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## THE LOWEST OF THE VERTEBRATES AND THEIR ORIGIN.\*

IN many seas have been found—and in almost all temperate and tropical seas may

\* *Columbia University Biological Series. II. Amphioxus and the Ancestry of the Vertebrates.* By ARTHUR WILLEY, B. Sc., Tutor in Biology, Columbia College.

be found—small animals of peculiar appearance and habits and of extraordinary interest. They have a translucent, compressed and elongated fusiform body attenuated at both ends, and therefore have received one of their names—*Amphioxus*; this form may be superficially modified, however, by the development of a membrane around the caudal portion of the body and the extension downwards of cirri from an oral ring. The existence of these cirri and the erroneous attribution to them of a respiratory function have given rise to another name for the group—*Branchiostoma*. *Lancelet* is a semi-popular equivalent of *Branchiostoma* and *Amphioxus*.

The animals thus distinguished externally are unique in their organization. The nervous system is manifest in an elongated tube without any expansion forwards into an *externally* specialized brain, and with its anterior portion only distinguished by the fact that there are (in front of the first myotome) two symmetrical pairs of sensory nerves which innervate the snout and have no corresponding ventral roots. A skeleton is represented by a simple notochord extending to both ends of the body, and there is no rudiment of a cerebral case or of sense capsules; the only other hard parts are developed around the anterior aperture, where

With a preface by HENRY FAIRFIELD OSBORN. Macmillan & Co. 1894. 8vo, xiv+316. Frontispiece. \$2.50.

a ring is formed by a number of subcartilaginous segments, which give rise to as many processes for the support of cirri just before their posterior ends, which connect with the succeeding segments. A specialized heart is also wanting, and so likewise are paired eyes, as well as auditory and olfactory organs. The sense of sight or light is subserved imperfectly by a median 'eye spot' sessile on the forward end of the nerve tube between the foremost pair of nerves. Immediately behind the eye spot is 'a small pit in the body-wall, reaching from the outer surface of the body to the anterior wall of the brain. This is known as *Kölliker's olfactory pit*, after its discoverer' (p. 19). Every other feature of the organization of the animals in question is noteworthy, and Mr. Willey tells about them in detail in the work which is here noticed, and to that reference may be made for further information.

The species of Lancelets are few; only nine or ten at most are known. They are of small size, ranging from about half an inch to little more than three inches in length. Most of them are found along sandy shores and are prone to bury almost the entire 'body in the sand, leaving only the mouth with the expanded buccal cirri protruding' (p. 9). Nevertheless one specimen was described in 1889 in the 'Report on the pelagic fishes' of the Challenger Expedition (p. 43), and affirmed to have been taken 'a few degrees north of Honolulu,' from 'a deep haul 1,000 fathoms' of an open-mouthed dredge.

Diverse are the views that have been held respecting the affinities of the Lancelets. From a single small specimen obtained on the Cornish coast, Pallas in seven lines described the species in 1774\* (not 1778, as Mr. Willey states) and called it *Limax lanceolatus* or *lanceolaris*. Under the

name *Limax*, Pallas included naked gastropods, whether broad or narrow, having a flat foot, and he mistook the metapleural folds and intermediate area of the new species for a foot. No further notice was taken of the species till 1834, when Costa described it anew as *Branchiostoma lubricum*, and in 1836 Yarrell redescribed it, and, with the assistance of John Edward Gray, identified it with the long-neglected *Limax* of Pallas and called it *Amphioxus lanceolatus*.

Both Costa and Yarrell thought that it belonged with the Lampreys and Hags. J. Müller first recognized how important were its peculiarities and in 1844 gave it subclass rank. Isidore Geoffroy St. Hilaire in 1852 and C. Bonaparte in 1856 first elevated it to class rank. Haeckel in 1866 advanced still further and contrasted the class of lancelets as a subphylum (Acrania) with all the other vertebrates (Craniota). This last view is adopted by Mr. Willey who however prefers the later name, Cephalochorda, for the 'division.' The family name, *Branchiostomidae*, was first given by Bonaparte in 1846.

With so much interest attached to them, the lancelets naturally have received much attention, and many elaborate memoirs on various parts of their structure have been published. Of the 140 (133 + 7) titles recorded by Mr. Willey in his bibliographical 'references' (pp. 295—309), 66 are under the head 'Anatomy of Amphioxus,' and 37 under the caption 'Development of Amphioxus.' Mr. Willey very properly adds that "this bibliography does not by any means include all that has been written on the anatomy of Amphioxus." Indeed, the titles could be more than doubled, but without material advantage to the value of the work for most readers. Really Mr. Willey has prepared a very useful and well made list and mainly with well considered restrictions. In view of such an abundant literature the need for a general work embodying

\*Spicilegia Zoologica [etc.]. Fasciculus decimus. Berolini [etc.], 1774. (p. 19, pl. 1., fig. 2.)

the most important data respecting the lancelets was urgent. Mr. Willey's volume to a very large extent administers to this need. He has judiciously combined the observations of himself and others and classified them under (I.) 'Anatomy of Amphioxus' and (II.) 'Development of Amphioxus;' under the former caption, he has data 'Historical,' on 'Habits and Distribution,' 'External Form,' and 'Internal Anatomy;' under the latter he treats of the 'Embryonic Development' and 'Larval Development,' enunciates certain 'General Considerations,' and concludes with a comparison of 'Amphioxus and Ammocœtes.' We need only refer specially to the section on 'The Excretory System' (pp. 55-75), because it contains information on 'organs' which were long undiscovered, or at least not appreciated. Mr. Willey is 'convinced as to the essential identity of the excretory tubules of Amphioxus with the pronephros of the craniate vertebrates.' The information respecting other structural features are up to date and the inferences as to homologies and functions reasonable and judicious, although there may be occasion sometimes (but rarely) for dissent. But we could have wished that the radical differences between the lancelets and true fishes had been emphasized by the use of terms indicating that analogous parts were not homologous. For instance, Mr. Willey correctly states that there is a dorsal fin 'supported by a series of gelatinous *fin-rays*, each of which lies in a chamber of its own,' and further says that 'the ventral portion of the fin in the region between atriopore and anus is supported by a similar series of fin-rays, but there are two of them placed side by side in each compartment.' Such structures are very unlike the specialized rays of teleostomous fishes, and to avoid the misleading tendency of such terms it has been recently proposed to designate the so-called rays of the lancelets *actinomimes* and their

inclosing chambers *actinodomes*, while the compound ventral fin has been designated as the *sympodium*. Such terms will be useful in systematic zoölogy as well as morphology.

The ground is now prepared for further advance, and one of the first of the problems that need examination is the amount of variability among the Branchiostomids. The first preliminary is the differentiation of known variation into generic and specific characters, instead of confounding all under one generic name, as Mr. Willey has done.

Applying the mode of valuation current for the higher groups, we have several modifications of different systems that are available for genera. Such are the development of the hinder end, the unilaterality or bilaterality of the gonads or sexual organs, the coördinate development of the metapleural folds, the presence or absence of a sympodium, and the development of the dorsal fin, and especially the relative extent of the actinomimes and actinodomes. Variations in these structures are expressible under five generic terms already named, *Branchiostoma*, *Paramphioxus*, *Epigonichthys*, *Asymmetron* and *Amphioxides*. Two of the genera (*Paramphioxus* and *Epigonichthys*) have recently been combined in one to which the new name *Heteropleuron* has been given, but even if such a union is favored, *Epigonichthys* should be used as the first distinctive name given to a member of the group; the two, however, appear to be sufficiently distinguished by the fins. *Epigonichthys* has an unusually high dorsal membrane and contracted actinomimes.

Eight species of lancelets are recognized by Willey, as had been previously by Dr. E. A. Andrews; one described in 1889 ('*B. pelagicum*') was overlooked and another (*Paramphioxus Singalensis* or *Heteropleuron Singalense*) has been described since.\*

\*On the species of Amphioxus. By J. W. Kirkaldy. Rep. Brit. Ass. Adv. Sc., 1894, pp. 625-686.

These have been simply distinguished by Mr. Willey by the number of myotomes, but most of them may be distinguished by other characters. Of the ten species, five belong to *Branchiostoma*, two to *Paramphioxus*, one to *Epigonichthys*, one to *Asymmetron*, and one to *Amphioxides*.

What are specific characters in any Branchiostomoid genus is a question as yet undetermined. The only one that has been generally used (exclusive of what are rather of generic importance) is the number of myotomes as a whole and in different regions. Even such a character has not been constantly adhered to. For example, in Dr. E. A. Andrews' useful and able memoir on 'An Undescribed Acraniate' two eastern American species are recognized, '*B. lanceolatum*' and '*B. caribæum*.' The former has an average of  $(35.6+13.6+11.8=)$  61 myotomes, and the latter an average of  $(34.8+14+8.9=)$  57.8 myotomes, but one individual from the Chesapeake Bay, referred to '*B. lanceolatum*,' has  $(36+16+7=)$  59 myotomes, and another Florida, referred to '*B. caribæum*,' has  $(35+17+7=)$  59 myotomes. Inasmuch as no other differential characters have been given, it is evident that Dr. Andrews was mainly influenced by the consideration of association or geographical distribution rather than morphological characters in the identification of the different specimens. The relations of the forms of our coast, indeed, still remain to be determined, and it is doubtful whether any American forms will prove to be conspecific with the European. Specific characters may perhaps be found in numerous details, *e. g.*, the number and proportions of the dorsal and ventral or sym-podial rays, the development of the cirri and skeletal bases; details of the velar tentacles and gillbars, form of the caudal, relative proportions of the various regions, etc. But numerous as have been the memoirs on *Branchiostoma lanceolatum*, no de-

tailed study of variations has yet been published. Until this is done much is left undone. The material now in museums, however, is generally insufficient for such studies and should be especially prepared therefore. If the labor of students, so often frittered away in verifying oft-repeated observations, could be in part directed to such preparation and observation, a boon to systematic zoölogy would be realized and certainly no less would be the benefit to the student. We may hope that Mr. Willey will continue studies so well begun and enlighten us on some of the many points still obscure. That we are ignorant as to the questions in point is not his fault.

The ancestry of the vertebrates is a fascinating subject for consideration, and the search for their nearest relatives began early in the century. Before the lancelet was known—at least as a vertebrate—Etienne Geoffroy Saint-Hilaire endeavored to homologize constituents of the bodies of insects and vertebrates. (We may here remark that Mr. Willey has repeatedly referred to the French naturalist as Saint Hilaire, but Saint Hilaire was only an agnomen, the true cognomen or family name being Geoffroy.) Long after the lancelet had been carefully investigated, and indeed very recently, a naturalist trained in modern methods, but who did not exercise a 'scientific use of the imagination,' actually contended that the vertebrates had arachnoid or rather limuloid ancestors! A less extravagant view has been that Annelid worms were nearest of kin to the vertebrate ancestors, and this has gained several followers. But the highly specialized character of annelids and still more of arthropods appears to forbid the serious consideration of such conceptions. Much more probable is the view that the nearest relatives of typical vertebrates are the Tunicates. This is the idea adopted by Mr. Willey, who has accepted a 'group' called 'Proto-

chordata' and included thereunder three divisions, (1) HEMICHORDA, or *Balanoglossids*, *Cephalodiscids* and *Rhabdopleurids*; (2) UROCHORDA, or *Ascidians*, and (3) CEPHALOCHORDA, or *Lancelets*. It is the present fashion to consider this affiliation as established, but it has not been proven beyond cavil. As a provisional hypothesis, however, it is the best of those that have been proposed, and there is no need to offer here any objections. Nevertheless, we should recall the fact that the lancelets and all other so-called 'Protochordata' must have very widely diverged from their common ancestors and that some of the characteristics of the first are probably the result of degeneration. When, for example, we find a specialized heart and auditory organs in Tunicates, as well as in many true invertebrates (even though they be not homologous), it is difficult to resist the inference that their absence in the lancelets is due to loss rather than to original failure of development. But now, with the necessary precautions and much hesitancy, we may assent to the possibility of the conclusions with which Mr. Willey closes his work.

"For the present we may conclude that the proximate ancestor of the Vertebrates was a free-swimming animal intermediate between the Ascidian tadpole and *Amphioxus*, possessing the dorsal mouth, hypophysis, and restricted notochord of the former; and the myotomes, coelomic epithelium, and straight alimentary canal of the latter. The ultimate or primordial ancestor of the Vertebrates [or Chordates] would, on the contrary, be a worm-like animal whose organisation was approximately on a level with that of the bilateral ancestors of the Echinoderms."

The length to which this notice has already extended forbids attention to various other features of Mr. Willey's work. It must suffice to add that the fourth and fifth sections are devoted respectively to 'the Ascidians'

(pp. 180-241) and 'the Protochordata in their relation to the problem of vertebrate descent' (pp. 242-293). For these we owe further thanks, and for all we feel assured future students of the groups in question will be grateful.

THEO. GILL.

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#### CURRENT NOTES ON ANTHROPOLOGY (IX). THE RITUAL CALENDAR OF CENTRAL AMERICA.

In the *Globus*, No. 18, 1895, Dr. E. Förstemann has one of his ingenious studies of the Central American Calendar, this time that portion of it called by the Nahuas the *Tonalamatl*, or Book of Days. This consisted of a period of 260 days, and strenuous efforts have been made by Mrs. Zelia Nuttall and other writers to treat it as a time-count, that is, as an aliquot part of the computation of astronomical years and cycles.

In this article Dr. Förstemann shows that this certainly does not hold good for the *Tonalamatl* as it constantly recurs in the Mayan manuscripts. In them it appears to be introduced for exclusively divinatory purposes, a basis for predicting events relating to persons or tribes, or else the weather, wars, disasters, etc. Not unfrequently a multiple of the period is embraced in the forecast, and very generally reference is made to the divinities assigned to the subdivisions of the *Tonalamatl*. Or, again, it is occasionally divided into its fourths, fifths or tenths; and what is noteworthy, the manuscripts present numerous similarities in these respects, proving that their writers were working on a like system of horoscopy.

I may add that the result of this investigation corroborates the position that I took in my 'Native Calendar of Central America and Mexico' (Phila. 1893), in which I maintained that the *Tonalamatl* was invented for and practically exclusively applied to divination, and not to the cyclical measure of astronomical time.