from the Cretaceous period. The Limnæidæ, which appear in the Jurassic, have a similar primitive radula. So, too, have the Siphonariidæ, but here, if *Hercynella* be correctly referred to this family, which seems doubtful, we have an ancestry dating from the Devonian.

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[1] In *Ovula ovum*, indeed, fusion has proceeded so far that the formula is 1:1:1:1:1.

[2] "Recherches sur divers Opisthobranches": Mém. Cour. 4° Acad. Sci. Belg., tome liii, p. 114.

The Stylommatophora, likewise, are primitive in the arrangement of the radula, most of them having a great number of similar teeth to the transverse row. The oldest of them, *Pyramidula* and *Jaminia*, appear, as well known, in the Coal-measures. The determination of the former is due to Pilsbry, than whom we have no greater living authority on helicoids. It was first referred to *Zonites*, and subsequently to *Archæozonites*, and under these names still masquerades in geological text-books, even the latest, so gyroscopic in their immutability are these works of instruction. *Zonites* proper, as typified by *Z. Algirus*, shows no diminution, but in *Vitrea* there is a considerable reduction in the number of teeth in each transverse row. Of the British species, *V. nitidula* has 36, the other species from 12 to 15 laterals in each row on either side of the median tooth, whereas in *Helix aspersa* there are about 55.

As regards the character of the individual teeth, Pilsbry[1] points out that the multicuspidate form of the primitive pulmonates gives way in the helicoids to the tricuspid type. In many Endodontidæ the teeth are all tricuspid, a form usually correlated with small size and strictly terrestrial habits. All modifications in the teeth proceed from the median line of the radula outwards, the outer marginal teeth being the last to be modified. A study of the marginal teeth, or of those of the embryo, therefore gives a clue in many cases to the ancestral condition of a much modified radula.

The yet more highly specialized of the pulmonates, the Agnatha, typified by the Testacellidæ, which date back to the Cretaceous, have likewise a primitive form of radula, in which, however, the individual teeth have become specialized to fit them for their actively carnivorous habits.

The radula of the Cephalopoda shows successive diminution in the number of teeth, but the gradation does not quite correspond with their taxonomy. Thus *Nautilus* on either side of the median has, first, two very similar admedians, then two long, pointed teeth, with a vestigeal basal plate between them and another on the outer margin, indicating that the primitive nautiloid radula had six teeth on either side of the central, or a transverse row of thirteen. The remaining members of the Class, with one exception, have only three laterals on either side; but *Loligo*, *Polypus*, and *Bolitæna* have a vestigeal plate on the outer side. The exceptional genus, *Gonatus*, has only two laterals on either side. Hoyle[2] has noticed that in the Cephalopoda there is a tendency in the corresponding teeth, especially the median, in following rows to vary slightly in a cycle, five or six rows going to each set.

[Since the above remarks on the radula were written, a most important paper has been published by Miss Igerna B. J. Sollas (Quart. Journ. Micro. Sci., vol. li, pp. 115–136) dealing with the composition and some points in the development of this organ.

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[1] Manual of Conchology, ser. II, vol. ix, p. xiii.

[2] "Challenger" Reports: Zoology, pt. xliv (1886), p. 54.

Miss Sollas finds that in all the odontophorous Mollusca the radula has an organic basis of chitine; that in the Docoglossa the teeth further contain as much as 27 per cent. of silica hydrate or opal in their composition, while in the rest of the Gastropoda the chitine is hardened superficially (*enamel layer*) by deposits containing calcium, iron, and phosphoric acid to the amount of from 2·4 to 6 per cent.; that the Chitons differ from this second group in alone having ferric oxide as the most important mineral constituent, which causes the dark colour of the teeth.

By employing Bethe's and other stains the interesting fact is brought out that the various tracts of the radula take the stains differently. A comparison of specimens thus treated should therefore enable a correct correlation to be made of the tracts of radulæ in the several stages of evolutionary development. Miss Sollas' results in this respect, so far as they go, bear out the conclusions set forth in the foregoing paragraphs; although obviously unaware of the opinion of previous writers on the subject concerning coalescence, she has been almost tempted to suggest that the "marginals are," as she puts it, "multiplied laterals."]

The circulatory system can be adduced as showing development if those of the tribe at the head of the phylum, the dibranchiate cephalopods, and the primitive gastropods be contrasted. For in the latter the circulatory system, instead of branching off into capillaries, is distended into swollen, irregular cavities, and sinuses, which are, so to speak, insinuated among the various organs of the body, while a certain amount of the blood finds its way back to the heart without passing through the respiratory organs. The Dibranchia, on the other hand, have the most complete circulatory system of any mollusc, the blood being nearly entirely contained in true vessels.

The molluscan heart, at the same time, offers some anomalies when the different groups are compared. It is most primitive, and more nearly approximates the annelidean type, in *Nautilus*, where the single ventrical (and no mollusc has more than one) is served by four auricles, whereas in all the other symmetrical mollusca it has but two auricles (except in the Scaphopoda and Aplacophora in which the heart is rudimentary). In the streptoneurous Gastropoda proportionately as the right (originally left) ctenidium becomes aborted in the higher Rhipidoglossa, and disappears in the rest, as the result of the general torsion of the body, so the corresponding auricle diminishes and disappears also. The simplification of the heart in this case, therefore, is not due to any progressive development from a less to a more perfect condition.

The respiratory system supplies some very interesting points, especially in those cases where a secondary system has been brought into play as in *Patella*, many Nudibranchia, and the Pulmonata. With these latter, howbeit, our present enquiry is not concerned, and we confine our attention to the true gills.

There is every indication that the primitive gill of the mollusca must have consisted of at least a pair of very simple, plume-like structures, and that as increased facilities for respiration were required, which of course implied increase of gill surface, it could only be obtained in one of two ways — the flattening out into a leaf-like expansion of the individual gill-filaments (aspidobranch), or their prolongation (pectinibranch). The former modification is the one that appears in all the archaic members of the different Classes, and may be recognized in the Polyplacophora, the rhipidoglossate Gastropoda, the protobranchiate Pelecypoda, and the Cephalopoda. This structure, nevertheless, is limited by the confined space of the pallial cavity, and further increase of surface can only be gained by the corrugation of the gill-filament. A beginning of such plication was observed by Martin Woodward in the case of *Pleurotomaria*,[1] and doubtless it exists in other aspidobranchs, but it is carried to a much greater degree in the cephalopods, in which the gill-filaments exhibit two series of plications crossing one another.

In the Gastropoda some changes, which would be startling if they were not so familiar, take place. In the first instance the right (morphologically left) ctenidium, as one ascends from lower to higher members, atrophies and disappears. Martin Woodward shows that this had begun in *Pleurotomaria*,[2] but it is far more marked in *Scissurella*. In the pectinibranchs not only has one ctenidium disappeared, but the other, except in the case of *Valvata*, has become attached by its whole length to the wall of the pallial cavity, and as a consequence has parted with the whole of the row of filaments on that side; so that three-quarters of the gill potentiality of the primitive mollusc is sacrificed. By way of partial compensation the individual gill-filaments have been somewhat lengthened till the familiar pectinibranch condition arises. In *Ianthina* these gill-filaments are, furthermore, plicated.

It is in the Pelecypoda, however, that the most extraordinary development of the gills takes place. The aspidobranch type of *Nucula* and the rest of the protobranchs is abandoned in the others for the pectinibranch type, and the lengthened filaments have to be folded back on themselves to keep them within the limits of the shell. The all-important monographs of Ménégaux[3] and Pelseneer,[4] crowned by the able memoir by Dr. Ridewood,[5] have made all malacologists familiar with the successive stages whereby these gill-filaments become united to form reticulate lamellæ, and afterwards by plication and further transverse unions from lamella to lamella give rise to the

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[1] Quart. Journ. Micro. Sci., N.S., vol. xliv, p. 224.

[2] Op. cit., p. 222.

[3] "Recherches sur la circulation des Lamellibranches marins": Thesis, 4to, Besançon, 1890.

[4] "Contribution à l'étude des Lamellibranches": Archives de Biol., tom. xi (1891), pp. 147–312.

[5] "On the structure of the Gills of the Lamellibranchia": Phil. Trans., ser. B, vol. cxcv (1903), pp. 147–284. The members of this Society had the advantage of a personal exposition of his work from Dr. Ridewood in March, 1904.

complicated, almost spongy structure met with in *Anodonta* and other specialized forms.[1]

The question then arises why there should be this remarkable development of gill in the Pelecypoda when the other Classes of the mollusca find their requirements amply met by far simpler structures.

The answer seems clearly that it is a matter of facility of respiration. The majority of the gill-bearing Gastropoda and the less specialized Pelecypoda live in waters that are constantly in a state of more or less agitation, and where, consequently, entangled oxygen is comparatively abundant; whereas the bivalves that burrow do not get the water in their lurking places so fully or so frequently aerated, and hence the necessity for being able to extract proportionately more oxygen from the water around them and the consequent development of the gill in response to this demand.

The fact, for instance, that *Anodonta* has developed such a complicated gill-structure becomes intelligible when it is borne in mind that it lives mostly in ponds or sluggish water, poor in oxygen, and has, moreover, for six or eight months out of the twelve to shelter within its gill-chamber hundreds of young, all like itself consuming oxygen from the same limited supply.

If this explanation be the right one, and complicated gill-structure be a result of environment, rather than progressive development, it may well happen that some of the groups of Pelecypoda founded on these gill-structures, particularly the more specialized ones, may prove to comprise forms that taxonomically are extremes of more than one family, just as the slugs have been shown to be. On this point it will be necessary to await further careful investigations of the type of those begun by Mr. Bloomer on the anatomy of the British Solenidæ, of which the latest have been laid before this Society.

All this tends to throw doubt on the taxonomic value of gill-structure *alone* for this group, and to lend greater weight to Dr. Dall's *caveat*, echoed by Dr. Ridewood, "that systems based on a single character . . . are bound to prove unsatisfactory as our knowledge of intermediate types advances; and that almost any group may have among its members some which retain archaicisms longer than the rest . . . Any permanent classification must necessarily be eclectic, considering all characters, and distinguishing sufficiently between genetic and adaptive features."[2]

So thoroughly has the nervous system of the Mollusca been worked at and described that, though much doubtless still remains to be done, it is possible to get a comprehension of the whole, and here at once a definite progressive development is traceable. In the earlier and more archaic Gastropoda the nervous system is diffuse, the nerve

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[1] For interesting papers on the circulation of the water through the Pelecypod gill and the part these currents play in conveying food to the mouth of the animal, see Wallengren, "Zur Biologie der Muscheln": Lunds Univ. Årskrift., N.F., Afd. ii, Bd. i, nos. 2 and 3 (1905).

[2] Dall: Trans. Wagner Free Institute, vol. iii, p. 505. Ridewood: Phil. Trans., ser. B, vol. cxcv, p. 185.

ganglions are comparatively widely separated, and the connectives and commissures that unite them are long. Passing to higher and higher representatives, the nerve-centres tend to become more and more concentrated, at first the sensory and motor nerve-centres and then all the others, till they form a ring round the anterior part of the œsophagus, and finally are intimately united and localized on the dorsal surface of the latter, as in *Pleurobranchus*, or the ventral side, as in the thecosomatous Pteropods. This progressive advance is observable also in the Cephalopoda, and to a lesser degree in the Pelecypoda and even the Amphineura.

In the Cephalopoda we meet for the first time in the Mollusca with internal structures of great import, namely, cartilages, which are especially developed in the head. In *Nautilus* there is the H-shaped capito-pedal cartilage, which supports the ventral portion of the nerve-centres, two of its branches extending to the base of the funnel. In the Dibranchia the cephalic cartilage completely invests the central nervous system, the œsophagus passing through it. Different Cephalopoda have additional cartilaginous pieces in other parts of the body, such as the bases of the fins and the arms, at the base of the neck (when the mantle is not fused to the head), at the internal extremities of the retractor muscles of the head and funnel, and even in the two branchial lamellæ. Here we have the bases of a possible internal skeleton that might conceivably be called into existence by the operation of circumstances at present unforeseen, but seeing that, despite the long geological ages of their existence, the Cephalopoda are still behind the earliest known fishes in this respect, much time must elapse before its evolution, and the further chronicle of any progress in this respect will fall to others than ourselves.

Summary.

Despite the plastic nature of the Mollusca, progressive development is traceable in certain characters, while in other conspicuous features the action of environment, or individual requirement, alone seems responsible.

In all the Classes there is a tendency to get rid of the shell, apparently as the result of the assumption of more active habits, especially among the carnivorous individuals.

The form of the body and the adaptations of the foot would appear to be solely influenced by considerations of habit and habitat.

In the Radula, on the other hand, there is consistent progress in the shape of the replacement of numerous, weak, little teeth by few, strong ones, especially in the carnivorous groups.

The Circulatory System shows advance from a diffuse form in the archaic to a well-defined one in the highest tribes.

The Respiratory System, *per contra*, develops in response to individual requirements rather than on any well-determined lines of progress.

Finally, the Nervous System shows distinct advance from the dispersed character that obtains in the primitive groups up to the concentrated form that it assumes in the highest types.

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