Address to the Zoological Section / by G. B. Howes.

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With kind regards.
G. B. Howes.

ADDRESS

TO THE

ZOOLOGICAL SECTION

BY

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PRESIDENT OF THE SECTION.

The Morphological Method and Progress

IT is now twenty-eight years since this Association last assembled in Belfast, and to those present who can recall the meeting the proceedings of Section D will be best remembered for the delivery of an address by Huxley 'On the Hypothesis that Animals are Automata, and its History,' one of the finest philosophic products of his mind.[1] At that date the zoological world were about to embark on a period of marked activity. Fired by the influence of the 'Origin of Species,' which had survived abuse and was taking immediate effect, the zoological mind, accepting the doctrine of evolution, had become eager to determine the lines of descent of animal forms. Marine observatories were in their infancy; the 'Challenger' was still at sea; the study of comparative embryology was but then becoming a science; and when, reflecting on this, we briefly survey the present field, we can but stand astonished at the enormity of the task which has been achieved.

Development has proceeded on every hand. The leavening influence, spreading with sure effect, has in due course extended to the Antipodes and the East, in each of which portions of the globe there have now arisen a band of earnest workers pledged to the investigation of their indigenous fauna, with which they are proceeding with might and main. Of the Japanese, let it be said that not only have they filled in gaps in our growing knowledge, for which they alone have the materials at hand, but that, with an acumen deserving the highest praise, they have put us right on first principles. I refer to the fact that they have shown, with respect to the embryonic membranes of the common chick, that we in the West, with our historic associations, our methods, and our skill, contenting ourselves with an ever-recurring restriction to the germinal area, have, by an error of orientation, missed an all-important septum, displaced under an inequality of growth.[2]

Those of us who have lived and worked throughout this memorable period have had a unique experience, for never has there been progress so rapid, accumulation of observations so extensive and exact. Of the 386,000 living animal species, to compute the estimate low,[3] every one available has been lain under hand, with the result that our annual literary output now amounts to close upon 10,000 contributions, the description of new genera and sub-genera, say 1,700. More than one half of this vast series refer to the Insecta alone; but notwithstanding this, the records of facts of structure and development, with which most of us are concerned, now amount to a formidable mass, calculated to awe the unlettered looker-on, to overwhelm the earnest devotee, unless by specialising he can secure relief. As an example of what may occur, it may be remarked that a recent exploration of the great African lakes has resulted in the discovery of over 130 new species.[4]

[1] For List of References see p. 19.

As to the nature of this unprecedented progress, it will suffice to consider the Earthworms. In 1874 few were known to us. An advance in our knowledge, which had then commenced, had made known but few more which seemed likely to yield result. Darwin's book upon them had not appeared. Some were exotic, it is true, but no one suspected that a group so restricted in their habits could reveal aught beyond a dull monotony of form and structure. Never was surmise more wide of the mark, for the combined investigations of a score of earnest workers in all parts of the world have in the interval recorded some 700 odd species of about 140 genera.[5] Mainly exotic, they exhibit among themselves a structural variation of the widest possible range. Not only do we recognise littoral and branchiate forms, but others achætous and leech-like in habit, to the extent of the discovery of a morphological overlap with the leeches, under which we are now compelled to remove them from their old association with the flat worms, and to unite them with the earthworms. And we even find these animals, as represented by the *Acanthodrilidæ*, coming prominently into considerations which involve the theory of a former antarctic continent, one of the most revolutionary zoo-geographical topics of our time.[6]

This case of the earthworm may be taken as typical of the rest, since for each and every class and order of animal forms, the progress of the period through which we have passed since last we assembled here has produced revolutionary results. Our knowledge of facts has become materially enhanced; our classifications, at best but the working expression of our ideas, have been to a large extent replaced in clearer, more comprehensive schemes; and we are to-day enabled to deduce, with an accuracy proportionate to our increased knowledge of fact, the nature of the interrelationships of the living forms which with ourselves inhabit the earth.

Satisfactory as is this result, it must be clearly borne in mind that its realisation could not have come about but for a knowledge of the animals of the past; and turning now to palæontology, it may be said that at the time of our last meeting in this city the scientific world were just becoming entranced, by the promise of unexpected results in the exploration of the American Tertiary beds, then being first opened up. The Rocky Mountain district was the area under investigation, and with this, as with the progress in our knowledge of recent forms, no one living was prepared for the discoveries which shortly came to pass. To consider a concrete case, we may premise that study of the placental mammals had justified the conclusion that their ancestors must have had equal and pentadactyle limbs, a complete ulna and fibula, a complete clavicle, and a skull with forty-four teeth; must have realised, that is, the predominant term of the living Insectivora as generally understood. Who among the zoologists of our time does not recall with enthusiasm the revelation which arose from the discovery, during these early days, in the Eocene of Central North America, of the genera at first described as *Eo-* and *Helohyus*?[7] The evidence of the existence, in the locality named, of these forty-four toothed peccaries, as they were held to be, rendered clearer the records of the later Tertiary deposits of the old world, which were those of hogs, and, in correlation with the facts then known, suggested that the Rocky Mountain area was the home of the ancestral porcine stock, and that in Early Tertiary times their descendants must have migrated, on the one hand, across the northern belt, of which the Aleutian Islands now mark the course, into the old world, to beget, with complication of their teeth, the pigs and hogs; and on the other into Central South America, to give rise, with numerical reduction of teeth and toes, to the peccaries, still extant.

Migration in opposite directions with diversity of modification was the refrain of this remarkable find, far-reaching in its morphological and zoo-geographical effects. Nor can we allude with less fervour to the still more striking case of the horses, indicating not merely a similar, though perhaps a later, migration, but a parallelism of modification in both the old and new worlds, culminating in the latter in extinction, whereby it became necessary, on the advent of civilised man, to carry back the old-world horse to its ancestral American home. No wonder that this should have provoked our Huxley to the remark that in it we have the

'demonstrative evidence of the occurrence of evolution,' and that the facts of palæontology came to be regarded as certainly not second to those of the fascinating but seductive department of embryology, at the time making giant strides.[8]

I have endeavoured thus to picture that state of zoological science at the time of our last meeting here; and I wish now to confine myself to some of the broader results since achieved on the morphological side. But let us first digress, in order to be clear as to the meaning of this phrase.

We do not expect the public to be accurate in their usage of scientific terms; but it is to me an astounding fact that among trained scientific experts, devotees to branches of science other than our own, there exists a gross misunderstanding as to the limitations of our departments. I quote from an official report in alluding to 'comparative anatomists, or biologists, as they call themselves,' and I but cite the words of an eminent scientific friend, in referring to biology and botany as coequal. In endeavouring to get rid of this prevailing error, let it be once more said that the term 'biology' was introduced at the beginning of the nineteenth century by Treviranus and Lamarck, and that in its usage it has come to signify two totally distinct things as employed by our Continental contemporaries and ourselves. By 'Biologie' they understand the study of the organism in relation to its environment. We, following Huxley, include in our term biology the study of all phenomena manifested by living matter; botany and zoology; and by morphology we zoologists mean the study of structure in all its forms, of anatomy, histology, and development, with palæontology—of all, that is, which can be preferably studied in the dead state, as distinct from physiology, the study of the living in action. Comparative morphology, the study of likeness and unlikeness, is the basis of our working classifications, and it is to the consideration of the morphological method, and the more salient of its recent results that I would now proceed, in so far as it may be said to have marked progress and given precision to our ideas within the last eight-and-twenty years. I would deal in the main with facts, with theories only where self-evident, ignoring that type of generalisation to which the exclusive study of embryology has lent itself, which characterises, but does not grace, a vast portion of our recent zoological literature.

To the earnest student of zoology, intent on current advance, the mental image of the interrelationships of the greater groups of animal forms is ever changing, kaleidoscopically it may be, but with diminishing effect in proportion as our knowledge becomes the more precise.

Returning now to American palæontology, we may at once continue our theme. In this vast field, expedition after expedition has returned with material rich and plentiful; and while, by study of it, our knowledge of every living mammalian order, to say the least, has been extended, and in some cases revolutionised, we have come to regard the Early Tertiary period as the heyday of the mammals, in the sense that the present epoch is that of the smaller birds. No wonder then that there should have been discovered group after group which has become extinct, or evidence that in matters such as tooth-structure there is reason to believe that types identical with those of to-day have been previously evolved but to disappear.[9] To contemplate the discovery of the Titanotheria,[10] the Amblyopoda,[11] the Dinocerata with their strange diminutive brain,[12] chief among the heavier ungulate forms, is to consider the Mammalia anew; and when it is found that among late discoveries we have (1) that of a series of Rhinoceratoidea, which though not yet known to extend so far back in time as the primitive tapirs and horses are complete as far as they go;[13] (2) that among the Ruminants we have, in the Oreodontidæ of the American Eocene, primitive forms with a dentition of forty-four teeth, an absence of diastemata, a pentadactyle manus, a tetradactyle pes with traces of a hallux, and, as would appear from an example of *Mesoreodon*, a bony clavicle, such as is unknown in any later ungulate, we are aroused to a pitch of eager enthusiasm as to the outcome of labours now in hand;[14] for, as I write, there reaches me a letter, to the effect that for most of the great vertebrate groups, and not the mammals alone, collections are still coming in, each more wonderful than the last.[15]

In the extension of our knowledge of the Ancylopoda,[16] an order of mammals named after the *Ancylotherium* of Pikermi and Samos, which occur in the Early Tertiary deposits of Europe, Asia, North America, and abundantly in Patagonia,[17] we have been made aware of the existence of genera whose salient structural features combine the dentition of an ungulate with the possession of pointed claws, believed to have been retractile like those of the living cats. Conversely to these unguiculate herbivores, which include genera with limbs on both the artio- and perisso-dactyle lines, there have been found, among the so-called Mesonychidæ, undoubted primitive carnivores, indications of a type of terminal phalanx seal-like and approximately non-unguiculate;[18] from all of which it is clear that we have in the rocks the remains of forms extinct which transpose the correlations of tooth and claw deducible from the living orders alone. Further, among the primitive pentadactyle Carnivora we meet, in the genus *Patriofelis*, with a reduction of the lower incisors to two, and characters of the fore limb which, with this, suggest the seals.[19] It is, however, probable that these characters are in no way indicative of direct genetic relationship between the two, for, inasmuch as these animals were accustomed to seek their food in the water of the lake by which they dwelt, their seal-like characters may be but the expression of adaptation to a partially aquatic mode of life—of parallelism of modification with the seals and nothing more.

Early in the history of their inquiry, our American confrères recorded from the Pliocene the discovery of camel-like forms possessed of a full upper incisor dentition; for example, the genera *Protolabis* and *Ithygrammodon*;[20] and now they have arrived at the conclusion that while the camels are of American origin one of their most characteristic ruminants, the Prongbuck (*Antilocapra*), would conversely appear to be the descendant of an ancestor (*Blastomeryx*) who migrated from the old world.

Sufficient this concerning the work in mammalogy of the American palæontologists. While we return them our devout and learned admiration, we would point out that the brilliance of their discoveries has but beclouded the recognition of equally important investigations going on elsewhere. In Argentina there have proceeded, side by side with the North American explorations, researches into the Pleistocene or Pampa fauna, which in result are not one whit behind,[21] as has been proved by the recognition of a whole order of primitive ungulates, the Toxodontia,[22] by that of toothed cetaceans with elongated nasals, as in the genera *Prosqualodon* and *Argyrocetus*, and of sperm whales with functional premaxillary teeth, viz., *Physodon* and *Hypocetus*, to say nothing of giant armadillos and pigmy glyptodons.[23]

It will be remembered by some present that, from Patagonian deposits of supposed Cretaceous age, there was exhibited at our Dover meeting the skull of a horned chelonian *Miolania*, which animal, we were informed, is barely distinguishable from the species originally discovered in Lord Howe's Island, and Queensland, and which, being a marsh turtle highly specialised, would seem in all probability to furnish a forcible defence for the theory of the antarctic continent.[24] But more than this, the results of renewed investigation of the Argentine beds by the members of the Princeton University of North America have recently resulted in collections which, we are informed, seem likely to surpass all precedent in their bearings upon our current ideas, not the least remarkable preliminary announcement being the statement that there occurs fossil a mole indistinguishable, so far as is known, from the golden mole (*Chrysochloris*) of South Africa.[25]

Before I dismiss this fascinating subject let me disarm the notion, which may have arisen, that the palæontological work of the old world is done. Far from it! Even our American cousins have to come to us for important fossil forms; as, for example, the genus *Pliohyrax* of Samos and the Egyptian desert,[26] while among the rodents and smaller carnivores there are large collections in our national museum waiting to be worked over afresh.

If one part of the globe more than another is just now the centre of interest concerning its vertebrate remains, it is the Egyptian desert. Here there have

recently been found the bones of a huge cetacean associated, as in South America, with those of a giant snake, one of the longest known, since it must have reached a length of thirty feet.[27] There also occur the remains of other snakes, of chelonians of remarkable adaptive type, of crocodilians, fishes, and other animals. Interest, however, is greatest concerning the Mammalia, which for novelty are quite up to the American standard, as with an upper and a lower jaw of an anomalous creature, concerning which we can only at present remark that it may be a marsupial, or more probably a carnivore, which has taken on the rodent type in a manner peculiarly its own.[28] Important beyond this, however, are a series of Eocene forms which more than fill a long-standing gap, viz., that of the ancestors of the Elephants and Mastodons, which hitherto stopped short in the Middle Miocene of both old and new worlds. As represented by the genus *Mæritherium*, they have three incisors above and two below, of which the second is in each case converted into a short but massive tusk. An upper canine is present, and in both upper and lower jaws a series of six cheek-teeth, distinct and bunodont in type.[29] In the allied *Barytherium*, of which a large part of the skeleton is known, the upper incisors were presumably reduced to two, the tusks enlarged, with resemblances in detail to the Dinoceratan type.[30]

So far as these remains are known, they appear to present in their combined characters all that the most ardent evolutionist could desire. There are with them Mastodons which simplify our knowledge of this group; and among the last discovered remains Sirenians, which, in presenting a certain similarity to the afore-named Mæritherium, strengthen the belief in the proboscidian relationships of these aquatic forms.[31] Finally, and perhaps most noticeable of all, there is the genus *Arsinoitherium*, a heavy brute with an olfactory vacuity which outrivals that of *Grypotherium* itself, and is surmounted by a monstrous fronto-nasal horn, swollen and bifid, for which the most formidable among the Titanotheres might yearn in vain. There is an occiput to match! The suggestion that this extraordinary beast has relationships with the Rhinoceridæ is absurd, since its tooth pattern alone inverts the order of this type. That it is proboscidian may be nearer the mark, and if so it shows once more how subtle were the mammals of the past.[32] Great as is this result, much remains to be done or done again, if only from the fact that in seeking to determine homologies our American brethren, in the opinion of some of us, have placed too much reliance on a so-called tritubercular theory of tooth genesis, of which we cannot admit the proof.[33] How, we would ask, is it conceivable that a transversely ridged molar of the *Diprotodon* type can be of tritubercular origin?

Sufficient for the moment of palæontological advance, except to remark that the zoologist who neglects this branch of morphology misses the one leavening influence; neglects the court on whose ruling arguments deduced from embryological data alone must either stand or fall. We may form our own conclusions from facts of the order before us; but it is when we find their influence on the master-mind prompting to action, like that of Huxley with his mighty memoir of 1880, in which he revised our sub-class terms, that we appreciate them to the full.[34]

With this consideration we pass to the living forms, and I have only time in dealing with these to comment on advance which affects our broadest conceptions and classifications of the past.

To commence with the Mammalia, we now know that the mammary gland when first it appears is in all forms tubular, and that this type is no longer distinctive of the Monotremata alone.[35] We know, too, that the intranarial position of the epiglottis when at rest, long known for certain forms, is a distinction of the class. It explains the presence of the velum palatinum, by its association with the glottis for the restriction of the respiratory passage, the connection being lost in man alone, under specialisation of the organ of the voice.[36]

Similarly, the doubly ossified condition of the coracoid may now be held diagnostic, for it is known that the epicoracoidal element, originally thought to characterise the monotremes alone, is always present, and that reduction to a varying degree characterises the metacoracoid, which retires, as in man, as the so-called coracoid epiphysis.[37]

Our conceptions of the interrelationships of the Marsupialia and Placentalia have during the period we are considering been delimited beyond expectation, by the discovery that an allantoic placenta in a polyprotodont marsupial, replaces the vitelline, present in its allies.[38] When it is remembered that in the formation of the placenta of the rabbit, bat, and hedgehog, there is a provisional vitelline stage,[39] it is tempting to suggest that the evidence for the direct relationship of the two mammalian sub-classes first named overlaps (there being a placental marsupial on one hand, a marsupial placental on the other), much as we have come to regard Archæopteryx as an avian reptile, the Odontornithes as reptilian birds. These facts, moreover, prove that the type of placenta inherited by the Placentalia must have been discoidal, and that from that all others were derived.

Equally important concerning our knowledge of the Marsupialia is the discovery, first made clear by Professor Symington, of this College, that Owen was correct in denying them a corpus callosum.[40] How Owen arrived at this conclusion it is difficult to conceive; but in these later days the history of discovery is largely that of method; and it is by the employment of chrome-silver, methylene-blue, and other reagents, which in differentiating the fibre-tracts enable us to delimit their course, that this conclusion has been proved. By the corpus callosum we now understand a series of neo-pallial fibres which transect the alveus and are present only in the Placentalia.[41]

There is no department of mammalogy in which recent work has been more luminous than this which concerns the brain; and, to mention but one result, it may be said that in the renewed study of the commissures there has been found a fibre-tract characteristic of the Diprotodontia alone, so situated as to prove that they and the Placentalia must have specialised on diverse lines from a polyprotodont stock.[42] Interesting this, the more, since the phalangers and kangaroos are known to be polyprotodont when young.[43] And when we add the discovery that in the form of its hippocampal commissure the brain of the Elephant Shrew, a lowly insectivore, alone among that of all Placentalia known realises the marsupial state,[44] as does its accessory organ of smell, we have to admit the existence of annectant conditions just where they should occur.[45]

The morphological method is sound!

The master hand which has given us this result has also reinvestigated the Lemurs. From an exhaustive study of the brain or its cast of all species of the order, living and extinct, there has come the proof that the distinctive characters of the lemuroid brain are intelligible only on a knowledge of the pithecoid type; that its structural simplicity in the so-called lower lemurs is due to retrogressive change, in some species proved to be ontogenetic; and that the Tarsier, recently claimed to be an insectivore, is a lemur of lemurs.[46] It is impossible to over-estimate the importance of this conclusion, which receives confirmation in recent palæontological work;[47] and there is demanded a reinvestigation of those early described Tertiary fossil forms placed on the Ungulo-lemuroid border line, as also a reconsideration of current views on the evolution of the primates and of man.[48]

In dismissing the Mammalia, we recall the capture during the period we review of three new genera, a fourth, the so-called *Neomylodon*,[49] having proved by its skull to be *Grypotherium Darwinii*, already known.[50] The African Okapi, an object of sensation beyond its deserts, has found its place at last. To have been dubbed a donkey, a zebra, and a primitive hornless giraffe, is distinction indeed; and we cannot refrain from contrasting the nonsensical statement that its discovery is 'the most important since Archæopteryx' with the truth that it is a giraffine, horned in the male, annectant between two groups well known.[51] As a discovery it does not compare with that of the Mole-marsupial,[52] and it falls into insignificance beside that of the South American diprotodont *Cœnolestes*, the survivor of a family which there flourished in Middle Tertiary times.[53]

Passing to Birds and Reptiles, it will be convenient to consider them together. A knowledge of their anatomy has extended on all hands, and in respect to nothing more instructively than their organs of respiration. Surprise must be expressed at the discovery, in the chelonian, of a mode of advancing complication of the lung suggestive of that of birds. On looking into this, I find that Huxley, who

rationalised our knowledge of the avian lung and its sacs,[54] was aware of the fact that in our common Water-tortoise (*Emys orbicularis*), the lung is sharply differentiated along the bronchial line into a postero-dorsal more cellular mass, an antero-ventral more saccular, of which the posterior vesicle, in its extension and bronchial relationships, strangely simulates the so-called abdominal sac of birds. He had already instituted comparison with the Crocodiles,[55] and was clearly coming to the conclusion that the arrangement in the bird is but the result of extreme specialisation of a type common to all Sauropsida with a 'cellular' lung. The respiratory process in the bird may be defined as *transpulmonary*, and it is an interesting coincidence that, as I write, there comes to hand a memoir, supporting Huxley's conclusion, and establishing the fact that there is a fundamental principle underlying the development and primary differentiation of all types of vertebrate lung.[56]

The discovery of the Odontornithes in the American Cretaceous is so well known, that it is but necessary to remark that nine genera and some twenty species are recognised.[57] To *Archæopteryx* I shall return. Before dismissing the Chelonia, however, it must be pointed out that palæontology has definitely clenched their supposed relationship to the Plesiosaurs. Of all recent palæontological collections there are none which, for care in collecting and skill in mounting, surpass the reptilian remains from the English Jurassic (Oxford Clay) now public in our national museum.[58] The Plesiosaurs of this series must be seen to be appreciated, and nothing short of a merciful Providence can have interposed, to ensure the generic name *Cryptocleidus*, which one of them has received, since the hiding of the clavicle, its diagnostic character, is an accomplished fact. It is due to secondary displacement, under the approximation in the middle line of a pair of proscapular lobes, present in the Plesiosauria and Chelonia alone, and until the advent of this discovery misinterpreted.[59] Taken in conjunction with other characters of little less importance, conspicuously those of the plastron and pelvis, this decides the question of affinity, and proves the Chelonia to have had a lowly ancestry, as has generally been maintained.[60]

Recent research has fully recorded the facts of development of the rare New Zealand reptile *Sphenodon*, and it has more than justified the conclusion that it is the sole survivor of an originally extensive and primitive group, the Rhynchocephalia, as now understood.[61] To confine our attention to its skeleton, as that portion of its body which can alone be compared with both the living and extinct, it may be said that positive proof has been for the first time obtained that the developing vertebral body of the terrestrial vertebrata passes through a paired cartilaginous stage, and that in its details the later development of this body is most nearly identical with that of the lower Batrachia.[62] There has long been a consensus of opinion that the forward extension of the pterygoids to meet the vomers in the middle line, known hitherto in this animal and the crocodiles alone, is for the terrestrial Vertebrata a primitive character; and proof of this has been obtained by its presence in all the Rhynchocephalia known. The same condition has also been found to exist in the Plesiosaurs,[63] the Ichthyosaurs,[64] the Pterodactyles,[65] the Dicynodontia,[66] the Dinosaurs,[67] and with modification in some Chelonians.[68] It has, moreover, been found in living birds;[69] a most welcome fact, since *Archæopteryx*, in the possession of a plastron, carries the avian type a stage lower than the Dinosaurs. It is pertinent here to remark that, inasmuch as in those Dinosaurs (e.g., *Compsognathus*) in which the characters of the hind limbs are most nearly avian, the pelvis, in respect to its pubis, is at the antipodes of that of all known birds, and the fore limb is shortened in excess of that of *Archæopteryx* itself, the long supposed dinosaurian ancestry for birds must be held in abeyance.[70]

Passing through the Rhynchocephalia to the Batrachia, we have to countenance progress most definite in its results. The skull, the limbs and their girdles, are chiefly concerned, and this in a very remarkable way.

In the year 1881 there was made known by Professor Froriep, of Tübingen, the discovery that the hypoglossus nerve of the embryo mammal is possessed of dorsal ganglionated roots.[71] Again and again have I heard Huxley insist on the fact that the ventral roots of this nerve are serial with the spinal set, but never did

he suspect the rest. It is, however, a most intensely interesting fact that, whereas by a Huxleian triumph the vertebral theory of the skull was overthrown, in these later Huxleian days the proof of the incorporation of a portion of the vertebral region of the trunk into the mammalian occiput should have marked the succeeding epoch in advance. The existence of twelve pairs of cranial nerves which all the Amniota possess involves them in this change; and the fact that in all Batrachia there are but ten, enables us to draw a hard-and-fast line between batrachian and amniote series.

It may be urged, as an objection, that since we have long been familiar with a fusion of vertebræ and skull in various piscine forms, the force of this distinction is weakened. But this cannot be; since, in respect to the investing sheaths and processes of development which lie at the root of the genesis of the vertebral skeleton, the fishes stand distinct from the Batrachia and Amniota, which are agreed.[72] So forcible is this consideration that it behoves us to express it in words, and I have elsewhere proposed to discriminate between the series of terrestrial Vertebrata as *archæ-* and *syn-craniate*.[73]

Similarly there is no proof that any batrachian, living or extinct (and in this I include the Stegocephala as a whole), possesses a costal sternum. So far as their development is known, the cartilages in these animals called 'sternal' are either coracoidal or *sui generis*.[74] The costal sternum, like the syncraniate skull, is distinctive of the Amniota alone. Had the Stegocephala possessed it even in cartilage, there is reason to think it might have been preserved, as it has been in the colossal Mososaur *Tylosaurus* of the American Cretaceous.[75] When to this it is added that whereas, in the presence of a costal sternum, the mechanism of inflation of the lung involves the body-wall, in its absence it mainly involves the mouth (as in all fishes and batrachians), the hard and sharp line between the Batrachia and Amniota may be expressed by the formula that the former are *archæcraniate* and *stomatophysous*, the latter *syncraniate* and *somatophysous*.

There are allied topics which might be considered did our time permit; but one certain outcome of this is that there is an end to the notion of a batrachian ancestry for the Mammalia. And when, on this basis, we sum up the characters demanded of the stock from which the Mammalia have been derived, we find them to be precisely those occurring outside the Mammalia in the Anomodont Reptiles alone. Beyond the sternum and skull, the chief characters are the possession of short and equal pentadactyle limbs, with never more than three phalanges to a digit, a complete fibula and clavicle, a doubly ossified coracoid, a heterodont dentition—a combination which, wholly or in part, we now associate with the Permian genera *Procolophon*, *Pariasaurus*, and others which might be named, the discovery of which constitutes one of the morphological triumphs of our time.[76]

Beyond this, it may be added, concerning the Batrachia, that among living pedate forms the Anura have alone retained the pentadactyle state and the complete maxillo-jugal arch, and that the Eastern *Tylototriton*, in the possession of the latter, becomes the least modified urodele extant.[77] These facts lead to the extraordinary conclusion that the living Urodela, while of general lowly organisation, are one and all aberrant; and it is not the least important sequel to this that, despite their total loss of limbs, the Apoda, in the retention of the dermal armour and other features which might be stated are the most primitive Batrachia that exist.[78]

The batrachian phalangeal formula 22343 was until quite recently a difficulty in the determination of the precise zoological position of the class; but it has now been overcome, by the discovery of a *Keraterpeton* in the Irish Carboniferous having three phalanges on the second digit of both fore and hind limbs,[79] and by that in the Permian of Saxony of a most remarkable creature, *Sclerocephalus*, which, if rightly referred to the Stegocephala, had a head encased, as its name implies, in an armature like that of a fish, and the phalangeal formula of a reptile, 23454.[80]

Passing from the Batrachia to the Fishes, we have still to admit a gap, since an interminable discussion on fingers and fins has not narrowed it in the least. In compensation for this, however, we have to record within the fish series itself

progress greater, perhaps, than with the higher groups. Certainly is this the case if, as to bulk, the literature in systematics and palæontology be alone taken into account.

Of the Dipnoi our knowledge is fast becoming complete. We know that *Lepidosiren* forms a burrow ;[81] and, in consideration of a former monstrous proposal to regard this animal, with its fifty-six pairs of ribs, and *Protopterus*, with its thirty to thirty-five, as varieties of a species,[82] it is the more interesting to find that the Congo has lately yielded a *Protopterus* (*P. Dolloi*) with the lepidosiren rib formula, viz., fifty-four pairs.[83]

As a foremost result of American palæontological research we have to record the occurrence, in the Devonian of Ohio, of a series of colossal fishes known as the Arthrodira, the supposed dipnoan affinities of which are still a matter of doubt.[84]

We have evidence that the osseous skeleton in a plate-like form first appeared as a protection for the eye of a primitive shark.[85] And coming to recent forms having special bearings on the teachings of the rocks, we have to acknowledge the capture in the Japanese seas of a couple of ancient sharks, of which one (*Cladoselachus*), since observed to have a distribution extending to the far North, is a survivor from Devonian times; the other (*Mitsukurina*), a genus whose grotesqueness leaves no doubt of its identity with the Cretaceous lamnoid *Scapanorhynchus*.[86] In the elucidation of the Sturiones and the determination of their affinities with the ancient Palæoniscidæ a master stroke has been achieved.[87] In the Old Red genus *Palæospondylus* we have become familiar with an unmistakable marsipobranch, possessing, as do certain living fishes, a notochord, annulated, but not vertebrated in the strict sense of the term.[88] The climax in Ichthyopalæontology, however, has been reached, in the discovery of Silurian forms, which, there is every reason to believe, explain in an unexpected way the hitherto anomalous Pteras- and Cephalaspidians, by involving them in a community of ancestry with the primitive Elasmobranchs. The genera *Thelodus*, *Drepanaspis*, *Ateleaspis*, and *Lanarkia*, chief among these annectant and ancestral forms, are among the most remarkable vertebrate fossils known.[89]

Passing to the Recent Fishes alone, the discovery which must take precedence is that of the mode of origin of the skeletogenous tissue of their vertebral column. The fishes, unlike all the higher Vertebrata, have, when young, a notochord invested in a double sheath, there being an inner chordal sheath, an outer cuticular, which latter is alone present in all the higher groups. The skeletogenous cells, by whose activity the cartilaginous vertebral skeleton is formed, arise outside these sheaths; but whereas, when proliferating, they in one series remain outside, they in the other, by the rupture of the cuticular sheath, invade the chordal. This distinction enables us to discriminate between a *Chordal series*, which embraces the Chimæroids, Elasmobranchs, and Dipnoi, and a *Perichordal*, consisting of the Teleosts, Ganoids, and Cyclostomes.[90]

In consideration of the enormity of the structural gap between the cyclostomes and the higher Vertebrata this is an extraordinary result. For be it remembered that, in addition to their well-known characters, the lampreys and hags (1) in the total absence of paired fins; (2) in the presence of branchiæ, ordinarily seven in number, fourteen in *Bdellostoma polytrema*,[91] numerically variable in individuals of certain species between six and fourteen, and doubtfully asserted in the young of one to be originally thirty-five ;[92] and (3) in the carrying up of their oral hypophysis by the nasal organ, whereby it perforates the cranium from above, as contrasted with all the higher Vertebrata, in which, carried in with the mouth-sac, it perforates it from beneath, exhibit morphological characters of an extraordinary kind. And if we are to express these characters in terms, we may distinguish the Cyclostomes as *apterygial* and *epicraniate*, the higher Vertebrata as *hypocraniate*.[93] [1] But this notwithstanding, the aforementioned subdivision of the

[1] It is an interesting circumstance, if their 'ciliated sac' is rightly homologised, that *Amphioxus* and the Tunicata present a corresponding dissimilarity, allowance being made for the fact that in *Botryllus*, *Goodsiria*, and *Polycarpa* the sac overlies the ganglion.[94] It is pertinent here to recall the ammocœte-like condition of the 'endostyle' in *Oikopleura flabellum*.[95]

Pisces into two series, which would associate the teleosts and ganoids with the cyclostomes, as distinct from the rest, receives support from recent study of the head-kidney by a Japanese, who seeks to show that the organ so called in the Elasmobranchs is of a late-formed type peculiar to itself;[96] and it is also in agreement with one set of conclusions previously deduced from the study of the reproductive organs.[97]

To deal further with the fishes is impossible in this Address, except to remark that recent discovery in the Gambia that the young of the Teleostean genera *Heterotis* and *Gymnarchus* bear filamentous external gills, renders significant beyond expectation the alleged presence of these among the loaches, and shows that adaptive organs of this type are valueless as criteria of affinity.[98]

In palæontology, as in recent anatomy, our records of detail have increased beyond precedent, often but to show how deficient in knowledge we are, how contradictory are our theories and facts.

In dismissing the fishes, I wish to comment upon our accepted terms of orientation. To speak of the median fins as dorsal, caudal, and anal, of the pelvic as ventral, and of the pectoral in its varying degrees of forward translocation as abdominal or thoracic, though a convention of the past, is to-day inaccurate and absurd. I question if the time has not come at which the terms thoracic (pulmocardiac) and abdominal are intolerable, as expressing either the subdivisions of the body-cavity or anything else, outside the Mammalia, which alone possess a diaphragm. Even in the birds, to grant the utmost, the subdivision of the cœlom if accurately described, must be into pulmonary, hyper-pulmonary, and cardio-abdominal chambers; while with the reptiles the modes of subdivision are so complex that a special terminology is necessary for each of the several types extant.

In the fishes, where the pericardium is alone shut off, the retention of the mammaliam terms but hampers progress. This was indeed felt by Duméril, when in 1865 he attempted a revisionary scheme.[99] Since, however, one less fantastic than his seems desirable, I would propose that for the future the 'anal' fin be termed *ventral*, the 'ventral' *pelvic*; and that for the several positions of the pelvic, that immediately in front of the vent, primitive and embryonic (which is the position for the Elasmobranchs, Sturiones, Lower Siluroids, and all the higher Vertebrata), be termed *proctal*, the so-called 'abdominal' *pro-proctal*, the so-called 'thoracic' *jugular* (in that it denotes association with the area of the 'collar-bone'), and the so-called 'jugular' *mental*. The necessity for this becomes the more desirable, now that it is known that a group of Cretaceous fishes (the Ctenothrissidæ), hitherto regarded as Berycoids, are in reality of clupeoid affinity, despite the fact that at this early geologic period they had translocated their pelvic fin into the jugular ('thoracic') position.[100]

The sum of our knowledge acquired during the last twenty-eight years proves to us that, among the bony fishes, the structural combination which would give us a premaxillo-maxillary gape dentigerous throughout, a proctal pelvic fin, a heart with conal valves, would be the lowest and most primitive. Inasmuch as this character of the heart, so far as at present known, exists only among the Clupesoces (pikes and herrings and their immediate allies), these must be regarded as lowly forms;[101] wherefore it follows that the possession of but a single dorsal fin is not, as might appear, a necessary index of a highly modified state.

Before I dismiss the vertebrates, a word or two upon a recent result of morphological inquiry which concerns them as a whole. I refer to the development of the skull. Up to 1878 it was everywhere thought and taught that the cartilaginous skull was a compound of paired elements, known as the trabeculæ cranii and parachordals, and that the former contributed the cranial wall. Huxley in 1874, from the study of the cranial nerves of fishes, had reiterated the suggestion he made in 1864, when dealing with the skull alone, that the trabeculæ might be a pair of præ-oral visceral arches, serial with those which support the mouth and carry the gills. The next step lay with the Sturgeon, in which in 1878 it was found that the cranial wall is originally distinct.[102] And later, when the facts were more fully studied in sharks, batrachians, reptiles, and birds, it became evident that the trabeculæ, though ultimately associated with the cranial wall,

take no share in its formation, and that when first they appear they are disposed at right angles to the parachordals and the axis, serially with the visceral arches behind.[103] Huxley was right; and although this consideration by no means exhausts the category of independent cartilages now known to contribute to the formation of the skull, it proves that the cartilaginous cranium, like the bony one, which in the higher vertebrate forms replaces it, is in its essence compound.

I now pass to the Invertebrata. Of the Oligochæta and Leeches I have spoken, and we may next consider the Arthropods. Of the Insecta, our knowledge has gained precision, by the conclusion that the primitive number of their Malpighian tubes is six, and by the study of development of these in the American cockroach *Doryphora*, which has rendered it probable they may be modified nephridia, carried in as are those of some oligochætes with the proctodeal invagination.[104] An apparent cervical placenta has been discovered in the orthopteran *Hemimerus*, which suggests homology with the so-called 'trophic vesicle' of the Peripatoids, as exemplified by *Parap. novæ-britannica*.[105] In this same orthopteran there have been recognised, in secondary proximity to the 'lingua,' reduced maxillulæ, which, fully developed and interposed between the mandible and first maxilla, in *Japyx*, *Machilis*, *Forficula*, and the *Ephemera* larva, give us a fifth constituent for the insectan head.[106] And when it is found that all the abdominal segments of a common cockroach, when young, are said to bear appendages, of which the cerci are the hindermost,[107] we have a series of facts which revolutionise our ideas. Little less striking is the discovery that in the caterpillar of the bombycine genera *Lagoa* and *Chrysopyga* seven pairs of pro-legs occur.[108]

The fuller study of the apertures of the tracheate body has resulted in the discovery that the Chilopoda are more nearly related to the Hexapoda than to the Diplopods; wherefore it is proposed to reclassify the Tracheata, in accordance with the position of the genital orifice, into *Pro-* and *Opistho-goneata*.[109] In a word the 'Myriapoda,' if a natural group, are diphyletic.

Our knowledge of the Peripatoids (Arthropoda malacopoda) has increased in all that concerns distribution and structure. They are now known, for example, from Africa, the West Indies, Australia, and New Zealand, and for examples from the two latter localities and Tasmania the generic name *Ooperipatus* has but lately been proposed, to include three species characterised by the possession of an ovipositor, of which two have been observed to lay eggs.[110]

Work upon the Crustacea in our own land, notorious for the tendencies of some of its devotees in their stickling for priority, has within the last twelve years advanced beyond all expectation. Much of our literature has been systematised, and an enormous increase in our knowledge of new forms has to be admitted, thanks to memoirs such as those of the 'Investigator,' 'Naples Zoological Station,' and others which might be named; while in the discovery and successful monographing, in the intervals of six years' labour at other groups, of a new family of minute Copepods (the Choniostomatidæ), parasitic on the Malacostraca, embracing forty-three species, difficult to find, we have an almost unique achievement.[111] The hand which gave us this has also provided a report which embraces the description of a nauplius of exceptional type, which, by a process of reasoning by elimination, masterly in its method, has been 'run to ground' as in every degree of probability the larva of Darwin's apodal barnacle *Protolepas bivincta*, of which only the original specimen is known.[112]

There is but one other crustacean record equal in rank with this, viz., the discovery of the genus *Anaspides*. Originally obtained from a fresh-water pool on Mount Wellington, Tasmania, at 4,000 feet, it has since been found in two other localities.[113] It is unique among all living forms, in combining within itself characters of at least three distinct sub-orders of 'prawns,' for with a schizopod body it combines the double epipodial lamellæ of an amphipod, the head of a decapod (pedunculated eyes and antennulary statocysts) apart from characters peculiarly its own. There is reason to believe that the nearest living ally to this remarkable creature is a small eyeless species (*Bathynella natana*) obtained from a Bohemian well;[114] and if its presumed relationships to the Palæozoic 'pod-shrimps' be correct, this heterogeneous assemblage may perhaps be

the representatives of a group of primitive Malacostraca, through which, by structural divergence, the establishment of the higher crustacean sub-orders may have come about.

It is pertinent to this to note that work upon cave-dwelling and terrestrial forms, upon 'well-shrimps' and the like, has produced important results. And interesting indeed is the recent discovery of three species, living at 800–900 feet above sea-level, in Gippsland, one an amphipod, two of them isopods, which, though surface-dwellers, are all blind.[115] While they prove to be species of genera normally eyed, they in their characters agree with well-known American forms; and the bleaching of their bodies and atrophy of their eyes proclaim them the descendants of cave-dwelling or subterranean ancestors, among whom the atrophy took place.

Huxley in 1880 rationalised our treatment of the higher Crustacea, by devising a classification by gills, expressive of the relationships of these to the limb-bases, interarticular membranes, and body-wall.[116] Hardly had his influence taken effect when, by work extending over the years 1886 to 1893, in the study of Penæus, the Phyllopods, Ostracods, and other forms, evidence had been accumulating to show that the crustacean appendage, even to the mandible itself, has primarily a basal constituent (protopodite) of three segments; that the branchiæ one and all are originally appendicular in origin; and that the numerical reduction of the basal (protopoditic) segments to two, with the assumption of a non-appendicular relationship by the gills, is due to coalescence of parts, with or without suppression.[117] The evidence for this epoch-making conclusion, which simplifies our conceptions and brings contradictory data into line, is as irresistible as it is important, and there has been nothing finer in the whole history of crustacean morphology. With it, the attempt to explain the supposed anomalous characters of the antennule by appeal to embryology goes to the wall; and, taking a deep breath, we view the Crustacea in a new light.

There remains for brief consideration one carcinological discovery second to none which bear on the significance of larval forms. It is that of the Trilobite *Triarthrus Becki*, obtained in abundance from the Lower Silurian near New York, with all its limbs preserved.[118] In the simplicity of its segmentation and the biramous condition of its limbs it is primitive to a degree. Chief among its characters are the total absence of jaws in the strict sense of the term, and the fact that of its three anterior pairs of appendages the third is certainly and the second is apparently biramous, the first uniramous and antenniform. In this we have a combination of characters known only in the nauplius larva among all living crustacean forms; and the conclusion that the adult trilobite, like the Euphausiacea, Sergestidæ, Penæidæ, the Ostracods, and Cirripedes of to-day, was derived by direct expansion of the nauplius larva can hardly be doubted. Much yet remains to be done with the study of the Triarthrus limbs; and the suggestion of a foliaceous condition by those of the pygidium, which are the youngest, is a remarkable fact, the meaning of which the future must decide.[119] We should expect the condition to be a provisional one, since while we admit the primitive nature of the phyllopods as an Order, we cannot regard the foliation of their appendages as anything but a specialisation. Be this as it may, the structural community between the nauplius larva and the trilobite is now proved; and when we add that in the yolk-bearing higher Crustacean types (e.g., *Astacus*) a perceptible halt in the development may be observed at the three-limb-bearing stage; that in *Mysis* the vitelline membrane is shed but to make way for a nauplius cuticle;[120] and that the median nauplius eye has long been found sessile on the adult brain of representative members of the higher crustacean groups, up to the lobster itself,[121] our belief in the ancestral significance of the nauplius larval form is established beyond doubt.

The thought of the nauplius suggests other larval forms. The gastrula is no longer accepted without reserve; the claims of the blastula, planula, parenchymella, not to say the plakula, have all to be borne in mind.[122] It is of the Trochophore, however, as familiar as the nauplius, that I would rather speak, as influenced by recent research. It is supposed to be primitive for the molluscs and chætopod worms at least; and various attempts have been made to bolster it up,

and to show that if we allow for adaptive change, its characters, well known, are constant within the limits of its simpler forms.[123]

It is now more than forty years ago that the late Lacaze-Duthiers described for *Dentalium* a larval stage, characterised by the possession of recurrently ciliated zones, which by reduction, with union and translocation forwards, give rise to the trochal lobe.[124] It is now known that in the American pelecypod *Yoldia limatula* a similar stage is found, in which a 'test,' of five rows of ciliated cells, is present; [125] and of the young of *Dondersia banyulensis* the like is true. But whereas in the *Yoldia* the ciliated sac is ultimately shed, in the Myzomenian the escape of the embryo is accompanied by rupture, which liberates the anterior series of ciliated zones in a manner strongly suggestive of forward concentration, leaving the posterior circlet with its cilia attached.[126]

This 'test' has also been seen in two species of *Nucula*, and pending fuller inquiry into the Myzomenian and a reinvestigation of Dentalium, I would suggest that this recurrently ciliated sac is representative of a larval stage antecedent to the trochophore, for which the term *protrochal* may suffice. This term has indeed been already applied to a larva of certain Polychæta, which might well represent a modification of that for which I am arguing;[127] and quite recently it appears to have been observed near Ceylon for a species of the genus *Marphysa*.[128]

The discovery of this larva in *Dondersia* was accompanied by that of a later-formed series of dorsal spicular plates, which for once and for all, in realising a chitonid stage, demolish the heresy of the 'Solenogastres,' mischievous as suggesting an affinity with the worms. Like that of the supposed cephalopod affinities of the so-called 'Pteropods,' it must be ignored as an error of the past.

Returning to the protrochal stage, whatever the future may reveal concerning it, by bringing together the Lamellibranchiata, Scaphopoda, and Polyplacophora, it associates in one natural series all the bilaterally symmetrical Mollusca except the cephalopods. In doing this, it deals the death-blow to the supposed Rhipidoglossan affinity of the Lamellibranchiata;[129] and in support of this conclusion I would point out that the recently discovered eyes of the mytilids are in the position of those of the embryo *Chiton*,[130] and that just as *Dentalium*, in the formation of its mantle, passes through a lamellibranchiate stage, so are there lamellibranchs in number in which a tubular investment is found.[131]

This protrochal larva has an important part to play. It may very possibly explain phenomena such as the compound nature of the trochal lobe of the limpet,[132] the presence of a post-oral ciliated band in the larva of the ship-worm,[133] and of a præ-anal one in that of various molluscan forms.[134] In view of it, we must hesitate before we fully accept the belief in the ancestral significance of the trochophore. And it is certain that an idea, at one time entertained, that the Rotifer (*Trochosphæra*) which so closely resembles it as to bear its name, is its persistent representative,[135] is wrong, since this is now known to be but the female of a species having a very ordinary male.

Through the Rhipidoglossa we pass to the Gastropods, which are one and all asymmetrical, for even *Fissurella*, *Patella*, and *Doris*, when young, develop a spiral shell; while Huxley in 1877 had observed that the shell of *Aplysia*, in its asymmetry, betrays its spiral source.

The notion, which until recently prevailed, that among these gastropods the non-twisted or so-called euthyneurous condition of the visceral nerve-cords, as exemplified by the Opisthobranchs, is a direct derivative of that of the Chitons has been proved to be erroneous, since the nerves in *Actæon* and *Chilina*, like those of the prosobranchs, are twisted or streptoneurous.[136] And as to the torsion of the gastropod body, recent research, in which my lamented demonstrator the late Mr. F. Woodward played a leading part, involving the discovery of paired reno-pericardial apertures in *Haliotis*, *Patella*, and *Trochus*, has resulted in proof that the dextral torsion which leads to the monotocardiac condition, does not affect all organs lying primitively to the left of the rectum, as we have been taught. Concerning the renal organs, it is the *primitively* (pretorsional) left one which remains as the functional kidney, its ostium as the genital aperture. Nor is the primitively right kidney necessarily lost, for while its ostium remains as the renal orifice, its

body, by modification and reduction, may become an appendage of the functional kidney, the so-called nephridial gland.[137] And we now know there are cases of sinistral torsion of the visceral hump, in which the order of suppression of the organs is not reversed, the arrangement being one of adaptation of a dextral organisation to a sinistral shell.[138]

Though thus specialised and asymmetrical as a group, the gastropods are yet plastic to an unexpected degree. Madagascar has yielded a Physa (*P. lamellata*) with a neomorphic gill, a character shared by species of *Planorbis* (*P. corneus* and *P. marginatus*), and an *Ancylus* in which the lung-sac is suppressed;[139] while St. Thomas's Island has given us a snail (*Thyrophorella Thomensis*), the peristome of whose shell is produced into a protective lid.[140]

In palæontology, history records the fact that in 1864 Huxley observed that the genus *Belemnites* appears to have borne but six free arms; a startling discovery which lay dormant till the present year.[141] And the recent study of the fauna of the great African lakes, in bringing to light the existence of a halolimnic molluscan series in Lake Tanganyika, has opened up new possibilities concerning the palæontological resources of enormous aqueous deposits, recently discovered in the interior, and has entirely changed our geological conceptions of the nature of Equatorial Africa.[142]

Time prevents my dealing with other groups, and it must suffice to state that with those I have not considered substantial work has been done. From what has been said, it is natural to expect that in some direction or another so vast an accumulation of facts must have extended the Darwinian teaching; and it is now quite clear that this has been the case with the two post-Darwinian principles known as 'Substitution' and Isomorphism or 'Convergence.'

The former may be exemplified by nothing better than the case of the Rays and Skates, in which, under the usurpation of the propelling function of the tail by the expanded pectoral fins, the tail, free to modify, becomes in one species a lengthy whiplash, in another a vestigial stump, in others, by the development of powerful spines, a formidable organ of defence.[143] In both the Rays and certain other fishes subject to the working of this law, modification goes further still, in the appearance of electric organs in remotely related genera and species, by specialisation of the muscular system of the trunk or tail, or, as in the case of *Malapterurus*, of 'tegumental glands.'[144] In this we have a difficulty admitted by Darwin himself, which now becomes clear and intelligible, since there is nothing new. There has simply come about the conversion, in one case of the energy of muscular contraction, in the other of glandular secretion, into that of electrical discharge, with accompanying structural change. The blind locust (*Pachyramina fuscifer*) of the New Zealand Limestone caves presents an allied case, since here, under the reduction of the eye, the antennæ, elongated to a remarkable degree, have become the more efficiently tactile; and it is an interesting question whether this principle may not explain the attenuation of the limbs in the recently discovered American Proteoid (*Typhlomolga Rathburni*) of the Texan subterranean waters.[145]

And as to isomorphism, by which we mean the assumption of a similar structural state by members of diverse or independent groups, I would recall the case of the Eocene Creodont *Patriofelis* and the Seals, and that of the Myriapods to which I have already alluded, and would cite that of the Dinosaurs and Birds, heterodox though it may appear, for reasons I have given.

As our knowledge increases, there is every reason to believe that, in the non-appreciation of these principles in the past, not a few of our classifications are wrong. We have even had our bogies, as, for example, the so-called Physemaria, which deceived the very elect;[146] and before I close I wish to deal briefly with a question of serious doubt, which these considerations suggest.

It is that of the position in the zoological series of the Limuloids, popularly termed the King Crabs. These creatures, best known from the opposite shores of the Northern Pacific, but found in the oriental seas as well as far south as Torres Strait,[147] have been since 1829 the subject of a difference of opinion as to their zoological position and affinities. Within the last twenty years there have been

three determined advances upon them, and of these the third and most recent may be first discussed. It has for its object the attempt to prove that they are intimately associated with the cephalaspidian and other shield-bearing fishes of the Devonian and Silurian epochs, and that through them they are ancestral to the Vertebrata. The latest phase of this idea is based on the supposed existence in a *Cephalaspis* of a series of twenty-five to thirty lateral appendages of arthropod type.[148] When, however, it is found that the would-be limbs are but the edges of body-scutes misinterpreted, suspicion is aroused; and when, working back from this, an earlier attempt reveals the fact that the author, compelled to find trabeculæ, in order to force a presupposed comparison between the architecture of the Cephalaspidian head-shield and the Limulus' prosomal hood, resorts to a comparison between the structure of the former in general and that of the cornu of the latter, with details which on the piscine side are not to date, the argument must be condemned.[149] It violates the first principles of comparative morphology, and is revolting to common sense; and as to the fishes concerned, we know that they have nothing whatever to do with the Limuloids, for we have already seen that, with their allies the Pteraspidiæ, they are a lateral branch of the ancestral piscine stem.[150]

The second advance upon the king crabs has very much in common with the first. It has engrossed the attention of an eminent physiologist for the last six or seven years, and by him it was in detail set before Section I at our meeting of 1896. Suffice it to say that it specially aims at establishing a structural community between the king crabs and certain vertebrates, favourable to the conviction that the Vertebrata have had an arthropod ancestry.[151] When we critically survey the appalling accumulation of words begotten of this task, it is sufficient to consider its opening and closing phases. At the outset, under the conclusion that the vertebrate nervous axis is the metamorphosed alimentary canal of the arthropod ancestor, the necessity for finding a digestive gland is mainly met by homologising the so-called liver of the arthropod with the cellular arachnoid of the larval lamprey, in violation of the first principles of comparative histology![152] At the close we find ingenious attempts to homologise nerve tracts and commissures related to the organs of sense, such as are invariably present wherever such organs occur.[153] Sufficient this to show that the comparison, in respect to its leading features, is in the opening case strained to an unnatural degree, in the closing case no comparison at all. Finding, as we do, that the rest of the work is on a par with this, we are compelled to reject the main conclusion as unnatural and unsound; and when we seek the explanation of this remarkable course of action, we are forced to believe that it lies in the failure to understand the nature of the morphological method. For the proper pursuit of comparative morphology, it is not sufficient that any two organisms chosen here and there should be compared, with total disregard of even elementary principles. Comparison should be first close and with nearly related forms, passing later into larger groups, with the progressive elimination of those characters which are found to be least constant. And necessary is it, above all things, that in instituting comparison it should be first ascertained what it is that constitutes a crustacean a crustacean, a marsipobranch a cyclostome, and so on for the rest. We have tried to accept this theory, fascinated both by the arguments employed and by the idea itself, which for ingenuity it would be difficult to beat, but we cannot; and we dismiss it as misleading, as a fallacy, begotten of a misconception of the nature of the morphological method of research.[154] It is of the order of events which led Owen to compare a cephalopod and a vertebrate,[155] led Lacaze-Duthiers to regard the Tunicates and Lamellibranchs as allied;[156] and with these and other heresies it must be denounced.

Passing to the third advance, extending over the last twenty years, it may be said to consist in the revival of a theory of 1829, which boldly asserts that Limulus is an Arachnid. In the development of the defence there have been two weak points but lately strengthened, viz., the insufficient consideration of the palæontological side of the question and of the presence of tracheæ among the Arachnida.[157] Under the former there was, until recently, assumed the absence of

the first pair of appendages in the Eurypterida; but it may be said that they have since been observed in *Eurypterus Fischeri* of the Russian Silurian,[158] and *E. scoticus* from the Pentland Hills,[159] in both of which they consist of small chelate appendages flexed and limuloid in detail, somewhat reduced perhaps, and enclosed by the bases of the succeeding limbs, which become apposed as the anterior end is reached. Since by this discovery the Limuloids, Eurypterids, and Scorpionids are brought into a numerical harmony of limb-bearing parts, we may at once proceed to other points at issue. So far as the broader structural plan of Limulus and the Scorpion are concerned, all will agree to a general community, except for the organs of respiration; but concerning the cœlom, the mobile spermatozoa, and the more detailed features under which Limulus is held to differ from the Crustacea and to resemble the Arachnida, I would remark that motile spermatozoa occur in the Cirripedes and Ostracods,[160] and that the rest of the argument is weakened, by the probability that the 'arachnidan' characters which remain may well have been possessed by the crustacean ancestors, and that Limulus, though specialised, being still an ancient form, might but have retained them. The difficulty does not seem to me to lie in this, nor with the excretory organs, if we are justified in accepting the aforementioned argument that the so-called Malpighian tubes may be inturned nephridia, ectodermal in origin, and in knowledge of the existence of endodermal excretory diverticula in the Amphipods.[161] These facts would seem to suggest that as our experience widens, differences of this kind will disappear.

As to the tracheal system, now adequately recognised by the upholders of the arachnid theory, the presumed origin of tracheæ from lung-books, the probability that the ram's-horn organ of the Chernetidæ may be tracheal,[162] the presence of tracheæ in a simple form in the Acari,[163] and, by way of an anomaly, in a highly organised form on the tibiæ of the walking legs of the harvestmen (Phalangidæ),[164] are all features to be borne in mind. While I am prepared to admit that this wide structural range and varied distribution of the tracheæ lessens their importance as a criterion of affinity, I cannot accept as conclusive the evidence for the assumed homology between lung-books and gills.[165] And here it may be remarked that a series of paired abdominal vesicles, recently found in the remarkable arachnid *Kœnenia*, invaginate as a rule but in one example everted, seized upon in defence of this homology, have not been so regarded by one most competent to judge.[166]

There remains the entosternite, an organ upon which much emphasis has been placed. Not only does a similar organ exist, apart from an endophragmal system, in the Phyllopod *Apus*, in *Cyclops*, and some Decapods;[167] but, regarding the question of its histology, it may be pointed out that from all that is at present known, the structural differences between these several entosternites do not exceed those between the cartilages of the Sepia body.[168] And when it is found that the figures and descriptions of the entosternite of *Mygale* ('Mygale sp.,' 'Mygalomorphous Spider,' *auct.*) have been twice presented upside down![169] the reliability of this portion of the argument is lessened, to say the least.

Recent observation has sought to clench the homology of the four posterior pairs of limbs of the King crab and Scorpion, by appeal to a furrow on the fourth segment in the former, believed to denote an original division into two; but I hesitate to accept this until myological proof has been sought.[170]

Returning, amidst so much that is problematic, to the sure ground of palæontology, I wish to point out that when all is considered in favour of the arachnid theory there still remains another way of interpreting the facts.

In both Limulus and the Scorpion the first six of the eighteen segments are well known to be fused into a prosoma bearing the limbs, but while in the Scorpion the remaining twelve are free, in Limulus they are united into a compact opisthosomal mass. In dealing with the living arthropods, there is no character determinative of position in the scale of this or that series more trustworthy than the antero-posterior fusion of segments. It has been called the process of 'cephalisation,' and the degree of its backward extension furnishes the most reliable standard of highness or lowness in a given assemblage of forms. In passing from the lower to the higher Crustacea, we find this fusion increasing as we ascend: and it therefore

becomes necessary to compare the Scorpion with the other Arachnida, Limulus with the Eurypterida, in order the better to determine the position of each in its respective series, by the application of this rule.

As to the number of segments present, variation is a matter of small concern, in consideration of the mode of origin of segmentation and the wide numerical range—from seven in the Ostracods to more than sixty in Apus—the segments of the crustacean class present.

On the arachnidan side, in the Solifugæ but the third and fourth segments are fused; the remaining four of the prosomal series with the ten which remain are free.[171] In *Kœnenia* four of the prosomal segments alone unite; the fifth and sixth with the rest are free.[172] And when we pass to the Limuloids and the descending series of their allies, we find it distinctive of the Eurypterida that all the opisthosomal segments are free. If we can trust these comparisons, we must conclude that the Eurypterida of the past, in respect to their segmentation, simplify the Limuloid type, on lines similar to that on which the Solifugæ and Kœnenia simplify the Higher Arachnid and Scorpionid type, and that therefore if the degree of antero-posterior fusion of segments has the significance attached to it, *Limulus* and *Scorpio* must each stand at the summit of its respective series. If this be admitted, it has next to be asked if, in comparing them, we may not be comparing culminating types, which might well be isomorphic.

The scorpions are known fossil by two genera, *Palæophonus* and *Proscorpius*, from the Silurian of Gotland and Lanarkshire, the Pentland Hills, and New York State;[173] while recent research, in the discovery of the genus *Strabops*, has traced the Eurypterida back to the Cambrian, leaving the scorpions far behind.[174] One striking feature of the limbs of the Palæozoic Eurypterids is their constantly recurring shortness and uniformly segmented character, long known in *Slimonia*, *Eurypterus*, and *Pterygotus*, retained with development of spines in some genera, and for three of the five known appendages of the recently described eurypterid giant *Stylonurus lacoanus*.[175] The minimum length observed for these appendages is that of the Silurian species *Eurypterus Fischeri*, discovered by Holm in Russia in 1898.[176] This creature is one of the few eurypterids in which all the appendages are preserved, and it is the more strange therefore that the advocates of the arachnid theory should ignore it in their most recent account. Allowing for the specialisation of its sixth prosomal appendage for swimming, the fifth is but little elongated, the second, third, and fourth are each in total length less, by far, than the transverse diameter of the prosoma, and uniformly segmented, giving the appearance of short antennæ. They seem to be seven-jointed, and are just such appendages as exist in the simpler crustacean and tracheate forms; and in the fact that their structural simplicity is correlated with the independence of the whole series of opisthosomal segments they lend support to the argument for isomorphism.

With this conclusion, we turn once more to the Scorpions, if perchance something akin to it may not be in them forthcoming. The Silurian genus *Palæophonus*, especially as represented by the Gotland specimen, reveals the one character desired. Its body does not appear to be in any marked degree simpler than that of the living forms; but on turning to its limbs, we find the four posterior pairs, in length much shorter than those of any living species, all but uniformly segmented.[177] In this they approximate towards the condition of the limbs of the Eurypterida just dismissed, and their condition is such that had they been found fossil in the isolated state they would have been described as the limbs of a Myriapod, and not of a scorpion at all. Indeed, their very details are what is required, since in the possession of a single terminal claw they differ from the limbs of the recent scorpions as do those of the Chilopoda from the hexapods.

With this the scorpionid type is carried back, with a structural simplification indicative of a parallelism with the other arthropod groups; and while the facts do not prove the total independence of the scorpionid and limuloid series, they bring the latter into closer harmony with the Eurypterida of the past. They prove that the Silurian Scorpions simplify the existing Scorpionid type, on precisely the lines on which the Eurypterida simplify the Limuloid; and they do so in a manner which suggests that a distinction between the *Crustacea vera* and the

Crustacea gigantostraca (to include the Eurypterida and Xiphosura) is the nearest expression of the truth. It becomes thereby the more regrettable that in a recent revision of the taxonomy of the Limuloids the generic name *Carcinoscorpius* should have found a place.[178]

I foresee the objection that the antenniform condition of the shorter limbs may be secondary and due to change. There is no proof of this. Against it, it may be said that the number of the segments is normal, and that where nature effects such a change, elongation is with the multi-articulate state the only process known; as, for example, with the second leg of the Phrynidæ, the so-called second pareiopod of the Polycarpidea, and the last abdominal appendage of *Apseudes*.[179]

That advances such as we have now considered should lead to new departures is a necessity of the case; and it but remains for me to remind you that within the last decade statistical and experimental methods have very properly come more prominently into vogue, in the desire to solve the problems of variation and heredity. Of the statistical method, by no means new, I have but time to recall to you the Presidential Address of 1898 by my friend and predecessor in this chair, himself a pioneer; and of the experimental method I can but cite an example, and that a most satisfactory one, justifying our confidence and support. It concerns the late Professor Milne-Edwards, who in 1864 described, from the Paris Museum, the head of a rock lobster (*Palinurus penicillatus*), having on the left side an antenniform eye-stalk.[180] With the perspicuity distinctive of his race, he argued in favour of the 'fundamental similarity of parts susceptible to revert to their opposite states.' The matter remained at this, till, on the removal of the ophthalmite of certain Crustacea, it was found that in regeneration it assumes a uniramous multiarticulate form; and it is an interesting circumstance that in the common crayfish the biramous condition normal to the antennule may occur. An example this of a fact which no other method could explain.[181]

When all is said and done, however, it is to the morphological method that I would appeal as most reliable and sound. And when we find (i.) that in certain Compound Tunicates the atrial wall, in the egg development delimited by a pair of ectoblastic invaginations, in the bud development may be formed from the parental endodermic branchial sac;[182] (ii.) that regenerated organs are by no means derivative of the blastemata whence they originally arose;[183] (iii.) that in the development of a familiar starfish the inner cells of the earliest segmentation stages, by intercalation among the outer, contribute half the fully formed blastula;[184] (iv.) that there are Diptera in existence in which, while it is well-nigh impossible to discriminate between the adult forms, there is reason to believe the pupa cases are markedly and constantly distinct; it becomes only too evident that the later embryonic and adult states are those most reliable for all purposes of comparison, and that it is by these that our animals can best be known and judged. Caution is, however, necessary with senility and age, since certain skulls have been found to assume at this period characters and proportions strikingly abnormal,[185] and by virtue of a most important discovery, which we owe to the Japanese, that in certain Holothurians, the calcareous skeletal deposits may so change with age, as to render specific diagnoses based on their presumed immutability invalid.[186] Advance, real and progressive, is in no department of zoological inquiry better marked than in comparative morphology, and it is for the pre-eminence of this that I would plead. Educationally, it affords a mental discipline second to none.

We live by ideas, we advance by a knowledge of facts, content to discover the meaning of phenomena, since the nature of things will be for ever beyond our grasp.

And now my task is done, except that I feel that we must not leave this place without a word of sympathy and respect for the memory of one of its sons, an earnest devotee to our cause. William Thompson, born in Belfast, 1806, became in due time known as 'the father of Irish natural history.' By his writings on the Irish fauna, and his numerous additions to its lists, he secured for himself a lasting

fame. In his desire to benefit others, he early associated himself with the work of the Natural History Society, which still flourishes in this city. He was President of this Section in 1843, and died in London in 1852, while in the service of our Association, in his forty-seventh year, beloved by all who knew him. His memory still survives; and if, as a result of this meeting, we can inspire in the members of the Natural History and Philosophic Society of this city, as it is now termed, and of its Naturalists' Field Club, an enthusiasm equal to his, we shall not have assembled in vain.

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