Remarks on some Recent Work on the Proto-chorda, with a Condensed Account of some Fresh Observations on the Enteropneusta.

By

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THE eighth volume of the well-known 'Traité de Zoologie Concrète,' by Professor Yves Delage and M. Edgard Hérouard, published in 1898, is devoted to what the authors style the Procordés or Prochordata, a group which is made to include three classes, namely, Hemichordia, Cephalochordia, and Uro-chordia. It is a pleasure to turn to a text-book in which the Enteropneusta are treated on equal terms with the Cephalo-chorda and the Urochorda, especially when, as in this case, the distinguished authors have aimed at impartiality—a quality which in one or two places has led them beyond the bounds of discrimination. It goes without saying that the work is an excellent one, and admirably calculated, on the whole, to give a just idea of these animals; but on the present occasion I am neither concerned with its many excellences nor with its few blemishes, but merely with the subject-matter.

No doubt the classification employed by the authors of this text-book answers not only their purpose, but that of their readers also. At the same time it should be borne in mind that it is in no sense a final classification, nor even one which corresponds to the present state of our knowledge. By not including the Pterobranchia in the same volume with the

Enteropneusta, the authors have neglected the opportunity of pointing an interesting and instructive analogy.

What the Urochorda are to the Cephalochorda, such are the Pterobranchia to the Enteropneusta.

The perpetual domination of the notochord in classification constitutes a noteworthy example of the manner in which zoological knowledge moves along well-worn grooves. There is strong reason to suppose that the gill-clefts have the priority of the notochord, or at least equal antiquity with it; and if this supposition should prove to be correct in principle, there ought to be some indication of it in the classificatory system.

I have treated this subject in some detail in a memoir on the Enteropneusta collected by me in the South Pacific, which will shortly be published;[1] and the following is a simplified form of the table of classification there constructed.

PHYLUM BRANCHIOTREMA, n. n.

I. HEMICHORDA, Bateson, 1884.

Class 1. PTEROBRANCHIA, Lankester, 1885.
Class 2. ENTEROPNEUSTA, Gegenbaur, 1870.

II. PROTOCHORDA, Balfour, 1882.

Class 1. UROCHORDA, Lankester, 1877.
Class 2. CEPHALOCHORDA, Lankester, 1877.

III. VERTEBRATA,[2] Lamarck and Cuvier.

Class 1. ACRANIA, Haeckel, 1866.
Class 2. CRANIOTA, Haeckel, 1866.

In the above system the group containing Amphioxus appears under two different names, Cephalochorda and Acrania. I see no objection to this procedure, nor any other way out of the difficulty.

[1] In Part iii of A. Willey's 'Zoological Results' (Cambridge University Press).

[2] Vertebrata = Holochorda, Gadow, 1898.

The justification for the new collective name, Branchiotrema, is contained in my forthcoming memoir, where it is introduced in connection with a new theory of gill-clefts, to which I have been led by my study of the Enteropneusta. This theory may be barely and briefly stated as follows :

The gonads and gill-slits were primarily unlimited in number and co-extensive in distribution, the gonads having a zonary disposition and the gill-slits occupying the interzonal depressions.

The primary function of the gill-slits was the oxygenation of the gonads, their secondary function being the respiration of the individual—the change of function having taken place pari passu with an elaboration of the vascular system.

Correlatively with the progressive regional differentiation of the body, the gonads and gill-slits became limited both anteriorly and posteriorly.   The anterior limitation of the gill-slits behind the collar region is constant in all Enteropneusta, but the posterior limitation is excessively variable.[1]   The emancipation of the gonads from their topographical relations with, and functional dependence on, the gill-slits has taken place in several ways, but the resultant tends to be, and eventually actually is, the restriction of the gonads to a post-branchial genital region.

Such, in outline, is the theory to which I have committed myself.   The Harmer-Brooks-Masterman theory of gill-clefts does not, in my opinion, account for their prime origin, but it does perhaps explain the retention of a single pair of gill-clefts in forms like Cephalodiscus and Appendicularia.

In recording the fact that Spengel divided the species of Enteropneusta into four genera, MM. Delage and Hérouard prefer to describe them "en bloc sous leur ancienne dénomination commune."   This conservative method of treatment is somewhat foreign to the general spirit of the book, since an endeavour has been made to incorporate the results contained in the most recent publications.   As a consequence, some

[1] Both anterior and posterior limits of the gonads are variable.

structures of first importance are relegated to foot-notes, e. g. the genital pleuræ (p. 5) and roots (p. 45) of Ptychoderidæ.

In a paper published in this Journal,[1] which our authors have overlooked, I have given reasons for supposing that a form like Ptychodera flava, in which the gill-slits open freely to the exterior and not first into gill-pouches, represents the most primitive existing type of Enteropneusta. Speaking from personal experience, I may at least say that this species has opened my eyes as to the significance of the enteropneustic organisation.

The figure of Ptychodera clavigera, given on pl. ii, facing page 64, is apt to be misleading. The pharynx in this figure appears to stand boldly forth as a cylindrical tube at the base of the open chamber formed by the arching genital pleuræ; and the parallel arcuate lines have the appearance which is actually presented by the true gill-bars in Ptychodera flava. The gill-bars of Pt. clavigera are, however, quite invisible externally, the genital pleuræ have a dorsal origin, the pharynx does not project beyond the level of the floor of the peribranchial space,[2] and the gill-pores are extremely small, lying at the base of the narrow branchial grooves.

The authors have very naturally followed Spengel in their explanation of the lateral septa of the Ptychoderidæ, as being the outer walls of a pair of cœlomic diverticula (p. 23, footnote).

The prolongations of the truncal cœlom into the collar region (viz. perihæmal and peripharyngeal cavities) are intelligible facts; but how the truncal cœlom could project a portion of itself into itself was a mystery to my mind until I realised that there is no question of a diverticulum at all.

[1] A. Willey, on Ptychodera flava, Eschscholtz, 'Quart. Journ. Micr. Sci.,' vol. 40, 1897, p. 165.

[2] Excepting that the branchial tract or gill-area, i. e. the area enclosed within the branchial grooves is somewhat arched. The blue-lined structure in the figure above referred to is simply the gill-area or Kiemenfeld of Spengel.

The fact that Ptychodera flava clears away this difficulty is alone sufficient to entitle it to be regarded with particular respect.   This remark no doubt applies to the sub-genus Chlamydothorax to which Pt. flava belongs.

In most Ptychoderidæ the lateral septa, as described by Spengel, have a limited anterior extension ; the point of their proximal or mesial origin from the basement membrane gradually approaches that of their distal insertion into the same membrane until the two points coincide ; and so the lateral septum on each side comes to an end in the posterior branchial region.   In this way there actually exists a portion of the cœlom, bounded mesially by the dorsal mesentery [1] and laterally by the lateral septum, which ends blindly in front ; and as long as this was all that was known on the subject there was perhaps no other alternative than to propound some such formal explanation as that put forward by Spengel.

In Ptychodera flava the lateral septa do not come to an end in the posterior branchial region, but they are co-extensive, in front and behind, with the genital pleuræ.   It can therefore hardly admit of question that the genital pleuræ and lateral septa are causally related to one another.

Where the genital pleuræ are at their maximum the lateral septa are entire.   As the genital pleuræ have become reduced, the reduction always taking place from before backwards, the the lateral septa have been subjected to the same process of limitation, and exhibit the effects of it in a more marked manner.

MM. Delage and Hérouard do not devote much space to the difficult subject of excretion in the Enteropneusta, being content to state that the essential organ of excretion is the glomerulus which forms part of the central complex of the proboscis, while the excretory products are said to be got rid of through the proboscis-pore.

[1] This holds good only for the post-branchial region. In front of the last gill-cleft on each side, the proximal origin of the lateral septum is transferred from the wall of the gut to the basement-membrane of the epidermis.

Bateson[1] found granules in nearly all the mesoblastic tissues, and he says (p. 526) "they may perhaps be excretory, and it is possible that they are more or less removed by the proboscis-pore and collar-funnels respectively. This does not explain their presence in large masses in the trunk body-cavity, from which no pore has been observed to open."

In the first place it should be remembered that it is not absolutely necessary that excretory products must be removed from the body; this is shown in the Ascidians, where there are no excretory ducts. The so-called pericardium (Herzblase) of the Enteropneusta which lies in the centre of the glomerulus, i.e. between the two halves of the latter, appears, from the curious way in which its endothelium proliferates into the cavity (to such an extent as sometimes to completely block up the cavity), to stand in functional as well as in topographical relation to the glomerulus. If this is so, it would, in its capacity as a closed sac associated with the renal function, be physiologically comparable to the organ of Bojanus of the Molgulidæ.

The glomerulus of the Enteropneusta is, so far as our present knowledge goes, a structure sui generis, and it is quite clear that it is the principal organ of excretion only in virtue of its having superseded something else, namely the paired excretory canals.

The proboscis-pores are highly variable; the collar-pores are constant; but neither the former nor the latter are any longer mere excretory pores. The collar-pores especially seem to promote locomotion by taking in water, and so causing the collar to swell (Spengel); this may happen also in the case of the proboscis-pores sometimes, but not always.

I have observed what I believe to be the vestiges of a pair of truncal canals and pores in two species of the genus Spengelia. In both Sp. porosa and Sp. alba, n. sp., there is a pair of canalicular extensions of the first pair of gill-pouches into the posterior end of the perihæmal cavities close to the level at which the latter pass into the truncal cœlom. They occur approximately at the same level as the collar-canals,

[1] 'Quart. Journ. Micr. Sci.,' vol. 26, 1886.

which likewise arise as canalicular extensions of the first gill-pouch into the collar cœlom on each side.[1] These truncal canals of Spengelia are such definite structures that I was for a long time perplexed as to their significance.

I have referred above to the fact that the collar-canals are actively functional; their walls consist of richly ciliated columnar epithelium, and they retain a uniform calibre from their external orifice to the wide semilunar funnel by which they open into the collar cœlom. The truncal canals, on the contrary, taper towards their internal ends, their walls contain ill-defined mucous cells, and, in short, they distinctly appear to be in a vestigial condition. The perihæmal prolongations of the truncal cœlom usually contain merely virtual cavities; in other words, their cavities are quite blocked up with muscular and connective tissue. This is the case in Sp. porosa, whereas in Sp. alba a true space appears in the posterior portion of the perihæmal cavities, namely, in the region in which the truncal canals occur.

I can neither state positively that there is an internal opening nor that there is not; one thing only is certain, namely, that the truncal canals are there. In Sp. porosa they are longer than in Sp. alba, but they present more the appearance of vestigial structures in a chronic state of mucoid degeneration in the former species than in the latter.

A minute terminal pore is always difficult to find in transverse section, or even in any kind of section, and it will be remembered that there was the same difficulty in the case of the atrio-cœlomic or brown funnels described by Professor Lankester in Amphioxus.

If the truncal canals of Spengelia [2] and the brown funnels

[1] This is Spengel's view. Morgan says the collar-pore and first gill-slit arise coincidently. I do not think this affects the present question. Bateson describes the collar-pores in B. kowalevskii as arising as thickenings of the outer "atrial" wall which become perforated. The so-called atrial cavities, formed by the overhanging lateral margins of the collar, are peculiar to B. kowalevskii (Spengel).

[2] It need be no cause for surprise that these structures only occur in one genus of Enteropneusta. Each species of Enteropneusta may and

of Amphioxus be regarded as vestigial structures, the impor-
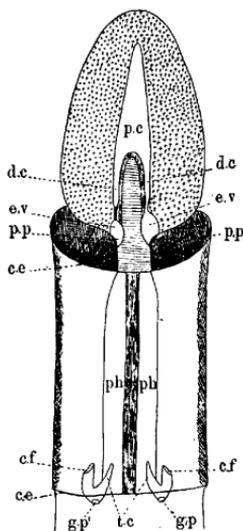tance of their possession of an internal opening is diminished.

Fig. 1.—Diagram of anterior end of an Enteropneust, to show the regional
canals and pores. The proboscis-pores are indicated as they sometimes
occur in Ptychodera flava; the collar and truncal pores as in
Spengelia. c. e. Anterior and posterior margins of collar. c. f. Collar
funnels. d. c. Dorsal canals of proboscis cœlom. e. v. End vesicles of
proboscis (Eichelpforten). g. p'. First gill-pores (only the most dorsal
portion of the first gill-pouch is indicated). p. c. Proboscis cœlom.
ph. Perihæmal cavities. p. p. Proboscis-pores. t. c. Truncal canals
(opening with the collar canals into the first gill-pouch).

In Ptychodera flava there are always two proboscis-
pores, one of which (either the right or the left) is smaller
than the other, and its terminal vesicle is usually not in

usually does present peculiar vestiges of structures which were presumably
associated together in the ancestral forms.

communication with the proboscis cœlom (see Fig. 1). Thus the internal opening of the proboscis canal (end vesicle or Eichelpforte) is lost, while the external opening remains; and it is probably a general rule that when these regional pores change their function, or lose their function and become vestiges, one of the first things to happen is likely to be the closure of the internal or cœlomic opening.[1]

In accordance with the above considerations, I regard the truncal canals of Spengelia and the atrio-cœlomic funnels of Amphioxus as the vestiges of a pair of functional truncal pores, which were homodynamous with collar-pores and proboscis-pores.   It is therefore of great interest to point out that in Amphioxus there are also traces of the other regional pores.

[1] As I have referred to this loss of the internal opening of the end vesicle of the proboscis canal, I will briefly state here what I believe to be some of the potentialities of this structure.

i. The proboscis-pore is frequently well in front of the anterior neuropore.

ii. Sometimes it is closely associated with the neuropore.

iii. Sometimes it opens into the medullary tube of the collar behind the neuropore.

iv. Frequently the end vesicle is prolonged behind the pore, as a cæcal follicle lying below the medullary tube.

v. Combining what sometimes happens into one phenomenon, we see the neuropore leading into the medullary tube, and a subneural organ opening into the latter.

vi. The entire medullary tube of the collar of Enteropneusta corresponds to the cerebral vesicle only of Amphioxus and of the Ascidian larva. The spinal cord is represented in Enteropneusta by the dorsal nerve which lies in the skin, and is not closed in.

vii. The subneural gland of the Ascidian larva opens by the neuropore into the dorsally placed mouth, and at the other end into the cerebral vesicle.

viii. The inner or cerebral opening of the subneural gland of the Ascidian larva is thus seen to correspond to the proboscis-pore, which has lost all relation to the cœlom.

ix. Hence the peculiar mode of development of the tunicate subneural gland is explained, and the apparent absence of a proboscis-pore in the tunicate larva is accounted for.

x. The roots of Ptychoderidæ are related to the epiphysial complex of the thalamencephalon of Craniota.

The structure in the larva of Amphioxus known as Hatschek's nephridium,[1] which opens at one end into the buccal cavity, has been shown by MacBride[2] to be, at an early stage, in open primary communication at its other end with the left archenteric pouch, which he has suggestively named the left collar-cavity. In spite of differences in the method of development, I regard Hatschek's nephridium as being in principle the vestige of a pair of collar canals.

Bateson tentatively compared the collar-pores of the Enteropneusta both to Hatschek's nephridium and to Lankester's brown funnels. The comparison of the enteropneustic proboscis-pore with the orifice of the amphioxine præoral pit is of old standing, and likewise originated with Bateson, who further compared them both to the craniate pituitary body, without carrying the comparison into any great detail.

In the Enteropneusta the excretory function of the regional pores has been superseded by the specialisation of the glomerulus; in Amphioxus by the evolution of the nephric tubules which were discovered by Weiss and Boveri.

It may indeed be said that in the Enteropneusta the primordia of the nephric tubules are present in the form of a minute diverticulum at the dorsal medial angle of each gill-pouch, or in a corresponding position in those cases where the gill-pouches are confluent, as in Pt. flava. These structures are particularly well seen in sections through Spengelia alba. Whether this be so or not there is undoubtedly a special significance in the remarkable fact that Boveri's tubules are precisely co-extensive with the gill-clefts, and a renewed importance should be attached to the connecting vessels observed by Paul Mayer between dorsal aorta and sub-intestinal vein in embryos of Pristiurus, which were shown by Rückert to occur in the same segments with the pronephric tubules and to furnish the latter with rudimentary glomeruli.

[1] If I understand them aright, MM. Delage and Hérouard have completely misunderstood this structure (p. 121, foot-note).

[2] E. W. MacBride, "The Early Development of Amphioxus," 'Quart. Journ. Micr. Sci.,' vol. 40, 1897, p. 589.

If Boveri's tubules open the way to a perception of the subsequent potentialities of the excretory system, Lankester's brown funnels, Hatschek's nephridium, and the præoral pit furnish a clue to its past history.
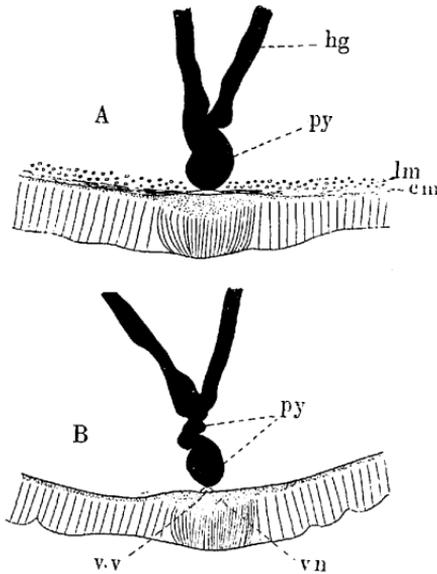

Fig. 2, A and B.—Portions of transverse sections through the caudal region of Ptychodera ruficollis, n. sp. A. Through the anterior caudal region. B. Through the mid-caudal region. cm. Circular muscles of body-wall. hg. Wall of hind gut. lm. Longitudinal muscles. py. Pygochord. vn. Ventral nerve-cord. vv. Ventral blood-vessel.

The substitution of nephric tubules in the truncal region for regional pores in the archimeric (Masterman) regions, which is displayed before our eyes in Amphioxus, is one of the most striking examples of the working of the principle of substitution that I can call to mind.

MM. Delage and Hérouard retain the designation noto-chord applied by Bateson to the diverticulum from the throat which projects into the proboscis, where it acquires a rigid consistency and sustaining properties. I prefer to call this struc-ture by a non-committal name, and propose the term stomo-chord. The stomochord is not the only skeletal product of the gut wall in the Enteropneusta. There is another structure which finds no mention in the text-book under consideration, but which is hardly second in interest to the stomochord itself. It occurs along the entire length of the hind gut in the caudal region on the ventral side in many Ptychoderidæ; it is a solid keel-like, ribbon-shaped band, with dilated distal border abut-ting upon the ventral blood-vessel, and united at its dorsal edge with the median ventral epithelium of the gut.

This structure, which I propose to call the pygochord, was first seen by Spengel in Pt. minuta, then by Hill in Pt. hedleyi, and I have found it in Pt. flava, Pt. carnosa, n. sp., and Pt. ruficollis, n. sp.

In Spengelia alba, n. sp., it appears to be represented by a vacuolar thickening of the ventral epithelium, which, how-ever, retains its epithelial position, and is not drawn out into a band.

I do not think that the enteropneustic stomochord corre-sponds to any definite part of the true notochord. The præ-oral extension of the notochord, far beyond the anterior limit of the neural tube in Amphioxus, is due to a forward growth of the notochord as such; whereas the præoral position of the stomochord in the Enteropneusta is due to a forward projection of a portion of the collar-gut or throat. Spengel calls it the Eicheldarm, but although he intended this name to be in-different, it is capable of misleading interpretation, since it does not belong to the proboscis at all in its primary quality of integral constituent of the gut, but only in its secondary quality of a skeletally metamorphosed derivative of the gut. Moreover, whereas the notochord is essentially a uniform, single, indivisible structure,[1] the stomochord exhibits strongly

[1] Tue anterior tip of the notochord presents certain properties which may

marked regional differentiation (Fig. 3). It is therefore not
sufficient to say that any structure in other forms is compar-
able to the enteropneustic stomochord, but it must be specified
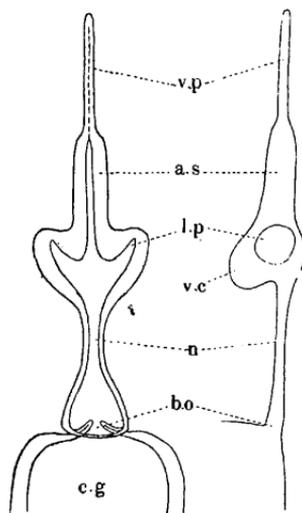which portion of this structure is referred to.

Fig. 3.—Diagram of a complete stomochord of an Enteropneust from the
    dorsal and lateral aspects, to show its regional differentiation. v.p.
    Vermiform process. a.s. Anterior region of body of stomochord. l.p.
    Lateral pouch. v.c. Ventral cæcum. n. Nuchal region. b.o. Buccal
    orifice of stomochord. c.g. Throat or collar-gut.

The lumen of the stomochord is highly variable; it may
safely be said that it is not the same in any two individuals of
a species. Sometimes it is in a fragmentary condition, some-

have an atavistic significance, but this does not affect my general proposition.
The most that could be looked for in the embryos of higher Chordata would
be a vestige of the buccal orifice of the stomochord, and perhaps this does
occur.

times it is locally obsolete, and sometimes it is unusually capacious. In all cases it is patently vestigial. In more than one of my species (e. g. Pt. carnosa, n. sp.) the stomochord undergoes fragmentation in the nuchal region, owing to the invasion of skeletal substance. In Balanoglossus canadensis Spengel found that the entire nuchal region of the stomochord was lacking.

The structure of which the stomochord, in its capacity as a portion of the gut, is a vestige, must originally have been post-oral,[1] and I have convinced myself that the structures recently described by Masterman [2] in the Actinotrocha of the Bay of St. Andrews are capable of being explained on this basis.

In its middle region the stomochord is greatly dilated, both dorso-ventrally and laterally. Spengel only emphasises the ventral cæcum of the stomochord in this region; but often there is a pair of lateral pouches which are particularly well-marked. In some cases the lateral pouches are less pronounced than the ventral cæcum, and sometimes the exact reverse is the truth. Sometimes the lateral pouches do and sometimes they do not unite with one another across the middle line by the intermediation of the ventral cæcum.

The interest of the situation has been increased rather than diminished by the recently published observations of Roule on the Actinotrocha of Phoronis sabatieri. Instead of the paired lateral diverticula or pleurochords described by Masterman, there is in Roule's larva a single median anterior ventral diverticulum, whose cells likewise undergo vacuolar degeneration, which gives it a semi-rigid consistency. According to Roule this ventral diverticulum arises at the anterior end of the intestine (in the same region as Masterman's pleurochords), and projects forwards ventrally below the œsophagus.

[1] I think it is universally admitted that the stomochord is a secondary projection into the proboscis cavity pushing the cœlomic epithelium or splanchnotheca of Spengel before it.

[2] A. T. Masterman, "On the Diplochorda," 'Quart. Journ. Micr. Sci., vol. 40, 1897, p. 281.

Thus in Masterman's pleurochords we have, as I believe, the representatives of the lateral pouches of the enteropneustic stomochord; while in Roule's ventral diverticulum we have the representative of the ventral cæcum of the stomochord.[1]

With regard to the structure in Actinotrocha which Masterman homologises with the so-called notochord described by Harmer in Cephalodiscus and by Fowler in Rhabdopleura, but which he (Masterman) labels "subneural gland," it is not easy to suggest a final explanation. Harmer[2] has pointed out its resemblance to the vermiform process of the stomochord which occurs in the Spengelidæ, and it may no doubt be compared with this structure.

What is doubtful is its primordial significance. As a first step in the discussion, the name arbitrarily given to it by Masterman should be dropped, because it involves a simple begging of the question.

The following proposition may therefore be stated categorically :—The "notochord" of the Pterobranchia represents the vermiform process of the stomochord of the Enteropneusta (Spengelidæ) ; but there is not sufficient evidence upon which to found an opinion as to its antecedent history.

In the process of regional differentiation of the entire body, which is such a characteristic feature of the Enteropneusta, the part of this influence devoted to cephalisation has, as has been already mentioned, led to serious changes at the anterior end

[1] The above view gives an adequate explanation of Roule's ventral diverticulum sufficient at least to show that the extraordinary theoretical excursion which this author makes is quite superfluous. Roule compares Actinotrocha directly with the Vertebrates because the Enteropneusta are "quelque peu aberrant." As a fact there is, in my opinion, reason to suppose that the Enteropneusta are even nearer the direct line of Craniate descent than Amphioxus. To set aside the Enteropneusta as aberrant forms argues ignorance of the group.

Reference.—Louis Roule, "Sur la place des Phoronidiens dans la classification des animaux, et sur leurs relations avec les Vertébrés," 'C. R.,' t. cxxvii, 1898, p. 633.

[2] S. F. Harmer, "On the Notochord of Cephalodiscus," 'Zool. Anz.,' 1897, p. 342. (Masterman's reply thereto, ibid., p. 443.)

of the trunk. Not only does a portion of the gut become pro-
jected into the proboscis, with the result that its lumen has
become vestigial and its walls rigid, but gill-slits have been
abolished from the anterior portion of the gut which lies in the
collar region.[1]   Masterman's pleurochords lie in the collar or
lophophoral region, and from his writings [2] they appear to be
vestiges of the gill-clefts which still persist in Cephalo-
discus.

As we have seen, the stomochord of the Enteropneusta is
a derivative of the collar-gut, and retains vestiges of structures
formerly serving another function in the post-oral collar region.
Thus we may conclude, in accordance with the preceding
considerations, that the pleurochords of Actinotrocha, the
gill-clefts of Cephalodiscus, and the lateral pouches of the
enteropneustic stomochord are the persistent vestiges of primi-
tive gill-clefts belonging to that portion of the body which, in
the Enteropneusta, is now specialised as the collar region.
The great series of truncal gill-clefts is entirely lacking in
the sessile forms, just as in the Ascidians there are strong
grounds for the interpretation of the numerous branchial stig-
mata as having originated by the subdivision of a single pair of
gill-slits[3] which persist in their undivided condition in Appen-
dicularia.[4]

[1] In Amphioxus the first larval gill-slit closes up.

[2] A. T. Masterman, "On the Further Anatomy and the Budding Processes
of Cephalodiscus dodecalophus," 'Trans. Roy. Soc. Edin.,' vol. xxxix,
1898, p. 507.

[3] From the mode of origin of the primary branchial stigmata in Ciona
intestinalis I thought three primary gill-clefts were represented in the
Ascidians, but a study of their formation in Molgula manhattensis con-
vinced me that such an interpretation could not be upheld; and on this point
I modified my views, and am now disposed to recognise the truth of Van
Beneden and Julin's hypothesis as to the presence of one pair only of primary
slits (see A. Willey, 'Amphioxus and the Ancestry of the Vertebrates,' 1894,
p. 232).

[4] It follows from what has gone before that the anterior portion of the
body of the stomochord in Enteropneusta, that is the part intervening be-
tween the vermiform process (when present) and the region of the cæcal
pouches (Fig. 3, *a. s.*), corresponds to the functional œsophagus of Actino-
trocha; not that Actinotrocha is itself an ancestral form, but it appears to

A word is necessary as to the development of the Entero-pneusta and the significance of the direct and indirect methods of development. In the text-book before us the authors consider the direct development as the more typical. This may be so in a certain sense, but it is necessary to bear certain facts in mind.

Spengel showed clearly that the Enteropneusta are divisible into three families, but he only named one of them, namely, the Ptychoderidæ. I propose to call the other two families the Spengelidæ and Balanoglossidæ respectively. Spengel was of the opinion that the Balanoglossidæ comprise the most primitive forms, and the Ptychoderidæ the highest or least primitive forms. As I have before stated, I hold the Ptychoderidæ to be the primitive family, emphatically not the Balanoglossidæ; I think the anatomy of Ptychodera flava shows this conclusively.

The Balanoglossidæ are all northern forms (White Sea, Greenland, Canada, Massachusetts), with relatively large eggs (from $\frac{1}{8}$ to $1\frac{1}{8}$ mm. in diameter), and from the size of the egg alone we are justified in concluding that they develop directly in the manner described by Bateson in B. kowalevskii. The Ptychoderidæ [1] have small eggs (rarely more than $\frac{1}{10}$ mm. in diameter) which develop into a Tornaria larva, i. e. indirectly.

have retained some of the characters of a primitive creature, just as the Ascidian tadpole retains primitive features which have quite disappeared from the larva of Amphioxus.

The difficulty will naturally arise as to how the portion of the primitive gut, represented in the stomochord, could have been projected past the mouth. I do not think we are obliged to make an obstacle of this difficulty. The principle of segregation will temporarily account for it. That segregation has taken place is shown by the origin of such a complex structure as the stomochord from a simple primordium (the mode of development of the vermiform process of the stomochord in Spengelidæ is unknown).

There is so much on the surface which demands explanation that I have ventured on dangerous ground in the endeavour to collate the various facts.

[1] Probably also the Spengelidæ (Schizocardium, Spengelia, Glandiceps).

It is therefore a striking fact that the more primitive forms
have the indirect method of development. There is probably
a special significance in this seeming paradox, and in order to
get at the meaning of it, it is important to call to mind a
parallel case. The difference in the method of development
followed by Peripatus capensis and by Peripatus novæ-
britanniæ is, allowing for the intra-uterine environment,
precisely the difference between direct and indirect develop-
ment. The egg of P. capensis (·5 mm.) is about five times as
large as the egg of P. novæ-britanniæ, and there are not
wanting anatomical features which point to the more primitive
character of the latter species.

Thus both in the Enteropneusta and in the Onychophora
the most primitive forms pass through an indirect development;
and in both cases it is the indirect development which yields
information about the proximal relationships of the respective
groups; while the direct development apparently instructs us
in the matter of the primordial significance of the organisation
(cf. blastopore of P. capensis and body-cavities of B. kowa-
levskii).

In their treatment of the development of Amphioxus, MM.
Delage and Hérouard expose themselves to criticism at several
points. They have apparently overlooked the works of Van
der Stricht and Sobotta,[1] especially the latter, in which the
question of the polar bodies of Amphioxus is practically settled.
These authors found that the first polar body is extruded while
the egg is still inside the ovary, and a portion of the egg-mem-
brane is constricted off with the first polar body, so that the
latter comes to lie quite outside the membrane. When the
latter springs away from the egg at the time of fertilisation,

[1] Van der Stricht's paper, "La maturation et la fécondation de l'œuf
d'Amphioxus lanceolatus" ('Arch. de Biol.,' xiv, 1895, p. 469), is
quoted in the bibliography at the end of the work, but Sobotta's latest important
paper on this subject is not quoted; perhaps it is too recent. J. Sobotta,
"Die Reifung und Befruchtung des Eies von Amphioxus lanceolatus,"
'Arch. f. mikr. Anat.,' vol. l, 1897, p. 15,

the first polar body is removed from the surface of the ovum and so is lost.[1]

In their account of the later development, the authors of the Traité have been seriously led astray by the recent work of R. Legros.[2] I regret to say that this author has produced a paper of a highly destructive character, from which it would appear, to the uninitiated, that his predecessors are incapable observers. As one of his principal results he seeks to show, by transverse sections through embryos preserved in a sublimate-acetic mixture, that the præoral pit, which is such a distinctive feature of the larva of Amphioxus, arises as a solid ectodermal proliferation which subsequently hollows out.

Hatschek's account of the origin of the præoral pit from the left head-cavity has recently been confirmed by MacBride (loc. cit.) by transverse sections through embryos preserved in osmic acid.

Hatschek's nephridium, according to Legros, arises as an outgrowth from the alleged ectodermal præoral pit, and the whole apparatus is subjected to an obvious and well-fitting comparison with the hypophysis of Ammocœtes, and hence with the hypophysis of Craniates in general; in fact, he makes it identical with the hypophysis of Ammocœtes, thus leaving no room for change of function nor for evolution.

The orifice of the præoral pit of Amphioxus, considered as a cœlomic cavity opening to the exterior, has generally been supposed to be related to the proboscis-pore of the Enteropneusta.[3] From what has been said above (p. 231) it follows that the præoral pit, like the mouth, has quitted its

[1] Sobotta describes two membranes round the egg, an inner and an outer, but makes no reference to the follicular membrane described and figured by Langerhasn.

[2] Robert Legros, "Développement de la cavité buccale de l'Amphioxus lanceolatus. Contribution à l'étude de la morphologie de la tête," 'Archives d'Anatomie microscopique,' tome i, No. 4, 1897; and tome ii, No. 1, 1898.

[3] For full treatment of this difficult subject see my memoir entitled 'Enteropneusta from the South Pacific, with Notes on the West Indian Species,' now in the press; Part iii, Zool. Results.

primary association with the neuropore, the notochord inter-
vening. I knew this had happened in the case of the mouth,
my views on this point being acceptable to MM. Delage and
Hérouard, but I had not, until recently, realised that a
similar change had affected the præoral pit.

It will therefore be seen that Legros has probably touched
upon the fringe of a fundamental truth, so far as the mor-
phology of the præoral pit is concerned, although led thereto
by erroneous premises; moreover the same truth was broached
by Bateson, to whose work the author makes no reference.

The contradictory result as to the origin of the præoral pit
arrived at by Legros would, if true, very seriously discredit the
work of Hatschek, but it has nevertheless been well received,
Klaatsch,[1] for example, ingenuously and uncritically rejoicing
at the "Correctur der Hatschek'schen Angabe;" and it has
been adopted by MM. Delage and Hérouard.

Hatschek's discovery of the conversion of the left head-cavity
into the præoral pit, which has been confirmed, let it be re-
peated, by MacBride, was a matter of unbiassed observation,
and must have come as a serious shock to his sense of cœlomic
propriety. To contradict Hatschek on this point in ignorance
of the living transparent embryos, and to base the contradic-
tion entirely upon sections through material preserved in sub-
limate and acetic, is surely very rash. The Belgian author
has obviously, in this matter, been a victim of the microtome,
but it is to be feared that his results will more or less dominate
the subject throughout the next decade, since they have already
found a home in a leading treatise.

The external orifice of the club-shaped gland is a minute
pore below the anterior end of the larval mouth ; it is invari-
ably to be seen in all living larvæ before the metamorphosis,
but is not always easy to find in transverse section. Of course
Legros does not find it, and he denies its existence.[2]

[1] Hermann Klaatsch, "Ueber den Bau und die Entwickelung des Tenta-
kelapparates des Amphioxus," 'Verh. Anat. Ges. (Anat. Anz.),' 1898,
p. 184.
[2] See also E. Ray Lankester and A. Willey, "The Development of the

In his remarks dealing with the larval mouth he attempts to set aside my work on the later larval development altogether; but he does not refer to a single figure of mine, so that I do not know whether he doubts the accuracy of all of them or only of some.

During the transition from the lateral larval mouth to the median adult velum the mouth maintains its integrity, but alters its shape and rotates through an angle of 90°.

Legros wastes pages of ink in denying this rotation, i.e. in denying a self-evident fact.

He goes on to say that the larval mouth does not, in its entirety, become converted into the definitive mouth, but only its anterior portion; the posterior portion closes up by fusion of the lips; and the evidence which he brings forward in support of this assertion is neither furnished by section nor by direct observation, but by measuring the relative distance of the posterior angle of the mouth from the tip of the snout.   It is quite true that this distance becomes somewhat shorter, a fact which my figures and description render completely intelligible by the change of shape and position which the mouth undergoes.   No soldering of the lips whatever takes place, and to assert that it does so on the evidence which Legros adduces is mere trifling.

The Ascidians naturally take up the most space in this volume of the Traité, and the treatment which they receive on the whole leaves little to be desired.   In the account of budding in the Botryllidæ the authors follow Pizon's work almost entirely.   On many points Pizon's results are in opposition to the work of Hjort.   It is a subject which requires more investigation.

The volume concludes with a useful summary of facts and of theories relating to the origin of the Vertebrata, from which I will make one quotation only.   On the subject of the præ-

Atrial Chamber of Amphioxus," 'Quart. Journ. Micr. Sci.,' vol. 31, 1890, where the external orifice of the club-shaped gland is figured both as seen in toto and as seen in section.

oral lobe (p. 315) the authors say, " Chez les Tuniciers adultes, il n'existe rien de tel, mais chez leur larve on retrouve des dispositions tout à fait comparables à celles de l'Amphioxus."

I have been treated to harsh words for holding the view that the organ of fixation of the Ascidian larva represents the præoral lobe. It is therefore possibly a matter for satisfaction that this view finds favour with the authors, but I could have wished that they had been more explicit. It may be worth while to add, in order to ward off possible misunderstanding, that for my own part I am more than ever convinced of its essential truth.

Klaatsch (loc. cit.) has recently made the suggestion " mit allem Vorbehalt," " dass das kolbenförmige Drüse [club-shaped gland of the larva of Amphioxus] die Anlage des Tentakelskelets darstellen könnte."

This is an astounding suggestion to make, and it will not survive criticism. The skeletal elements of the buccal cirri commence to appear long before the disintegration and consequent disappearance of the club-shaped gland.[1]

[1] I venture to refer Dr. Klaatsch to my paper entitled "The Later Larval Development of Amphioxus," 'Quart. Journ. Micr. Sci.,' vol. 32, 1891; and to the figures on Pl. 15 accompanying the paper. He may there see for himself the vindication of what I have said above. If he doubts the accuracy of these figures, possibly in his next publication he will kindly inform us why he does so.