













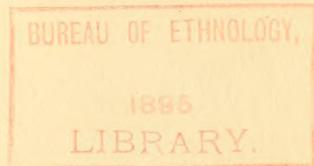
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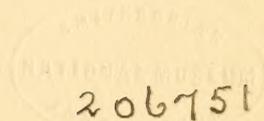
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the ali-sphenoids is rather small, and on each side of the basi-sphenoid they flatten out into broad surfaces which slope gradually to the glenoid cavities, the latter being but little above the level of the cranial axis. This shape of the ali-sphenoids does not occur in the recent species, as in correlation with the heightening of the molar crowns the glenoid cavity is placed at a higher level, so that this portion of the ali-sphenoids has become almost vertical. The orbito-sphenoids seem to have about the shape and proportions seen in the llama.

The tympanics are inflated into enormous bullæ, which in both species of *Pæbrotherium* are relatively much larger than in the recent genera, and are more rounded. In the small species, *P. Wilsoni*, they are larger and less compressed than in *P. labiatum*, and in both the long diameter is directed nearly parallel to the cranial axis, while in the modern forms it is placed at a wide angle with it. The postero-external angle of the bulla shows a deep styloid groove, "a vertical gutter ending below in a pit with a process for the conjunction of the styloid bone" (Leidy, No. 19, p. 143). The pit is decidedly smaller and shallower than in *Auchenia*, and is less distinctly separated from the groove. The stylo-hyal does not appear to have been ankylosed with the tympanic; at all events, I find no trace of it in any of the specimens which I have examined. As in the Tylopoda generally the bulla is filled with cancellous bony tissue. The external auditory meatus is a closed ring, opening slightly upwards and backwards; its rim does not project at all beyond the surrounding parts of the squamosal. The mastoid portion of the petiotic is exposed on the occipital surface, filling a very narrow space between the squamosal and the ex-occipital.

The parietals are very long, and form almost the whole of the roof of the cranium, but for most of their length they are narrowed by the great extension of the squamosals, in front of which they send down very long descending processes to meet the orbito-sphenoids. Throughout their entire length they unite to form the low and very thin sagittal crest which rises posteriorly to join the crest of the inion. Anteriorly the parietals diverge to receive the pointed ends of the frontals, and are thus much shorter in the median line than on the sides. This part of the cranium is very like the corresponding part in the modern forms, but the sagittal crest is not so prominent and the parietal

zone hardly so long; in the llama this zone is very much shorter and the sagittal crest is reduced to very small limits. The shape of the cranium in *Auchenia* is very different from that of *Pæbrotherium*, being dome-shaped with its highest point at the fronto-parietal suture, and the upper contour sloping downwards and backwards to the occiput and anteriorly to the forehead, while in *Pæbrotherium* and the camel the highest point is at the crest of the inion, and from here the upper contour inclines downward to the forehead.

The squamosals are very large and form most of the side walls of the cranium. The root of the zygomatic process is less extended antero-posteriorly than in the llama, and the process itself is rather shorter and straighter; it is received anteriorly into a deep notch of the jugal. The glenoid cavity is much extended from before backwards, and is nearly flat; the postglenoid is high and broad but very thin, and in close contact with the bulla; its articular surface is continuous with that of the glenoid cavity, but in some specimens they are slightly separated, while in the recent genera a wide and deep depression intervenes between the two. There is no elevation of the outer margin of the glenoid cavity into a process, such as occurs in the camel. The post-tympanic process of the squamosal is short and closely united with the posterior lip of the meatus auditorius. This process is placed much farther in advance of the occipital condyles than in the existing species, and in consequence the lambdoidal crest, when viewed from the side, has a much more oblique course downward and forward. This elongation of the posterior region of the cranium is common to the primitive forms of many mammalian groups, and is brought about, so far as we can judge, by the greater proportionate size of the medulla oblongata and cerebellum.

The jugal has a nearly straight course, running forward nearly parallel with the axis of the skull and forming the lower rim of the orbit in such a manner that it opens nearly straight outwards and but little forward, though this eversion of the posterior part is more strongly marked in the larger specimens of *P. labiatum*. The postorbital process of the jugal is long, slender, and curved, but does not quite reach the corresponding process of the frontal, so that the orbit is not completely enclosed by bone. The jugal extends further forward upon the

and need not here detain us; the question is rather as to how far *homological* structures may arise independently, and how far they may undergo similar modifications. Clearly, until this problem can be definitely settled one way or the other, the difficulty of making out phylogenetic series must be very great, and especially so in those cases where our information as to extinct forms is incomplete, or even sometimes where the entire skeletal structure is before us. A notable example of such a difficulty is afforded by the extraordinary animal *Chalicotherium*, the skull and teeth of which were for many years referred to the ungulates, while the feet, under the names of *Macrotherium*, *Ancylotherium*, *Morotherium*, etc., were ascribed to the edentates, but of late the researches of Forsyth Major, and Filhol have shown that they all belong to the same type. The curious little artiodactyl, *Leptomeryx*, is known in almost every detail of its skeleton, and yet its relations to the other members of its suborder are very far from clear, as it has been variously referred to the traguline, the deer, and the camel series. This is simply because we cannot yet determine how far its resemblances to other groups are due to actual relationships, and how far to parallel development. In other families of extinct mammals we are continually encountering the same difficulty, and opinions on the subject of genetic connections are in a constant state of flux. One school of observers tacitly denies all such parallelism, and this assumption leads them to regard all similarities of structure as due to phylogenetic relation, and this again results in the most complicated cross-connections and reticulations instead of the ordinary view of diverging lines. In some treatises it is gravely argued that because a given specimen has been referred by one anatomist to one group, and by another to another group, the connection between the two series is thereby made at least probable.

(3) Even more difficult to decide is the question as to how far *convergence* of development is possible, meaning by this a similar result which is reached by two or more independent lines having a different starting-point. The view which is held with regard to this point is to a great extent conditioned by opinions as to the nature of heredity, and so some naturalists deny the possibility of any real convergence, while others accept it and push it to extreme limits. Mivart, for example (No. 22, p. 509),

seems inclined to believe that the South American monkeys have an entirely different origin from those of the Old World; or an even more striking example is the supposed dual origin of the horse in the Old World and the New.

Another aspect of this same question is the consideration of the relative value to be given to resemblances and differences in discussing the relationship between various groups. Huxley (No. 13, p. 657) believes that, in forming natural orders, "it is more important that similarities should not be neglected than that differences should be overlooked." This, again, requires the consideration of the nature of the resemblances and differences, whether they are due to advancing differentiation or to the retention of primitive characters, whether the characters be adaptive or inadapative. Thus Flower says: "Too exclusive attention has been paid to the characters of the teeth in defining the family divisions of the order. The difficulty in the taxonomic use of these organs arises from the fact that the teeth of all the members of such a limited and well-defined group as the terrestrial or fissipedal Carnivora are formed on the same general type, but with infinite modifications of this type. And as these modifications are mainly adaptive, and not essentially indicative of affinity, they reappear in various degrees and combinations in many of the great natural divisions of the order" (No. 10, p. 5). Wallace, on the other hand, insists upon the instability of inadapative characters (No. 34, p. 138). The classification of the Carnivora by the characters afforded by the base of the skull, as proposed by Turner and Flower, is rejected by Schlosser (No. 28, p. 236) on the ground of his studies of extinct forms. "Aus all dem gesagten geht so viel hervor, dass die als Aeluroidea zusammengefassten Formen in *einigen* Punkten einen gemeinsamen Entwicklungsprocess verfolgen. Das berechtigt aber noch lange nicht, auf eine nähere Verwandtschaft zu schliessen." In the same way the relations of the various forms of marsupials to the placental orders form the subject of endless diversities of opinion. The question as to the relative taxonomic value of the feet and the teeth has been very hotly disputed, and the list might be indefinitely extended, showing how the construction of phylogenies depends upon the answer to this problem of convergence in its protean forms.

(4) Can a structure which has once been lost ever be regained? Here again we find that assumptions, generally tacit, but sometimes very explicit, underlie the discussion of relationships. Schlosser, for example, holds very decided views upon this point. "Dass eine Regenerirung dieser Knochen stattgefunden hätte, ist ganz undenkbar; es gibt kein einziges Beispiel, wo ein rudimentär gewordenes Organ sich wieder vervollständigt hätte. Es wird sich vielmehr höchst wahrscheinlich herausstellen, dass in Fällen, die allenfalls in dieser Weise gedeutet werden könnten, das betreffende Organ nur durch andere vorübergehend verdeckt war und dann wieder deutlich hervorgetreten ist" (No. 29, p. 420). Boas, on the other hand, does not share this opinion. "Während die Metacarpalia, resp. Metatarsalia, 2 und 5 bei den ausgebildeten typischen Wiederkäuern stets nur fragmentarisch vorhanden oder gänzlich rückgebildet sind, werden dieselben bekanntlich bei den Embryonen in ihrer ganzen Länge knorpelig angelegt und es erscheint deshalb die Deutung nicht ohne Weiteres unberechtigt die vollständige Elemente bei den erwachsenen Traguliden als einen retardirten embryonalen resp. atavistischen Charakter aufzufassen" (No. 2, p. 514).

(5) Analogous to this is the problem as to whether the differentiation of any group is a steadily advancing one (or retrograding, as the case may be), interrupted only by stationary periods of rest, or whether it should rather be regarded as progressing in a spiral, advancing on the whole and in the long run, but with many set-backs and retrogressions; such a process, in short, as Wallace has supposed to occur in the history of the flowering plants, in order to account for the endless variety and complexity in the arrangements for cross and self-fertilization (No. 32, p. 331).

(6) Another question arises with regard to the higher animals, whether advancing differentiation is always by means of the reduction of parts, or whether these may not sometimes be increased in number. More depends upon this than would at first sight appear to be the case. The question is usually answered in the negative, and nearly all phyletic series are constructed on this presupposition. If this assumption be invariably correct, it will of itself solve some of the problems which have already engaged our attention. With regard to the

teeth, Wortman says: "There are no cases known to me in which teeth have been added. On the contrary, I am firmly of the opinion that not so much as a single tooth has ever been added to the diphyodont mammalian dentition in the course of development, but that specialization has invariably gone in the other direction, as almost all evidence of palæontology goes to show" (No. 34, p. 454).

The bearing of this question upon phylogenetic discussions will be made clear by a single example. Among the *Canidæ*, as in other placental mammals, the normal number of true molars is not more than three, and, except as a rare and occasional variation, this number is not exceeded by any known fossil member of the family, or even by any creodont, even as far back as the earliest Eocene; yet the existing genus *Otocyon* has four molars, though in other points of structure this genus shows no important differences from other dogs. Nearly all palæontologists have agreed in regarding this as proof that the ancestors of the *Canidæ* had four molars, which have been retained only in *Otocyon*, and that the occasional appearance of a fourth molar in other genera of the family is clearly due to reversion (Huxley, No. 14, p. 262), and it is further argued that the dogs must be connected with the carnivorous marsupials. This view may be entirely correct, and yet it involves consequences which have an important bearing upon phylogenetic reasoning. We may suppose: (a) that all the fossil forms with three molars, which are ordinarily regarded as ancestral to the recent dogs, such as *Miacis*, *Daphænus*, *Cynodictis*, etc., etc., are in reality not connected with them at all, but that when the cynoid series is made out, it will be found to consist of forms with four molars down to comparatively recent geological times; or, (b) that there are two lines, one of which is through *Miacis*, *Daphænus*, etc., to *Canis*, and the other through unknown ancestors to *Otocyon*, both starting from a type with four molars. This alternative, however, involves the assumption of a remarkable degree of convergence, for the early forms of the *Canidæ* differ much from the recent members in the structure of the brain, skull, vertebral column, and limbs, while in all these points *Otocyon* presents no differences of importance from the other recent genera, and must therefore have reached its present identity with them by an entirely different path. (c) This fourth molar of *Otocyon*

might be regarded as being re-acquired, and therefore atavistic. If none of these alternatives can be accepted, it only remains to assume that the accessory molar has been added *de novo*. A somewhat similar case is that of the llama with four lower molars recorded by Rüttimeyer (No. 25, p. 55).

(7) In cases of the reduction of parts, is such reduction always accomplished in the same manner? For example, Fürbringer maintains that the reduction of vertebræ must always proceed from the hinder end of the column, and that interpolation or reduction of vertebræ in the median or anterior region does not take place (No. 11, p. 328). Ihering, on the contrary, expressly states that such interpolation and suppression does take place (No. 15), a view which is adopted by Parker on the basis of his studies of the development of *Chelone viridis*: "In the adult I can find only 41 developed vertebræ; viz. 8 cervical, 10 dorsals, 2 sacral, 21 caudal. But in the third and fourth stages there are at least 15 somatomes in the cervical region; in the dorso-lumbar-sacral, 12 (as in the adult); and 24 in the caudal — 51 in all. Thus we miss in the adult 7 in the cervical and 3 in the caudal — 10 in all" (No. 23, p. 47).

(8) Besides the questions of a more general nature already mentioned, there are many obvious ones of a special character, of which we may select as an example the following: What are the effects which follow as a mechanical necessity from great increase or diminution of the size of the body?

This list of "open questions" with regard to the mode in which evolution operates in any given case might, of course, be greatly extended; but for the purposes of the present investigation it will suffice. At first sight it might seem that the questions here propounded were unanswerable, because the solution of them must be drawn from the careful study of phyletic series, while the proper construction of the latter depends upon a correct understanding of the method of development. Fortunately, however, certain series of extinct mammals offer us a way of escape from this "vicious circle," because they present us a series of forms which we have every reason to believe stand to each other in the relation of ancestor and descendant, a relationship which may be verified by tracing the changes of form and function through the minutest gradations back to starting-points very different from the final results. Furthermore, in

these cases we are not restricted to a study of fragments and conjectural restorations, but of many genera we have nearly complete skeletons and satisfactory information as to geographical and geological distribution. Of course, our knowledge of these phyla is very far from complete, but it is sufficiently so to promise very important aids to the solution of the evolutionary problems which have been enumerated.

Aside from the questions as to the mode in which development operates, there are others of more fundamental importance; viz. those as to the efficient causes or factors of development and the laws of heredity. The essays of Weismann have of late aroused widespread discussion as to these factors, and have thrown grave doubts upon the transmission of acquired characters, which we have hitherto accepted as a fundamental axiom. Weismann's objections to assuming such transmission are twofold: (1) the impossibility of imagining how changes in the adult organism can so affect the germ-plasm as to cause corresponding changes in the offspring; and (2) the entire absence of proof that characters so acquired ever are transmitted. Of course neither of these reasons can be conclusive, as Weismann unhesitatingly admits. "It is perfectly right to defer all explanation and to hesitate before we declare a supposed phenomenon to be impossible, because we are unable to refer it to any of the known forces. No one can believe that we are acquainted with all the forces of nature. But, on the other hand, we must use the greatest caution in dealing with unknown forces, and clear and indubitable facts must be brought forward to prove that the supposed phenomena have a real existence, and that their acceptance is unavoidable" (No. 33, pp. 80, 81). "It appeared to me to be necessary to state this weighty and fundamental question, and to formulate it concisely and definitely, for only in this way will it be possible to arrive at a true and lasting solution of the problem. We must, however, be clear on this point — that the understanding of the phenomena of heredity is only possible on the fundamental supposition of the continuity of the germ-plasm. The value of experiment in relation to this question is somewhat doubtful. A careful collection and arrangement of facts is far more likely to decide whether, and to what extent, the continuity of germ-plasm is reconcilable with the assumption of the transmission of acquired characters from the parent body to the germ,

and from the germ to the body of the offspring. At present such transmission is neither proved as a fact, nor has its assumption been shown to be unquestionably necessary" (pp. 104, 105). "If, as I believe, these phenomena can be explained without the Lamarckian principle, we have no right to assume a form of transmission of which we cannot prove the existence. Only if it could be shown that we cannot now or ever dispense with the principle, should we be justified in accepting it. . . . Only if the phenomena presented by the progress of organic evolution are proved to be inexplicable without the hypothesis of the transmission of acquired characters, shall we be justified in retaining such an hypothesis" (p. 448).

Closely akin to this most important problem is the question whether development is always by minute gradations or whether it may not be *per saltum*.

The study, detailed and minute as it must be, of mammalian phyla, which can be regarded as at least approximately determined, promises to throw much very welcome light upon these vexed questions; for we have here, as it were, a great series of physiological experiments carried out, not through a few generations or even centuries, but through long ages. It would certainly seem that an examination of the steps of gradual and progressive change must afford weighty evidence upon one side or the other, and make clear which hypothesis best accords with the observed facts.

One of the series which will prove the most serviceable for our purpose is undoubtedly that of the Tylopoda, which has been so satisfactorily worked out by Cope (No. 6, p. 341; No. 9) both on account of their great numbers, their excellent preservation, and their persistence with steadily advancing differentiation through long periods of time. Leaving aside for the present the discussion of the mutual relationships of the various genera of this series, we have here merely to enumerate these forms in the order of their appearance in geological time. The earliest member of the series would appear to be the genus *Pantolestes*, Cope, of the Wasatch, which is followed by *Homacodon*, Marsh, of the Bridger, a genus which is very closely allied to, if not identical with, the European *Dichobune*, from which Schlosser derives the true ruminants and the tragulines. In the Bridger also occurs *Ithygrammodon*, O. S. and S., but

this form is very imperfectly known and is of no importance for our purpose. The Uinta representative of the series is *Leptotragulus*, Scott and Osborn; *Parameryx*, Marsh, of the same formation, is a mere *nomen nudum*, as to which we have no information. In the White River beds is found *Pæbrotherium*, which also occurs in the John Day, and is followed by *Protolabis*, Cope, of the Deep River and Loup Fork, *Procamelus*, Leidy, *Homocamelus*, Leidy, *Protomeryx*, Leidy, and *Megalomeryx*, Leidy, and *Pliuchaenia*, Cope, of the Loup Fork. The Pliocene yields the genera *Holomeniscus* and *Eschatius* of Cope and *Protauchaenia*, Branco, the line terminating in *Auchaenia* and *Camelus* of the existing fauna.

The Princeton expedition of 1890 had the good fortune to obtain an almost complete skeleton of *Pæbrotherium* of the lower or White River Miocene, the middle member of the Tylopodan series. This beautiful specimen, which was discovered by Professor W. F. Magie, with other specimens in the Princeton museum, and some which have been very kindly put at my disposal by Professors Cope and Agassiz, forms the main subject of this paper. The plan proposed is to give a detailed description of *Pæbrotherium*, followed by a discussion of the evolution of the skeletal and dental structures of the *Camelidæ*, the phylogeny of the family and its relation to other artiodactyls. In the second paper a similar plan will be followed for other mammalian series, and then an attempt will be made to apply the results of these studies to the solution of the evolutionary problems already enumerated.

#### PÆBROTHERIUM, Leidy.

This genus is quite abundant in the lower and middle Miocene formations of the West (White River and John Day). Hitherto it has not been adequately described. Leidy's type specimen is the much-fractured skull of an immature animal, which does not allow a complete account to be given. Cope has published some very valuable notes (Nos. 6, 8, 9, etc.) upon the vertebræ, limbs, and teeth; but these are all too brief to serve our purpose, which requires a careful consideration of all the minute points of structure.

I. *The Dentition* (Pl. I, Figs. 8 and 9).

A. *Upper Jaw*. — I have not seen any specimens of the superior incisors, but there can be no doubt that they were present in the typical number. The canine is short, compressed, and trenchant, and is relatively much smaller than in the recent genera. There is, however, not a sufficient number of specimens available to determine accurately whether or not this small size of the canine is a sexual characteristic. The first premolar is isolated by a diastema, both in front of and behind it; it is implanted by two fangs, and has a very simple, compressed, and trenchant crown, which is remarkable for its antero-posterior elongation. Pm. 2 and 3 are similar in general character, but are even more elongated; on the outer side they exhibit a prominent median ridge with anterior and posterior depressions. Some specimens show a well-marked antero-external buttress on pm. 3; in others this is but feebly developed. A very small internal festoon is shown on the posterior half of the crown in some individuals; others have no trace of it. Pm. 4 is much less elongate (antero-posteriorly) than the anterior premolars, and resembles the corresponding tooth in the ruminants generally in being made up of two crescents, an external and an internal one.

The true molars are all brachyodont, and are not strongly extended antero-posteriorly, the true molar series but slightly exceeding the premolar in length. M. 1 is the smallest of the three in both dimensions. M. 2 is slightly longer and narrower than m. 3. In each of them the crown is composed of four crescents, no trace of the unpaired fifth lobe ever appearing; the valleys are very narrow and rather shallow, so that they are obliterated at a comparatively early stage of wear. The outer wall of the crown has a distinct, though very much compressed, median buttress, and a much less prominent anterior buttress: each crescent has a well-defined median ridge. In the recent genera, and especially in *Camelus*, the posterior half of m. 3 is decidedly narrower than the anterior half; in *Pæbrotherium* this difference is indicated but slightly. The presence of internal basal pillars is subject to much variation. In one specimen I find a minute trace of such a structure on m. 1 and 2, and a fairly well developed pillar on m. 3; a second specimen shows

a trace on m. 3, and none on the others, while a third specimen is entirely devoid of them.

B. *Lower Jaw.* — The incisors are small, and have simple, compressed crowns, very different from the curious, shovel-like teeth of existing species. They differ also from the latter in relative size, the median incisor being the smallest and the external the largest of the series. In position they are quite strongly procumbent. The canine, in all the specimens which I have seen, is very small, though larger than the incisors; it is more erect than the latter, and has a very much compressed crown, the anterior and posterior edges of which meet at nearly a right angle. The first premolar, as in the upper jaw, stands isolated, both from the canine and from pm. 2; it is implanted by a single stout fang, and has a very small simple crown. The other premolars increase in size from pm. 2 to 4, and are all much alike, have elongate and very much compressed crowns, with an acute apex and trenchant edges; each has a distinct anterior basal cusp, and on pm. 3 and 4 there is an internal ridge which runs backwards from the median apex. This is barely indicated on pm. 3, but is well shown in 4, and in some specimens encloses a distinct "lake" with the external wall; in others it is open internally. The molars are elongate but very narrow, and show a distinct tendency toward hypsodonty; the valleys are very narrow, but perfectly simple, and not complicated by any projections from the walls; the internal faces are much flattened, and there are no pillars or anterior "compression-folds," which are so conspicuous in *Auchenia*. The fifth crescent of m. 3 varies very much in size, being nearly twice as large in some specimens as in others. Basal pillars are much less frequent than in the upper molars. I have seen them in but one specimen, and then as a mere rudiment on m. 1.

The chief peculiarity of the dentition of *Pæbrotherium* consists in the very elongate, simple, and trenchant premolars which recall those of *Xiphodon* rather than those of any existing ruminant.

*The Milk Dentition.* — I have not been able to determine whether the first premolar has a predecessor or not; at all events, the tooth which represents it in the temporary series is of similar size and constitution. The second upper milk-molar (D. 2) is like its successor pm. 2 in the permanent set, but the

third one is very different ; it consists of a posterior pair of crescents, internal and external, while the anterior portion of the tooth is a long cutting blade with hardly a rudiment of the antero-internal lobe. In the structure of D. 3 *Pæbrotherium* thus agrees with the tragulines and the more ancient selenodonts generally ; seen from the outer side there are three cusps, but only one internal one, the posterior. In *Pæbrotherium*, however, the anterior blade is very much elongated. Rüttimeyer has laid great stress upon the construction of this tooth in his classification of the selenodonts, but, as will be seen later, it is of very doubtful value. D. 4 is composed of four crescents like a true molar, but is proportionately broader. In the lower jaw the three anterior milk-molars are very similar to their successors in the permanent series ; as to the first one, it is not certain whether it is changed, though it probably is, at least in some cases. Thus in all the adults which I have seen pm. 1 is implanted by a single fang, while in some young animals the first milk-molar is inserted by two fangs, in others by only one. D. 4 is like that of the selenodonts generally, consisting of three pairs of crescents, of which the posterior pair is markedly broader than the others.

The milk dentition remains long in place, until the true molars have all appeared and are in full use.

## II. *The Skull* (Pl. I, Figs. 1-3, 7).

In general appearance the skull of *Pæbrotherium* is decidedly like that of the llama, though with many important differences. The cranium is short and rounded, the face very long and tapering ; the upper contour of the skull is nearly straight, the orbits very large and prominent and situated further back than in either of the living genera ; the occiput is rather high and narrow, the face very shallow, especially anteriorly, and the narial opening is low, narrow, and nearly vertical. The zygomatic arches are rather short and very slender. The cranio-facial axis is straight, and the sagittal crest is long, but low and thin.

Examined more in detail, the skull of *Pæbrotherium* exhibits its tylopodan affinities very clearly, though, as would naturally be expected, in a less extreme degree than in the existing forms. The basi-occipital differs in shape in the two species ;

in *P. Wilsoni* it is long, narrow, and rounded, being reduced to a mere rod by the enormously inflated tympanic bullæ, while in *P. labiatum* the more moderate size of the bullæ allows it to expand into quite a broad plate, with well-defined keel and lateral rugosities. The condyles are sessile, not projecting at all behind the plane of the occiput; inferiorly they meet in the median line, and are not separated by a groove, as is the case in the recent species. Though the articular surface is continued well forward on the basi-occipital, there is not formed that accessory surface for the inferior arch of the atlas, which is to be found in the camel. The ex-occipitals are broad and low; the supra-occipital high and narrow, forming a prominent lambdoidal crest, and is continued well forward upon the roof of the cranium. The shape of the occiput and especially of the crest is rather more like the condition found in *Camelus* than in the llama; the median line is strongly prominent, caused partly by the shape and position of the vermis of the cerebellum, partly by a thickening of the bone in this region and development of a diploëtic structure. The foramen magnum is nearly circular in outline, and differs from that of the recent species chiefly in the character of the upper margin, which is more horizontally directed, and in the median line is notched, with a slight projection on each side of it. The paroccipital processes are quite long, broad, and very thin plates, ending in an obtuse point; they are flattened antero-posteriorly, and when seen from the side present hardly more than their edges to view; for most of their length they are closely applied to the auditory bullæ. These paroccipital processes are placed more in advance of the condyles than in the recent species, and are separated from them by deep fossæ.

The basi-sphenoid is longer and narrower than the basi-occipital, and, like it, is different in the two species, being decidedly broader and more flattened in *P. labiatum*; its anterior termination is just within the pterygoids. The presphenoid is so much obscured by the long, sloping vomer that very little of it is visible. The alisphenoids have narrow descending pterygoid plates, which, compared with those of the llama and more especially the camel, are extremely short, and terminate in distinct hamular processes, which, however, are by no means so prominent as in the modern species. The ascending portion of

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ON THE OSTEOLOGY OF PÆBROTHERIUM: A  
CONTRIBUTION TO THE PHYLOGENY OF THE  
TYLOPODA.

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ALTHOUGH the theory of evolution is now accepted as an established fact by almost all naturalists, this general agreement does not extend beyond the point of believing that the present organic world has arisen by descent from simpler forms. The application of the theory to concrete cases is beset with grave difficulties, and gives rise to the most divergent views. The uninitiated reader who takes up a monograph upon some animal group may well be surprised to see the minuteness and accuracy with which the genealogy of the series is set forth, and the relationships of the various genera and species marshalled in orderly array. But another treatise upon the same animals will contain an equally complete family tree, which contradicts the first in almost every particular. To some extent this almost hopeless divergence is inherent in the very nature of the problem, it being largely a question of the value of evidence and of the balance of probabilities, as to which men must be expected to differ; but there is another potent cause of the discrepancy. When the contradictory phylogenetic schemes are analyzed, it is frequently found to be the case that the discussion rests upon certain postulates and assumptions, sometimes explicit, generally only implied, and even apparently uncon-

scious. Generally these postulates are, in the present state of knowledge, incapable of proof, and they appeal with very different force to different minds: what to one appears almost self-evident, another regards as not even probable. To remove this confusion, the first step is obviously to enumerate the assumptions upon which so much morphological reasoning is founded, and a few of them are therefore here stated, taking, however, only those which are applicable to the problems of mammalian phylogeny. No doubt every morphologist will find it easy to make a list of many such open questions which confront him in his own field, and perhaps they will need to be separately answered for each of the greater groups of living things, for we have as yet no right to assume that what may prove to be true of one group may safely be applied to another. These questions may be grouped together under the general inquiry as to the *laws of evolution*, or the *mode* of its operation.

As examples of the more obvious of these problems which especially affect the discussion of mammalian phylogeny, the following may be selected:—

(1) Is a genus which consists of several species, of single or multiple origin? Let us assume that genus A is descended from genus B, from which it differs by the presence or absence of some character. Now have all the species of A been derived from a single species of B, which first assumed the structure characteristic of A and then differentiated along diverging lines, thus forming several species of the new genus? Or, on the other hand, have several species of B independently assumed the new common character, so that species of one genus may be more closely related to those of the other genus than to each other? Or, again, does sometimes one method obtain and sometimes another?

(2) This question may be stated in more general terms by inquiring how far *parallelism* of development is possible; meaning by parallelism that forms having a common origin may independently run through a similar course of evolution, and finally arrive at similar results. The question here becomes of great importance, but of immense complexity and difficulty, because if we admit the possibility of such a mode of development, how is the extent to which it may go to be determined? The principle of analogical structures is thoroughly recognized,

face than in either of the living genera, and there is a marked rugosity for the attachment of the masseter muscle. The lachrymal is rather small, but extends more on the face than in the camel, and articulates with the frontal, maxillary, and jugal, but not with the nasal, from which it is separated by a process of the maxillary. There is, however, no such vacuity at this point, as occurs in the llama and to a less extent in the camel. The lachrymal foramen is double, and is situated within the rim of the orbit.

The frontals are broad but short; they are widest just above the orbits, and from this point they taper in posteriorly and are received into a deep notch formed by the diverging parietals. From the anterior end of the sagittal crest distinctly marked supra-orbital ridges diverge, and curving forward and outward, terminate in the long and rugose postorbital processes. Near the front of the upper rim of the orbits there is a deep and widely open notch. Anteriorly the frontals terminate little if any in advance of the front of the orbits. There are considerable frontal sinuses, but they do not produce any bulging of the skull. The frontal zone of the cranium is less developed than even in the camel, and has hardly any share in roofing over the cerebral hemispheres. The orbits are very large and situated low down in the face; they are much farther back than in the camel, the anterior rim being over the second molar, and in some specimens over the third. This is a decided advance over the condition found in the primitive selenodonts generally. The alveolus of the third molar makes a hardly noticeable projection into the antero-inferior portion of the orbit. The orbits are also remarkable for their depth, which is so great that a veritable interorbital septum is formed as in the tragulines. In existing tylopodans there is no such appearance.

The nasals are very different from those of either of the recent genera, especially in their greater length. At their junction with the frontals they are quite broad, but rapidly taper, and for most of their length they are extremely narrow: anteriorly they extend nearly to the tips of the premaxillaries.

The maxillaries are long and low; the alveolar portion is especially low, in correspondence with the brachyodont condition of the molars, and thus the inferior rim of the orbit is separated from the teeth by a much narrower space than in the

modern types. But even the facial portion of the maxillaries is very low, especially in front, and the nasal chamber is not nearly so high as in the camel and llama. Just below the line of suture with the nasals there is a long depression in the maxillaries, which is constant in all the specimens, and cannot therefore be entirely due to pressure. Seen in section the nasal passage thus has a curious shape, very narrow above, but broad and very low beneath. Posteriorly the maxillary sends up a short process between the lachrymal and nasal, which reaches the frontal, as in *Camelus*, while in *Auchenia* the vacuity developed at this point prevents more than the minutest contact with the frontal. The alveolar border is prolonged much farther back of the last molar than in the existing forms. The face of *Pæbrotherium* does not exhibit the sudden constriction in advance of pm. 3, which is so characteristic of recent Tylopoda, but tapers gradually to the muzzle, and as the premolars are still present in unreduced number, there is a much shorter edentulous region of the maxillary than in the camel and llama.

The premaxillaries are only partially preserved in any specimen which I have examined, but it can be seen that the ascending rami are short and nearly vertical, and that they are in contact with the nasals. The anterior nares have thus the low, narrow shape and nearly vertical position which occurs in *Anoplotherium*, *Cainotherium*, *Oreodon*, and in fact most of the primitive selenodonts, and very different from the long, obliquely placed opening of the recent tylopodans. Apparently the palatine plates of the premaxillaries are large in proportion and but little reduced by the incisive foramina. The palatine processes of the maxillaries are long, narrow, and tapering anteriorly, giving to the palate the triangular shape, very narrow in front, which is characteristic of the *Camelidæ*, but there is hardly any indication of the constriction of the palatal surface at the diastema behind the first premolar and re-expansion at the canine alveoli, which is so marked in the recent genera. The palatine fissure between the alveolus and the posterior nares is very shallow, though subject to considerable variation: in some specimens it hardly reaches the third molar.

The palatines are narrow and are intermediate in character between those of *Camelus* and those of *Auchenia*; they extend well forward, as far as the first molar, and have their anterior

edges truncate as in the camel, but do not form so much of the hard palate as in that animal, on account of the more anterior position of the nares: on the other hand, they have a greater extension on the roof of the mouth than in *Auchenia*. The posterior nares resemble those of *Auchenia* in shape and position; they are very long and narrow and with a lancet-shaped anterior margin which extends as far forward as the interval between the second and third molars. The canal is, however, very much lower than in the existing forms. The pterygoids are short and end in very small hamular processes, and the pterygoid fossa is a mere shallow slit. The vomer is conspicuous as a septum through nearly the whole length of the posterior nares.

The mandible has a very long and slender horizontal ramus with sinuous lower border; the symphysis is long and spout-like, but is shorter than in the modern genera; and as all of the premolars are present, the edentulous portion is very much shorter. The angle is prolonged into a great hook-like process which is far more conspicuous, though of much less vertical extent, than in the recent genera. The ascending ramus is low and more sloping than in the recent forms; the coronoid process is more recurved and pointed, and the masseteric fossa is deep but of small extent and situated very high up. The condyle is more transversely extended and less rounded than in the camel and llama, and the articular surface for the postglenoid process is very small. Aside from the great production of the angle, the ascending ramus of the jaw is more like that of a true ruminant than of the llama.

The *Foramina* of the skull of *Pæbrotherium* are for the most part like those of the modern Tylopoda. The external opening of the supra-orbital canal is placed near the median line, as in the camel; the infra-orbital foramen is over the fourth premolar, the position which it occupies in the existing species, but the less height of the alveolus brings it nearer to the teeth. The posterior palatine foramina are very far forward, opposite the third premolars, and I can detect but a single pair of them. The two optic foramina are placed low down and very close together, though not quite in contact: the outer lip is not produced into a spine. The foramen lacerum anterius and the foramen rotundum have coalesced, but the opening is not so

large as in the recent species. The foramen ovale and foramen lacerum medium occupy the same position as in *Auchenia*. There is a large postglenoid foramen which does not occur in the llama. The carotid canal is distinct from the foramen lacerum posterius. In *Auchenia* there are at the root of the zygomatic process of the squamosal three venous foramina, the anterior one of which is small, the two posterior very large: only the former is present in *Pæbrotherium*, and in both of the modern genera there is a large foramen between the mastoid and exoccipital, which is very minute in *Pæbrotherium*.

### III. *The Brain* (Pl. II, Fig. 10).

The brain of *Pæbrotherium* has been described by Bruce (No. 5, p. 39), but we shall need to examine it from a somewhat different point of view. To render the significance of the description clear, the following account of the camel's brain is quoted from Krueg (No. 18, p. 322): "Beide Gehirne [*i.e.* of camel and dromedary] fallen hauptsächlich auf durch die Charakteristica der Gehirne grosser Thiere, und zwar jenes des Kamels noch mehr als das, von einem jungen Thiere stammende, des Dromedars: gedrungene Gestalt, übergrosser, fast verwirrender Furchenreichthum und ausserordentlich starke Pronation. Zwischen Fissura Sylvii und Fissura suprasylvia sind mancherlei accessorische Furchen eingeschoben, welche die Fissura suprasylvia so hoch nach aufwärts drängen, dass sie bei seitlicher Ansicht eben nur noch sichtbar bleibt. Auf der obern Seite rückt in gleicher Weise die Fissura lateralis so stark an den (abgerundeten) medialen Rand, dass sie schon mehr der medialen als der obern Fläche anzugehören scheint. Gleicherweise rückt das hintere Ende der Fissura coronalis sammt dem Bügel auch dem medialen Rand zu, und noch über diesen hinaus. . . .

"Die Fissura rostralis ist vorhanden, bezugs der Fissura postica bestehen, eben wegen des Reichthums an Furchen, einige Zweifel über die richtige Deutung. Aehnliche Zweifel bleiben auch bezugs der Fissura diagonalis. Endlich sei noch erwähnt, dass sich die Fissura rhinalis wie gewöhnlich bei reich gefurchten Gehirnen nach vorne oben in eine Furche fortsetzt und dass der Lobus pyriformis eine Längsfurche trägt.

“Alle bisher angegebene Merkmale sind vielmehr durch die Grösse als durch die Art des Thieres bedingt. Das einzige auffallende Merkmal, wodurch sich die Tylopoden dann allerdings von den meisten Hufthieren unterscheiden würden, besteht in der schiefen Stellung der Fissura coronalis, die von hinten median, nach vorn lateral gerichtet ist.”

In *Pæbrotherium* the hemispheres are rather short and narrow, ending posteriorly a little in advance of the auditory meatus and tapering anteriorly, as in the brains of the smaller ungulates, such as the tragulines, *Moschus*, etc. In the anterior part of the hemispheres the vertical depth is conspicuously small. The cerebellum is large and completely uncovered, the cerebrum not extending over it at all. The frontal lobes of the hemispheres are extremely small, while the parietal, occipital, and temporo-sphenoidal lobes are fairly well developed. The cortex is much less richly and complexly convoluted than in the camel and llama, and the convolutions are but very slightly sinuous. The sulci which are present are, with few exceptions, those which Krueg has mentioned as being characteristic of all ungulates. In general shape and appearance the brain of *Moschus* is very like that of *Pæbrotherium*; but there are important differences, especially in the degree of “pronation” and “supination” (to use Krueg’s terms). In *Moschus*, as in *Tragulus*, the hemispheres are strongly supinated; *i.e.* the sulci, which are typically confined to the medial surface, make their appearance on the dorsal side. In *Pæbrotherium* the opposite tendency is apparent; *viz.* for the sulci of the dorsal surface to move toward the middle line. The fissura lateralis is thus brought close to the medial edge, from which it is separated only by a very narrow median gyrus; it is long and nearly straight, and is closed in front by the union of the median and medi-lateral gyri. An accessory sulcus runs parallel with the lateral for about three-fourths of its length. The suprasylvian sulcus is placed very high up, nearly, though not quite so high as in the camel: it is very long and but slightly sinuous, and anteriorly passes into the coronal sulcus. The latter, if correctly identified, is placed higher than in the recent species; and its posterior limb runs inward and forward, almost reaching the median line. The diagonal fissure, if present at all, is represented by a very short sulcus which connects the sylvian fissure at its anterior end with the suprasylvian. The

fissura postica is longer than in the camel, and has a somewhat less oblique position, running nearly parallel with the suprasylvian. Between these two sulci there is a short accessory sulcus which runs from the hinder edge of the hemisphere, and then curves downward to join the suprasylvian. The sylvian fissure is quite long and nearly straight, and passes somewhat obliquely upward and forward; it appears to be both straighter and longer than in the camel, especially the *pars posterior*, which in the camel is very short. The cast shows no indication of a *processus acuminis*. The rhinal sulcus is but very faintly marked.

The cerebellum is too much damaged in the two available specimens for accurate description. It is relatively large, both transversely and antero-posteriorly, and has a very broad, prominent vermis, which rises from the medulla at nearly a right angle, and when the skull is placed in a horizontal position, is seen to project somewhat above the plane of the hemispheres. The lateral lobes of the cerebellum are broader than the vermis, and have high, nearly vertical, posterior faces.

#### IV. *The Vertebral Column* (Pl. II, Figs. 11-23).

1. *Cervical Vertebrae*.—The atlas, as compared with that of the recent Tylopoda, differs in some important respects, especially in its greater elongation in proportion to its transverse breadth, and has a shape not altogether unlike that of *Anoplotherium*. The anterior cotyli for the occipital condyles are deeply concave and quite depressed; inferiorly, they are almost in contact in the median line; superiorly, they are separated by a deep emargination which is wider than in the existing tylopodans. In the latter the external margin of each cotylus is marked by a deep notch, which is but slightly indicated in *Pæbrotherium*. The neural arch is higher, narrower, and more convex than in the camel and llama, in which it is flattened, and the neural spine is more distinctly indicated. The inferior arch in the larger species, *P. labiatum*, resembles that of *Auchenia* in having a strong median keel with a deep depression on each side of it; in the smaller *P. Wilsoni*, this appearance is less distinct, and in the camel the arch is regularly convex from side to side. In the latter genus the anterior edge of the inferior

arch shows on each side of the median line an articular surface for the accessory facets on the basi-occipital: *Pæbrotherium* agrees with *Auchenia* in showing no trace of this. The posterior facets for the axis are high and narrow, and are reflected upon the inner surface of the arch; the facets of the two sides have a somewhat more oblique position than in the recent genera, where they lie in nearly the same transverse plane. The transverse processes differ from those of the recent genera in their much greater antero-posterior extension, as they are produced considerably behind the condyles for the axis, and terminate posteriorly in blunt points, as in the ordinary ruminants; from these points the thickened margins of the transverse processes sweep forward in gentle curves, dying away upon the anterior cotyli. Seen from the side, the edge of the process is not sinuous, but nearly straight. In *Auchenia* the transverse processes project hardly at all behind the facets for the axis, and in the camel they terminate in advance of these surfaces. In both of the living forms the edge of the transverse process is bent in a sigmoid curve, running anteriorly and dorsally. The foramina of the atlas are much as in the recent genera. The neural arch is perforated by a foramen for the superior branch of the first spinal nerve, and the forward extension of the transverse process converts the anterior notch at its root into a foramen. The posterior opening of the vertebrarterial canal enters the base of the transverse process from behind, while in the camel and llama it is placed upon the dorsal side.

The axis has already assumed a strikingly tylopodan character. The centrum is very long, narrow, and depressed, and is faintly keeled throughout its length, the keel terminating behind in a high and quite rugose hypapophysial tubercle. The anterior end of the centrum is quite suddenly expanded to form the articular surfaces for the atlas, which rise high upon the sides of the neural canal, and inferiorly are continuous with each other and with the facet upon the ventral face of the odontoid process. The lower edge of this compound facet is, however, emarginated in the middle line, indicating that formerly the surfaces of the two sides were separated, while in the existing forms of both Pecora and Tylopoda this margin is uninterruptedly curved from side to side. The odontoid process is peculiar in being exceedingly short and semi-cylindrical in shape,

the inferior surface being convex and the superior flattened, and the free anterior margin is gently rounded, not abruptly truncated. In the existing genera of the *Camelidæ*, as well as in the true ruminants, the odontoid process is spout-like, with deeply concave dorsal surface, while that of *Pæbrotherium* resembles rather the odontoid of *Anoplotherium*, the *Oreodontidæ*, and other primitive selenodonts, except that it is decidedly smaller. The anterior end of the axis in *Pæbrotherium* differs from that in *Camelus* in being much less oblique, and in the fact that the odontoid is not directed dorsally as well as forwards: in these respects it is more like the axis of the llama. The posterior face of the centrum is slightly concave. The neural arch is high and narrow, and the neural spine is expanded into a high thin plate, which is very different in character from the spine of the recent genera, in that it is both higher and longer (antero-posteriorly), projecting behind the postzygapophyses, while in the llama, and especially in the camel, it terminates some distance in front of the zygapophyses, ending in a bifid rugosity, which is not indicated in *Pæbrotherium*. The postzygapophyses are small and slightly concave from side to side. The transverse processes are broken away in all the specimens which I have had the opportunity of examining, but it is evident that they were short and very thin, depressed plates. The anterior opening of the vertebrarterial canal is placed laterally, as in the camel (but not so far forward); in the llama the opening is inferior rather than lateral. This canal appears to enter the neural canal a little more than half-way toward the posterior end, though it is difficult to decide this question with accuracy from the available specimens. The pedicels of the neural arch are perforated by the second pair of spinal nerves.

The third cervical is slightly longer than the axis, and has a narrow, depressed centrum which broadens posteriorly, so that the hinder face is much broader than the front: the latter is slightly convex, the former concave. Throughout the entire length of the centrum there is an inferior keel, which, for the anterior two-thirds of its course, is a faintly marked ridge, but then becomes much more prominent and ends behind in a rugose tubercle. The transverse processes expand posteriorly and terminate in flat, depressed wing-like projections. There is already an indication of a division of the process into anterior

and posterior portions, but the former has not attained any such development as appears in the camel. The neural arch is low in front and rises behind, and the pedicels are deeply notched anteriorly for the passage of the spinal nerves. The neural spine is represented only by a very feebly marked ridge. The postzygapophyses are much larger and diverge much more strongly than the prezygapophyses, and from the base of the latter a sharp ridge runs posteriorly along the side of the pedicel of the neural arch. There is in this vertebra no visible opening for the vertebrarterial canal.

The fourth cervical is slightly shorter than the third, measuring about six-sevenths of its length, but is otherwise very much like it. The anterior portion of the transverse process is, however, more developed, and more clearly distinguished from the posterior portion, and projects downward, somewhat as in the recent forms, but to a much less marked degree. The inferior keel and tubercle are more prominent than on the third vertebra.

The fifth cervical is shorter than the fourth, about five-sevenths of its length, but differs from it in no other important respect, except that the separation of the transverse process into anterior and posterior portions is more distinct. On both of these vertebræ the down-projecting anterior portion of the transverse process is very different in shape from that which occurs in the recent genera, being much less massive and rugose, and having thickened and regularly curved margins, which extend somewhat in advance of the anterior face of the centrum. Neither this vertebra nor its predecessor has a neural spine or visible vertebrarterial canal.

The sixth cervical is strikingly different from the others, and is less like its representative in the modern genera than any other vertebra of the neck. The centrum is considerably shorter than that of the fifth vertebra, which, in the specimen we are describing, measures 56 mm. in length, while the sixth measures but 45 mm., and is higher in proportion to its breadth. The anterior face is quite strongly convex and nearly hemispherical in shape, the posterior as strongly concave. The inferior keel and tubercle are almost obsolete. The neural arch is high and is occupied throughout its length by a thick neural spine, which is unfortunately broken away in the only

specimen before me, so that its height cannot be determined, but it was obviously much better developed than in the llama, and was apparently quite as large in proportion as in the camel. The pedicels of the neural arch are higher than in the recent genera, and the zygapophyses project farther in front of and behind the centrum. The transverse process is a long, stout, depressed plate, which is much more prominent, and has a greater antero-posterior extent than in the living species, and the base of the process is perforated throughout its entire length by the vertebrarterial canal, which is not the case in the camel or llama. Beneath, and slightly in advance of the posterior opening of the vertebrarterial canal, there is another large foramen, which, however, merely enters the bone and does not perforate it (Pl. II, Fig. 16 *vc'*). This second foramen is likewise absent in the modern Tylopoda. The inferior lamella is a very large and massive plate, which is longer than the centrum and very different in shape from that of the llama. In the latter the lamella is separated into two portions, an anterior one, which is compressed and projects downward, and a posterior one, which is depressed and projects outward. In *Pæbrotherium* this separation does not occur, the lower margin of the lamella being entire, and giving the whole vertebra an appearance quite like that of the horse. The vertebra is decidedly shorter in proportion than is the case in the llama. The sixth cervical of *Camelus dromedarius*, as figured by De Blainville, resembles that of the llama in the division of the lamella, while in a specimen of *C. bactrianus* I find this vertebra more like that of *Pæbrotherium*.

The seventh cervical is the shortest vertebra of the series, much shorter, proportionally, than in either of the living types. The centrum is broad and depressed for most of its length, but in advance of the transverse processes becomes suddenly constricted to form the small and nearly hemispherical anterior face. The posterior face is concave, broad, and low, and shows facets for the first pair of ribs. The pedicels of the neural arch are high, the neural spine thick and inclined forward, the prezygapophyses large, widely separated, and projecting more in advance of the centrum than is the case in the recent species. There is only the faintest trace of the hypapophysial keel and tubercle. In a specimen of this species kindly lent to me by

Professor Cope I find a minute canal through the base of the transverse process, but this is probably an individual peculiarity.

It will be plain from the foregoing description that the cervical vertebræ of *Pæbrotherium* have already assumed the features characteristic of the Tylopoda, but in a somewhat less marked degree than in the recent forms of that group. Indications of a more primitive condition are found in the structure of the transverse processes, the retention of the vertebrarterial canal in the sixth vertebra, the shape of the atlas, the character of the odontoid process, and the less elongated and less massive development of the neck as a whole. If we take the length of the humerus as a standard, and call that 100, the length of the neck in *Pæbrotherium* would be 197; in *Auchenia*, 280; and in *Camelus*, 286.

*The Dorsal Vertebræ.* — The number of dorsals characteristic of *Pæbrotherium* cannot yet be definitely determined, as no specimen has as yet been found with the series complete. In the individual upon which this description is for the most part founded, there are preserved twelve vertebræ of this region and, in addition, a fragment of a centrum which probably represents a thirteenth, though it may perhaps belong to a lumbar. The first dorsal has a centrum which is nearly as long as the last cervical, and is broad and flattened from above downward; the anterior rib-facets are nearly flat, but are on projecting processes, very much as in the llama. The inferior face of the centrum has on its anterior part a broad ridge with raised and rounded margins, and on each side of this a small pit, all of which occur also in *Auchenia*, the first dorsal of which this vertebra closely resembles, though its centrum is decidedly longer in proportion. The prezygapophyses are larger, higher, and project more in advance of the centrum than in the recent forms; the transverse processes, on the other hand, are rather shorter, and end in a large, deeply concave facet for the tubercle of the first rib.

The second, third, and fourth dorsals have centra which are shaped very much like that of the first, but they gradually become less distinctly opisthocœlous, shorter, narrower, and less depressed. In the middle region of the thorax the vertebræ are relatively large and heavy, with large spines which slope strongly backward; but these spines are very much more slen-

der than in the existing tylopodans, and so far as can be judged from the specimens at hand were also proportionately longer. Metapophyses first appear on the ninth vertebra, rising from the transverse process just above the facet for the tubercle of the rib; they increase in size on the tenth and eleventh, but retaining the same position, while on the twelfth and thirteenth they shift to the prezygapophyses. The centra of the posterior dorsals become elongated, broad, and depressed, and have nearly flat faces. The spines are strongly inclined backward until the twelfth vertebra is reached, which is the anticlinal, and has a curious plate-like spine, with deeply concave anterior and nearly straight and vertical posterior margin. The last dorsal has a broad, plate-like spine, like that of a lumbar vertebra. On the eleventh vertebra the postzygapophyses tend to become cylindrical, and are received into the concave prezygapophyses of the twelfth, on which vertebra and the thirteenth these processes are of the interlocking cylindrical type common to all artiodactyls. The spinal nerves pass out between the neural arches, and in no case are the pedicles perforated by them. The chief difference between the dorsal vertebræ of *Pæbrotherium* and those of the recent Tylopoda lies in the character of the spines, which in the latter, and more especially in the camel, are extremely massive, while in the Miocene genus they are very slender.

The *lumbar vertebræ* probably number six, or perhaps seven, and are relatively large. The centra are long, broad, and depressed, and become more so as we pass backward: they have nearly flat or slightly opisthocœlous faces, and are keeled inferiorly; while in the posterior part of the region there is a faintly marked ridge on each side of this keel. Both the neural spines and the transverse processes are, unfortunately, broken away in all the specimens which I have seen; but from the fractured surfaces, it is clear that the latter had a greater antero-posterior extent than in the recent genera, and that the neural spines were more compressed and decidedly less massive. The zygapophyses are of the typical interlocking shape, but they differ in detail from the structure seen in the modern genera. In the camel an additional complication has arisen, in the appearance of a concave surface above the postzygapophyses, the episphe-nial process, which also occurs in several of the true ruminants.

Naturally, the prezygapophyses are modified to fit them. In the llama these processes appear irregularly, sometimes present on one side and not on the other, and are often absent altogether. In *Pæbrotherium* a slight beginning of the same structure may be observed on some of the lumbar vertebræ (Pl. II, Fig. 23). In this genus, also, the postzygapophyses are more angulated than in the llama, the superior and inferior articular surfaces not passing into each other by such a gentle, regular curvature.

No sacral or caudal vertebræ are preserved in any of the specimens at my disposal; but if we may judge from the analogy of its contemporaries, *Pæbrotherium* probably had a longer tail than the modern representatives of the group.

#### V. *The Ribs.*

The ribs of *Pæbrotherium* differ decidedly from those of the camel and llama in their much greater slenderness. The anterior ribs are short and flattened, but by no means so broad as in the existing species; while those of the median and posterior regions are much more slender than is usual among recent artiodactyls, and are rather to be compared to the ribs of carnivores. This is, however, usually the case among the more ancient ungulates, and *Hyrax* still retains this type of rib-structure. In the existing Tylopoda, and especially the camel, the ribs are very irregularly curved, but in *Pæbrotherium* they have only the usual outward and forward curvature.

#### VI. *The Fore Limb.*

The scapula (Pl. II, Figs. 24, 25) is, on the whole, rather more like that of the llama than that of the camel, though individual variations of considerable extent occur, which approximate the condition found in *Camelus*. In the latter the scapula is much higher and narrower than in the llama; the spine rises nearer to the glenoid cavity, and runs in a nearly median position, dividing the blade into nearly equal pre- and post-scapular fossæ; the acromion is less developed, the neck is longer and broader, the coraco-scapular notch higher and more gently curved, and the coracoid much more massive and rugose. In *Pæbrotherium* the neck is very slender and contracted (in some speci-

mens it is considerably broader than in others), and the spine rises nearer to the coracoid than to the glenoid border, making the prescapular fossa much broader than the postscapular, but the difference is not so great as in *Auchenia*, and the outline formed by the coracoid border is rather more like what we find in the camel than in the llama. The spine rises abruptly to a considerable height and runs in a somewhat straighter and less sinuous line than in either of the recent genera; the acromion is very long, expanded at the free end, and somewhat retroverted. The glenoid cavity is shallow and nearly circular in outline, the antero-posterior diameter but slightly exceeding the transverse; this varies, however, in different specimens, as does also the degree of thickening and rugosity shown by the edge of the glenoid cavity. The coracoid process is less prominent than in the existing genera and very much less massive and rugose; as in them, however, it is curved inward at the free extremity.

The *humerus* (Pl. II, Figs. 26-28) is strikingly different from that of the modern representatives of the group, and in the same way as the humerus of *Mesohippus* differs from that of the existing horses. In *Pæbrotherium* the humerus is relatively long and slender, with feebly developed ridges for muscular attachments; the deltoid ridge and hook, so conspicuous in the recent forms, are here but a roughened line; and the supinator ridge, though running far up upon the shaft, is but faintly indicated. The shaft shows the same sigmoidal curve as in *Camelus* and *Auchenia*, but to a less degree, and is very much more slender, especially when seen from the front, for the antero-posterior extent of the proximal part of the shaft is considerable. The head is strongly convex, is more sharply constricted off from the shaft, and presents more decidedly backward than in the recent genera. The external tuberosity is a high and roughened ridge, which extends across nearly the entire anterior face of the bone, and ending in a prolonged and massive hook which overhangs the bicipital groove. The upper margin of this tuberosity is slanting on the external side, projecting but little above the head, but rising high above it on the internal side. The internal tuberosity is small and is separated from the outer one only by the narrow and deep bicipital groove, the bottom of which is occupied by the very small beginning of

what Kowalevsky has named the "bicipital tubercle" (No. 16, p. 6). The bicipital groove is thus confined to the antero-internal angle of the head, and is overhung by the external tuberosity so as to be hardly visible at all when viewed from the front. At first sight, therefore, the proximal end of the humerus of *Pæbrotherium* appears to be totally different from that of the modern Tylopoda, in which the external tuberosity is but little larger than the internal, from which it is separated by a very wide interval: the bicipital groove has immensely broadened, and is separated into two parts by the bicipital tubercle, which has become almost as large as the tuberosities proper, and is situated in the median line of the humerus. Great as this difference is, it is entirely bridged over, as we shall see later, by the intermediate genera.

The distal end of the humerus is proportionally narrow; the trochlea is set somewhat more obliquely to the long axis of the shaft than is the case in the modern forms, and has a considerably greater height on the internal than on the external side—a difference which is hardly indicated in the camel and llama. The intercondylar ridge is a faintly marked, low, narrow, and rounded swelling, and differs strikingly from the broad and prominent ridge of *Camelus* and *Auchenia*. The external epicondyle is but little developed, forming merely a stout ridge, but the internal one is quite large and forms a prominent rugose projection at the postero-internal angle, very much as in the camel: in the llama this is considerably reduced. The trochlea is higher than in the recent species, and especially is carried up on the posterior side of the bone very much higher than in the camel—a mode of development which reverses that which occurs in the true ruminants. The anconeal fossa is small but deep and perforates the shaft, thus forming a small supratrochlear foramen.

The ulna and radius (Pl. II, Figs. 29–32) are firmly co-ossified throughout their length, and are remarkably long and slender, though not quite so long as in the existing Tylopoda. Assuming the length of the humerus to be 100, that of the radius is 115, while in the camel it is 125. Just below the proximal end there is a small interosseous foramen which penetrates from side to side, and above the distal end there appears to be another; at all events there is a very deep anterior fossa between the two bones at this point.

In correspondence with the narrowness of the humeral trochlea, the head of the radius is but slightly broader than the shaft. The articular surface is divided into two concave facets by a very low ridge which forms an inconspicuous projection on the anterior margin. As the external facet is much larger than the internal, this projection is internal to the median line of the head, but placed nearly in that of the shaft, for the expansion of the head is principally towards the outer side. The shaft of the radius is very slender and of transversely oval section, with the inner border somewhat sharper than the outer: it gradually thickens below the middle of its length, as well as becoming broader. The bicipital tuberosity is very small and inconspicuous, and is placed some distance below the head, on the internal border. The distal end is much thicker and broader than the proximal, though less expanded than in the modern genera. The anterior face is slightly roughened and exhibits the grooves for the extensor tendons even more distinctly than in the camel. The distal face exhibits three well-separated facets for the proximal row of carpals, which are placed somewhat obliquely to the transverse axis of the radius. The surface for the scaphoid is concave in front, convex behind, and is reflected far up upon the posterior side of the radius, giving the bone greater depth (antero-posteriorly) here than elsewhere. The lunar facet is separated from the scaphoidal by a sharp ridge: it also is concave in front, convex behind, but is not reflected upon the posterior side of the radius, except for a small articular surface which is visible on the ulnar side of the projecting posterior portion of the scaphoidal facet. The cuneiform surface is large, and covers almost the whole of that bone, the ulnar contact with it being very much reduced. The cuneiform surface of the radius is saddle-shaped, concave from side to side, and convex from before backwards, and reflected upon the posterior side of the radius, passes into the surface for the pisiform, which is more on the radius than on the ulna. There is, however, no such projection at this point as is formed by the scaphoidal facet. Large as it is, the cuneiform facet of the radius is relatively smaller than in the modern forms, where it covers the entire proximal surface of the cuneiform when viewed from the front, the ulna being pushed to the postero-external angle.

The humeral facets of the ulna are peculiar in the Tylopoda, and quite different from those which occur in the ordinary ruminants: the peculiarity is already well established in *Pæbrotherium*. Externally the articular surface is confined to the superior border of the sigmoid notch, whereas on the inner border it is continued down the anterior face of the notch, and passes without interruption into the corresponding facet of the radius. The olecranon is high, but compressed and not massive; it is continued upward in almost the same straight line as the shaft, and is abruptly truncated at the end, its superior margin sloping downward and forward, and deeply grooved by a sulcus for the extensor tendons. Both the anterior and posterior margins of the olecranon are nearly vertical. In *Camelus* and *Auchenia* the olecranon is very different, in that it projects strongly behind the line of the shaft; and the superior margin is rounded, rugose, and not grooved by a tendinal sulcus.

The shaft of the ulna is much reduced, but decidedly less so than in the modern forms, in which it is almost entirely posterior in position, and even the distal end is concealed by the expansion of the radius. In *Pæbrotherium*, on the other hand, the shaft is visible from the front for its whole length, and when viewed from behind covers half the width of the radial shaft. The distal portion of the ulna is enlarged both in thickness and depth, fitting into a deep depression of the radius just above its distal expansion. From this point the ulna tapers rapidly to its distal end, terminating in a small tip which projects somewhat below the level of the radius, and showing facets for the cuneiform and pisiform, which in old animals pass into the corresponding facets of the radius without any visible line of separation.

The *carpus* (Pl. II, Figs. 33-35) has been figured, and briefly described by Cope, who has called attention to its more important characters, but a more detailed account is necessary for the purpose which we have in view. As a whole the carpus is broad and low—a change which has chiefly affected the distal row, as the height of the proximal series is still considerable. The scaphoid is narrow but deep antero-posteriorly; its radial surface forms a low broad ridge in front, and behind a deep concavity, terminating in an elevated hook, which extends well up upon the posterior surface of the radius, and necessitates the

peculiar facet on that bone which has been described. As the inner angle of the distal end of the radius is not so prominent as in the llama, the corresponding part of the scaphoid is but slightly depressed, and its internal surface is nearly plane, aside from minute rugosities. Distally, the scaphoid shows three facets, for articulation with the trapezium, trapezoid, and magnum respectively. The first is extremely small, and is placed at the postero-internal angle of the bone. The facet for the trapezoid is concave, and relatively decidedly smaller than in the llama, which fact is intelligible when we remember that in the existing forms the trapezoid plays a much more important part than it does in *Pæbrotherium*. The facet for the magnum is nearly flat, and is relatively very large, occupying nearly the entire width of the anterior part of the bone.

The lunar is rather higher and broader than the scaphoid, but of somewhat less antero-posterior diameter. Its proximal surface is convex, and irregularly quadrate in shape. The internal or radial side is nearly vertical, and abuts against the scaphoid without the distinct excavation which occurs in the llama. There is no superior facet for the scaphoid, but the inferior facet extends almost to the upper border. Posteriorly the lunar has a bifid projection, the longer and stouter arm of which curves toward the scaphoid, the other toward the cuneiform. The distal beak is long; the magnum facet is longer and more obliquely placed than that for the unciform, the two meeting at an acute angle. In the llama they are of about the same size, and meet at a right angle.

The cuneiform is a high, narrow, and deep bone, much less cubical and massive than in *Auchenia*; its proximal surface is shaped somewhat like that of the scaphoid, but is narrower, and the facet is carried farther down upon the external side to allow for the downward projection of the ulna. This is decidedly more marked than in the recent species. Posteriorly there is a narrow, oblique surface for the pisiform, and the distal surface is entirely taken up by the narrow and somewhat concave facet for the unciform.

The pisiform is short, and differs much in shape from that of the llama and camel. The neck is small and much contracted, but rapidly expands to form the thickened, rugose, and somewhat incurved free end. The facet for the cuneiform is long

but narrow, that for the radius and ulna very small. In the llama the pisiform has a much greater vertical depth and a much less constricted neck; the facet for the ulno-radius is even larger than that for the cuneiform, and the whole bone is longer, higher, and more compressed.

The presence of the trapezium in the carpus of *Pæbrotherium* is a very interesting fact, which was first demonstrated by Cope. It is a very small bone of nodular shape, attached to the scaphoid by a minute facet, and connected also with the trapezoid and the rudimentary second metacarpal. Baur has shown (No. 1, p. 117) that the trapezium probably still occurs sometimes in the *Camelidæ*.

The trapezoid is relatively smaller than in the recent genera, and as in them shows no tendency to coalesce with the magnum. There is a single, slightly convex surface for articulation with the scaphoid; the surface for the magnum is not separated into superior and inferior facets, as it is in the llama. Distally there are two facets which meet at a very open angle: the larger one is on the radial side, and is for the rudimentary second metacarpal; the smaller one is for a process of the third metacarpal. This is another example of Kowalevsky's "adaptive reduction."

The magnum is broad and low, hardly more than half the height of the unciform. The greater part of the proximal surface is occupied by the facet for the scaphoid, which is flat in front, but behind rises upon the convexity which articulates on one side with the scaphoid and on the other with the lunar. This convexity is decidedly more prominent than in the existing genera. The anterior portion of the lunar facet slopes downward at an open angle from the scaphoidal, and is decidedly smaller. The distal surface for metacarpal III is nearly flat and of triangular shape, with the apex behind. There is, of course, no facet for mc. II, which is excluded from contact with the magnum by the connection of No. III with the trapezium. The posterior hook of the magnum has become rudimentary.

The unciform is rather high and narrow, and so descends considerably below the level of the magnum. The proximal surface is unequally divided between the small oblique lunar facet and the large transverse but sinuously curved cuneiform facet, but the disproportion is not nearly so striking as in the modern genera. In the llama, for example, the cuneiform facet is many

times broader than that for the lunar, the proportion being 3 to 1; in *Pachrotherium* it is as 9 to 5. Distally, the unciform is taken up, for the most part, by the large surface for the fourth metacarpal, but in addition there is a small but distinct facet at the inner angle for a projection of mc. III, and on the external side another and still smaller one for the rudimentary fifth digit. Both of these facets are, however, lateral rather than distal. The posterior process is well developed and forms a stout decurved hook, which is relatively longer than in the llama.

The *metacarpus* (Pl. II, Figs. 36, 37) consists of two functional digits, the third and fourth, with small scale-like rudiments of the second and fifth, all of them separate. Mc. II is very short, with a somewhat enlarged and thickened head, but tapering rapidly to a blunt point; it lies in an excavation in the radial side of mc. III, and is very closely applied to but not co-ossified with it. The proximal end is convex, and shows two very small facets, the larger of which is posterior and articulates with the trapezium, while the anterior one articulates with part of the trapezoid, but is altogether excluded from the magnum.

Mc. III is considerably elongated, but has not reached the relative length which occurs in the modern genera; its length is to that of the humerus as 85 to 100, while in the modern types the length is about 95, and in some individuals even exceeds the length of the humerus. The shaft is very slender throughout, especially in the distal third. The proximal portion of the shaft is of trihedral section, with flattened ulnar side which is closely applied to mc. IV, while the anterior surface is rounded. Near the distal end the flattening of the ulnar side disappears and the shaft becomes nearly cylindrical. The distal ends of the median metacarpals show a slight tendency to diverge, obviously the beginning of the peculiar structure which characterizes the cannon-bone of the *Camelidae*. The proximal articular surface presents a large, slightly concave facet for the magnum, and a much smaller, though very distinct one, for the trapezoid. The head rises above that of mc. IV and sends out a process which abuts against the unciform, and thus mc. III articulates with three of the carpal elements; beneath this process there is a fossa which receives the fourth

metacarpal. The distal trochlea is very narrow, hardly expanding at all beyond the shaft, and is simply convex from before backwards. The carina is entirely confined to the palmar side, and is less prominent even than in the existing members of the family. In position, it is slightly to the medial side of the middle line. Besides the carina the elevation of the medial and external borders produce keels which are much sharper and more prominent than in the llama.

Mc. IV is the counterpart of mc. III, but is decidedly more slender and flattened in its proximal half. Its head is decidedly narrower, and its apparent breadth is reduced by the overlapping process from mc. III to the unciform. On the ulnar side of the proximal end there is a deep excavation in which lies the rudimentary fifth metacarpal.

Mc. V is a very much reduced and flattened scale, even smaller than the rudimentary second digit, and is attached to the side of the unciform by a minute facet.

The *phalanges* (Pl. III, Figs. 48, 49) of the manus are very different from those of the recent Tylopoda, and would seem to indicate that *Pæbrotherium* possessed a foot like that of the typical ruminants; not the broad pad or cushion which characterizes the existing forms. The phalanges of the first row are long and slender, but much shorter, relatively, than in the llama; nor are the proximal and distal ends so much expanded as in that animal: their shape is likewise more asymmetrical, owing to the less degree of divergence of the toes. In the true ruminants the strong degree of convergence produces decided asymmetry of the phalangeal articular surfaces. In *Pæbrotherium* the groove for the carina of the metacarpals is a mere emargination of the posterior edge. The phalanges of the second row are even more unlike those of the recent genera, in that they are short and much compressed, but of considerable antero-posterior diameter, while in the camel and llama they are broad and much depressed and flattened. The ungual phalanges resemble those of the antelope and deer much more than they do those of the recent Tylopoda; they are long, high, and pointed, somewhat rounded on the outer, but quite flattened on the medial surfaces. These phalanges are sufficient to show that *Pæbrotherium* could not have had anything more than a rudimentary pad.

VII. *The Hind Limb.*

Of the *pelvis* but little is preserved in any of the specimens. The best is one consisting of the acetabulum, a considerable portion of the ilium, and the base of the ischium; this specimen is of *P. Wilsoni*, and belongs to the Museum of Comparative Zoölogy at Cambridge. The acetabulum is slightly more depressed and less circular than in the existing species and has a somewhat less prominent rim. The ilium is remarkable for its very long, shallow, and compressed peduncle. The fragment is preserved as far forward as the hinder edge of the surface for the attachment of the sacral vertebræ, and for this entire distance the ischial and acetabular borders are nearly parallel, giving to this region of the bone a very different appearance from that which occurs in the recent forms: in the llama the neck of the ilium is especially reduced in length. The expanded plate of the ilium is unfortunately broken away, but it obviously was not very large. The ischium, so far as it is preserved, is also shallow with nearly parallel borders; it does not show the high, thin, and arched crest, which is so prominent in the llama (but not to the same degree in the camel) above and behind the acetabulum. In the recent species there are above the acetabulum several prominent and rugose ridges for the attachment of the deep gluteus muscle, while in *Pæbrotherium* these are very faintly shown. The pubis, at its origin below the acetabulum, is slender and of trihedral section; it forms a somewhat more open angle with the axis of the ilium than in the camel and llama.

The *femur* (Pl. II, Figs. 38, 39) is characteristically tylopodan in appearance. Kowalevsky has called attention to the peculiarities of this bone in the *Camelidæ*, "in which the superior end of the femur is shaped on a plan entirely different from other ruminants, presenting a great resemblance to the *Imparidigitata* (*Rhinoceros*) in the breadth of the connecting bridge and the shape and position of the great trochanter." (No. 17, p. 30). In *Pæbrotherium* the proximal end is less expanded laterally than in the living cameline genera; the head is small and projects less obliquely upward than in *Auchenia*, but is set upon a somewhat more distinct neck. The pit for the round ligament is an oval depression placed upon the posterior

aspect of the head, and is shorter, shallower, and nearer the border of the head than in the llama. The bridge connecting the head and the great trochanter is narrower, shorter, and less rugose, and the great trochanter rises higher above it, producing a decided notch. Though the great trochanter is higher than in the recent forms, it is much less massive and thickened antero-posteriorly, and in consequence the digital fossa is much shallower. The second trochanter is also less developed, especially in the vertical direction, than in the llama, though relatively larger than in *Camelus*, and forms a small conical protuberance. The shaft is long, slender, and arched forward, and except for its greater slenderness, very similar to the proportions found in the recent species. With the length of the humerus taken as 100, that of the femur in *Pæbrotherium* is 125, in *Camelus* 127, and in *Auchenia* 134. The rotular trochlea is broad and shallow, with sharp external and thickened internal lip, the latter being also somewhat the higher of the two—a more decided difference than occurs in either of the modern genera. The condyles are smaller, less strongly projecting, and less widely separated than in the latter. The trochlea rises higher upon the shaft, is less strongly arched, and less oblique to the transverse axis of the distal end of the bone, than in the recent genera. The external condyle is somewhat larger than the internal, and there is no such decided notch above the latter as occurs in *Auchenia*. *Pæbrotherium* agrees with most of the true ruminants, and differs from the *Camelidæ* in the presence of a distinct pit for the insertion of the plantaris muscle above the external condyle.

It is clear from the foregoing that the femur of *Pæbrotherium* departs but little from the cameline type, and that such divergences as are observable are in the direction of the more generalized artiodactyls.

The *tibia* (Pl. III, Figs. 40-42), like all the other limb bones, is long and slender; longer as compared with the humerus than in either of the existing genera, its length being 141, as compared with 130 in *Auchenia*, and 111 in *Camelus*. The facets for the femoral condyles are large and nearly flat, and separated by a prominent bifid spine; the external facet is considerably larger than the internal, but shows no tendency to assume the peculiar recurvature which occurs in the camel. The cnemial crest is

very prominent and runs far down the shaft; on the inner side of its proximal end there is the usual deep tendinal sulcus. The lower half of the shaft is flattened antero-posteriorly and is transversely oval in section. The distal end is somewhat expanded and thickened; the external astragalar facet is somewhat larger than the internal, from which it is separated by a tongue, much more prominent than in the existing types. In each of these astragalar facets there is a shallow depression, the beginning of the interruptions of the articular surfaces which are so noticeable in the camel. The internal malleolus is very prominent and is anterior in position. The fibular facet is continuous from before backward, and though emarginated by the groove for the rudimentary shaft of the fibula, this groove is not nearly so deep as in the camel, where it divides the facet into anterior and posterior portions.

The *fibula* (Pl. III, Fig. 41) is quite as much reduced as in the modern representatives of the *Camelidæ*. The proximal end is a small spine ankylosed with the tibia, and the distal portion is a nodule which is wedged in between the tibia and the calcaneum, forming a heavy external malleolus. It projects further beyond the line of the tibia than in the recent genera, and is deeply grooved on its outer side by the sulcus for the peroneal tendons. The nodule presents articular facets upon three of its sides, a proximal one for the tibia which is not interrupted in the middle, a distal one for the calcaneum, and an internal one for the astragalus.

The *tarsus* (Pl. III, Figs. 43-47) is essentially like that of the llama, but in correspondence with the lighter construction of the limbs, is higher and narrower. The astragalus has a narrower groove for the tongue of the tibia, and, indeed, is narrower throughout. The external condyle is separated quite widely from the distal trochlea, while the internal one is separated from the navicular facet only by a small prominence. The surface for the cuboid is quite narrow, that for the navicular much wider and hour-glass-shaped. The calcaneum is relatively longer and more slender than in the llama, and is especially of less antero-posterior depth towards its distal portion, nor is there any groove above the sustentaculum, to receive a process from the tibia. When the calcaneum of the llama is viewed from behind, there is seen a projection from the posterior part of the

distal end, which embraces the lower end of the astragalus, and between which and the sustentaculum there is a deep notch: nothing of the kind is observable in *Pæbrotherium*, and the sustentaculum itself is not so prominent. The fibular facet of the calcaneum is longer, lower, and less abruptly truncated in front than in the llama, and the cuboidal surface is likewise narrower. The tuber calcis is proportionately thicker, of less depth, and with the free end less thickened and rugose: its borders are also more nearly parallel.

The cuboid is decidedly higher and narrower than in the living genera, and its facets differently proportioned; that for the calcaneum being somewhat broader than that for the navicular, while in the recent forms the reverse is the case, though the difference is not very striking. The calcaneal facet in *Pæbrotherium* is a broad overhanging shelf, strongly convex from before backwards: a small fossa intervenes between it and the astragalar surface, where the two are on the same level. The astragalar facet is narrow and simply concave from before backward; in the middle of its course it is emarginated on both sides and greatly narrowed, though not entirely interrupted, by the fossa already mentioned, on the outer side and by another on the inner side; anteriorly it rises much higher above the calcaneal facet than in the llama. The posterior hook of the cuboid is very stout, but not quite so long as in the recent species, and fits closely against the projection from the fourth metatarsal. On the internal or tibial side of the cuboid are two facets for the navicular, — the hinder one a large projecting ledge, the front one a mere smooth surface. The distal end of the cuboid displays a large, somewhat triangular and concave surface for the fourth metatarsal, which is not emarginated and interrupted as in the camel. External to this is a minute facet for the rudimentary fifth digit, but this facet is entirely lateral in position, not at all distal.

The navicular is entirely free from the cuboid, never showing any tendency to coalesce with it; it is comparatively high and narrow, but of less antero-posterior depth than in the recent forms, and is devoid of a posterior hook. The astragalar surface is concave from before backwards, saddle-shaped from side to side, and is emarginated in the middle by a fossa on the fibular side. The posterior facet for the cuboid does not form a prom-

inence as in the llama. The distal surface displays two facets, — a large and nearly plane anterior one for the coalesced ecto- and meso-cuneiforms, and behind this a small and somewhat concave one for the ento-cuneiform.

Cope has incorrectly stated that the ento-cuneiform was missing, and that the ecto-cuneiform alone supported the third digit (No. 8, p. 487). As a matter of fact, the third digit is supported by a compound bone, composed of the coalesced ecto- and meso-cuneiforms, while the ento-cuneiform is also present. The latter is the smallest of the tarsal bones; it is wedged in between the navicular and the rudimentary second metatarsal, and behind is in contact with the stout posterior hook of metatarsal III, but does not touch the latter in front. The compound cuneiform is relatively higher and narrower than in the recent genera: it has no contact with mt. II. Except for differences of proportion and a few variations in details, the tarsus of the Tylopoda had already attained in *Pæbrotherium* to substantially the same condition which it still retains.

The *metatarsus* (Pl. III, Figs. 50, 51), like the metacarpus, consists of two functional digits, the third and fourth, and of two reduced, scale-like rudiments, the second and fifth. Mt. II has an enlarged head with an oblique facet, directed downward and backward, which articulates with the ento-cuneiform; it is entirely excluded from any contact with the meso-cuneiform by the extension of mt. III over that bone. In some specimens mt. II is free, while in others it is firmly co-ossified with mt. III, though its limits are always plainly visible; it is considerably longer than the corresponding metacarpal, but is nevertheless short, and rapidly tapers to a point.

Mt. III and IV are much longer than the metacarpals, while in the recent genera the fore and hind cannon-bones are of almost the same length. In *Pæbrotherium* the length of the metacarpus is 85, that of the metatarsus 95 (that of the humerus being 100); in *Camelus* these proportions become 93 and 97, in *Auchenia* 101 and 99; so that the Miocene genus has nearly attained the modern standard so far as the length of the metatarsus is concerned. Mt. III is considerably stouter than its fellow, to which it is very closely applied, and the two were held together by the manner in which the long hook-like processes from the plantar side of the proximal ends are wedged in

between the ento-cuneiform on the one side and the posterior hook of the cuboid on the other. On the tibial side of mt. III and the fibular side of mt. IV there are near the proximal end small deep fossæ for the rudimentary metatarsals. Mt. V is never, in any specimen which I have seen, ankylosed with mt. IV, and its contact with the cuboid is very small and almost entirely lateral—a fact which we shall see to be not without importance. The distal ends of the functional metatarsals are broader than those of the metacarpals, but the carinæ are not more prominent, and are likewise entirely confined to the plantar side.

The *phalanges* of the pes are in general like those of the manus, but those of the proximal row appear to be decidedly shorter (which is not sufficiently indicated in the restoration) in the hind foot than in the fore foot. Kowalevsky has pointed out the same difference in *Anchitherium* and the horse (No. 16, p. 65).

The metapodials of *Pæbrotherium*, even the rudimentary ones, are very similar in form and proportions to those of *Xiphodon*, but with the important difference that in the latter genus the reduction is an inadaptive one, while in the former it is adaptive. Schlosser, following Cope's description of the pes, has regarded *Pæbrotherium* as inadaptively reduced (No. 27, p. 114); but this is incorrect. In the manus, mc. III is in contact with the trapezoid and has entirely excluded mc. II from the magnum, though the contact of mc. III with the unciform is still considerable. In the pes, mt. III is supported solely by the entocuneiform, the extension of mt. III taking up the whole of the mesocuneiform, and excluding mt. II from it altogether: the heads of Nos. III and IV are also on the same level, and mt. III is no longer in connection with the cuboid. This is "adaptive" reduction in its most typical form, and so far as the Tylopoda are concerned, Kowalevsky's law holds good.

#### VIII. Restoration (Fig. A).

The abundant material now at command, and especially the larger part of a skeleton belonging to a single individual, enables us to give a restoration of this curious animal, in which there would seem to be but little opportunity for error. *Pæbrotherium* was a long-limbed, slender, and graceful animal with a long neck and delicate, pointed head. In general appearance it

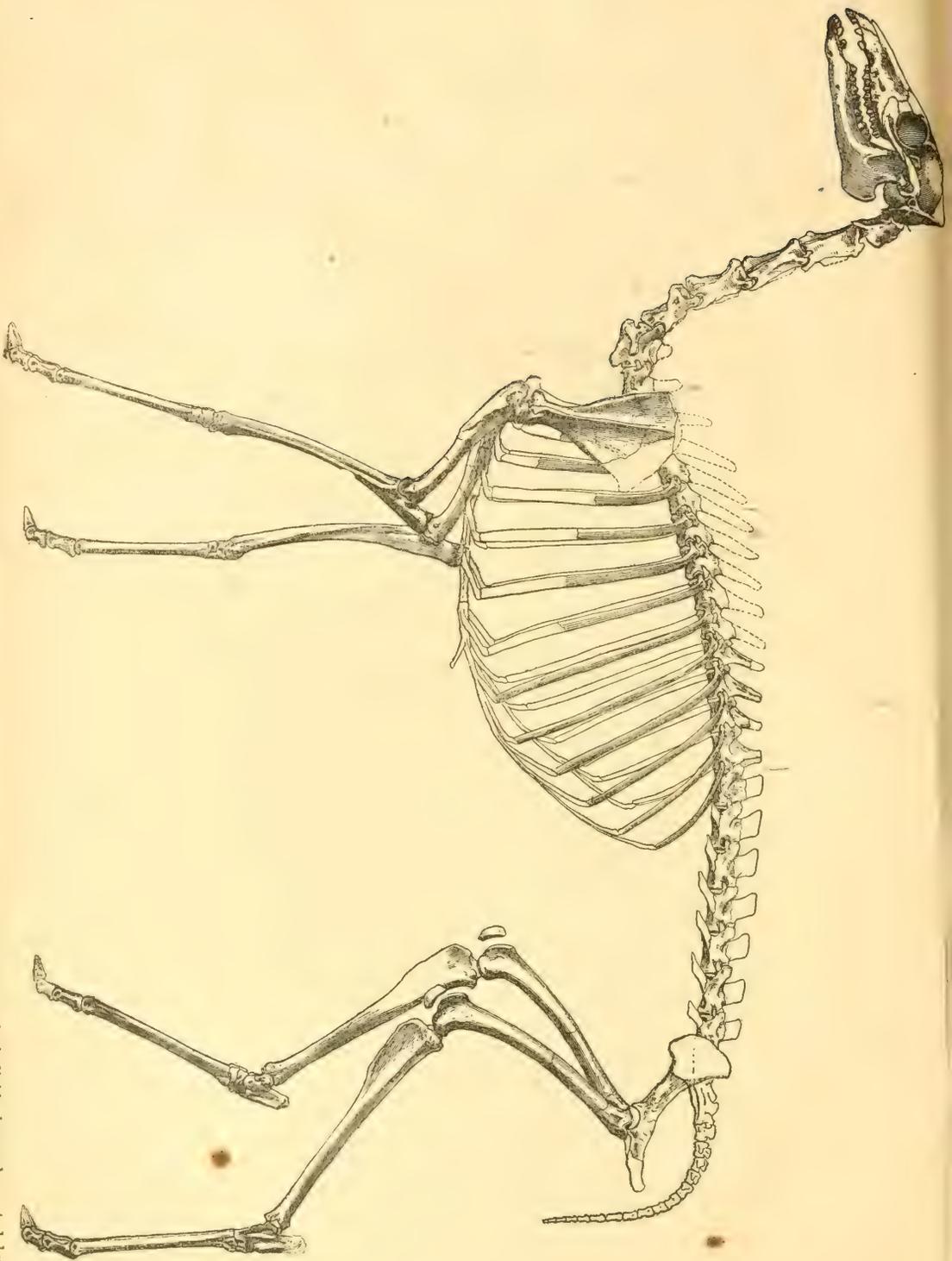


FIG. A. — *Pelecanus tibialis*, Cope. — Restoration  $\times 1/6$ . The drawing is for the most part from the skeleton of a single individual, supplemented by specimens belonging to Professor Cope and the Museum of Comparative Zoology.

was not unlike the llama, but with manifold differences. In size, the Miocene genus is very inferior to the recent one. A llama skeleton is about 112 cm. high at the shoulder, while the tallest individuals of the large species, *P. labiatum*, which I have seen, do not exceed 69 cm. in height. The head of *Pæbrotherium*, and especially the face, is longer, lower, and more pointed, and the neck, though much elongated, is still distinctly shorter than in the living genus. The thorax is longer, and, owing to the lightness of the ribs, more open in appearance; the lumbar region, on the other hand, is rather shorter. The limbs are quite as long, if not longer, and in particular more slender, giving the animal quite the look of some of the antelopes, which is increased by the fact that the metatarsals are decidedly longer than the metacarpals, and the ungual phalanges are long and pointed, very different from the nodules of the modern Tylopoda.

No other known genus from the White River beds had even a remote resemblance to *Pæbrotherium*; among European animals *Xiphodon* at once suggests itself as the one most like it in appearance, though, of course, no question of near relationship between these genera can be entertained.

#### STRUCTURAL CHANGES IN THE CAMELINE SERIES.

We have next to consider the steps by which the *Camelidæ* have reached their present differentiation, assuming for the present that the series of genera usually referred to this group represent the stages in its evolution, and reserving the discussion of relationships until the facts of structure have been presented.

##### I. *The Dentition.*

The oldest member of the Cameline series is, according to Cope (No. 9), the genus *Pantolestes* of the Wasatch Eocene. In this form the superior molars are of the primitive tritubercular type, which originally caused the reference of the genus to the pseudo-lemuroids, but are complicated by the addition of the para- and metaconules, making five in all, but the protocone is still median in position. The inferior molars correspond in structure, being of the type which Cope has named

“tuberculo-sectorial,” and consisting of an anterior triangle composed of the proto-, para-, and metaconids, and a low posterior heel or talon. The paraconid is much reduced, and in some species cannot be distinguished. The talon is more or less distinctly basin-shaped, and two cusps (the hypo- and entoconids) can be observed in it; on the last molar there is an additional median lobe, which represents the fifth cusp so universal among the artiodactyls. No other known artiodactyl (except the problematical genus *Leptochærus*, Leidy) has such a primitive molar dentition as this. There is nothing to distinguish it from some of the Condylarthra, the pseudo-lemuroids, or even certain creodonts, which is to say that it has still preserved the plan common to all these groups—a fact of the highest morphological interest.

In view of the fact first pointed out by Schlosser (No. 30, p. 267), that the premolars even when entirely like the molars in structure, have passed through an entirely distinct course of development, and that the similar parts in the two series are not homologous, the premolars of *Pantolestes* deserve careful examination. Of the superior series only the fourth is known, and this is entirely like the corresponding tooth of most creodonts, consisting of a single compressed and trenchant external cusp, the protocone, and a conical internal cusp, which may be called the deutocone. It is important to remember that the protocone is external in position, while in the superior molars it is internal. The inferior premolars are all simple, compressed, and trenchant cusps, implanted, except the first, by two fangs. More or less distinct anterior and posterior basal cusps are present, and in one specimen of *P. brachystomus* I find in the fourth premolar of one side (but not of the other side) a distinct *deutoconid* occupying the same position as in the supposed creodont genus *Chriacus*.

The second member of the series is the genus *Homacodon*, Marsh, from the Bridger, which presents us with a great advance in the dentition, in that the molars have become quadrate in outline and quadrituberculate in structure. In the upper series this change is brought about by the addition of the hypocone; strictly speaking, these molars are sextituberculate; for though the metaconule has become larger, the protoconule is frequently, if not generally, present as well, though evidently about to dis-

appear. The principal cusps are now pyramidal in shape, so that when worn they exhibit the first step toward the acquisition of the selenodont pattern. The lower molars still retain a trace of the paraconid, the talon has been raised to the height of the anterior triangle, and the hypo- and entoconids have completely separated. *Homacodon* is evidently very closely allied to *Dichobune*, and may well be identical with it, but in the absence of more complete information it will be best to separate them provisionally.

The superior dentition of the Uinta genus, *Leptotragulus*, is unfortunately not known. The lower molars are distinctly selenodont, but show their connection with the buno-selenodont type of *Homacodon* by the fact that the inner cusps are thick and conical, not flattened out into thin plates, and the outer crescents are somewhat trihedral in section, and rather angular than curved. The valleys are widely open above, but narrow rapidly below, becoming mere slits after a moderate degree of attrition. External basal pillars appear on some of the molars. The premolars are simple and trenchant, much as in the tragulines: the fourth is, however, somewhat more complicated than its predecessors, and consists of a high, acute, and compressed cone, with a small and sharp antero-internal cusp. From the inner side of the apex of the principal cusp there runs downwards and backwards a thin ridge enclosing a very narrow valley; this ridge appears to represent the deutoconid. All the teeth of *Leptotragulus* are very brachyodont, and the molars are rather broad in proportion to their antero-posterior extension; the premolars have but a moderate extension in the same direction.

In the White River genus *Pæbrotherium* the dentition is still unreduced; the canines are small; the first premolar in each jaw has become isolated by diastemata both in front and behind it, and the inferior one is implanted by a single fang. The other lower premolars are still very simple, but have become greatly elongated antero-posteriorly, and the enlargement of the antero-internal tubercle gives rise to an anterior valley. The inferior molars show a decided advance toward the modern type of structure as compared with those of *Leptotragulus*. The inner crescents are much flattened, the outer more curved; the crown has become narrower and higher, and shows a distinct tendency to assume the hyposodont condition. The upper

molars are still very brachyodont and of the typical tetra-selenodont character; the median ribs of the external crescents are still prominent, and the antero-external buttresses small. Premolars 1 to 3 are simple, compressed, and trenchant cones, much elongated antero-posteriorly; pm. 4, on the other hand, has assumed the structure which it has in all ruminants, consisting of an internal and an external crescent. Apparently this tooth corresponds to half a molar, but from what we have seen in *Pantolestes* it is plain that the protocone is here the outer crescent, while in a true molar it forms the antero-internal crescent, and the deutocone, which forms the inner crescent, has no strict homologue in the molar crown at all. It is rarely the case among Artiodactyla that the premolars become molariform, but this does occasionally occur (e.g. *Agriochærus*, *Dicotyles*); and though the molar pattern may be fully attained, the elements which compose the crown are differently arranged and are not homologous with those which occupy similar positions in the crowns of the true molars. The first step towards the assumption of the molar pattern in the last upper premolar, is the addition of a second external cusp behind the protocone, which may be called the *tritocone*. This occupies the same place as the metacone of the true molars; but as its position with reference to the protocone is entirely different, it cannot be given the same name. The addition of the tritocone produces a tritubercular crown similar to that of the primitive molars, but with the elements which compose it not homologous with those of the molar crown. A second internal cusp, which may be called the *tetartocone*, is next added, and this corresponds to the hypocone of the true molars, and completes the molar pattern. In *Agriochærus* (Fig. B) this tetartocone is still very small, in some specimens hardly noticeable.

The steps of differentiation by which the inferior premolars become molariform are not quite so clear, but they may be made out in *Agriochærus* and *Dicotyles*. Comparing pm. 4 of *Oreodon* with that of *Agriochærus*, we see that the first addition to the protoconid is a cusp on the inner side, which may be called the deutoconid, and then the only further step which is necessary to the assumption of the molar pattern, is the elevation of the talon and its division into hypo- and entoconids. The almost perfectly molariform pm. 4 of this genus retains an inter-

esting reminiscence of its previous condition, in that the deuteroconid is a conical tubercle, and that the anterior valley opens inwards in front of it, as in the true molars of *Lophiomeryx*, while in the molars of *Agriochærus* the functionally equivalent metaconid expands into a plate which closes the anterior valley. Likewise, if we compare the fourth lower premolar of *Thinohyus* from the John Day beds with that of *Dicotyles*, the same process of development may be made out: first, the addition of the deu-

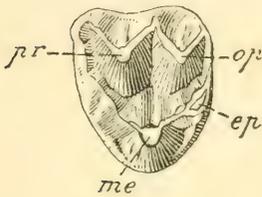


FIG. B, p. 4 of *Agriochærus latifrons*. *pr*, protocone. *me*, deuterocone. *op*, tritocone. *ep*, tetartocone.

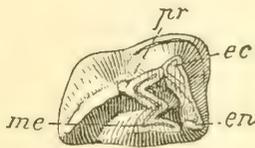


FIG. C, p. 4 of *Oreodon Culbertsoni*. *pr*, protoconid. *me*, deuteroconid. *ec*, hypoconid. *en*, entoconid.



FIG. D, p. 4 of *Agriochærus latifrons*. (Letters as in Fig. C.)

teroconid, and then the elevation and division of the talon into hypo- and entoconids. It is plain, therefore, that the parts of an inferior molariform premolar are much more nearly homologous with the corresponding elements of the molars than is the case in the superior series; the protoconid having the same position; viz., forming the antero-external crescent or cusp, as have also the hypo- and entoconids. In the upper series only one element, the protocone, is common to both premolars and molars; and while in the former it is the antero-external cusp, in the latter it is the antero-internal. It is not asserted that the transformation of the premolars always takes place in this manner, but it may be regarded as the usual method.

The camels of the John Day formation do not present any important modifications of the dentition; in some of them the first upper premolar has but a single fang, and others are decidedly reduced in size: the former Cope has erected into a separate genus, *Gomphotherium*. It seems probable that these forms are not in the direct line of cameline descent.

In the succeeding formation, the Deep River (*Ticholeptus* beds of Cope), occurs the genus *Protolabis*, Cope, which is also

continued up into the overlying Loup Fork. This animal retains the full number of teeth, but the superior premolars (the inferior are not known, unless, as is very improbable, *Protomeryx*, Leidy, should belong to the same form), are much reduced in size and especially in antero-posterior length, as compared with those of *Pæbrotherium*. The canine is longer and more pointed, and the external incisor has become caniniform and larger than the true canine. The true molars are still very brachyodont. In the Loup Fork species of *Protolabis*, *P. heterodontus*, the external incisor and canine have become very large, quite as large in proportion as in the camel and much larger than in *Procamelus*. I suspect, however, that this species will prove to belong to the genus *Homocamelus*, Leidy. Leidy describes the teeth of this genus as follows: "The caniniform incisor, the canine, and the first premolar were all separated from each other, and from the succeeding continuous row of premolars and true molars by wide-arching intervals.

"The second and third premolars (Figs. 16, 17), forming the advanced pair of teeth of the closed molar series, differ from those occupying the jaw fragments ascribed to *Procamelus occidentalis*, both in shape and relative position to each other. In *P. occidentalis* the antero-posterior diameter of the two teeth mentioned extends along the same line, and this is parallel with the alveolar border. In the present fossil the two teeth have their antero-posterior diameter directed obliquely, so that the back part of the first premolar is external to the fore part of the second. Both teeth are inserted by distinct pairs of fangs.

"The crown of the second premolar, slightly worn, is moderately compressed, conical, with its posterior portion curving outward and backward in a wing-like expansion. Internally it is bounded by a crescentoid basal ridge.

"The crown of the third premolar is a more developed form of that of the preceding tooth. The internal basal ridge is produced into a thick fold or process before and behind, extending towards the triturating border. It has nearly the constitution of the corresponding tooth, or first premolar, of the camel, but is relatively shorter and wider, and has the antero-internal fold relatively better developed. The worn triturating border exhibits a uniform surface of dentine, with the notch outward" (No. 19, p. 158).

The most abundant of the Loup Fork camels is *Procamelus*, which is represented by several species. In this genus the upper incisor series is as reduced as in the existing forms, but the first and second persist for a somewhat longer time, as Cope has pointed out. The premolars are not reduced in number: the first is implanted by two fangs, though they show a strong tendency to coalesce. The second is likewise small, with a compressed trenchant crown and small anterior basal cusp. Except for its relatively small size this tooth has changed very little from the condition found in *Pæbrotherium*. The third premolar differs considerably in the specimen of *P. occidentalis* figured by Cope from that given by Leidy. In the former it "consists of a small anterior cusp and a long posterior blade. A strong basal cingulum represents the interior crescent" (No. 6, p. 332, Pl. LXXVI, Fig. 2). This tooth is decidedly the most extended antero-posteriorly of the premolar series. In Leidy's specimen (No. 19, Pl. XX, Fig. 1) the third premolar is decidedly shorter and shows a strong tendency to form an internal crescent, by the elevation and extension of the anterior and posterior basal cusps, but which is incomplete in the middle. We have here, therefore, the formation of a tooth very similar to pm. 4, but in quite a different manner. The fourth premolar is of the typical pattern, and need not detain us. The upper true molars differ from those of the earlier genera only in their tendency to form prismatic crowns, and in the greater prominence of the anterior and median external buttresses. The median ribs on the outer walls of the external crescents are still distinct.

In the lower jaw the premolars are undiminished in number, but considerably reduced in size. The first is a small, simple cone, implanted by a single fang. The second is larger and compressed, with indications of internal basal cusps. The third and fourth are much more elongate and compressed; when viewed from the outer side, they show two concavities separated by a median convexity: internally there are parallel ridges which enclose one or two valleys. The true molars are more hypsodont than in the earlier forms, more flattened on their inner walls, and the fifth lobe of the last one is larger and contains a more distinct valley.

Contemporary with *Procamelus* is the genus *Pliauchenia*, Cope,

which resembles the former in the character of its dentition, but has lost one premolar, the second, in the lower jaw. "The canine and first premolar are especially short, and separated by a very short diastema; that separating the first and third premolars is also short, being less than that which separates the first and second in *Procamelus occidentalis*" (Cope, No. 6, p. 344).

In the Pliocene beds occur the highly specialized genera *Holomeniscus* and *Eschatius*, Cope. In these the reduction of the premolars has reached its maximum, there being but one left in each series. In the former genus the fourth superior premolar is of the ordinary pattern, composed of an external and an internal crescent, while in *Eschatius* this tooth is reduced to a simple cone.

In the existing genera the changes in the dentition are chiefly confined to the increased size and trenchant shape of the external upper incisors and canines, and the reduction in number and size of the premolars; in *Camelus* the number is  $\frac{3}{2}$ , and the first superior premolar is a large caniniform tooth. In *Auchenia* this tooth is lost, and the premolars reduced to  $\frac{2}{1}$ ; the molars are prismatic, though by no means to the same degree as in the Cavicornia, and the anterior and median buttresses of the upper ones much more strongly developed. In *Auchenia* there are strong transverse "compression folds" on the anterior walls of the lower molars.

The *milk dentition* is not known in any of the older genera of the series. In *Pæbrotherium* it agrees essentially with that of the tragulines and the more ancient selenodonts generally. The last upper milk molar resembles a true molar in form and construction. D. 3 is composed of a posterior pair of crescents and a long anterior blade consisting of two imperfectly separated external cusps and but the rudiment of an internal cusp. D. 1 and 2 resemble the corresponding teeth in the permanent series, if, indeed, the first one changes at all. In the lower jaw D. 1 appears to change, at least sometimes, for in some specimens it is implanted by two fangs, whereas pm. 1 has but a single root; in other specimens the first tooth in the temporary series is like that in the permanent set. D. 2 and 3 are not different in any important respect from pm. 2 and 3. D. 4 has the constitution usual among the selenodonts, consisting of three pairs of cres-

cents arranged in transverse pairs, of which the anterior pair is by far the largest. In *Procamelus*, to which genus I attribute the "milk dentition of a camel" figured by Cope (No. 6, Pl. LXXVII, Fig. 4), the character of the temporary molars has undergone an important change. D. 2 is like pm. 2, consisting of an elongated and trenchant external cusp, and an imperfect internal crescent formed by the elevation and extension of the anterior and posterior basal cusps in the manner already described. D. 3 is the longest tooth, antero-posteriorly, in the temporary series. It consists of two pairs of crescents, of which the anterior pair is the smaller and especially narrower: the rudimentary antero-internal cusp of *Pæbrotherium* has now become a complete crescent. The accessory anterior basal cusps of the White River genus now forms a transverse "compression fold" across the whole of the front face of the tooth. D. 4 is like a true molar in constitution, and has a fairly well developed basal pillar at the junction of the two inner crescents. The upper milk incisors and canines, as well as the entire lower temporary dentition, are unknown to me.

In the recent genera of the *Camelidæ* the milk molars are very much reduced. In the upper jaw D. 3 has a compressed anterior half, and is of irregular molar form. D. 2 is rudimentary. In the lower jaw D. 4 is of the usual selenodont pattern; D. 3 is very much reduced with the anterior portion trenchant, and D. 2 is wanting. There is thus in the cameline phylum a similar change in the character of the milk dentition to that which occurs in the true ruminants, *Gelocus* and *Prodremotherium* agreeing in this respect with *Pæbrotherium* and the tragulines. As I have pointed out elsewhere (No. 31, p. 370), the same transition occurs in the *Oreodontidæ*, *Oreodon* having the older type of milk dentition, in which D. 3 consists of a posterior pair of crescents and an elongated antero-external blade, but no antero-internal cusp, while in *Merychynus* this tooth is molariform and consists of two pairs of crescents. The transformation has occurred, therefore, at least three times independently among the selenodonts, in the true ruminants, the camels, and the oreodonts.

## II. *The Skull.*

The skull of the more ancient genera of the tylopodan series, *Pantolestes*, *Homacodon*, and *Leptrotragulus*, is quite unknown;

and we can therefore follow the evolution of this region only from the lower Miocene upward. The recent *Camelidæ* have a peculiar type of skull, markedly different from that of the true ruminants. Rüttimeyer has summed up these peculiarities as follows: Characteristic of the *Camelina* is the presence of upper and lower canines and the approximation of the molar series, the properly masticating surface of which is very short, to the premaxillary dentition and the corresponding part of the inferior dentition. The premaxillæ are very complete, and reduced only by small incisive foramina. Nevertheless, the skull is distinguished by the very rapid tapering of the face anteriorly, which is expressed particularly in the triangular form of the palate and in the very oblique position of the molar series (somewhat as in the *Toxodontia*). The maxillary region of the skull is peculiarly limited, and mainly taken up in the formation of the nasal passage, having but a low alveolus and very limited muscular surfaces. Even the jugal, as well as in the lachrymal (which at least in the camel hardly appears on the face), takes almost no share in the formation of the face. The infra-orbital foramen lies far back, above the last premolar. There is no masseter crest, and the masseter surface is almost obsolete. The nasal canal is high, and roofed over by short nasals, which in the llama are very broad posteriorly. The posterior nares are also very high, especially in the pterygoid portion. The pterygoid wings are placed vertically; and in the llama, as in young animals, are perforated by unusually large sphen-orbital foramina. Characteristic in the cranium is the small extent of the frontal zone as compared with the parietal zone, in the formation of which the very high squamosals take a large share. The orbits are very prominent, in spite of which the external openings of the supra-orbital canal are in the camel almost median in position, less so in the llama. A further consequence of these relations is the displacement of the orbits into the facial region above the molar alveoli, and the extraordinary length of the temporal fossa, at least in the camel. Of the occipital bones, only the supra-occipital extends upon the roof of the cranium, and in the camel is raised into a great crest. The paroccipital processes are in both forms reduced to a minimum; the auditory bullæ are much inflated in the llama, in the camel they are strongly compressed, and with a very deep styloid groove.

The glenoid cavity is very small, but has a high post-glenoid process, as in the horse. The sphenoid region has the relations general among artiodactyls; the foramen ovale lies in the *ala posteriora*, and there is no ali-sphenoid canal. The condyle of the lower jaw is spherical, instead of being transversely extended as in the true ruminants; the coronoid process is straight and pointed, not curved, and a process for muscular attachment arises from the *angulus mandibulæ*.

Of the two genera, *Camelus* presents the family characteristics in excess, as compared with the llama, which is in so far a less extreme form. In the latter the frontal zone is more extended, and encroaches upon the parietal zone behind the orbits. The orbits are not placed so far forward, and the jugal and lachrymal are more extended upon the face. In front of the jugal there is a considerable vacuity. The premaxillæ reach the nasals. The posterior nares are not so high, but extend farther forward than in the camel; and the speno-maxillary fossa is, even in old animals, not entirely obliterated. The external supra-orbital openings are opposite the internal ones.

“All this probably places the group of the camels outside of any other relations to existing ruminants than those of physiological similarity, and even the selenodont type of dentition appears to be rather analogical to than identical with that of the ruminants proper. Among living ungulates no group stands nearer to the camels, with regard to the plan of skull-structure, than that of the perissodactyl horse” (No. 26, p. 19).

These peculiarities occur in a less marked degree in the skull of *Pæbrotherium*. The cranium is shorter, narrower, less capacious and less rounded. The orbits are placed further back even than in the llama, and approach very near together, so that an inter-orbital septum is formed, almost as in the tragulines. They are not so prominent, nor directed so much anteriorly as in the recent forms, and are not quite enclosed by bone; the supra-orbital fissure is widely open, though not so deep as in the recent genera. The face is very low, especially in front; and its upper contour descends regularly from above the orbits to the anterior nares. Owing to the completely brachyodont condition of the upper molars, the alveolus is extremely low, and the orbit is separated from the molars by a very small space. The nasals are extremely long and narrow, and do not show the

posterior expansion in width which is so characteristic of the llama. Below the suture of the nasals and maxillaries the latter show a long, deep depression. The anterior nares have an altogether different shape from that seen in the existing genera; they are very low, and their lateral edges are not nearly so oblique, but more vertical in position. The lachrymal and jugal are about as much extended upon the face as in *Auchenia*; but the notch in the latter, which receives the anterior end of the zygomatic process of the squamosal, is not deep as in the modern species. There is no fontanelle between the nasal, frontal, and maxillary, as is so markedly the case in the llama; and sometimes even in the camel there is a small vacuity present. The face is not abruptly constricted in front of pm. 4, but tapers gradually forward. The nasal chamber is very low, especially in front; and in consequence the maxillary has no such vertical extension as in the recent species. The palate is also very different in shape, especially in the absence of the deep constriction in front of the molar series and the very much shorter diastema behind pm. 1. The alveolus is continued further back of the last molar, and forms a very small projection into the orbit; the palatal notches between the alveoli and the palatines are very short, and the posterior nares have a much less vertical extent. The latter are in shape and position very like those of *Auchenia*, being long, narrow, and pointed anteriorly, extending to the space between m. 2 and 3. The vomer extends lower, and is more conspicuous than in the modern genera. The descending plates of the ali-sphenoids are shorter, somewhat broader, and do not terminate in such distinct hamular processes; the same statement applies to the pterygoids, of which the free ends are short and inconspicuous. The tympanic bullæ are relatively larger and more rounded, and the styloid groove and pit are shallower and more widely open behind. The zygomatic process of the squamosal is shorter, and the glenoid cavity is not separated into two parts. The occiput is rather high and narrow, and there is a strong lambdoid crest, as in the camel. The construction of the roof of the cranium agrees best with the latter genus, as is seen in the shortness of the frontal zone, the long sagittal crest, and prominent lambdoid crest; but owing to the more posterior position of the orbits, the zygomatic arch and temporal fossa are much shorter. A primitive feature is the

length of the posterior region of the cranium and the anterior position of the paroccipital processes.

In the lower jaw the horizontal ramus is relatively longer and more slender than in the recent genera, the symphysis is much shorter, and the ascending ramus much lower, in correspondence with the more brachyodont dentition; the angular process is very much longer, extending far back of the line of the condyle, but much lower from above downwards. The condyle is more extended transversely, and the articular surface for the postglenoid process much less developed, and in general the condyle departs less decidedly from the ordinary ruminant pattern than does that of the living Tylopoda. The coronoid process is shorter, more regularly recurved, and more like that of the Pecora: it is compressed and thin, and shows no tendency to assume the massive condition found in *Camelus*. There is a rather small but deep masseteric fossa.

Though the skull of the more ancient genera referred to the cameline series is unknown, yet from the analogy of other ungulate lines we may infer with considerable confidence that several features of the skull structure of *Pæbrotherium* indicate advance and differentiation, as, for example, the posterior position of the orbit, the shortened cranium, and very long face; the great size of the auditory bullæ, etc., etc. Indeed, in some respects *Pæbrotherium* is more modernized than the camel.

The skull of *Protolabis* exhibits no very important changes; the nasals are somewhat shortened, and the anterior nares higher and more obliquely placed than in *Pæbrotherium*; the face is deeper and the orbit rather smaller; the face is constricted in front of pm. 2, and the distance from the tip of the premaxillaries to the infra-orbital foramen, which is still placed above pm. 4, is considerably lessened; the posterior nares are situated further back, apparently altogether behind the molars. The superior alveolus is continued some distance back of the third molar.

The skull of *Procamelus* (Pl. I, Figs. 4-6) has two well-distinguished types of structure, one of which, *P. occidentalis*, Leidy, resembles the llama; the other, *P. angustidens*, Cope, is more like the camel (cf. Cope, No. 6, Pl. LXXVII, Fig. 1, and our Pl. I, Fig. 6). In both the orbit is decidedly smaller than in *Pæbrotherium* and separated by a wider interval from the molars

The whole face has become shorter and deeper, and the anterior nares are much higher and more oblique, while the posterior nares have increased in height and are placed behind the molar series. In *P. occidentalis* there is a small prelachrymal vacuity, and the shape of the cranium is much like that of the llama, with extended frontal zone, much shortened sagittal crest, and very low occiput and inconspicuous lambdoid crest. There is a small prelachrymal vacuity. On the other hand, the orbit, though situated far back, is in relative size more like that of the camel, and the posterior nares are almost precisely like those of that genus. In *P. angustidens*, for an opportunity to study which I am indebted to the kindness of Professor Cope, there is no prelachrymal vacuity, the sagittal crest is much higher and longer, and the lambdoid crest is much more prominent. In this cranium the highest point is at the junction of the two crests: in *P. occidentalis* it is in the middle of the parietal zone. The cranium of *P. angustidens* thus strongly recalls that of the camel, as that of the other species does the llama. In both the orbits are enclosed by bone, and the palatal notches are deeper than in the White River genus, while the nasals remain much longer and narrower than in either of the recent genera.

The mandible is known only in the case of *P. occidentalis*, and this is most like that of the llama; but the ascending ramus is relatively lower and wider, and the masseteric fossa is much better developed. As compared with the mandible of *Pæbrotherium*, the most important changes, aside from the general increase in size, are the greater depth and robustness of the horizontal ramus, the reduction of the angular process in length, and its increase in height, and the less clear definition of the masseteric fossa.

The differences between the skull structure of *Procamelus* and that of the modern genera are sufficiently indicated in Rüttimeyer's description already quoted. Unfortunately we know too little about the skulls of the Pliocene and Quaternary forms to enable us to trace these changes step by step. It should be emphasized, however, that the skull of *Procamelus* unites peculiarities both of *Camelus* and *Auchenia*, and that these characters are not merely primitive features which have been retained by one or other of the modern genera, but actual specializations; e.g. the position of the orbit and construction of the cranium on the

one hand, the shape and position of the posterior nares, on the other, in *P. occidentalis*; in *P. angustidens* the extension of the frontal zone and posterior position of the orbits, combined with the very camel-like cranium.

### III. *The Brain.*

The salient features of the brain of *Pæbrotherium* are the large relative size of the cerebellum and medulla, the short, narrow, and tapering hemispheres, which in the anterior region have very slight vertical depth. The convolutions are few, simple, and straight; and the sulci present are, with the exception of a few accessory ones, those which are common to the whole series of ungulates, and closely resemble those of a foetal sheep. The frontal lobes are strikingly small.

The brain of *Procamelus*, as described and figured by Cope, shows a decided advance upon that of *Pæbrotherium*. The cerebellum is relatively smaller and the hemispheres larger, and they have assumed a more rounded and less tapering shape: the frontal lobes are decidedly enlarged, the accessory sulci have become more numerous, and the convolutions somewhat more sinuous, though they are still much simpler and straighter than in the recent genera. This brain is "not materially smaller than that of the llama, an animal which *Procamelus* equalled in general proportions. The hemispheres are, however, not produced so far posteriorly as in the *Auchenia*, reaching only to the line of the meatus auditorius externus.

"The orbital portion of the hemispheres is extensive and nearly smooth from the olfactory lobes to the supra-orbital border. This is not prominent, but is represented by a short longitudinal ridge. Above each of these, on the superior or front aspect of the hemispheres, is a massive convolution, but crescent-shaped, with the convexity inwards. The posterior part of the convolution is a sub-round tuberosity, which stands opposite to, and in front of, the furrow separating the Sylvian and median convolutions" (No. 6, p. 339).

The change from *Procamelus* to the recent species in brain structure consists less in increase of size, though there is some such increase, than in the rounder and deeper shape of the hemispheres, and in the very much more numerous and more

sinuous convolutions. The main sulci are already present in *Pæbrotherium*, so that the brain of this genus stands to that of the recent genera in the relation of embryo to adult, and affords an interesting confirmation of Krueg's results obtained by embryological investigation.

#### IV. *The Vertebral Column.*

Cope states (No. 7, p. 718) that the lumbar vertebræ of *Pantolestes* have flat articular faces.

The vertebræ of *Pæbrotherium* have reached a stage of development which, except in a few points, is almost like that of the existing forms. The neck is elongated, though decidedly shorter than in the recent genera; the transverse processes are not so distinctly separated into anterior and posterior portions, and on the sixth cervical the vertebrarterial canal is clearly visible. The atlas has longer and more recurved transverse processes; the anterior cotyli are not notched; there is no accessory articular surface on the anterior face of the inferior arch, and the vertebrarterial canal has its posterior opening at the base of the transverse process, not on the dorsal side of it. The axis has a high, thin, plate-like neural arch, more expanded antero-posteriorly, but much less massive and rugose than in the modern genera; the odontoid process is short and flattened on the dorsal side, with a rounded tip.

The dorsal vertebræ appear to number 13; they have long, slender, backwardly directed spines and elongated compressed centra.

The lumbar vertebræ have depressed centra with inferior median keels and lateral ridges; the spines are thinner and more compressed, and the zygapophyses show the faint beginnings of the epispheial processes which are so well developed in the camel.

The cervicals of *Procamelus* described and figured by Cope (No. 6, p. 335, Pl. LXXVIII) are intermediate between those of the recent genera and those of *Pæbrotherium*. The atlas agrees with the latter in the continuation of the transverse processes behind the surfaces for the axis, and with the former in the position of the vertebrarterial canal, the deep emargination of the outer rims of the occipital cotyli, and, apparently, in the

presence of an articular surface on the anterior edge of the inferior arch. The odontoid process of the axis is somewhat more concave on its superior surface than in *Pæbrotherium*, much less so than in the recent forms. The other cervicals are relatively smaller than in the llama, the transverse processes more expanded and less completely separated into anterior and posterior portions, and there are no neural spines. As in the recent genera, the third and fourth vertebræ are of nearly equal length, while in *Pæbrotherium* the third is considerably the longer.

The dorsal vertebræ of *Procamelus* are imperfectly known, but the character of the spines agrees best with that of the recent genera, except that they are rather longer.

The lumbar vertebræ have in the anterior region an inferior angulate keel, while in the posterior ones there is an angle on each side of the median one. The epispheial processes of the zygapophyses are quite distinct and much better developed than in *Pæbrotherium*.

The ribs of *Procamelus*, so far as they are known, agree best with those of the recent species, being much broader and more flattened than in *Pæbrotherium*. They appear, however, to be more simply and regularly curved than in the camel.

#### V. *The Fore Limb.*

The fore limb is entirely unknown in *Pantolestes*; and with regard to *Homacodon*, we know only that the manus contains four digits. Of *Leptotragulus*, fragments of the fore limb are preserved which throw some welcome light upon the questions at issue.

The glenoid cavity of the scapula is oval in shape, the antero-posterior diameter exceeding the transverse, and is placed somewhat obliquely to the vertical axis of the bone; the coracoid is much less prominent than in the later genera, and is not at all rugose, and but little recurved at the tip. The spine is placed nearly in the median line, but not quite, so that the postscapular fossa is slightly larger than the prescapular.

The distal end of the humerus is narrow; the internal epicondyle is pushed to the posterior angle; the outer condyle of the trochlea is narrow, the inner somewhat broader, and the

intercondylar ridge is narrow and sharp. The articular surface is high both in front and behind; the anconeal fossa is deep and appears to penetrate the shaft.

The ulna and radius are closely applied together, but do not coalesce, except partially at one point in the proximal portion, whatever may be true of the distal. The former has a heavy and prominent olecranon, which, so far as it is preserved, is continued upward in the line of the shaft, and does not project backward at all; the sigmoid notch is deeply incised with a decurved proximal margin; both internal and external humeral facets are continued down the anterior face of the notch. At the level of the head of the radius the shaft is quite broad and thick, but rapidly tapers below this point. The head of the radius is narrow, and the groove for the intercondylar ridge is very shallow and does not notch the front margin. The shaft, so far as preserved, is much more slender and rounded than in *Pæbrotherium*.

In *Pæbrotherium*, the shape of the scapula agrees best with that of the llama, as do also the position of the spine, shape of the acromion, and relative size of the pre- and post-scapular fossæ, but the coracoid, though much larger than in *Leptotragulus*, is much smaller and less rugose than in the llama. The neck and coraco-scapular notch are more like those of the camel.

The humerus is very different from those of the later genera; the distal end is like that of *Leptotragulus*, but the intercondylar ridge is broader and more rounded, though less so than in the existing genera. The shaft is much more slender than in the latter, the proximal end remarkably different; the external tuberosity is very high and broad, extending across the whole anterior face of the bone and overhanging the bicipital groove. This groove is narrow, deep, and placed at the antero-internal angle of the head, and the very small rudiment of a bicipital tubercle may be seen at the bottom of it. The internal tuberosity is very small.

The ulna and radius are firmly co-ossified throughout, but are separated at two points by the proximal and distal interosseous foramina. The shaft of the radius is much broader and flatter than in *Leptotragulus*, though much more slender than in the recent species. The head is also narrower than in the latter;

the groove for the intercondylar ridge of the humerus is very shallow, and to the inner side of the median line there is an elevation of the anterior margin, which is more prominent than in *Leptotragulus*. The distal end is but moderately expanded, and the three carpal facets are of nearly the same transverse breadth. The olecranon is very high and in the line of the shaft, projecting backwards but slightly, and has a deep tendinal sulcus on its extremity. The shaft of the ulna is decidedly less reduced than in the modern species.

The proximal row of carpals is of considerably greater height than the distal: in width the three bones of this row are nearly equal. The radial facet of the scaphoid is considerably broader in front than behind and is not emarginated on the internal side. The proximal articular surface of the lunar is nearly quadrate in outline; distally there is a long median beak formed by the junction of the facets for the magnum and unciform, which meet at an acute angle; the former is the longer and so obliquely placed as to be rather lateral than distal. The cuneiform has considerable antero-posterior depth, but is relatively narrow. The pisiform is short and very much compressed, with a very contracted neck, and expanded, rugose, and incurved free end; its articulation with the ulno-radius is much less extensive than in the recent genera. The trapezium is present and forms a small nodule, which is applied to the scaphoid and the rudimentary second metacarpal. The trapezoid is free; it is a very small bone, little larger than the trapezium; distally it is divided into two facets of unequal size — a small one for mc. II, and a somewhat larger for mc. III. The magnum is broad and very low; it is broadest in front, and narrows almost to a point behind; its proximal surface is chiefly occupied by the scaphoid, the lunar facet being much narrower and more obliquely placed; distally it is in contact only with mc. III, the extension of which upon the trapezoid excludes mc. II from the magnum. The unciform is a large bone, chiefly remarkable for its vertical height, which is nearly double that of the magnum, thus extending much below the level of that bone; the lunar facet is relatively larger than in the recent species. The unciform is connected with three metacarpals; the whole distal surface proper is occupied by mc. IV, but on the radial border there is a small facet for the projection of mc. II, and on the ulnar border a still smaller one for mc. V.

The metacarpus consists of two functional and two rudimentary digits. Mc. II is a short scale which is closely applied to and apparently sometimes even slightly co-ossified with mc. III: it articulates with the trapezium and trapezoid, but not with the magnum. Mc. III is very long, though relatively shorter than in the recent forms, and very slender, especially in the distal portion. Owing to the different levels at which the distal surfaces of the magnum and the unciform stand, mc. III rises higher than mc. IV, and so abuts against the unciform; on the radial side its head has extended over so as to occupy much of the trapezoid. Mc. IV is a trifle shorter and somewhat more slender than No. III, but is otherwise shaped like it. The distal ends are very slightly expanded; the carinæ are low and entirely confined to the palmar side. Mc. V is even smaller than No. II.

The phalanges are very unlike those of the existing species; those of the first row are not so long, less expanded at the extremities, and more regularly rounded. Those of the second row are short, slender, and rounded: their greatest diameter is from the dorsal to the palmar side. The unguals are long, pointed, and slender, with the medial surfaces flattened; the external rounded, and altogether much more like the unguals of antelopes or deer than like the nodules of the Tylopoda.

The skeleton of the John Day genus, *Gomphotherium*, so far as it is known, does not differ sufficiently from that of *Pæbrotherium* to require description, and the skeleton of *Protolabis* is quite unknown.

The fore limb of *Procamelus occidentalis* (that of *P. angustidens* is not known) has been described and figured by Cope. It is very like that of the llama, which it about equals in size, but is decidedly more slender.

In the scapula the spine rises close to the coracoid border; the coracoid process has very greatly increased in size and massiveness, and its free end forms a long recurved hook.

The humerus has become markedly stouter than that of *Pæbrotherium*, but less so than that of the llama, and the deltoid ridge and hook much more prominent; the distal end is broader, the supracondylar foramen no longer present, and the intercondylar ridge broader and more rounded. The external tuberosity is very much reduced in width, but it still rises high above

the head, higher, indeed, than in *Pæbrotherium*, terminating in a long, massive, and incurved hook. The internal tuberosity is increased in size, and the bicipital groove becomes very much wider, occupying nearly half the width of the proximal end, and the rudimentary bicipital tubercle of *Pæbrotherium* has become a prominent ridge dividing the groove into two parts.

The radius, though still slender, is much broader and more flattened than in the White River genus, and has received the inward curvature of the recent forms; the head is expanded, especially towards the outer side; the distal end has also expanded, and the carpal facets are no longer of equal width, that for the cuneiform being now the broadest. The shaft of the ulna is still further reduced, and is no longer visible from the front, except just above the distal end. The interosseous foramina penetrate, as in *Pæbrotherium*. The olecranon is not so high, and projects more strongly backward than in the latter, but it descends more steeply from the coracoid process.

In the carpus (Pl. III, Fig. 52) the scaphoid has become more massive and broader in front, producing a notch on the internal side. The lunar is relatively narrower; its distal beak is less prominent, the magnum and unciform facets being more nearly equal and inclining to each other at a more open angle. The cuneiform is heavier and wider and is less excavated upon the outer side for the descending distal end of the ulna. The pisiform is more thickened and increased in depth. No facets on the scaphoid or trapezoid indicate the presence of the trapezium, though it may have been preserved. The trapezoid is larger than in *Pæbrotherium*; the magnum is higher in proportion to its breadth; the lunar surface is broader and less oblique. The unciform, on the other hand, has become

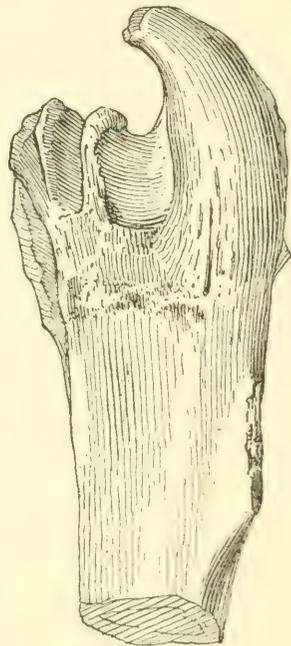


FIG. E.

Humerus of *Procamelus occidentalis*; anterior view of proximal end (after Cope).

reduced in height, and its distal surface projects but little below that of the magnum.

The metacarpus is now represented by a cannon-bone, which is as long as, but more slender than in the llama. The lateral metacarpal rudiments have disappeared, unless, as I believe to be the case, the proximal end of mc. II be ankylosed with mc. III, forming the projection at the inner side of the cannon-bone. Even in *Pæbrotherium* there is a tendency for this co-ossification to occur. The fifth metacarpal, on the other hand, appears to have vanished completely. The cleft at the distal end of the cannon-bone is wider and deeper than in the llama, and the articular facets wider.

The phalanges of the first row only differ from those of the llama "in the greater prominence of the proximal ligamentous insertions and the rather more slender shafts." The unguals are very different from those of *Pæbrotherium*, being broad, depressed, and flattened with obtuse points; but they are relatively larger than in the recent genera.

The changes from *Procamelus* to the existing forms in regard to the structure of the fore limb are not very striking. They consist in an increased robustness of all the shafts, articulations, and ridges for muscular attachment, and naturally to a greater degree in the camel. The most important change is in the proximal end of the humerus, where the external tuberosity is much reduced and the internal tuberosity and the bicipital tubercle increased, so that all three are nearly of the same size, and the bicipital groove is much widened. The shaft of the ulna is further reduced, and the olecranon receives a different shape. In the carpus the lunar is reduced in width, and the proximal row of carpals is higher in comparison with the distal row; the pisiform becomes wider and more compressed. The ungual phalanges are reduced to mere nodules.

## VI. *The Hind Limb.*

The pelvis of *Pantolestes* is peculiar in many ways. The ilium has a long and very deep peduncle, and a very wide iliac surface. Both the pubic and acetabular borders are raised into arched prominences just in advance of the acetabulum. There is little to suggest that this belongs to an artiodactyl at all.

The femur is long, with a slender rounded shaft. The head is nearly hemispherical, set upon a very distinct neck, and has a minute circular depression for the round ligament. The great trochanter is relatively very large and massive, but does not rise above the level of the head, and encloses a deep digital fossa. The lesser trochanter is also prominent, but not much extended vertically. Cope states (No. 7, p. 718) that there is no third trochanter; but I find what I conceive to be a remnant of it on the outer side of the shaft, a considerable distance below the great trochanter. The distal end is much thickened, and the rotular trochlea very prominent, but narrow. The distal end of the tibia shows a very large internal malleolus, and deeply excavated condyles for the astragalus. The fibula seems to have been complete; its distal end is much enlarged, and shows a tendinal sulcus upon the outer side.

The tarsus is typically artiodactyl, and shows considerable differentiation. The calcaneum is long and compressed, with a high fibular facet, a prominent sustentaculum, and a broad surface for the cuboid. The astragalus is high and narrow, and has the usual double pulley. The cuboid is also high and narrow. The navicular is low, especially behind, where there is a relatively large facet for the ento-cuneiform. The meso- and ecto-cuneiforms have coalesced in such a fashion that there seems to be a step cut in the compound bone, caused by the fact that the meso-cuneiform is much lower than the ecto-cuneiform; and while the proximal surfaces of the two are on the same level, distally the latter projects much below the former.

Only the third metatarsal is preserved; but the facets of the tarsus show that the pes was tetradactyl, with the median digits enlarged, and the lateral much reduced. The reduction is so far inadapative that mt. II occupies the whole of the meso-cuneiform, and is in contact with the side of the ecto-cuneiform.

The hind limb of *Homacodon* has not been described further than the statement that the pes has four digits, and that the astragalus is "suilline" (Marsh, No. 20, p. 120; and No. 21, p. 364). In *Leptotragulus* the proximal end of the femur is broad, with a hemispherical head set upon a long and very distinct neck; the second trochanter is relatively large.

The distal end of the tibia has a narrow facet for the fibula, showing that the latter had begun to shift beneath the tibia;

but the narrowness of this facet, the absence of any groove on the outer side of the tibia, and the presence of a large rugose surface in place of it, make it probable that though the reduction of the fibula had begun, it was by no means complete.

The tarsus of *Leptotragulus* is very like that of *Pæbrotherium*. The calcaneum is long and compressed and of less vertical extent (*i.e.* from the dorsal to the plantar side) than in the Miocene genus. The astragalus is high and narrow, with the proximal trochlea deeply and widely grooved. The cuboidal surface is very narrow. The cuboid is remarkably high, narrow, and deep. Both the surfaces for the astragalus and calcaneum are narrow, the latter a little the broader of the two; the posterior hook is longer and less massive than in *Pæbrotherium*; the distal surfaces for mts. IV and V are very much as in that genus.

The mts. III and IV are enlarged, but, though broken, obviously elongate and slender; their distal ends are almost exactly like those of *Pæbrotherium*. Judging by the fossæ upon the median metatarsals, it appears probable that the lateral ones are not quite so much reduced as in the White River type.

The phalanges of the first row are very slender and rounded and the unguals are long, compressed, and pointed like those of the antelopes.

In *Pæbrotherium* the ilium has a very long and narrow peduncle and a plate, which apparently was not much expanded; the ischium is also slender and compressed and without the arched prominence above and behind the acetabulum, so prominent in the recent forms. The femur is very tylopodan in appearance; but the bridge connecting the great trochanter and the head is shorter and narrower, and the great trochanter less massive there than in the living forms. The condyles are smaller and less prominent and the rotular trochlea wider and shallower; a pit for the insertion of the plantaris muscle is present.

The tibia is long and slender, with very prominent and extended cnemial crest. The distal facets for the astragalus are partly interrupted on each side of the tongue. The fibula is very much reduced, the shaft having disappeared, and the distal end moved beneath the tibia; but the groove for it on the latter

is not so deep, nor does it divide the fibular facets into two parts, as in the recent genera.

The tarsus is high and narrow. The calcaneum is long and slender, the astragalus high; the cuboid is likewise high and narrow, and the calcaneal facet deeply incised and broader than the astragalar; the latter and the astragalar facet of the navicular are emarginated by a median but shallow and small fossa. The ecto- and meso-cuneiforms are co-ossified.

The median metatarsals are longer and stouter than the metacarpals, the increased diameter being the antero-posterior rather than the transverse, and the posterior hooks are very long and stout. Mts. II and V are small scale-like rudiments; the former sometimes, but not always ankylosed with No. III, the latter always free.

Of the hind limb of *Procamelus* (Pl. III, Fig. 53) I have the distal end of the tibia, proximal end of the cannon-bone, the calcaneum, astragalus, and navicular of a large species from the Loup Fork of Oregon, and Cope has figured the cuboid. Judging from these remains, it would appear that the hind limb of this genus has very nearly reached the modern condition. The distal end of the tibia is broad and heavy; the malleolus is shorter and more massive than in *Pæbrotherium*; the intercondylar ridge, lower and broader, and its articular surface is interrupted by a deep fossa. The groove for the fibula is very deep, and separates the fibular facet into a smaller anterior and larger posterior portion.

The astragalus has become much broader in proportion to its height, and the rim of the external condyle much thicker. The calcaneum is compressed and deep, with prominent sustentaculum and long narrow cuboidal facet. On the inner side of the distal end can be seen the beginning of the projection which in the llama extends far inwards behind the astragalus; the distal end extends little if any below that of the astragalus. The navicular is very low; the fossa, which in *Pæbrotherium* emarginates the fibular edge of the astragalar surface, is here larger and deeper. The cuboid is also very low vertically; the calcaneal facet is but little incised.

The upper end of the cannon-bone is heavy and deep antero-posteriorly. The posterior hook-like projections are relatively shorter but more massive than in *Pæbrotherium*. The prox-

imal end of mt. II is clearly a part of the cannon-bone, forming a large facet for the ento-cuneiform; its line of suture with mt. III is still visible. A comparison with the modern forms shows that in them also this bone is preserved, as Boas (No. 3, p. 52) and Gaudry (No. 12, p. 117) have found to be the case in the true ruminants. I find, however, no trace of mt. V, and from its altogether lateral attachment to the cuboid in *Pæbrotherium* it appears probable that it has entirely disappeared.

The changes in the structure of the hind limb from *Procamelus* to the recent genera are not sufficiently important to call for description.

#### THE PHYLOGENY OF THE TYLOPODA.

The immediate ancestors of the modern *Camelidæ* are, unfortunately, not known to us, though the *Protauchenia* of Branco (No. 4, p. 110) not improbably stands in this relation to the llama series, the forms which occur in the Pliocene of the United States being highly specialized side branches, which have died out without leaving successors. Toward the end of the Miocene the ancestors of the modern forms probably migrated from North America to South America and the Old World, as is indicated by the Siwalik fossils and others. In the upper Miocene, or Loup Fork beds, we meet a large number of species of this group. *Homocamelus*, so far as known, is very camel-like, and it might seem at first sight that we have here a direct ancestor of the camels; but the peculiar and reduced character of the premolars, though still present in full numbers, renders it probable that this genus is not in the direct line, but is perhaps the forerunner of *Holomeniscus* or *Eschatius*. *Plianchenia* has frequently been regarded as the forerunner of the llamas, but the known remains of it are altogether too imperfect to enable us to form a decision on this question, and the great shortening of the disastema would seem to oppose this view.

*Procamelus*, on the other hand, if not itself the common ancestor of the two recent lines, obviously stands very near to their point of divergence. It may be objected that this genus has already become too highly specialized in both directions to be the ancestor of either series; *e.g.* agreeing with the llama in

the position of the orbits and the extension of the frontal zone, with the camel in the shape and position of the posterior nares. But this objection is of no great weight, for this differentiation is as difficult to explain on the assumption that *Procamelus* is a side branch. The two species *P. occidentalis* and *P. angustidens* very strongly suggest themselves as the starting-points of the llama and camel series respectively.

*Protolabis* is obviously the connecting link between *Procamelus* and *Pæbrotherium*; and so far as known, is exactly what it should be to assume this position.

*Pæbrotherium* has frequently been regarded as ancestral to the camels only, but its relation to the llamas is quite as unmistakable. Branco's suggestion (No. 4), which was adopted by Schlosser (No. 27, p. 49), that *Leptauchenia* is the earliest known member of the *Auchenia* line, I have elsewhere shown to be entirely untenable (No. 31, p. 356).

*Leptotragulus* is so very like *Pæbrotherium* that no one can hesitate to regard it as the forerunner of the White River genus. Every known detail of its structure thoroughly confirms this view.

The position of the Bridger genus *Homacodon* is much less clear, for as yet only the most meagre accounts of that form have been published; but so far as it is known, it gives us every reason to believe that it is connected on the one hand with *Pantolestes* and on the other with *Leptotragulus*.

If these conclusions are correct, it follows that the Tylopoda are but remotely connected with the true ruminants, and that they have no common ancestors nearer than the *Dichobunidae*, to which Schlosser also traces the Pecora. However this may be, no one will dispute the view that *Pæbrotherium* cannot be ancestral to any of the ordinary ruminants; and, therefore, that all the structural points in which the modern *Camelidae* agree with the Pecora, but which do not occur in *Pæbrotherium*, must have been independently acquired. As we have already seen, Rüttimeyer reached this same conclusion from the study of the existing forms alone.

I have elsewhere given my reasons (No. 31, p. 389) for believing that the oft-repeated view of the connection between the *Oreodontidae* and the *Camelidae* is altogether untenable, and I need not repeat them here. The present investigation further

confirms the position reached in the article cited; viz. that all the great groups of selenodont artiodactyls when traced back are seen to arise independently from the abundant and widespread Eocene type, which may be called the Buno-Selenodonta; and which forms, as it were, a lake from which several streams, flowing partly in parallel, partly in diverging directions, are derived. It seems very clear that the term "selenodont," though most useful as a descriptive word, has no value as a term of classification.

In the discussion of the structure and succession of the Tylopoda, I have merely endeavored to establish the facts, reserving for the second paper all attempts at explaining those facts; for such explanation will be rendered easier by the study of some other lines of mammalian descent, and by the comparison of the facts thus obtained with those which the history of the camels offers for our consideration.

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## EXPLANATION OF PLATE I.

FIG. 1. *Pebrotherium Wilsoni*. Skull of a young animal, side view  $\times \frac{4}{3}$ . Museum of Comparative Zoölogy.

FIG. 2. *Pebrotherium Wilsoni*. The same, top view  $\times \frac{4}{3}$ .

FIG. 3. *Pebrotherium Wilsoni*. The same, base view  $\times \frac{4}{3}$ .

*f. ov.* foramen ovale; *f. opt.* optic foramen; *f. l. a.* foramen lacerum anterius and foramen rotundum.

*par. oc.* paroccipital process; *p. sp.* presphenoid; *b. sp.* basisphenoid; *f. l. p.* foramen lacerum posterius; *pal.* palatines.

FIG. 4. *Procamelus occidentalis*. Skull, top view  $\times \frac{1}{3}$ , after Cope.

FIG. 5. *Procamelus occidentalis*. Skull, base view  $\times \frac{1}{3}$ , after Cope.

FIG. 6. *Procamelus angustidens*. Skull, side view  $\times \frac{1}{3}$ . Cope collection. *p. gl.* for. postglenoid foramen; *po. ty.* post-tympanic process of squamosal; *p. oc.* paroccipital process.

FIG. 7. *Pebrotherium labiatum*. Tympanic region, natural size. *con.* occipital condyle; *par.* paroccipital process; *ty.* tympanic bulla; *m. a. e.* external auditory meatus.

FIG. 8. *Pebrotherium Wilsoni*. Superior molar series, crown view, natural size.

FIG. 9. *Pebrotherium Wilsoni*, inferior molar series, crown view, natural size.











## EXPLANATION OF PLATE II.

- FIG. 10. *Pæbrotherium Wilsoni*. Intracranial cast. *cb.* cerebellum; *i.* median convolution; *2.* medi-lateral; *3.* lateral; *4.* suprasylvian.
- FIG. 11. *Pæbrotherium labiatum*. Atlas, base  $\times \frac{2}{3}$ . Cope collection. *v. c.* vertebrarterial canal.
- FIG. 12. *Pæbrotherium labiatum*. Atlas, side  $\times \frac{2}{3}$ . Cope collection.
- FIG. 13. *Pæbrotherium labiatum*. Atlas, rear  $\times \frac{2}{3}$ . Cope collection.
- FIG. 14. *Pæbrotherium labiatum*. Axis, side  $\times \frac{2}{3}$ . *o.* odontoid process; *pt. z.* postzygapophysis.
- FIG. 15. *Pæbrotherium labiatum*. Fourth cervical, side  $\times \frac{2}{3}$ .
- FIG. 16. *Pæbrotherium labiatum*. Sixth cervical, side  $\times \frac{2}{3}$ . *v. c.* vertebrarterial canal; *v. c.!* accessory foramen.
- FIG. 17. *Pæbrotherium labiatum*. Sixth cervical, rear  $\times \frac{2}{3}$ .
- FIG. 18. *Pæbrotherium labiatum*. Seventh cervical, side  $\times \frac{2}{3}$ .
- FIG. 19. *Pæbrotherium labiatum*. Seventh cervical, base  $\times \frac{2}{3}$ .
- FIG. 20. *Pæbrotherium labiatum*. First dorsal, base  $\times \frac{2}{3}$ .
- FIG. 21. *Pæbrotherium labiatum*. Ninth dorsal, side  $\times \frac{2}{3}$ .
- FIG. 22. *Pæbrotherium labiatum*. Lumbar vertebra, side  $\times \frac{2}{3}$ . *pt. z.* postzygapophysis. Cope collection.
- FIG. 23. *Pæbrotherium labiatum*. Lumbar vertebra, rear  $\times \frac{2}{3}$ . Cope collection.
- FIG. 24. *Pæbrotherium labiatum*. Scapula, side  $\times \frac{1}{2}$ . *c.* coracoid; *a.* acromion.
- FIG. 25. *Pæbrotherium labiatum*. Scapula, distal end, natural size.
- FIG. 26. *Pæbrotherium labiatum*. Humerus, front  $\times \frac{1}{2}$ . *e. t.* external tuberosity.
- FIG. 27. *Pæbrotherium labiatum*. Humerus, proximal end, natural size. *e. t.* external tuberosity; *i. t.* internal tuberosity; *bc. t.* bicipital tubercle.
- FIG. 28. *Pæbrotherium labiatum*. Humerus, distal end, natural size.
- FIG. 29. *Pæbrotherium labiatum*. Ulna-radius, front  $\times \frac{1}{2}$ . *R.* radius; *U.* ulna.
- FIG. 30. *Pæbrotherium labiatum*. Ulna-radius, rear  $\times \frac{1}{2}$ .
- FIG. 31. *Pæbrotherium labiatum*. Ulna-radius, distal end, natural size. *s.!* *l.!* *c.!* facets for the scaphoid, lunar, and cuneiform.
- FIG. 32. *Pæbrotherium labiatum*. Ulna-radius, proximal end, natural size.
- FIG. 33. *Pæbrotherium labiatum*. Carpus, front. Cope collection. *s.* scaphoid; *l.* lunar; *c.* cuneiform; *td.* trapezoid; *m.* magnum; *u.* unciform; natural size.
- FIG. 34. *Pæbrotherium labiatum*. The same, proximal face.
- FIG. 35. *Pæbrotherium labiatum*. The same, distal face.
- FIG. 36. *Pæbrotherium labiatum*. Metacarpals, front  $\times \frac{1}{2}$ .
- FIG. 37. *Pæbrotherium labiatum*. The same, proximal end, natural size.
- FIG. 38. *Pæbrotherium labiatum*. Femur, proximal end, front view, natural size. Cope collection.
- FIG. 39. *Pæbrotherium labiatum*. The same, proximal end, top view.





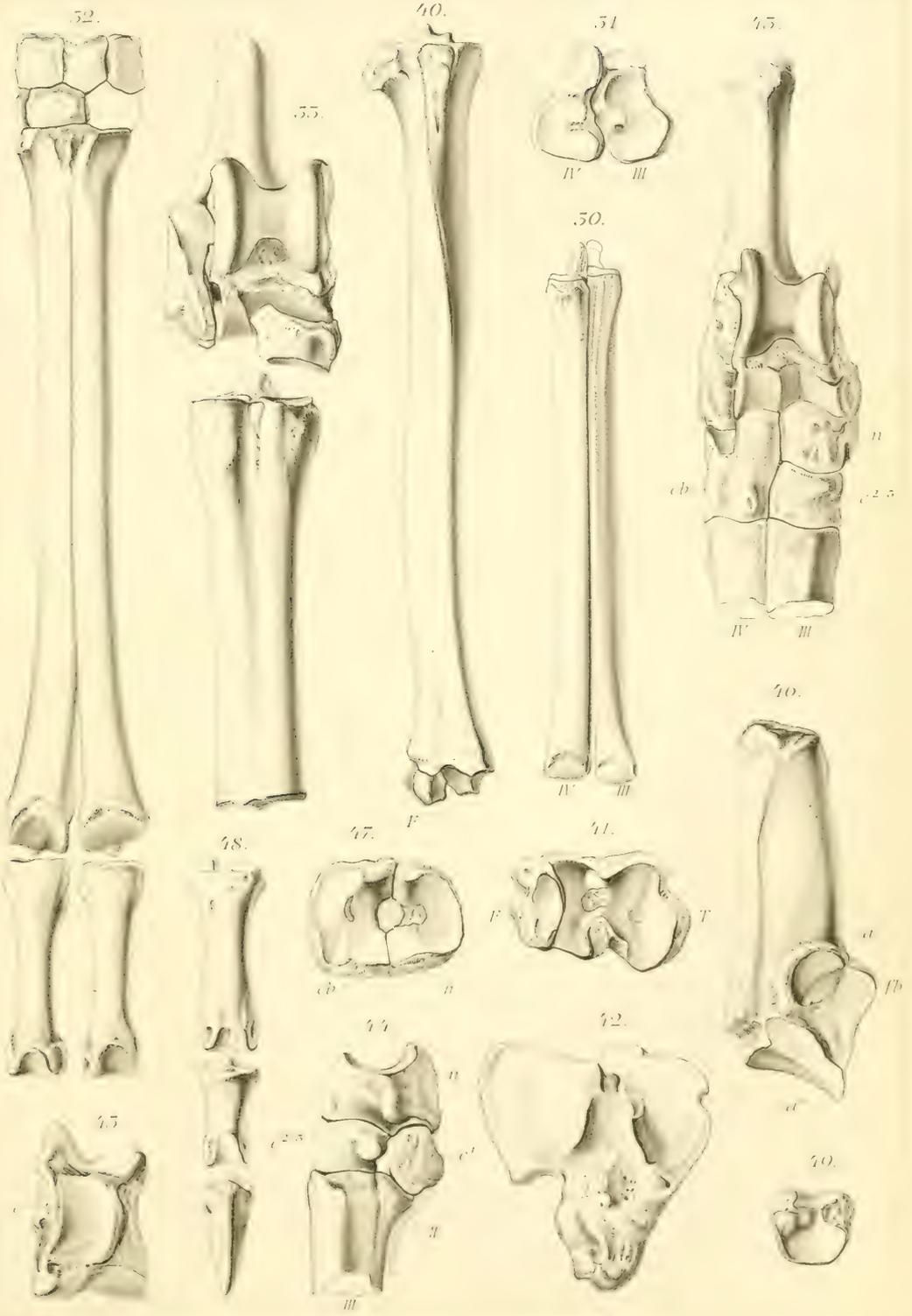






## EXPLANATION OF PLATE III.

- FIG. 40. *Pebrotherium labiatum*. Tibia, front  $\times \frac{1}{2}$ .
- FIG. 41. *Pebrotherium labiatum*. The same, distal end, natural size. *T.* tibia; *F.* fibula.
- FIG. 42. *Pebrotherium labiatum*. The same, proximal end, natural size.
- FIG. 43. *Pebrotherium Wilsoni*. Tarsus, front, natural size. *cb.* cuboid; *n.* navicular; *c.* 2 + 3, coalesced meso- and ento-cuneiforms.
- FIG. 44. *Pebrotherium Wilsoni*. The same from the inner side. *II.* rudiment of second metatarsal; *III.* third metatarsal.
- FIG. 45. *Pebrotherium Wilsoni*. Astragalus, plantar surface, natural size.
- FIG. 46. *Pebrotherium Wilsoni*. Calcaneum, tibial side, natural size. *fb.* fibular facet; *a' a''* astragalar facets.
- FIG. 47. *Pebrotherium Wilsoni*. Cuboid and navicular, proximal surface, natural size.
- FIG. 48. *Pebrotherium labiatum*. Phalanges of manus, natural size.
- FIG. 49. *Pebrotherium labiatum*. First phalanx, proximal end.
- FIG. 50. *Pebrotherium labiatum*. Metatarsals, front  $\times \frac{1}{2}$ .
- FIG. 51. *Pebrotherium labiatum*. The same, proximal end, natural size.
- FIG. 52. *Procamelus occidentalis*. Manus, front  $\times \frac{1}{2}$ . After Cope.
- FIG. 53. *Procamelus sp.?* Tarsus, front  $\times \frac{1}{2}$ . This specimen is of an undetermined species from the Loup Fork of Eastern Oregon, which was presented to the Princeton Expedition of 1890 by Mr. William Day.





A CONTRIBUTION TO THE MORPHOLOGY OF  
THE VERTEBRATE HEAD, BASED ON A  
STUDY OF *ACANTHIAS VULGARIS*.

JULIA B. PLATT.

THESE studies, begun under the direction of Dr. C. O. Whitman, were completed in the summer of 1890, at the Marine Biological Laboratory of Wood's Holl. I acknowledge gratefully the valuable criticism and suggestion with which Dr. Whitman has followed my work.

My material consisted of nearly a thousand specimens, collected on the coast of Massachusetts at Lanesville and North Truro. Among the hardening reagents employed, micro-sulphuric acid proved the most reliable. However, specimens hardened in Perenyi's fluid were also good, while osmic acid and gold chloride have given some valuable results. For differentiation the common hæmatoxylin and carmine stains were used. The reconstructions, showing the development of the eye-muscles, were obtained from series of camera outlines, which were projected on paper ruled to a scale corresponding to the magnification of the drawings, and to the thickness of the sections from which they were taken. The flat projections thus obtained were then shaded in order to represent more clearly the relative depth of different parts. By these reconstructions I have endeavored to give a definite idea of the successive changes through which the head cavities pass in the process of transformation. Although the final results do not differ from those obtained by Van Wijhe (No. 16) nearly ten years ago, it is hoped that a more complete presentation of the steps by which these results are reached may not be devoid of interest. The scientific value of an exact knowledge of the position in which the eye-muscles arise is sufficiently evinced by the stress which Rabl (No. 15) lays upon the location of the primary somatic muscles, as determining, to a degree, the homologies of head and body somites.

I have not attempted a complete account of any of the systems of the head, thinking it sufficient to note those points in which I have found *Acanthias* to differ from Selachians hitherto described.

#### A. HEAD CAVITIES AND MUSCLES.

The origin and the relations of the first four or five head cavities in *Acanthias* are in several respects exceptional. To make these differences clear, I shall refer briefly to the appearance of these cavities in other Selachians, as described by Balfour, Marshall, Van Wijhe, and Dohrn.

In regard to the head cavities in *Scyllium*, Marshall (No. 10) says that by stage D the "separation of somatic and splanchnic layers . . . has gone so far as to give rise to a distinct cavity in the head region on either side, while at a considerably later period the separation extends further back, so as to form in the trunk the peritoneal or body cavity. The whole of the cavity so formed may be termed *cœlom*." This cavity is then divided into anterior and posterior parts by the appearance of the hyomandibular clefts. In regard to succeeding stages, Marshall quotes from Balfour (No. 1) as follows: "During stage I, this front section of the head cavity (the part in front of the hyomandibular cleft) grows forward and becomes divided, without the intervention of a visceral cleft, into an anterior and a posterior division. . . . Between stages I and K, the anterior (premandibular) cavities of the two sides are prolonged ventralwards, and meet below the base of the fore brain." Therefore, according to Marshall, the premandibular cavity in *Scyllium* is cut off from the anterior part of the original *cœlomic* cavity. This is not the case in *Acanthias*. Here, the premandibular cavity arises independently in the wide mass of cells in which, at an early stage, the anterior end of the notochord is lost. This mass of cells gives rise to two pairs of cavities laterally situated, and to two or three or even more median cavities. Of the paired cavities, the more lateral and anterior are as yet unnamed; the more median and posterior form the lateral portions of the future premandibular cavity. Both pairs of cavities have definite walls and are constant in their appearance. The median cavities, on the other hand, have irregular outlines, and their number varies, unless I mistake, in different embryos at

the same stage of development. These median cavities are probably the homologues of the anterior cavities in *Torpedo*, recently described by Dohrn (No. 8), in which he thinks he sees the rudiments of several lost somites. I find in *Acanthias* little evidence to favor such a view. The median cavities lack definite walls, are irregular in number and in outline, and are surrounded by tissue which appears to be disintegrating rather than passing through a process of normal development. Sooner or later these median cavities fuse with one another and with the posterior of the paired cavities, forming together the pre-mandibular cavity.

Kastschenko (No. 9) says that the entire premandibular cavity arises "aus der . . . praechordalen Höhle, welche einer ganzen Reihe verschiedener Umgestaltungen unterworfen wird," and that the resulting cavity cannot be homologized with a true head somite. Views so at variance as those of Kastschenko, Van Wijhe, and Dohrn show that the true significance of the pre-mandibular cavity is still extremely problematic. For while Kastschenko claims that the cavity is non-somatic, Van Wijhe thinks it is formed by the fusion of one pair of somites, and Dohrn by the fusion of many.

Of the paired lateral cavities above described, the anterior are first to appear. They are found shortly before the breaking through of the first visceral clefts, and their appearance is immediately followed by that of the lateral portions of the pre-mandibular cavity, after which the median cavities arise. The fusion by which the entire premandibular cavity is formed takes place just after the first visceral clefts appear.

I have spoken of these cavities as arising from the mass of cells in which the notochord ends. This is true; but at the time when the cavities appear, the original mass of cells in which the chorda ended has been increased by the addition of cells proliferated from the walls of the mandibular cavity. Exactly what part of the resultant tissue is derived from each of these two sources, I am unable to say. I believe, however, that the lateral cells in which the paired cavities arise, are in great part, if not entirely, the result of proliferation from the walls of the mandibular cavity.

Although the anterior pair of cavities, and the lateral portions of the premandibular cavity, arise independently in *Acanthias*,

they have undoubtedly the morphological value of spaces cut off from the primitive cœlom. The position, the independence, and the time of origin of the anterior pair of cavities, tend to show that these cavities have a segmental value equal to that of the lateral parts of the premandibular cavity. Van Wijhe (No. 16) found in *Galeus* a pair of head cavities anterior to the premandibular, and thinking them recently cut off from the premandibular cavity, homologized them with prolongations of that cavity which he had seen in *Scyllium*. Denying to them, therefore, a value equal to that assigned by him to the lateral portions of the premandibular cavity, he considered them, and their homologues in *Scyllium*, to represent the visceral portions of the premandibular cavity. It may be mentioned here that the median portion of the premandibular cavity is not ventral to the lateral prolongations of that cavity, as claimed by Marshall for *Scyllium*, but dorsal, as more recently shown by Dohrn in his studies on *Torpedo* (No. 8).

Longitudinal sections through *Acanthias* embryos at a stage when the anterior gill clefts are as yet but pockets from the alimentary canal, show serial divisions of the mesoderm that differ somewhat from the divisions in *Scyllium* described and figured by Van Wijhe (No. 16). I shall merely note the differences here, hoping later to give the subject more careful study. From the anterior limit of the head to the tail the neural cord is marked, at this stage, by a series of constrictions, opposite each of which there lies, in the body, a mesodermic somite, or protovertebra. The line of somites alternating with the neuromeres is continued into the head as far forwards as the alimentary pocket, which is to form the second visceral cleft. Here complete divisions of the mesoderm cease, but serial depressions in its dorsal wall indicate incomplete divisions into three parts above the hyoid arch (Van Wijhe found *two* somites here) and two parts above the mandibular arch. Like the somites of the trunk, the divisions thus marked off alternate with the neuromeres, lying opposite successive constrictions of the brain. The anterior division of the mandibular cavity corresponds to the constriction that separates the mid-brain from the hind-brain, or to that from which the trochlear nerve arises.

In Fig. 1, Pl. IV, the four anterior cavities of the right side of the head are represented at a stage when the hyomandibular

(spiracular) cleft alone has broken through. The median part of the premandibular cavity (1) is indicated as if seen through the walls of the mandibular cavity (2). I have designated the new head cavity (*a*), "anterior," rather than "first," as the numerals, 1, 2, 3, have been already assigned to the premandibular, mandibular, and "third" head cavities respectively. The walls of all four cavities are but one cell in thickness, and are as yet undifferentiated, save that the cells forming the wall of the ventral portion of the mandibular cavity are deeper than those found elsewhere, and the walls of this part of the cavity are somewhat irregular, owing probably to the rapid proliferation of cells from the surrounding mesoderm. The "third" head cavity (3) occupies the place of the most anterior of the three incomplete divisions of the mesoderm which were found at an earlier stage above the hyoid arch.

Between the stages represented in Figs. 1 and 2 the embryo has increased from 6 to 12 mm. in length. The relative increase in size is shown by the reconstructions, as they are made from camera outlines of a like magnification. The diameter of the last two reconstructions (Figs. 6 and 7), however, has been reduced one-half. In the embryo from which Fig. 2 is reconstructed, the *anterior* head cavity (*a*) has increased in size, but its shape is little changed. In relation to the eye, the cavity maintains approximately the same position. In relation to the other head cavities, however, its position is greatly changed, owing in part to the increased cranial flexure, which has carried the cavity to a position apparently posterior to that originally occupied, and in part to the rapid growth of the lateral portions of the premandibular cavity (1), against the outer walls of which the *anterior* cavity (*a*) has now come to lie. The median portion of the premandibular cavity has reached its maximum development, and posteriorly the cavity is becoming constricted, prior to the formation of the inferior oblique muscle. As yet no muscle cells have appeared in its walls. The anterior prolongation of the mandibular cavity (2) now lies in a plane more nearly horizontal, a change due chiefly to the increased cranial flexure, and to the accompanying rapid growth of the dorsal region of the head. The inner wall of the anterior prolongation of the mandibular cavity has become concave, as shown in sec. 10, Pl. VI, which passes

through a horizontal plane in the line sec. 10, Fig. 2, Pl. VI, and represents the mandibular cavity of the opposite side of the head from that seen in the reconstruction. From the same section (sec. 10) it is also seen that the inner wall of the body of the mandibular cavity has become very thin, anticipating its absorption into the general mesoderm. This enlarged part of the cavity is followed by a region where the walls are closely compressed, and this in turn is followed by the rudiment of the large mandibular muscle, "*Kaumuskel*" (*mus.* 2). The third head cavity (3) has become elongated in an antero-posterior direction, and its posterior wall has opened to the general mesoderm. The walls of these cavities are now developing muscle cells in three places; namely, in the ventral part of the mandibular cavity to form the "*Kaumuskel*" above mentioned, in the inner wall at the base of the anterior prolongation of the mandibular cavity (sec. 10, *mus. e*, Pl. VI), and in the inner wall of the *anterior* head cavity (*a*). The oculomotor (III) and abducent (VI) nerves have appeared, and are distributed to the walls of the premandibular and third head cavities respectively.

In Fig. 3, Pl. IV, the point of view has changed. The head cavities are now seen from the median plane of the embryo. I thought it well to picture the primary cavities as they would appear if looked at from the side of the head, but I also wished to project the eye-muscles upon the eyeball, and it consequently became necessary to change the point of view at some stage. I have chosen to do so here. Because of this change, the *anterior* head cavity (*a*) is represented as if seen through the walls of the premandibular cavity. From sec. 4, Pl. V, which passes through the line sec. 4, Fig. 3, Pl. IV, it will be seen that many cells from the median wall of the *anterior* cavity (*a*) have migrated into the centre of the cavity, while the cells bounding the inner wall above and below have the elongated contour of muscle cells. The size and shape of the *anterior* cavity is little changed. The premandibular cavity, however, has grown greatly. The posterior constriction (1 *i.e.*) which appeared in Fig. 2 has increased, and the walls of the portion of the cavity thus cut off are fast developing muscle cells. Cross or horizontal sections through an embryo at this stage show the portion constricted from the premandibular cavity to resemble so closely the *anterior* head cavity (*a*) that the two cavities are only to be

distinguished by their different positions. In both, the cells of the inner wall are becoming muscular, and in both these cells are migrating to the centre of the cavity. Sec. 4 shows that the walls of the premandibular cavity are but one cell in thickness, except where they are about to be continued into the process which forms the inferior oblique muscle (*inf. obl.*).

A break (Fig. 3, *b*, Pl. IV) has appeared in the inner wall of the mandibular cavity, where, posterior to the rudimentary muscle (*mus. e.*) of secs. 10 and 4, the wall was seen in sec. 10, Pl. VI, to be very thin. The division thus begun ultimately separates the cavity into two parts, of which the posterior and central part belongs to the mandible, the anterior and dorsal part to the region of the eye. I have not traced the history of the mandibular muscles, but may mention that a small muscle arises just posterior to the break (Fig. 3, *b*), which I believe to be permanent. It is found later in the neighborhood of the inferior oblique eye-muscle. The muscle *mus. e.* of Fig. 2, has become greatly enlarged in the stage represented by Fig. 3. It continues the line of the external rectus muscle which is now forming from the walls of the *third* head cavity. These two muscles are so intimately connected that for some time I believed the mandibular cavity to take part with the *third* in the formation of the external rectus muscle. The walls of the anterior prolongation of the mandibular cavity have begun their metamorphosis into the superior oblique muscle. Both outer and inner walls take part in the change, but the inner wall is the more active. Their relative thickness does not vary essentially from that represented in sec. 10, Pl. VI. Cells from the posterior wall of the *third* head cavity are fast dropping off into the general mesoderm. It will be noticed that the direction of the long axis of this cavity is changing. The ultimate change is one of 180°, so that the anterior limit of the original cavity forms the posterior or distal attachment of the external rectus muscle.

Between the stages represented in Figs. 3 and 4 the length of the embryo has increased from 16 to 22 mm. In Fig. 4 the outline of the *anterior* head cavity (seen through the walls of the premandibular) appears much as in Fig. 3, but the cavity no longer exists. Its place is occupied by a compact mass of cells. That part of the premandibular cavity which was cut off to

form the inferior oblique muscle has also been filled by the ingrowth of muscle cells, and the solid muscle thus formed has begun to extend in a ventral direction (*inf. obl.*, Fig. 4). Sections through this muscle and through the muscle formed from the walls of the *anterior* head cavity still closely resemble one another. The dorsal wall of the premandibular cavity has now become thickened to form posteriorly the rudiment of the inferior rectus muscle (*inf. rec.*), anteriorly the rudiments of the superior (*sup. rec.*) and the internal (*int. rec.*) recti muscles, which are separated from one another by a slight depression in the wall of the cavity. The internal rectus is the more median of the two anterior muscles. The walls of the premandibular cavity are elsewhere thin. The visceral part of the mandibular cavity has now become entirely severed from the remainder of the cavity, and is omitted in the reconstruction (Fig. 4). The dorsal part of the cavity is now represented by a solid mass of cells, forming anteriorly the superior oblique muscle, posteriorly the muscle marked *mus. e.* The connection between these two muscles has been almost obliterated in the region where the ramus ophthalmicus profundus trigemini crosses the mandibular cavity in passing from the Gasserian ganglion, which is situated lateral to the cavity, to the ciliary ganglion, which lies median to the cavity. The third head cavity has become completely filled by muscle cells that have migrated to the centre of the cavity from its inner wall, as shown in sec. 5, Pl. V. This section also shows the peculiar relation existing between the external rectus muscle, now forming in the third head cavity, and the mandibular muscle, *mus. e.* If this cross-section be compared with a similar section through an older embryo, represented in sec. 6, it will be seen that were the cells of the mandibular muscle (*mus. e.*) to fuse with those of the third head cavity (*ext. rec.*) at the stage represented by sec. 5, the resulting muscle would closely resemble in shape the external rectus of sec. 6. I am convinced, however, that such a fusion does not take place, for the limiting wall of the third head cavity can be traced until the muscle here formed comes to occupy the entire place once occupied (sec. 5) by the cells of the two muscles (*ext. rec.* and *mus. e.*). The cells of the mandibular muscle (*mus. e.*) gradually yield their place to those of the third head cavity and are ultimately lost in the general mesoderm. Thus a muscle, the rudi-

ment of which appeared in the walls of the mandibular cavity prior to the origin of any of the eye-muscles, completely disappears, although in the embryo of 22 mm. it is still relatively large as compared with the eye-muscles.

Fig. 5, Pl. IV, shows the eye-muscles of an embryo of 27 mm. Between this stage and that last reconstructed (Fig. 4) the outline of the anterior head cavity has become indistinct, and its cells, undergoing retrogressive development, have lost their muscular character and are finally indistinguishable from the cells of the general mesoderm which surrounds the eye. We have reason therefore to believe that two large muscles are lost in this region of the head; namely, that formed from the *anterior* head cavity and the rudimentary muscle of the mandibular cavity (*mus. e.*). What the function of these muscles may have been I am unable to guess, unless they possibly belong to the lost gill arches said once to have existed anterior to the mandibular arch. In Fig. 5 the premandibular cavity is still found. The four muscles to which its walls give rise are beginning to radiate towards the points of their ultimate attachment. The cells of the rudimentary muscle (*mus. e.*), so closely related to the external rectus, are now indistinguishable from the surrounding mesoderm, and the superior oblique eye-muscle represents all that is left of the walls of the dorsal part of the mandibular cavity.

In an embryo of 35 mm. (Fig. 6) the premandibular cavity has disappeared. The principal changes in the position of the eye-muscles relate to the external rectus and to the superior and inferior oblique muscles. What was originally the posterior limit of the external rectus now lies anterior to the remainder of the muscle. The superior and inferior oblique muscles are approaching one another. In still older embryos the approximation is continued until the points of their proximal attachment meet.

In the embryo of 55 mm. (Fig. 7) the eye-muscles conform so closely to the adult condition that it is unnecessary to trace their development further.

In concluding, I would say in regard to the anterior head cavities that their primary position and the time of their origin both point to their serial position as between the mandibular and premandibular cavities. Van Wijhe suggests that the

homologues of these anterior cavities in Galeus and Scyllium may be regarded as the visceral portions of the premandibular cavity cut off by the mouth involution. Such a view is not warranted by the position of the cavities in Acanthias. They lie dorsal to the premandibular cavity, and if an independent segmental value is not to be ascribed to them, it is much more probable that they represent the visceral portion of the anterior division of the mandibular cavity than that of the premandibular, as suggested by Van Wijhe (No. 16).

#### B. CIRCULATION.

The early development of the circulatory system in Acanthias corresponds quite closely to the development in Pristiurus as described and figured by Dohrn (No. 6). A few differences, however, may be noticed.

At the stage from which Fig. 8 is reconstructed, from the enlarged end of the primitive heart, two arteries ascend in the mandibular arches to the dorsal aorta. At the base of the mandible each artery becomes enlarged, and a downward projection of its ventral wall as the artery turns inward to meet that of the opposite side, is the budding arteria ophthalmica magna. Anterior and lateral to the two projections thus formed lie the lateral portions of the premandibular cavity. The ophthalmicæ magnæ are thus seen to maintain in their position the same relations to the lateral portions of the premandibular cavity that the hyoid and mandibular arteries maintain to their respective head cavities. Their position is median and slightly posterior to that of the cavities. If the ophthalmica magna is, as Dohrn (No. 7) suggests, to be regarded as the remains of a premandibular aortic arch, then it would seem reasonable from the position of the vessel to connect it with the premandibular cavity, as both belonging to the same body segment.

As the mandibular arteries fuse with one another, they send forward two small branches, which, passing to either side of the notochord, open into a wide blood-space *posterior* to the point of the chorda. From this space two branches extend laterally downwards and forwards (Fig. 8, *ac*, Pl. IV). These branches lie at either side of the premandibular cavity, but meet the

median walls of the *anterior* head cavities, from which it would seem that they may be segmentally related to these anterior cavities.

A glance at the reconstruction (Fig. 8) makes evident the significance of the blood-space now lying dorsal to the point of the notochord. Originally the aorta, or aortæ, lay straight below the chorda, extending as paired vessels to fuse anteriorly in a single wide chamber, from which two or, if we include the arteriæ ophthalmicæ magnæ, three pairs of aortic branches were given off. When the flexure of the chorda occurred, the point of the chorda passed through the aorta, almost severing an anterior portion of the vessel, with one pair of branches from the main aorta, and placing them in their present abnormal position apparently dorsal to the notochord. If the ophthalmicæ magnæ are to be viewed as the remains of aortic arches, what shall we say of these anterior branches which are well developed when but one complete aortic arch exists, and when the ophthalmicæ magnæ and the hyoid arteries are represented as small pockets in the wall of the aorta? Whether or not these vessels ever functioned as aortic arches, and aside from any consideration of imaginary gills they may once have supplied, we may surely view them as segmental vessels, giving one further clue to the lost metamery of the head.

At the stage of development from which Fig. 8 is reconstructed no cardinal veins are to be found, unless a few isolated spaces in the neighborhood of the vagus, facial, and trigeminal ganglia are scattered beginnings of a more definite channel.

In the next stage that I have figured (Fig. 9), two pairs of aortic arches are complete; namely, the mandibular and the hyoid. Two posterior pairs of arches may be traced a short distance from the aorta. The condition of the anterior vessels is much the same as represented in Fig. 8, save that a pair of small branches (*cd.*<sup>1</sup>) are now seen to arise from the anterior and dorsal wall of the aorta. They may be traced backward a short distance, but soon disappear. These vessels are the first definite rudiments of the cardinal veins. They soon separate from the aorta, taking with them as they part the aortic space posterior to the chorda, with its pair of aortic branches. Fig. 10 represents the completed separation. There are now six aortic arches, and the arteriæ ophthalmicæ magnæ (*oph. m.*) are well developed.

The anterior limit of the dorsal aorta has begun to recede from the point of the chorda. The irregular blood-spaces about the brain and cranial ganglia have become more or less confluent, and now open into the main venous branches. From the anterior cardinals plus anterior aorta, three pairs of vessels, with the irregular outlines of the primitive venous system, extend towards the dorsal wall of the brain. It will be noticed that as the cardinals pass the chorda each divides to reunite before opening into the aortic space posterior to the chorda (*aa'*). I believe this division and reunion to be of constant occurrence at this stage, but can assign no reason for it.

Dohrn (No. 6) finds that in *Pristiurus*, before the artery and posterior vein of a gill arch have separated from the anterior vein, there are *two* commissures, between the anterior and posterior veins of each arch. These he figures, giving also a later stage in *Scyllium*, where the artery and the posterior vein have separated from the anterior vein and from one another, the posterior vein having now united with the anterior vein of the following arch. In this later stage but *one* vein commissure exists in each arch. In *Acanthias*, at a stage between the two above described, when the artery and the posterior vein have separated from the anterior vein (except in the fourth gill arch), but when the posterior vein is not connected with the vein of the following arch, I find at least five vein commissures in both the first and second branchial arches, and at least four vein commissures in the third and fourth arches. The more or less complete division of some of these commissures points to the possible existence of seven or more commissures in each arch, while the fact that many sections show the commissures to be directly continued, without perceptible change in diameter, into the veins of the long external gill filaments, suggests that there may once have been as many commissures as filaments.

The vessel which unites the hyoid vein with the first aortic arch (mandibular) has been homologized by Dohrn with the vein commissure of the true gill arches, and he considers the position of this vessel decisive in determining the serial homologies of the mesodermic structures which it parts. Now, in *Acanthias*, the final vein commissures of the gill arches must represent five or seven, or possibly more, original commissures, extending in all over the entire curve of the gill vein from the point where, in

ascending the arch the vessel leaves the horizontal plane, to the point where, in turning towards the aorta, it becomes again horizontal. Supposing, as seems probable, that the commissure which unites the vein of the hyoid arch with the mandibular artery, is really the homologue of a commissure of the gill arches, this assumption would not necessarily involve the further assumption that its position is identical with that of the final commissures of the arches, since these must represent a reduction of five or more primary commissures, extending in all over quite a wide space. Yet this second assumption would be necessary in order to argue from the position of the hyoid commissure to the homologies of structures lying above or below it.

At this stage, in which the gill arches possess several commissures, the walls of the mandibular artery have become very thin below the commissure that connects this artery with the hyoid vein, and it is difficult to follow the artery in its ventral portion until it again becomes distinct on turning towards the axial line of the body. Retrogressive development is evidently taking place. The hyoid vein and the anterior vein of the first branchial arch are now prolonged ventrally towards the inner limit of the first gill cleft. Here the branchial vein is continued in a small vessel with thick walls, which, passing below the inner opening of the cleft, unites with the ventral prolongation of the hyoid vein, and is then further continued over the dorsal wall of the hyoid artery to unite with the ventral end of the mandibular artery, which has now lost its connection with the aorta (Fig. 11, \*, Pl. ). Maurer (No. 12) says that he has seen in several series of *Acanthias* embryos a ventral continuation (as in the Teleosts) of the first gill vein, which united with the first arterial arch (mandibular). He does not mention a union with the hyoid vein at the same point. Yet this anastomosis seems to me of interest, since it gives an intermediate stage in the successive reductions by which one passes from the hyoid circulation in the Selachians to that of the Teleosts and Amphibians.

In Selachians, at an early stage, a single aortic arch exists in each of the mandibular, hyoid, and successive branchial arches. In the branchial arches this vessel soon divides into three, the artery, and the anterior and posterior branchial veins. In the hyoid arch the primary vessel divides into but two, the artery and the posterior vein, while in the mandibular arch the vessel remains undivided.

In the Teleosts, where the hyoid has no gill, its primitive aortic arch does not divide, but a ventral prolongation of the vein of the first branchial arch anastomoses with the common root of the mandibular and hyoid arteries, which lose their connection with the ventral aorta.

According to Maurer (No. 12), no hyoid artery develops in the Amphibians; consequently the artery of the first branchial arch follows immediately upon the mandibular artery, which is then seen to arise from the base of the first branchial artery, rather than independently from the aorta. When, as soon happens, the mandibular artery loses its connection with the ventral aorta, it still remains connected with the base of the first branchial artery, which is at the same time severed from the aorta. Later, the first gill vein develops from this branchial artery. Thus it happens that the ventral prolongation of the first gill vein is continued into the mandibular artery, forming the *artera carotis externa*.

To review: in the Selachians the branchial circulation becomes hyoidean by the loss of the anterior gill vein. The hyoid circulation of *Acanthias* in the stage described becomes Teleostean by the loss of the hyoid artery or becomes Amphibian by the loss of both artery and vein. The progressive change is a simple reduction by loss of parts, and not a modification by the introduction of new relationships not found in the Selachians.

### C. THE NERVES.

While my studies on the medulla of the chick (No. 14) and the salmon confirmed the results obtained by Béranek (Nos. 4, 5) and Orr (No. 13) in regard to the number, position, and constancy of the "neuromeres" of the medulla, they led me to believe that the primary attachment of the cranial nerves was between consecutive neuromeres, rather than from the convexity of a neuromere. I carefully examined successive constrictions of the brain in the chick, but was unable to find any nerves arising from the neural crest anterior to the trigeminus. Renewing the search with my present Elasmobranch material, and examining the first constriction anterior to the medulla, I found there a nerve, which proved to be the primitive trochlearis. By comparing longitudinal sections through older embryos with

like sections figured by Marshall (No. 11), in which he represents the trochlear nerve as it first appears in Scyllium, I found that in later stages of *Acanthias* embryos, the nerve resembles its earliest appearance in Scyllium; the proximal portion then consisting of a mere knob of cells upon the dorsal surface of the brain. This difference in the time at which the trochlear nerve first appears in Scyllium and in *Acanthias* is explained by Van Wijhe, who tells us (No. 16) that in Scyllium there are two long outgrowths from the neural crest anterior to the facial nerve. One lies anterior to the second (mandibular) somite; the other is situated at its posterior and lateral side. The neural crest then gradually vanishes from before backwards, and with its disappearance the anterior outgrowth approaches the posterior, at the same time relinquishing its attachment to the mid-brain. It finally comes to arise by a common root with the trigeminus from the anterior end of the medulla. Thus Van Wijhe failed to recognize, in the anterior prolongation of the neural crest, the primary trochlear nerve, and the ramus ophthalmicus superficialis trigemini seemed in Scyllium and in *Pristiurus* simply a branch of the main trigeminal root. In *Acanthias*, however, the trochlearis retains its original attachment after the disappearance of the neural crest in the region between this nerve root and the trigeminus. Later, when the proximal part of the trochlearis atrophies, the distal part remains and is seen by its position to be the ramus ophthalmicus superficialis trigemini.

The history of the trochlear nerve in *Acanthias* is as follows: primarily, a wide sheet of cells extends down the walls of the brain from mid-brain to medulla. This sheet of cells then divides into three parts, connected above and below. These divisions lie opposite successive constrictions of the brain, and are consequently separated from one another by two neuromeres. The two posterior parts fuse into a single nerve root, the trigeminal. The anterior part retains its original attachment to the brain, and as the dorsal wall of the brain grows, becomes further removed from the trigeminus, changing at the same time the line of its direction, so that ultimately, while the trigeminal root meets the Gasserian ganglion in a vertical plane, the trochlearis, lying in a plane nearly horizontal, meets the ganglion at the point where the ramus ophthalmicus profundus trigemini leaves it.

Sec. 9, Pl. VI, shows the trochlearis in horizontal section at the time when two gill clefts have broken through, and when the Gasserian ganglion is attached by its trigeminal root to the side of the medulla. Along the line where the trochlearis arises, the mid-dorsal wall of the brain is elevated, indicating a rapid proliferation and migration of cells. This crest disappears at either side of the nerve root, and the upper surface of the brain becomes quite level. It will be noticed that the cells of the trochlear closely underlie the ectoderm. Many sections indicate that they maintain a closer relationship to the ectoderm than that of mere propinquity. Soon after the stage represented in sec. 9, the primary root of the trochlearis begins to atrophy. This takes place in a somewhat irregular manner. Fragments of the nerve are to be found at varying points of its original course, for a long time after the nerve in its entirety has ceased to exist. The most common positions for these fragments are at either side of the mid-dorsal line of the brain (resembling Marshall's figure of the first appearance of the trochlearis in *Scyllium*), or at a point about half-way between the original attachment of the nerve and the Gasserian ganglion. They are frequently asymmetrically placed on opposite sides of the embryo, and may be wanting in either of the above-mentioned positions, or found in both. Sooner or later the fragments disappear, and all that is then left of the original nerve is a line of cells extending forwards from the Gasserian ganglion. In whatever way the primary trochlearis breaks down, these cells are constantly left. They are the homologues of the trigeminal branch of the ophthalmicus superficialis, described and figured by Van Wijhe. In *Galeus*, as in *Acanthias*, this nerve does not arise, as is the case with *Scyllium* and *Pristiurus*, from the ganglion root of the trigeminus, but in common with the ramus ophthalmicus profundus from the anterior portion of the Gasserian ganglion. The cells thus left by the trochlearis lie above the anterior part of the mandibular cavity, and give rise to a nerve which runs forwards over the wall of this cavity, and to a mass of deeply staining cells, surrounding the nerve anteriorly. As the superior oblique muscle develops, these cells lie upon its dorsal surface.

In describing the disappearance of the primary trochlearis in *Torpedo*, Dohrn (No. 8) mentions an isolated mass of cells which

the nerve leaves, as it atrophies, on either side of the brain. These cells soon vanish, but Dohrn suggests that they may be the remains of a pristine trochlear ganglion. The position and early disappearance of the cells makes me think them homologues of the fragments (sec. 8, IV<sup>2</sup>) found in *Acanthias* at the side of the brain, rather than homologous to the cells lying above the superior oblique muscle; for the latter do not soon disappear, but may be found after the entire trochlear nerve is re-established. They represent probably but part of the original trochlear ganglion, the greater part of which is to be looked for in the anterior portion of the Gasserian ganglion.

In the reconstructions, showing the development of the eye-muscles, I have indicated the position and general direction of the anterior cranial nerves at the several stages reconstructed. Although this was done with the view to establish more surely the relations of the head cavities, and although many large branches have been omitted, the reconstructions may still be helpful in showing the relations of such nerves as are there outlined. Fig. 1, Pl. IV, shows the position of the trochlear and trigeminal nerves at a stage somewhat earlier than that from which sec. 9, Pl. VI, is drawn. In Figs. 2, 3, 4, the distal portion of the trochlearis (*V, an.*) is seen as it extends forwards over the anterior prolongation of the mandibular cavity or over the superior oblique eye-muscle.

Between the stages represented in Figs. 4 and 5, and long after all trace of the proximal part of the primary trochlearis has vanished, a small fibrous nerve (sec. 11) grows from the brain at the point where the original trochlearis grew from the neural crest. The nerve can be followed a short distance into the mesoderm, but becoming extremely attenuated, is soon lost. Sec. 11 shows that a fibrous commissure, crossing the dorsal wall of the brain, connects the two nerve roots (IV) of opposite sides. Soon after the appearance of this small nerve, which is the root of the permanent trochlearis, cells are proliferated to meet it, from the ganglion cells that lie above the superior oblique muscle. Thus the permanent trochlearis (sec. 7, Pl. V) arises from two sources, from the brain and from ganglion cells.

At least two objections may be raised on the ground of *a priori* improbability against this account of the development of the trochlearis. In the first place, it seems highly improbable

that the nerve, after losing its primary attachment to the brain, should grow back through so great a distance to the point whence it originally arose, unless its continuity had been but seemingly interrupted. In the second place, it seems improbable that the nerve should result by the fusion of two outgrowths, one from the ganglion, and one from the brain.

In regard to the first of these objections, it will be noticed that the position of the primary trochlearis is not the same as that of the permanent nerve (compare secs. 9 and 7). The former lies close against the ectoderm, the latter deep in the mesoderm. Further, at the time when the primary trochlearis atrophies, it is a compact cord, measuring three or four cells in diameter, and when it breaks into fragments, as mentioned above, they retain the width of the primary nerve (sec. 8). In order that the final nerve should be the same as the original trochlearis, it would therefore be necessary to bridge two, or sometimes three, wide breaks in a solid cord, the cells of which still retain their primary rounded contour, and are not prolonged into fibres. Evidently such connection, if it existed, could not be overlooked.

In regard to the second objection, the *cells* of the permanent trochlearis cannot arise from the brain, because no cells are to be found in the root of attachment, as would certainly be the case if cells migrated from the brain to the distal portion of the nerve. The *fibrous root* of the nerve cannot be composed of prolongations from the distal cells, because the fibrous or proximal part of the permanent trochlearis arises before the distal and cellular part; further, the fibrous root is thickest as it comes from the brain, becoming gradually attenuated as it proceeds into the mesoderm.

Therefore the permanent trochlearis is a new nerve, arising from two sources..

Before the permanent trochlearis is formed, branches of the ramus ophthalmicus superficialis trigemini (all that is left of the original trochlearis) are quite widely distributed in the region surrounding the anterior limit of the superior oblique eye-muscle. When the permanent trochlearis is established, its relation to the superior oblique muscle, and to the ramus ophthalmicus superficialis, is such, that the ophthalmicus, rather than the trochlearis, appears to supply the muscle. A single

sagittal section passes through nearly the entire length of the ophthalmicus superficialis, including the distal distribution of its branches upon the surface of the superior oblique muscle, while the trochlearis, in passing from the brain to the muscle, turns at a right angle where it meets the ophthalmicus superficialis. The relation of the nerves to the muscle is shown in Fig. 6, Pl. IV. In fact, the trochlearis and the ramus ophthalmicus superficialis trigemini are simply parts of one and the same nerve, from which nerve a branch passes to the surface of the superior oblique muscle. In older embryos the path of the trochlearis becomes more direct, and its connection with the ophthalmicus superficialis then appears as a mere anastomosis between two independent nerves.

Sec. 7, Pl. V, shows the permanent trochlearis when first entirely developed. The drawing is put together from several sections, one of which passes through the fibrous part of the nerve, and one through the distal third of the nerve. The two sections were united, and the median portion of the nerve interpolated by the aid of the camera. The sections make an angle of  $45^\circ$  with the long axis of the body, which is approximately the plane of the nerve. Sec. 13 shows the structure of the median portion of the trochlearis at about the same stage. The section is drawn especially to show that the body of the nerve is cellular, and that the nuclei belong to the nerve, and not to a mesodermic sheath.

Returning to the stage when the primary trochlearis and the trigeminus have not yet separated, but are represented in a continuous sheet of cells, and examining the constriction of the brain next anterior to that from which the trochlearis grows, one finds here a cord of nerve cells, which, arising in the mid-dorsal wall of the brain, extend downwards back of the eye, to meet there a line of cells continued forward from the Gasserian ganglion. Dohrn finds in *Torpedo* a prolongation of the neural crest which is undoubtedly the homologue of this nerve in *Acanthias*. At the stage described, the neural crest has disappeared between this nerve and the sheet of cells representing the united trochlear and trigeminal nerves. The nerve passes ventrally into a group of cells that are undoubtedly the rudiments of a ganglion. The connection between these cells and the Gasserian ganglion is the path of the future ramus ophthal-

micus profundus trigemini. Along the same line the rudimentary ganglion is continued forwards to unite with cells, which, arising from the anterior lips of the neuropore, have fused with the primary nasal epithelium. Successive stages in the early development of this nerve have not been figured, from lack of abundant material. Recently, however, the needed material has been obtained, and I hope soon to give the development and relations of the nerve more careful study than has hitherto been possible.

The nerve arises from the constriction that separates mesencephalon and thalamencephalon. As the term "mesocephalic" has been applied by Beard (No. 3) to the ganglion usually called "ciliary," I suggest that this new nerve, in consideration of its origin, be called the "thalamic" nerve. With the growth of the dorsal wall of the brain, the nerve is carried forwards and comes to lie directly above the optic stalk. In Fig. 1, Th, Pl. IV, the position of the nerve is outlined at the time when one gill cleft has broken through. Sec. 12, Pl. VI, passes through the root of the thalamic nerve at the time when two pairs of branchial clefts have broken through, and the third is only closed by the thinnest ectoderm. The plane of this section is indicated in Fig. 1, sec. 11, Pl. IV: the section, however, is from an older embryo. The nerve at this stage is a round fibrous cord containing many nuclei. Its fibres can be traced into the brain, but vanish distally in the mesoderm above the eye. The primitive character of undifferentiated cells from the neural crest has been entirely lost. Later the thalamic nerve atrophies in much the same manner as does the primary trochlear.

In the series from which sec. 3 is drawn, the remains of the thalamic nerve are still to be found as two masses of cells, one connected with the brain in the mid-dorsal line, the other lying isolated at the side of the brain. This tells us that the thalamic nerve does not entirely disappear before the oculomotorius is established, or before four pairs of branchial clefts have broken through. The phylogenetic significance of these facts is surely great; and although the homologue of this nerve, found in other Selachians is a quickly vanishing prolongation of the neural crest, it is not therefore to be lightly overlooked.

When Rabl (No. 15) says, "Vor allem haben wir daran festzuhalten, dass der Vorderkopf nur zwei primäre Nerven, den Tri-

geminus und Acustico-facialis besitzt," "vor allem" surely cannot mean that we are to hold by the above dictum even though it be contradicted by facts.

The peculiar development of the trochlearis led me to look with great interest for the origin of the oculomotorius. This nerve arises in the stage when three branchial clefts have appeared, or when the length of the embryo is about 1 cm. At first the nerve lies in a plane nearly horizontal, and extends from the inner and dorsal angle of the ciliary ganglion to the brain. Its path crosses that of the veins  $c^2$ , Fig. 10, Pl. IV, and lies from two to four sections ( $\frac{2}{300}$  to  $\frac{1}{100}$  mm. in thickness) above these vessels. Horizontal sections through the venous space  $aa'$ , Fig. 10, pass above the nerve; sections through the branches,  $c^2$ , Fig. 10, pass below it. Hence the region to be searched for the origin of the oculomotorius is limited. Sec. 2, Pl. V, shows the oculomotorius when it consists of but one cell, extending from the ciliary ganglion to the brain. To judge from the position of this cell, it might have migrated either from the brain or from the ganglion, although the appearance of the inner and dorsal angle of the ganglion indicates that a migration of other cells may be about to take place. I was so fortunate as to obtain another series of sections in which the oculomotorius is also represented by but one cell (sec. 1, Pl. V) and in which the position of the cell leaves no doubt that its migration from the ciliary ganglion has recently taken place. In sec. 3, Pl. V, at a stage when four branchial clefts are through, the nerve is well established. These three sections tell together the story of the origin of the oculomotorius, or at least trace its source back to the inner cells of the ciliary ganglion. Whence these cells are derived, I am unable to say, and upon the answer to this question depends the true position of the oculomotorius in the series of segmental nerves. The "Anlage" of the ciliary ganglion lies in the region where the prolongation from the neural crest that forms the thalamic nerve meets that from which the trochlear and trigeminal nerves arise. Later, when the ciliary ganglion is well developed, the connection with the thalamic nerve is lost, and the ophthalmicus profundus is seen to unite the ciliary ganglion with the Gasserian at the point where the primary trochlearis enters. Three cranial nerves are therefore intimately connected with the formation of the ciliary

ganglion. I believe, however, that the proper ganglion of the thalamic nerve atrophies between the optic vesicle and the brain, where a group of cells are long found which stain differently from the surrounding cells. The ciliary ganglion can hardly be the proper ganglion of the trochlearis, since this nerve has its own ganglion lying above the superior oblique eye-muscle; and if all of the original ganglion cells of the trochlearis are not here represented, they are surely to be looked for along the line of the original connection between this ganglion and the Gasserian; in other words, on the path of the ramus ophthalmicus superficialis trigemini, and not on that of the ramus ophthalmicus profundus. The latter never occupies the position of that remnant of the neural crest which ventrally united the rudiments of the trigeminal, trochlear, thalamic, and olfactory nerves. I therefore consider the ramus ophthalmicus profundus a commissural nerve, resembling that nerve which connects the several vagus ganglia, and must leave the question to which of the main divisions of the neural crest the ciliary ganglion primarily belongs, quite unanswered.

The fact that both the oculomotorius and the permanent trochlearis are formed by the proliferation of ganglion cells towards the brain makes it highly probable that these nerves are both primarily sensory. At an early stage the ciliary ganglion is intimately connected with a thickening of the epithelium, which, if sensory, as seems probable, would transmit to the brain any impulses it received most directly by way of the oculomotorius. It may also be remembered that the walls of the premandibular cavity do not develop muscle cells for some time after the first appearance of the oculomotorius, from which it seems that the nerve is sensory prior to the acquisition of its motor function. The connection of the ciliary ganglion with the floor of the mid-brain by means of the oculomotorius, I believe to be a secondary attachment, homologous to the secondary attachments of other ganglia to the brain. Van Wijhe (No. 16) suggests that the optic nerve is morphologically anterior to the olfactory. I think that he is right, and I sometimes suspect that the oculomotorius is morphologically anterior to the opticus.

The development of oculomotorius and trochlearis in *Acanthias* tends to show that Balfour (No. 2) was right in considering the

roots of efferent and afferent nerves primarily united. If these two nerves are originally mixed nerves, then no purely motor nerves are to be found in the anterior part of the head until the abducens is reached. In regard to this nerve, I have nothing to add to the little already known. It arises in *Acanthias* by two main roots, and is at first distributed not only to the walls of the *third* head cavity, but also to the general mesoderm posterior to that cavity. Few nuclei are found throughout its course, and the peripheral position of these indicates that they are probably mesodermic, belonging to the nerve sheath, rather than to the nerve itself.

#### SUMMARY.

1. The curved end of the notochord passes through the dorsal aorta, thus almost severing from the main vessel an anterior portion, which gives rise to a pair of relatively large branches.

2. At first the cardinal veins open into the aorta at a point dorsal to the origin of the mandibular arteries. In later development, as the anterior limit of the aorta recedes, these veins lose their direct connection with it, retaining, however, their connection with that part of the primary aorta which was almost cut off by the flexure of the chorda. Hence this part of the aorta, with its pair of aortic branches, becomes incorporated into the venous system.

3. Anterior to the premandibular cavity there is a pair of head cavities. These cavities arise independently, and are at no time continuous with the premandibular cavity. The cells of their walls are so modified, in the course of development, as to resemble the muscle cells forming simultaneously in the walls of the adjacent head cavities. No permanent muscle is formed, and the cells are later lost in the general mesoderm about the eye. These cavities are probably homologues of those found by Van Wijhe (No. 16) in *Galeus*. Their lateral position leads me to think that they cannot be homologized with any of the head cavities recently described by Dohrn (No. 8) in *Torpedo*.

4. In relation to the new head cavities, the position of the anterior arterial branches above described (1) is similar to the position of the first aortic arch, in relation to the mandibular cavity, or to the position of the arteriæ ophthalmicæ magnæ

in relation to the lateral portions of the premandibular cavity, suggesting that the arteries and cavities thus in their position similarly related may be associated segmentally.

5. The number of primary commissures connecting the branchial veins in each arch is not limited to two, as seems from Dohrn's (No. 6) description to be the case in *Pristiurus*. In *Acanthias* I have counted as many as five commissures in each of the anterior branchial arches, and the partial division of many of these commissures indicates that their original number may be even greater.

6. The first aortic arch, *i.e.* the mandibular, unites ventrally with both the hyoid vein and the anterior vein of the first branchial arch. This union gives a connecting link in the hyoid circulation of Selachian, Teleost, and Batrachian.

7. The walls of the premandibular cavity give rise to the superior, inferior, and internal recti muscles, and to the inferior oblique muscle. The walls of an anterior prolongation of the mandibular cavity give rise to the superior oblique muscle, and from the walls of the so-called *third* head cavity is formed the external rectus muscle. These observations merely confirm those of Van Wijhe (No. 16), whose study of the development of the eye-muscles in the Selachians did not include those of *Acanthias*.

8. The rudiment of a large muscle is found in the walls of the mandibular cavity, in close proximity to the external rectus muscle. This rudimentary muscle, like that which arises from the walls of the *anterior* head cavity, is later lost in indifferent mesoderm.

9. My study of successive stages in the development of the eye-muscles shows that the muscle cells of the external rectus first appear in the *median* wall of the *third* head cavity. The cells pass from this wall into the cavity, ultimately filling it. This is also the case with the rudimentary muscle formed from the walls of the *anterior* head cavity. The superior oblique muscle and the rudimentary muscle of the mandibular cavity appear first in the *median* wall of this cavity. The premandibular cavity is formed by the fusion of a pair of lateral cavities with a median space, which is generally supposed to have a morphological value widely different from that of the two cavities which it unites. If the *median* walls of the originally paired cavi-

ties are represented in the resulting single cavity, they are surely to be looked for at the line where the lateral cavities have fused with the central space. The four premandibular eye-muscles arise from the dorsal wall of the lateral portions of the premandibular cavity, approximating closely, in their place of origin, the line of fusion between the paired cavities and the central space. In view of these facts it is difficult to understand the ground of one of the chief objections advanced by Rabl (No. 15) against considering the premandibular, the mandibular, and the *third* head cavities homologues of the body somites. He says, "Während ferner die Muskulatur der Urwirbel ausschliesslich aus der medialen Wand entsteht, nimmt sie im Vorderkopf zum grössten Theil aus der lateralen und zum kleineren Theil aus den hinteren Wand der sogenannten Somite den Ursprung."

10. The trochlear and trigeminal nerves arise as a continuous sheet of cells, extending from the neural crest down the walls of the brain. The two nerves soon separate. The trochlearis is then seen to arise anterior to the cerebellar division of the brain, and the trigeminus posterior to this division. The proximal cells of the trochlearis, *i.e.* the cells which connect the nerve with the brain, soon disappear, leaving the distal cells of the primary nerve still connected with the trigeminal ganglion at the point of origin of the ramus ophthalmicus profundus. From these cells a nerve is formed which extends forwards over the anterior prolongation of the mandibular cavity. This nerve is surrounded anteriorly by a mass of deeply staining cells, which lie above the forming superior oblique muscle. They are the remains of the primary trochlearis, and from them cells are proliferated towards the brain to meet the small fibrous outgrowth of the permanent trochlearis. Thus a portion of the original trochlear nerve, which was an outgrowth from the neural crest, does not entirely disappear, but is known later as the ramus ophthalmicus superficialis trigemini, and the permanent trochlearis is formed by the growth of ganglion cells towards the brain, and of nerve fibres from the brain.

11. Anterior to the mid-brain there is an outgrowth from the neural crest, which extends downward back of the eye, meeting the ganglion line ventrally in the neighborhood of the ciliary ganglion. This outgrowth persists after the disappearance of the neural crest. It is carried forward by the growth of the

dorsal wall of the brain, and comes to lie, in horizontal section, above the optic stalk, arising now as a differentiated nerve from the depression between the mesencephalon and thalamencephalon, it passes down the sides of the brain, and is lost in the mesoderm above the eye. It finally atrophies at about the time and in the same manner as does the proximal part of the primary trochlearis. Dohrn (No. 8) has described in *Torpedo* an homologous prolongation of the neural crest.

12. From the point where the primary trochlearis unites with the trigeminal ganglion a line of nerve cells extends forward, which soon enlarges into the rudiment of the ciliary ganglion, then meets the anterior prolongation from the neural crest, which develops into the nerve that I have called "thalamic," and finally ends in a mass of cells which, arising from the anterior margin of the neuropore, have united with the primary nasal epithelium. This line of nerve cells is later represented by the ramus ophthalmicus profundus trigemini. The nerve is therefore primarily a commissural nerve. It unites the original ganglionic cells of the trigeminus, trochlearis, oculomotorius, thalamicus, and olfactorius.

13. The oculomotorius first appears as a cellular proliferation from the inner cells of the ciliary ganglion. The nerve grows from the ganglion towards the brain, with which it becomes united in the floor of the mid-brain. It is therefore probable that the oculomotorius is primarily sensory; a conclusion which is strengthened by remembering that at the time when the nerve arises, the ciliary ganglion is connected with a large patch of thickened epithelium, while the walls of the premandibular cavity have not yet developed muscle cells.

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 LETTERING.

## II.-VII. Cranial nerves.

- V, *an*, distal portion of the primary trochlearis.
- I-3, head cavities.
- I<sup>i.o.</sup>, part of the premandibular cavity forming the inferior oblique eye-muscle.
- 2<sup>s.o.</sup>, part of the mandibular cavity forming the superior oblique eye-muscle.
- a*, anterior head cavity.
- aa*, anterior part of the dorsal aorta.
- aa'*, anterior part of the dorsal aorta taken into the cardinal system.
- ac*, branches of the dorsal aorta.
- ac'*, branches of the dorsal aorta taken into the cardinal system.
- aud.*, auditory vesicle.
- b.*, break in the walls of the mandibular cavity.

- b. c. g.*, connection of oculomotorius and ciliary ganglion.  
*br.*, brain.  
*br. a.*, branchial artery.  
*br. v.*, branchial vein.  
*c<sup>1</sup>, c<sup>2</sup>, c<sup>3</sup>*, branches of cardinal veins.  
*Cd.*, cardinal vein.  
*cd.<sup>1</sup>*, rudiment of cardinal vein.  
*c. g.*, ciliary ganglion.  
*Ch.*, chorda dorsalis.  
*com.*, commissure from hyoid vein to mandibular artery.  
*D. A.*, dorsal aorta.  
*dis.*, distal.  
*ect.*, ectoderm.  
*ext. rec.*, external rectus eye-muscle.  
*hy. a.*, hyoid aortic arch.  
*hy. art.*, hyoid artery.  
*hy. v.*, hyoid vein.  
*inf. obl.*, inferior oblique eye-muscle.  
*inf. rec.*, inferior rectus eye-muscle.  
*int. rec.*, internal rectus eye-muscle.  
*md. a.*, mandibular aortic arch.  
*mus<sup>2</sup>.*, mandibular muscle (Kaumuskel).  
*mus<sup>4</sup>.*, rudimentary muscle of mandibular cavity.  
*oph. m.*, arteria ophthalmica magna.  
*oph. m.<sup>1</sup>*, rudiment of arteria ophthalmica magna.  
*oph. sup.*, ramus ophthalmicus superficialis facialis.  
*opt.*, optic vesicle.  
*pr.*, proximal.  
*prof.*, ramus ophthalmicus profundus trigemini.  
*prof.<sup>3</sup>*, branch from the profundus in the direction of the anterior head cavity.  
*s. c. g.*, ectodermic thickening connected with the ciliary ganglion.  
*sec.*, section.  
*sup. obl.*, superior oblique eye-muscle.  
*sup. rec.*, superior rectus eye-muscle.  
*Th.*, thalamic nerve.  
*v. br.*, floor of brain.  
*v. com.*, vein commissures of first branchial arch.

\* Anastomosis of  $\left\{ \begin{array}{l} \text{mandibular artery.} \\ \text{hyoid vein.} \\ \text{first branchial vein.} \end{array} \right.$



## DESCRIPTION OF PLATE IV.

- FIG. 1. Embryo of 6 mm. The four anterior head cavities are shaded, and the anterior cranial nerves outlined.
- FIG. 2. Anterior head cavities from an embryo of 12 mm.
- FIG. 3. Anterior head cavities from an embryo of 16 mm.
- FIG. 4. Eye-muscles from an embryo of 22 mm.
- FIG. 5. Eye-muscles from an embryo of 27 mm.
- FIG. 6. Eye-muscles from an embryo of 35 mm.
- FIG. 7. Eye-muscles from an embryo of 55 mm.
- FIG. 8. Anterior part of the dorsal aorta in an embryo with one complete aortic arch.
- FIG. 9. Anterior part of the dorsal aorta in an embryo with two complete aortic arches.
- FIG. 10. Anterior part of the dorsal aorta and of the cardinal veins in an embryo with six complete aortic arches.
- FIG. 11. The anastomosis of mandibular artery, hyoid vein, and first branchial vein. The figure also shows the five vein commissures of the first branchial arch.

aud.

10

11

12

sup. rec.  
extrec

13

14

extrec

15

16

17

18

19

20

21

22

23



hy. art.  
md. a.









## DESCRIPTION OF PLATE V.

SECS. 1 and 2. Horizontal sections through the oculomotorius when it consists of but one cell.

SEC. 3. The oculomotorius completely established in horizontal section.

SEC. 4. Cross-section, showing the median wall of the *anterior* head cavity (*a*) giving rise to muscle cells that partly fill the cavity, showing also the rudimentary muscle (*mus. e.*) of the mandibular cavity.

SEC. 5. Cross-section, showing the relation of the external rectus muscle to the rudimentary mandibular muscle (*mus. e.*).

SEC. 6. Cross-section, showing that the cells of the external rectus muscle have come to occupy the space occupied at an earlier stage by the cells of this muscle, together with those of the mandibular muscle (*mus. e.*).

SEC. 7. The permanent trochlearis as it first appears.

SEC. 8. Horizontal section, showing the fragments left by the primary trochlearis when the nerve atrophies.

See 7.

See 6.

2.7

See 11.

See 10.

2

W

W

W

See 10.

See 8.

See 10.

W

W

W

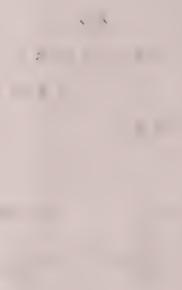
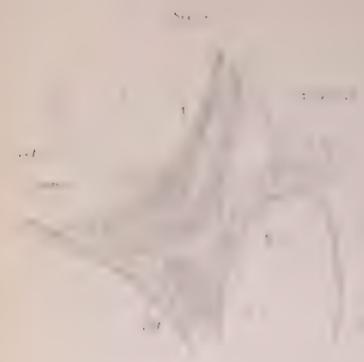
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## DESCRIPTION OF PLATE VI.

- SEC. 9. Horizontal section through the primary trochlearis.
- SEC. 10. Horizontal section through the mandibular cavity, showing the anterior prolongation of this cavity, from which the superior oblique eye-muscle is formed, and also showing the beginning of the rudimentary muscle (*mus. e.*).
- SEC. 11. The fibrous root of the permanent trochlearis.
- SEC. 12. Cross-section through the root of the "thalamic" nerve.
- SEC. 13. Median portion of the permanent trochlearis at the stage represented in sec. 7.





## REPRODUCTIVE ORGANS OF DIOPATRA.

E. A. ANDREWS.

IN dissecting a large species of the annelid *Diopatra* at Beaufort, North Carolina, in June, 1888, my attention was attracted by certain peculiar strings of green cells occurring abundantly in the body cavity. From the chlorophyll-like appearance of the pigment, the definite cell walls and linear arrangement of the cells in these strings, as well as from the marked shrinkage of the protoplasm, after the manner of a primordial utricle, these objects were at first mistaken for parasitic algæ. Examination, however, soon showed that the cell strings were connected with ova both free in the body cavity and when in the ovary, and that they were in fact merely ovarian cells liberated along with the ova, and remaining for a time attached to them as peculiar processes. Such cell strings were found not only in the above species, described below as *Diopatra magna*, but also in *D. cuprea*, Bosc, which is less abundant at Beaufort. Moreover, the same cell strings were found and studied in this latter species at Wood's Holl, Massachusetts, later in the same summer.

As these cell strings and their connection with the ova present some unique aspects of the history of ovarian cells, a detailed account of them may not be without interest. The general appearance of one of these cell strings is shown in Fig. 1, where the spherical ovum is seen to be provided with two nearly equal tails or strings of cells, larger where attached to the ovum, and diminishing towards the free tip. Each cell, and the ovum also, has its nucleus, and, at this stage, its nucleolus, while bright green pigment is especially noticeable in the ovum. This pigment varies in amount, some cases observed at Beaufort, in *D. magna* particularly, showing the green color much more conspicuously than the majority of those seen at Wood's Holl.

Floating about freely in the body cavity, these strings increase in diameter and in length, while the ovum grows still more markedly. Various stages of this gradual growth are represented in Fig. 2: here it will be noticed that the branching of

one or both cell strings is common, as in *b*, *d*, *e*. This branching is the rule in *D. magna*, while in *D. cuprea* it is rare. In only one case observed, *c*, the strings of two ova were continuous as in that figure.

Regarding the cell arrangement in the branching of the strings of *D. magna*, we may say that the usual method of division, with planes at right angles to the length of the string, is sometimes replaced by the occurrence of an oblique plane (Fig. 3, *c*) resulting in a side bud, or small cell, which, however, may be formed as a marked lateral growth previous to division, as in *f*. When this plane coincides with the long axis of the string, as at the tip of *e*, a bifurcation probably results, such as is illustrated in *b* and *d*, yet this may also be due to great growth of a side branch.

However complex the branching of the cell strings of *D. magna* may become, the egg finally, in a stage between *f* and *g* (Fig. 2), gets rid of these appendages altogether, and completes its growth as a simple, spherical cell, which is characterized superficially by an area of greenish pigment surrounding a clearer protoplasmic area on one side. This area coincides with the nucleus as to size, but the latter is now no longer seen, since the egg has become opaque owing to the accumulation of yolk granules.

The actual dimensions of these floating eggs and cell strings in *D. magna* are about as follows: the smallest measure  $40\ \mu$ ., with a nucleus  $20\ \mu$ . and nucleolus  $6\ \mu$ .; each appendage is now  $380\ \mu$ . long, and  $10\ \mu$ . and  $20\ \mu$ . wide at the two ends, often containing about 15 cells, exclusive of those in any small branches that may be present.

At this period little or no green pigment is perceptible. When the egg has become  $100\ \mu$ . in diameter, with a nucleus  $50\ \mu$ . and nucleolus  $13\ \mu$ ., the appendage is about  $430\ \mu$ ., with about 40 cells, having diameters of  $30\ \mu$ . and  $20\ \mu$ . at the two ends of the series. The strings may become longer, but in most ova about  $500\ \mu$ . thick they seem to have shortened again, and finally disappear in these  $550\ \mu$ ., so that ripe ova measuring  $600\ \mu$ . have no trace of such appendages.

The fate of the cell strings could not be determined, but some observations indicate that they gradually disintegrate and fall off, cases being observed in which only one or two cells were left adhering to the ovum: yet these may have been, partly, at least, pathological changes occurring in the sea-water, which, at

the high temperature experienced at Beaufort, seems to rapidly set up degeneration in the cells.

In the ripe ovum  $600\ \mu$ . in diameter, as already noted, the green pigment is aggregated about a clear area  $125\ \mu$ . in diameter. On section of the ovum it is found that this is a clear protoplasmic part intervening between the eccentric nucleus and the thick egg membrane. The relation of the clear region, the nucleus with its peripheral nuclei, and the green pigment, is shown in the section, Fig. 4. The main mass of the ova is filled with large, round yolk bodies imbedded in a fine granular or reticulated protoplasmic matrix, while the clear area, *a*, alone is entirely free from yolk and from pigment also. The yolk is not found in ova  $100\ \mu$ . in diameter, and must therefore be formed while the ovum and its appendages float freely in the body-cavity liquid: younger eggs are uniformly granular throughout, though the peripheral part of the protoplasm is easily affected by reagents, and seems less solid than that nearer the nucleus. In fresh material the egg membrane is seen to be perforated by innumerable pores, though not seen in sections.

That the egg as represented in Fig. 4 is ripe seems indicated by its size, occurrence in great numbers, packing the body cavity full, and by the occasional finding of like eggs amongst the larvæ of this season of the year in the gelatinous egg masses: yet attempts at artificial fertilization were unsuccessful.

These larvæ are spherical, at the earliest stage obtainable at this time of year, and revolve within the jelly by equatorial and terminal cilia. Each is only about  $550\ \mu$ . in diameter in preserved specimens, and retains the egg membrane as a cuticle  $5\ \mu$ . thick. At this early stage the body is sprinkled over with irregular green patches of pigment, derived in all probability from the green pigment of the egg.<sup>1</sup>

<sup>1</sup> The remarkable slimy gelatinous egg mass of *D. magna* forms a conspicuous and common cylindrical slender body, several feet long, lying on the sand where the adult lives. The larvæ found in this gelatinous common envelop have been figured and described by Professor Wilson (Studies Biological Laboratory, S.H.V., Vol. II, 1883) as belonging to *D. cuprea*.

The production of these great gelatinous masses is undoubtedly accomplished by the secretion of unicellular, epidermal glands along the lateral aspect of the posterior region of the body of the female, where there are two white, swollen masses of epidermal cells both anterior to and posterior to each parapodium.

These masses readily swell in water and produce the above jelly: one of them seems to surround the nephridial opening.

In *D. cuprea*, the ova and cell strings in the body cavity present the same general appearance as in *D. magna*; but, as already observed, the strings rarely branch, and the ova are actually smaller.

More numerous measurements in this species give even greater certainty to the conclusion that the ovum and its appendages grow while floating in the body cavity.

Thus in one individual ova vary from 30 to 325  $\mu$ ., while the strings measure 150  $\mu$ . to 875  $\mu$ . in length and 10 to 30  $\mu$ . in diameter in extreme cases. Other measurements in various individuals emphasize the increase in diameter of the ovum and the simultaneous growth in length and thickness of the cell strings, though this is relatively less than in the ovum.

The smallest of these floating ova measured 15  $\mu$ ., and had two strings 70 and 150  $\mu$ . long and 11  $\mu$ . wide: the number of cells in these smallest strings is frequently 15, as in the larger species. The strings fall off after the ovum is 300  $\mu$ . in diameter and do not appear to diminish before then, but to drop off intact, though this requires re-investigation. The ovum having lost its strings, increases to 400  $\mu$ ., when it is apparently ripe, and has a membrane 2  $\mu$ . thick perforated by pores or canals. As strings 400  $\mu$ . long frequently have 30 cells, an increase in number as well as growth of individual cells may be assumed to take place during the floating period. The yolk granules of the mature egg do not appear in the youngest stages, but when about 50  $\mu$ . in diameter sections show a peculiar vacuolation of the protoplasm, indicating a deposition of liquid or solid yolk bodies in the protoplasmic meshwork of the cell body.

In both species of *Diopatra* these cell strings may be traced back to the ovaries, which differ but little, though larger, in my sections, in *D. cuprea* than in *D. magna*. The size, however, varies much in different individuals and even in different regions of the same individual.

In either the ovary is a transverse band along the posterior face of a septum, on each side the body, extending from the cavity of the parapodium towards the digestive tract, and ending as a protuberant, rounded mass. The ovaries occur in very many somites, and appear to be simply aggregations of peritonæal cells, or cells projecting freely into the body cavity, with no special

membranous investment.<sup>1</sup> Each mass surrounds a large blood-vessel and its lateral branches, and may be regarded as consisting of two portions, the one applied to the septum, a densely aggregated collection of nuclei in a protoplasmic matrix; the other projecting into the body cavity freely, a festoon-like collection of cell strings or necklace-like loops, each capped by an ovum at its most protuberant, free part (Fig. 5).

These projecting loops are most abundant at the largest part of the organ, nearest to the digestive tract, and are identical with the smallest cell strings found floating freely in the body cavity. In *D. cuprea* the ova at the ends of the loops measure 11 to 16  $\mu$ . in preserved specimens, and are thus as large as the smallest ones found free in the body-cavity liquid. In *D. magna* the largest ovarian ova measured only 22  $\mu$ ., or half the dimensions of those found free in the body cavity; but I have no doubt sufficient material would show identity in size, as there is in all other respects, between the smallest free ova and those still attached to the ovary.

The smallest ova in the strings are but little in excess of the other string cells in diameter, and form but slight departures from the general shape and structure of the cells of the entire series (Fig. 6). Thus from a series of nearly identical cells there is formed by great relative growth of the central one a condition in which the latter becomes distinguished as a large ovum with the lateral parts of the string now attached to one side of it as two cellular appendages. The cells of the loop are largest nearest to the central ovum, and diminish towards the two ends attached to the ovary. At first attached on opposite poles of the ovum, the two halves of a string or loop become gradually carried around on to one side by the unequal increase or growth of the surface of the ovum, the side turned away from the ovary projecting into the body cavity at the apex of the loop, growing more than the opposite side. In attempting to follow the cell strings back to their first appearance in the ovary, we find the cell walls no longer visible in that part spoken of as the solid matrix near the septum, but there the nuclei are small and

<sup>1</sup> The nephidium in *D. cuprea* opens by a wide, transversely elongated funnel, projecting anteriorly from the septum and separated by it from the ovary of the next posterior somite. It passes laterally in the septum as a tube opening ventrally at the base of the parapodium.

closely packed in a common protoplasmic mass (Fig. 5). Immediately about the blood capillaries the nuclei remain small, (Fig. 7, *a*), while towards the periphery of the mass they increase in size and often show a linear arrangement (*b*), and then when still larger exhibit cell boundaries (*c*). In these faintly outlined cell strings, while part of the solid ovarian matrix, certain cells increase in size, and may be recognized as ova (*ov*). Such linear series of cells become detached from the general matrix except at the tips, and so form loops or cell strings projecting more and more freely from the solid part of the ovary. Eventually, such cell loops (Fig. 5) break away even at the tips, and then float off in the body-cavity liquid, each with a growing centrally placed ovum.

In certain parts of the ovarian matrix nuclear division appears to take place actively, but neither this nor the subsequent linear arrangement of nuclei and cells could be referred directly to the arrangement of the blood-vessels around and upon which the ovary is, as it were, built up.

In the males of both species the body cavity may be filled with spermatozoa and the masses of cells giving rise to them, but no strings of cells comparable to those of the female are found. The testis has the same position and relation as the ovary, and is also to be regarded as a mass of peritonæal cells. It may, however, be distinguished from the ovary by the size and arrangement of the cells or nuclei, which in both species are uniformly about  $7 \mu$ . in diameter, with nuclei  $5 \mu$ ., and present no such linear arrangement as is conspicuous in the peripheral part of the ovary. The nuclei are thus noticeably larger in the testis than in the ovary, excepting the older nuclei of the ova themselves.

The method of formation of spermatozoa was studied in preserved specimens in which sections show various stages inside the body cavity. Though the nuclei are not arranged in linear series in the testis, they grow out from its surface into the body cavity as irregular, many-celled processes, which break off and float free as clumps of generally but few cells (Fig. 8, *a*). By division and multiplication of these few nuclei, characteristic clusters about  $55 \mu. \times 18 \mu. \times 37 \mu.$  are formed, having an elongated, somewhat flattened ellipsoidal form, and made up of many small nuclei surrounded by little protoplasm (*b*). These

clusters were found separating or dividing into halves, in each of which the nuclei became much smaller and apparently homogeneous (*c*). These smallest, ultimate nuclei lose their cohesion, and separating, float freely in body-cavity liquid, where each becomes converted into a mature spermatozoon, having the general form shown in Fig. 9, *m*. Crescent-shaped intermediate forms often float about, marked on one side by a conspicuous, deeply stained, drop-like body.

In *D. cuprea* the general development of the spermatozoa is the same as in the above description of *D. magna*, yet the form of the perfect spermatozoon is strikingly different (Fig. 9, *c*), considering that we have here two species of the same genus, furnishing a case of dimorphism similar to that of certain species of the common frog, *Rana*.

The most noticeable feature in the formation of the reproductive cells in these Annelids lies in the fact that the ova of the female are accompanied during a considerable part of their growth, while free in the body-cavity liquid, by a collection of ovarian cells, cell strings, having no apparent function, though at first identical with the ovum itself.

The survival of one ovarian cell at the expense of others is common, and the linear arrangement of such sets of cells in the ovary is not unknown; but I know of no case in which such sister cells of the ova remain so long as peculiar appendages to the ovum. In this case there seems no ground for assuming that the ova derive nourishment directly from the ovarian cells, or at least from the separated ones of the cell strings; the early presence of a firm egg membrane precluding any ingestion of entire cells, while the radial pores in the membrane, even if they are present at an early period, are too small to take in yolk bodies as solids, much less entire cells. Of course it cannot be denied that pseudopodia-like processes, or continuity of protoplasm, may exist between ovum and cell strings, but the small area of the ovum occupied by the attachment of these strings would seem to be insufficient to account for the large increase of bulk taking place in the ovum. That the cell strings play but little if any part in the supply of nourishment to the ovum is also indicated by their insignificance when the yolk spherules appear, and by their entire absence during the later stage of growth of the ovum.

If the suspension of the ovum at an early stage by means of cell strings has any direct utility, I would incline to seek it in the advantage derived from a greater free access to the body-cavity nutriment thus attained, and regard the cell strings as chiefly, if not entirely, mechanical supports subsequently retained for a while as, possibly, furnishing some advantages by keeping the ova separate and well surrounded by the nutrient liquid while floating about. They are eventually lost when the ovum approaches maturity and prepares to pass out of the body cavity into the nephridial tubes.

Perhaps, however, the whole arrangement is only the necessary result of unknown laws of growth of the ovarian cells, and results in no advantage at all comparable to the peculiarity of the structure produced.

Whatever may prove to be the function of these cell strings, if any, their occurrence seems to be confined to *Diopatra*, as far as I know. The nearest approach to this condition of things is seen, perhaps, in *Bonellia*, where also the ovum is armed with a collection of cells adhering to its periphery at one point, and of no apparent use. These cells form, to be sure, a spherical mass, but agree with the cell strings of *Diopatra* in having the same origin as the ovum, which in both cases is differentiated by growth beyond the condition attained by the majority of the ovarian cells. Sections of the cell mass given by Spengel show a striking resemblance to the connection of ovum and cell string in *Diopatra*. Moreover, the resulting cell mass remains upon the pole of the ovum remote from the eccentric nucleus, and this, I am inclined to think, is the case with the cell strings in *Diopatra*. The relative position of the auxiliary cells with reference to the ovum and ovary is, however, opposite in the two cases, and it does not appear that even a suspensory function could be ascribed to them in *Bonellia*.

BALTIMORE, Dec. 8, 1890.

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As the large *Diopatra* upon which the above observations were first made does not occur upon our Northern coast, and as it is as yet undescribed, a brief description of it, with illustrations of some of its characters, may be here appended, indicating its considerable departure from the common *D. cuprea*.

DIOPATRA MAGNA *sp. n.*

Body flat, elongated; first five or six somites convex and elevated dorsally, so that mouth is terminal; buccal somite small, widened at sides, as narrow dorsally as first setigerous somite, bearing at middle of each side a smooth tentacular cirrus as long as first two setigerous somites. Head withdrawn into buccal somite; palps large, globose with nodules anteriorly; antennæ smooth, with short annulated bases about as long as first setigerous somite; median antenna and intermediate ones four times as long as tentacular cirrus, outer one about half length of median one; tentacles cylindrical, with conical tips, and as long as bases of antennæ. Anterior five parapodia very stout, three directed forward. Branchiæ pectinate, beginning upon the sixth setigerous somite as a simple filament; pinnules increasing to about 12 by the 13th somite, where the branchiæ meet over the back; posterior to middle of body the number of pinnules decreases gradually, the branchiæ becoming flabellate, bifid, and finally simply filiform on the posterior somites.

Setæ in first five parapodia, about 13 to each, imperfectly jointed, with the hooked tip and tooth below it enclosed in a delicate hood: other parapodia bear about 30 simple, pointed setæ, two stout hook setæ, and delicate, asymmetrical, finely serrated, chisel-shaped setæ. Jaw pieces dark; lower jaws with whitish tips, indented on the edge; dental plates with 8 teeth on right and 7 on left; large pair of paragnaths with 8 teeth on right and 6 on left, unpaired piece on left with 8 teeth; two small pairs of paragnaths, the one smooth, the other with a rounded boss.

Color dark, except anterior end, which is flesh color with sprinkling of dark dots; branchiæ dark brown; antennæ reddish brown; body translucent posteriorly; posterior intestine full of dark fragments of eel-grass, etc. Anus very large; anal cirri shorter, more slender than median antenna.

Length, up to 1 m.; breadth without parapodia, 16 mm.; median antenna, 10 mm.

Found in pure sand of outer parts of "Bird Shoal," Beaufort, North Carolina. Constructing stout, conspicuous tubes projecting vertically some inches above sand, and turned to one side at orifice.

Eggs laid in greatly elongated, large cylindrical mass of jelly. Young often constructing small tubes on outside of those of adult.

## EXPLANATION OF PLATE I.

FIG. 1. General appearance of young ovum and cell strings, floating in body cavity. *D. cuprea*. Camera, Zeiss. 2. F.

FIG. 2. Successive stages of growth of ova while floating in body cavity. *g*, ripe ovum with green pigment about clear area, *a*. *D. magna*.  $\times 250$  diameter.

FIG. 3. Various methods of branch formation in cell strings of *D. magna*.

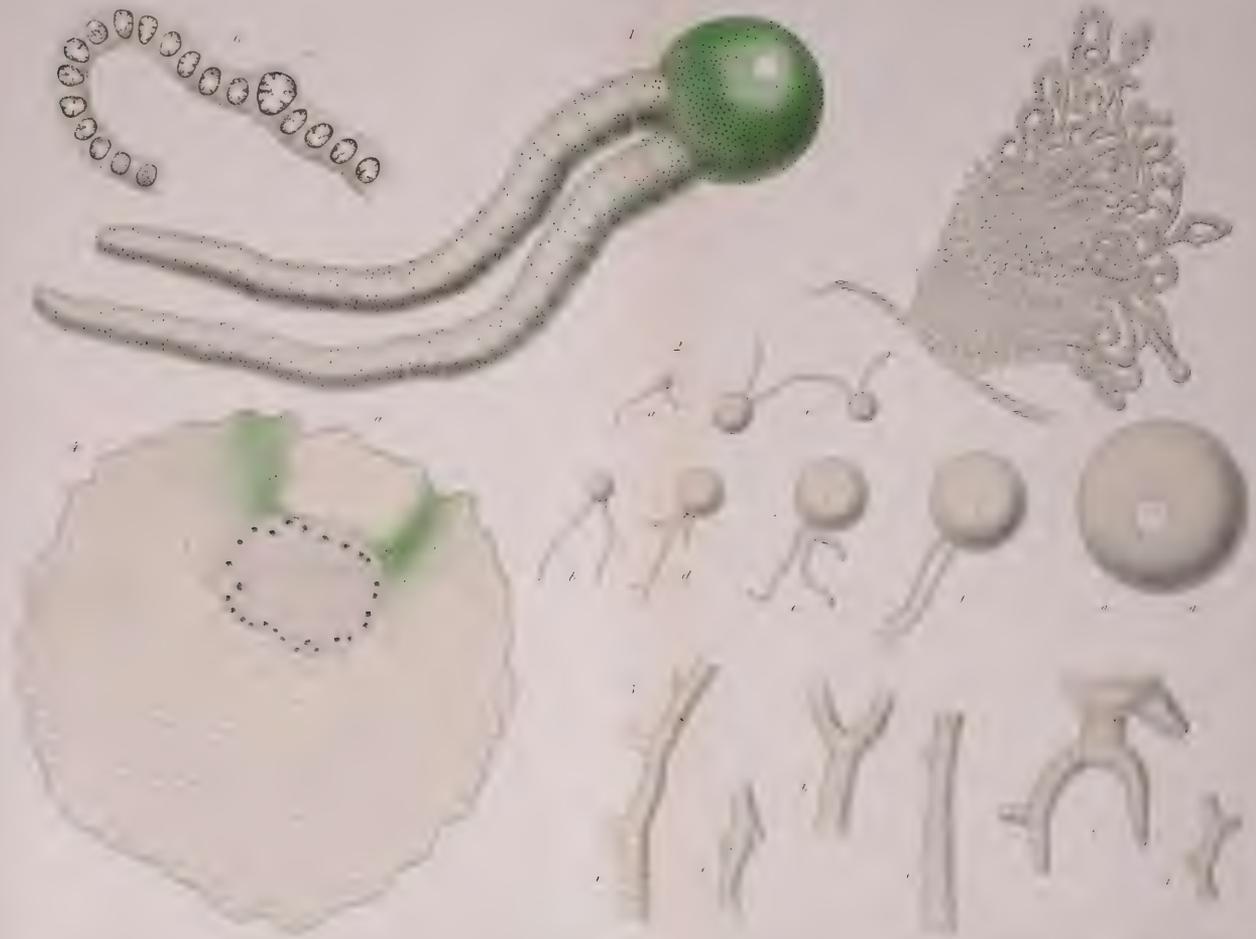
FIG. 4. Section of ripe ovum of *D. magna* from body cavity. Camera, Zeiss. 2. D. *a*, clear protoplasm. Green pigment remaining after hardening in Perenyi's fluid. Hæmatoxylin and borax carmine stain.

FIG. 5. Section of ovary of *D. cuprea*. Camera, Zeiss. 2. D.

FIG. 6. Young cell string still attached to ovary. *D. cuprea*. Camera, Zeiss. 4. F.











## EXPLANATION OF PLATE II.

FIG. 7. Section of ovary of *D. cuprea*. *s*, septum; *v*, blood-vessel; *ov*, enlarged cell forming an ovum; *a*, cluster of small nuclei around a capillary; *b*, linear arrangement of nuclei; *c*, cell string not yet free from matrix. Camera, Zeiss. 2. F.

FIG. 8. Three successive stages in the formation of spermatozoa in *D. magna*. *a*, small group of cells first liberated from testis; *b*, mass resulting from division and growth of *a*; *c*, final product of one-half of group *b*. Camera, Zeiss. 4. F.

FIG. 9. Ripe, active spermatozoa. Camera, Zeiss. 4. *D. m*, of *D. magna*; *c*, of *D. cuprea*.

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 DESCRIPTION OF FIGURES, ILLUSTRATING CHARACTERS OF *D. Magna*.

FIG. 1. Pointed seta.

FIG. 2. Hook seta of first parapodium.

FIG. 3. Side view of anterior region.

FIG. 4. Dorsal view of posterior end.

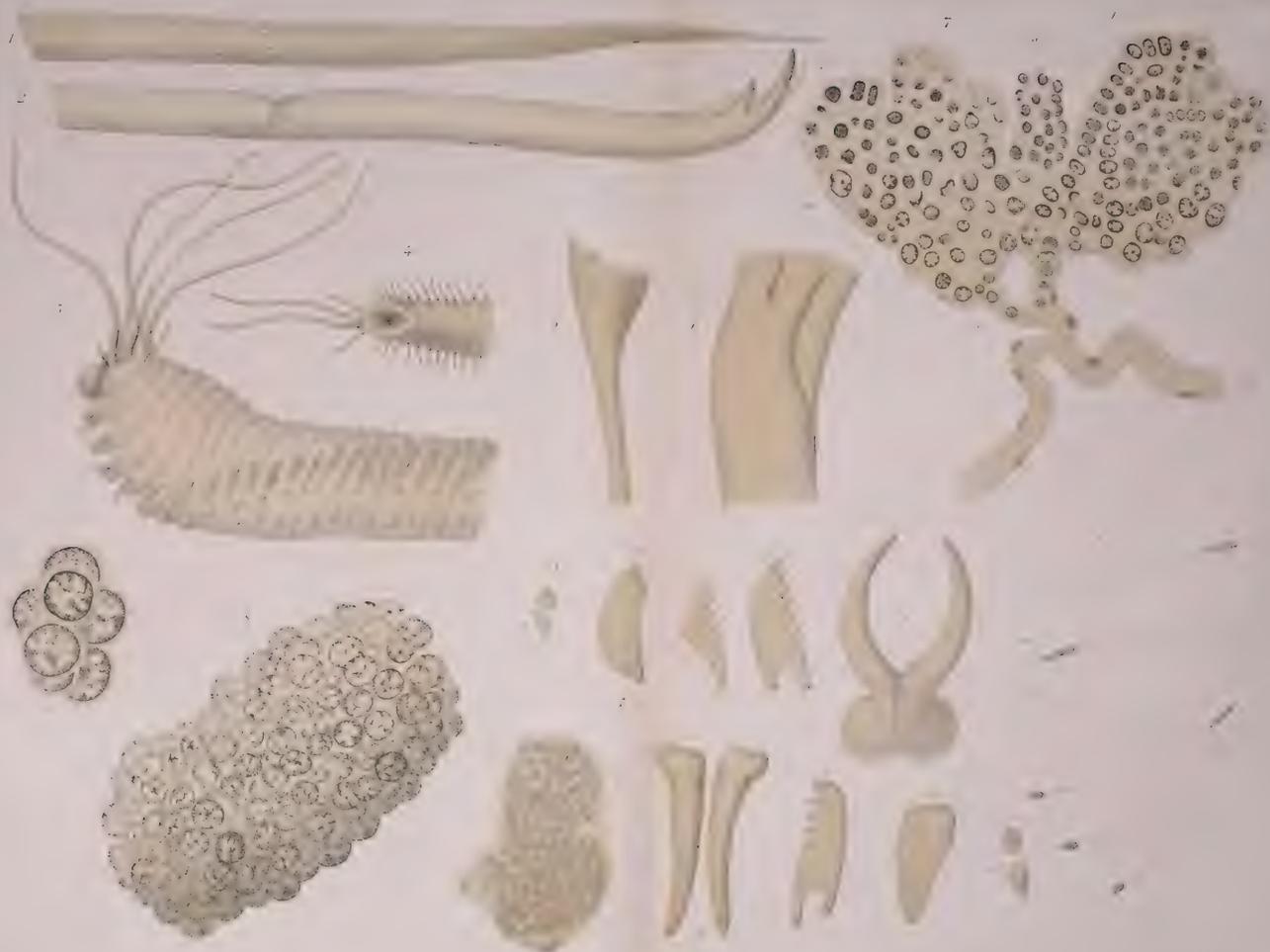
FIG. 5. Chisel-shaped seta.

FIG. 6. Hook seta of 40th somite.

FIG. 7. Jaws: *A*, dorsal jaw pieces; *B*, ventral jaw pieces; *l* and *r*, left and right dental plates; *l*<sup>1</sup>, unpaired left piece; *l*<sup>2</sup>, *l*<sup>3</sup>, *l*<sup>4</sup>, and *r*<sup>2</sup>, *r*<sup>3</sup>, *r*<sup>4</sup>, left and right paragnaths.









CONTRIBUTIONS ON THE MORPHOLOGY OF THE  
ACTINOZOA.

III. THE PHYLOGENY OF THE ACTINOZOA.

J. PLAYFAIR McMURRICH.

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A DISCUSSION of the phylogeny of the Actinozoa may seem superfluous after the admirable paper by Boveri ('90) which has appeared so recently. Prior to its publication I had accumulated a considerable number of facts bearing upon the questions discussed in it, and, before it reached me, had written several pages of a paper whose purpose was to set forth my deductions from these facts. This paper seemed, however, unnecessary, since many of Boveri's conclusions coincided with my own, and it was destroyed. In regard to certain points, however, I was not in perfect harmony with Boveri, and having had the opportunity since the publication of this paper of studying some forms, very interesting from a phylogenetic standpoint, I have determined

to describe the important features of these forms, and, at the same time, to set forth my views upon the relationships of the various tribes of Actinians, and the affinities which they bear to the other Actinozoa.

The advances which have been made during the last few years in our knowledge of the Actinians have been very remarkable, and have been largely due to the scientific expeditions sent out by various governments. A number of adult forms of great phylogenetic importance have been discovered, the structure of known forms has been more accurately studied, and, at the same time, embryological observations have given a significance to structural peculiarities, and have pointed out the proper lines for future investigation. As a result of these factors, we are now able to picture, with a tolerable amount of assurance, the phylogeny of many groups of the Actinozoa. Much still remains to be done, however, and it is hoped that the present paper will form one more step in advance, and bring the goal which is sought a little nearer.

I propose in the first place to call attention to certain phenomena in the formation of the mesenteries, and to describe some observations bearing upon their arrangement and order of appearance in certain groups of the Actinozoa, and in the second place I shall discuss the relationships of the various groups to one another, and so endeavor to deduce their phylogeny.

#### I. EDWARDSIÆ.

Very little is known at present concerning the development of the Edwardsiæ. Mark ('84) has figured some stages of a larval *Edwardsia* which is found parasitic in the Ctenophore, *Mnemiopsis Leidyi*, Ag., of our Eastern Coast, and Boveri has described the larva of *Edwardsia Claparedii*. I have been able to examine the larvæ of the Ctenophore parasite, infested specimens of *Mnemiopsis* having been very abundant at Wood's Holl, Massachusetts, during the summer of 1888, but none of the specimens at my disposal throw any certain light upon the sequence of formation of the mesenteries. Notwithstanding the very great variation in size of the parasitic individuals, all those I obtained were in the same stage of development, possessing eight perfect mesenteries, one pair only, the ventro-laterals, being provided with mesenterial filaments.

The larvæ studied by Boveri were in a corresponding stage.

The inference to be drawn seems to be that in the *Edwardsia* the ventro-lateral mesenteries are the first formed, and this is borne out by a specimen figured by Mark (Pl. XII, Fig. 2), in which these are the only mesenteries present. The lines of origin of two other pairs are indicated by depressions of the endoderm, the depression for the dorso-lateral pair being most distinct, those for the ventral pair less so, while there is no indication as yet of the fourth pair. It is probable that the relative distinctness of the three pairs indicates the succession of their development. The absence of any trace of the fourth pair of mesenteries renders it uncertain as to whether they made their appearance on each side of the dorsal line, or between the first and third pairs. In this latter case the third pair would constitute the dorsal directives, and the order of appearance would correspond with what Lacaze-Duthiers ('72) has described, but the wide separation of the mesenteries of the third pair seems to indicate that the fourth pair will form the dorsal directives, and the order of formation of the mesenteries will therefore correspond with what H. V. Wilson ('88) has described for *Manicina*, and I ('91) for *Rhodactis*.

## II. HEXACTINIÆ.

There are two points regarding the order of appearance of the mesenteries of the Hexactiniæ, which must be referred to here. These are (1), Is it the second or fourth pair of mesenteries that is destined to become the dorsal directives? and (2), Which is the more primitive method of passing from the *Edwardsia* to the *Halcampa* condition,—that which Boveri has termed the bilateral type, or that which he designated the biradial type?

There seems to be little doubt that the account given by Kowalewsky ('75) of the development of the mesenteries in *Actinia*, sp. (?) is incorrect. In addition to this, two sequences of formation have been described. Lacaze-Duthiers ('72) is the authority for one, in which the second pair of mesenteries become the dorsal directives, the third pair the ventral directives, and the fourth pair make their appearance between the first and second pairs. The correctness of this succession was called in question by the Hertwigs ('79). It seemed to them more

probable, though they had no definite evidence on the subject, that the fourth and second pairs of Lacaze-Duthiers' description should be reversed. According to this succession, the second pair of mesenteries appears in the larger chamber formed by the first mesenteries, dividing it into a dorsal and two dorso-lateral chambers; the third mesenteries develop in the ventral chamber and become the ventral directives; while the fourth mesenteries appear in the dorsal chamber, and become the dorsal directives. The first reason the Hertwigs give in support of their supposition is, that since all the later mesenteries are known to develop in pairs, it is probable that the first eight mesenteries likewise did so. We know now that the four mesenteries which convert the *Edwardsia* stage into the Hexactinian are in certain cases not developed in pairs, and therefore the Hertwigs' first argument must be considered as having little weight. Their second reason seems, however, stronger. They point out that the filaments of the mesenteries which Lacaze-Duthiers considers to be the fourth pair develop earlier than those of either his second or his third pair. It seems to be a general rule that the succession of development of the filaments corresponds with that of the mesenteries, and therefore it would seem probable that there is an error in Lacaze-Duthiers' observations, explainable by the fact that he made no use of sections.

This probability is rendered stronger by the observations of H. V. Wilson ('88) on *Manicina*, mine ('90) on *Rhodactis*, and those of Faurot ('90) on *Halcampa*, in all of which cases it seems certain that the fourth pair of mesenteries are the dorsal directives.

Haddon ('89), however, states very positively that F. Dixon, working under his direction, has been able to confirm by the study of sections Lacaze-Duthiers' observations. The only conclusion that seems possible is, that there may be considerable variation in the order of appearance of the first eight mesenteries. I believe from the occurrence of the order which I have found in *Rhodactis* in such widely separated forms as that genus, the Madreporæ and the Halcampidæ, that it must be regarded as the more primitive and normal. Lacaze-Duthiers' arrangement may be explained, not by a supposed transformation of the second pair of mesenteries into the dorsal direc-

tives, but by a retardation of their formation. The fourth formed mesenteries of *Bunodes verrucosus* are equivalent morphologically to the second pair of *Rhodactis*, but their appearance is delayed until after the formation of the directives. The development of their mesenterial filaments before those of the directives is thus explicable.

A possible explanation of the earlier development of the fourth pair is suggested by their relation to the dorsal siphonoglyphe. It may be that the development of a second siphonoglyphe in the Hexactiniæ has made it of advantage to the animals that the mesenteries in connection with it should be early developed. It may be noted in this connection that in *Rhodactis*, in which in the adult two well-marked siphonoglyphes are present, the original arrangement obtains, and at the same time the development of the siphonoglyphes is not evident in the larva until the formation of the third and fourth pairs of mesenteries. In other words, the siphonoglyphes and the directives appear simultaneously. If an early development of the dorsal siphonoglyphe be of advantage to the embryo, there would naturally be an early development of the dorsal directives.

As regards the formation of the fifth and sixth mesenteries, which convert the embryo from the *Edwardsia* stage to the *Halcampa* stage, Lacaze-Duthiers found that they developed between the ventral directives and the ventro-lateral mesenteries, and between the ventro- and dorso-laterals. This observation has been abundantly corroborated, and there can be no question as to its correctness. The Hertwigs ('79), however, found a different arrangement in *Adamsia*; here the fifth and sixth mesenteries form in pairs on each side between the dorso- and ventro-laterals (Fig. I.). This arrangement has likewise been confirmed by Boveri.

We have consequently two different methods for the arrangement of the fifth and sixth pairs of mesenteries, showing again

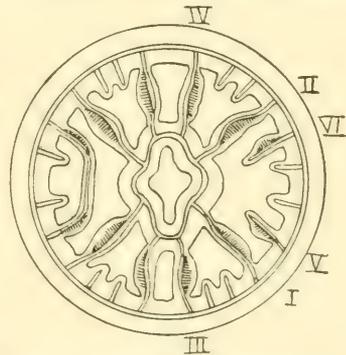


FIG. I.—Transverse section through larva of *Adamsia* (after Hertwig).

that variation in the manner of appearance of the mesenteries may readily occur. It is interesting to note also that not only is the relation of the newly formed mesenteries to their predecessors different in the two cases, but likewise the arrangement of the longitudinal muscles on the older mesenteries is different. Boveri ('90) terms that arrangement found in *Adamsia* the biradial type, and that of Lacaze-Duthiers the bilateral, and correctly assumes that the latter, in which the arrangement of the mesenterial muscles agrees with what is found in adult *Edwardsia*, is the original type, the biradial type having been derived from it by an abbreviation of the development. The symmetry of the Actinozoa, and especially of the larvæ, is bilateral; in the Hexactinæ a radial arrangement of parts is superposed upon this, giving what may be termed a biradial arrangement; this secondary symmetry is thrown back in the ontogeny of certain forms producing the biradial type of development.

The superposition of a secondary radial symmetry upon an original bilateral one is also to be seen in the Ctenophores, giving rise to the characteristic biradial symmetry of these forms.

A feature of the development in the biradial types calls for special mention; that is, the reversal of the arrangement of the musculature of the first pair of mesenteries. In the original arrangement seen in the bilateral type, their longitudinal muscles are upon their ventral faces and the transverse muscles on the dorsal faces. In the biradial type this arrangement is reversed, so that the longitudinal muscles are upon the dorsal face.

There can be no doubt but that the arrangement of the mesenterial musculature is an important feature in determining the relationships of the Actinozoa, but the occurrence of the biradial type of development shows that it cannot be considered a fixed and unalterable character, but must be regarded as a feature which may with comparative readiness undergo modification. This idea is confirmed by the occurrence of abnormalities in the arrangement of the musculature in Hexactinian forms, where constancy of arrangement is perhaps more to be expected than in some of the less specialized groups. I have already ('89) described an abnormality of this kind in *Aulactinia stelloides*, a

primary mesentery of which possessed longitudinal muscles on both the dorsal and ventral face.

But more important examples of a change from the normal arrangement of the muscles are to be found among the Sagaritidæ. G. F. Dixon ('88) has shown that in three species of *Sagartia* (*S. venusta*, *S. nivea*, and *S. miniata*) a single siphonoglyphe only is frequently present, and in *S. venusta* he found that a form with only one siphonoglyphe possessed only a single pair of directives. F. Dixon ('88) confirmed this observation, and showed that it is the rule with *S. nivea* and *S. rosea* also; and I have found the same state of things to occur in *Metridium marginatum*. In this species, of which I have had an opportunity of examining a large number of individuals, the presence of a single siphonoglyphe is almost, if not quite, as frequent as the more normal arrangement.

The arrangement of the mesenteries in one specimen examined is shown diagrammatically in Fig. 1, Pl. IX. It will be seen that apparently only one siphonoglyphe is present, and with it is connected a pair of directive mesenteries (III). At the other extremity of the stomatodæum is a pair of mesenteries (IV) corresponding to the directives of other forms, but having their longitudinal muscles upon the contiguous faces, as is the rule in the lateral pairs of mesenteries. Now, there can be no question here as to the identity of the forms with only one pair of directives and one siphonoglyphe with those with two, nor can there be any doubt that the forms with two pairs of directives are the more normal ones, the condition in which there is only one pair being a secondary modification, since the former arrangement is characteristic of the ancestral Halcampidæ and Edwardsiæ. If we consider the siphonoglyphe which persists to be in all cases the ventral one, we have a case in which there is a secondary reversal of the arrangement of the musculature of the fourth pair of primary mesenteries in nearly half the individuals of a species.

A further point of interest lies in the fact that this reversal is associated with the absence of a siphonoglyphe.

G. F. and A. Y. Dixon ('89) have described an interesting abnormality in *Bunodes thallia*, one specimen of which possessed *three* pairs of directives in connection with *three* siphonoglyphes. Blochmann and Hilger also describe a variation in the

arrangement of the mesenteries of *Gonactinia* ('88). Between the dorso-lateral pair of imperfect mesenteries and the dorsal genital mesentery a pair of perfect mesenteries intervened, having their longitudinal muscles arranged as in the directive mesenteries, the stomatodæum showing indications of a siphonoglyphe at the region of their insertion into it.

It seems probable that the ancestral Anthozoa did not possess a siphonoglyphe. In the simple Alcyonaria (*Monoxenia*, *Hartea*, and *Haima*) it seems to be absent. In other Alcyonaria it is, as a rule, present, varying, however, greatly in its development, as has been shown by Hickson ('83), and in all cases is single, marking the ventral surface of the polyp. In the Edwardsiæ two siphonoglyphes appear to be the rule, and in these forms, in contradistinction to what occurs in the Alcyonaria, two pairs of directives are present. It appears as if there was some reason why, when there are two siphonoglyphes, the longitudinal muscles should not be upon the same sides of the mesenteries which are in connection with them; in other words, it is necessary, for the proper action of the siphonoglyphes, that the longitudinal muscles of the mesenteries in connection with one of them should be upon the dorsal faces, those in connection with the other siphonoglyphe having them upon the ventral faces. It is possible that this arrangement has something to do with the preservation of the lumen of the siphonoglyphe when the lips of the stomatodæum elsewhere are in contact.

Since the Edwardsiæ are provided with two siphonoglyphes, that is the condition to be expected in all forms derived from them, and with the majority it seems to be the case. There are, however, numerous exceptions, as in the Sagartids mentioned above, in certain Halcampidæ (*Peachia*), in the Ceriantheæ, and in the Zoantheæ. It is evident, however, that the forms of these last three groups have been derived from ancestors with two siphonoglyphes, since they are provided with two pairs of directives. The arrangement of the musculature of the mesenteries of the Alcyonaria is probably the most primitive one, since it is the most symmetrical. The alternation of the arrangement of the musculature of the ventral directives consequent upon the formation of a second siphonoglyphe came to be so thoroughly impressed upon the development of more recent forms, that it still persists as a rule when one of the siphonoglyphes

has secondarily disappeared. The condition which is found in the Sagartids, mentioned above, cannot be regarded as a reversion to a more primitive condition, however. This is clearly shown by the arrangement of the mesenteries. The ventral surface of the body is indicated by the development of the musculature of the first and second pairs of mesenteries (I, II), in which the longitudinal muscles in bilateral types always are on the ventral face, and by the development of the mesenteries V and VI, which form always (in the bilateral types) in the lateral and ventro-lateral intermesenterial spaces of the embryo. It is evident from this that it is, as might be expected, the ventral siphonoglyphe in all cases that persists, the dorsal one disappearing. The mesenteries of the dorsal siphonoglyphe in the Edwardsiæ retain the original arrangement of the muscles; it is the ventral ones in which the arrangement has been modified. These, in the Sagartids with a single siphonoglyphe, retain the modified arrangement, while it is the dorsal ones in which a secondary or tertiary modification ensues. If we imagine one of these Sagartids with only the eight primary mesenteries, it will be seen that the arrangement of the musculature is entirely different from what is found in the Edwardsiæ.

In their paper on *Bunodes thallia*, already referred to, Messrs. G. F. and A. Y. Dixon ('89) describe an exceedingly interesting observation. They found that the paired mesenteries forming the second cycle of the hexamerous Actiniæ are more developed in the lower part of the embryo than in the upper. Near the base all six pairs are present at a certain stage; a little higher up only two of the pairs on each side can be found, and still higher only one pair, that nearest the dorsal directives. They point out that in the middle region the arrangement is similar to what occurs in *Peachia*,<sup>1</sup> and in the upper the arrangement found in *Gonactinia* is recalled. If this difference of development of these paired mesenteries indicates a primitive want of simultaneity in their development, we have an important clew to the explanation of the occurrence of such forms as *Peachia* and *Gonactinia*. I have examined my preparations of embryos of *Aulactinia stelloides* for indications of what the

<sup>1</sup> It will be seen later that the arrangement in the middle region is *not the same* as that of *Peachia*, but differs from what is found there in a very important particular.

Messrs. Dixon describe, but my results have not been perfectly satisfactory. I find that apparently all six pairs of mesenteries of the second hexamerous cycle appear simultaneously, but that the pair on each side of the dorsal directives develops more rapidly than the others and soon surpasses them in size.

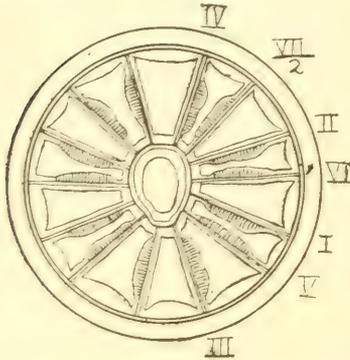


FIG. II.—Transverse sections through *Scytophorus striatus*.

which he erected the new tribe *Monauleæ*. Hertwig recognizes in this form (Fig. II) a single pair of directives only; but it is to be noticed that we have at the dorsal surface two mesenteries

The evidence from adult forms seems to point, however, to the development of the first cycle of paired mesenteries successively. I shall return to the discussion of the question later on; in the meantime I wish to describe briefly the forms which yield the evidence such as it is.

The form which shows the slightest advance upon the *Edwardsia* condition is Hertwig's *Scytophorus striatus* ('82), for the reception of which he erected the new tribe *Monauleæ*. Hertwig recognizes in this form (Fig. II) a single pair of directives only; but it is to be noticed that we have at the dorsal surface two mesenteries (IV) with their longitudinal muscles on the ventral faces, exactly the condition which we find in the dorsal directives of *Edwardsiæ*. I cannot see any reason for not regarding them as the dorsal directives. The mesenteries present in *Scytophorus* represent, I believe, the twelve *Halcampa* mesenteries with the addition of one mesentery on each side ( $\frac{VII}{2}$ ) in the spaces between the dorsal directives and the second mesenteries (II). Boveri

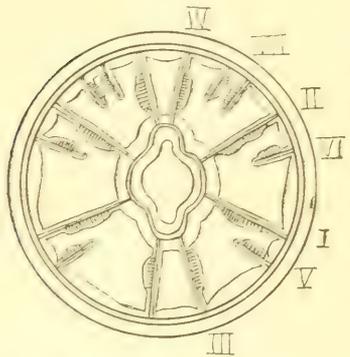


FIG. III.—Transverse section of *Gonactinia prolifera*.

('90) recognizes the eight *Edwardsia* mesenteries in *Scytophorus*, but derives it directly from that group, not disregarding, however, the possibility of its derivation from an *Halcampa* condition, which I prefer to accept.

In the form described originally by Sars as *Actinia prolifera*, and more recently by Blochmann and Hilger ('88) as *Gonactinia*

*prolifera* (Fig. III) eight *Edwardsia* mesenteries (I-IV) are present, perfectly developed; in addition to these it has the two *Halcampa* mesenteries (V-VI), which, however, have not yet reached their perfect development, remaining in an immature condition; and finally a pair corresponding to the dorsal pair of paired mesenteries of the Hexactiniæ (VII) is developed.

Amongst the Actiniaria collected by the United States Fish Commission steamer "Albatross" during the winter of 1887-8, I have found a form which is very interesting in this connection. It was dredged in the neighborhood of the Santa Barbara Islands off the coast of California, in fourteen fathoms. I propose to name it *Oractis diomedææ*.

All the specimens are more or less contracted, and the external ectoderm has been macerated away, leaving the mesogloea exposed. It is consequently impossible to distinguish between a capitulum, scapus, and physa which may have been present. The base is rounded, and apparently was not adherent, and the column is marked by *twenty* longitudinal furrows corresponding to the insertion of as many mesenteries. On the portion corresponding to the capitulum are *ten* prominent ridges or tubercles, but I could not distinguish any perforations of the physal portion of the column, such as Haddon ('86) has described in *Peachia hastata*. There are apparently ten simple, rather blunt-pointed tentacles, with well-marked muscle-processes for the ectodermal muscles, the radial musculature of the disc being also supported on similar processes. The stomatodæum has only a single siphonoglyphe, which is very deep with thick mesogloea, its ectodermal epithelium being destitute of gland-cells, and resembling in appearance the epithelium of the lateral streaks of the mesenterial filaments of the Hexactinians. On the general surface of the stomatodæum are *six* strong longitudinal ridges, each one corresponding to the insertion of a mesentery. I could find no trace of a conchula.

The arrangement of the mesenteries may be seen from Fig. 2, Pl. IX. There are two pairs of directive mesenteries (III and IV), the ventral pairs (IV) being inserted into the bottom of the siphonoglyphe. On each side of the ventral directives is a small mesentery (V), imperfect, and without mesenterial filaments and reproductive organs, having its longitudinal muscle on the dorsal face. Next to it comes a perfect mesentery (I)

with its longitudinal muscle on the ventral face, forming a pair consequently with the imperfect mesentery just described. All the perfect mesenteries, including the directives, possess mesenterial filaments and reproductive organs. Dorsal to the mesentery last mentioned is a pair of imperfect mesenteries (VIII), followed by a pair consisting of a ventral imperfect (VI) and a dorsal perfect mesentery (II), and dorsal to this pair is a second pair of imperfect mesenteries (VII), and then come the dorsal directives. The figure given is somewhat diagrammatic, since the longitudinal muscles of the imperfect mesenteries are only distinct in their uppermost part, while those of the perfect mesenteries are more clearly marked out lower down.

On the supposition that the paired mesenteries develop successively, this form represents a stage succeeding *Gonactinia*, from which it differs only in the development of the second pair of paired mesenteries.

Another arrangement occurs in *Peachia*, whose internal structure has been described by Haddon ('89) and Faurot ('90). Instead of referring to the accounts of these observers, however, I shall take the opportunity of describing the structure of a form which agrees closely with *Peachia*, and which occurs upon our Eastern Coast, being found at Nantucket and the neighboring coasts, in Long Island Sound, and probably as far south as Charleston, South Carolina.

I refer to the form originally described by L. Agassiz ('59) as *Corynactis albida*, but referred by Verrill ('64) to the genus *Halcampa*. Previous to Agassiz' description, however, Stimpson ('56) had described under the name of *Actinia producta* a form from the coast of South Carolina. Verrill also assigned this to the genus *Halcampa*, considering it distinct from the more northern *H. albida*, but later united the two forms under the name *Halcampa (sic) producta*. This union seems to be perfectly justifiable, there being apparently no well-marked characters upon which to base a separation.

*Halcampa producta* has been figured and described, so far as its external characteristics are concerned, by Verrill ('64), so that I shall confine my attention here solely to some points in the internal anatomy. The stomatodæum is comparatively short, and is marked by longitudinal ridges corresponding in number with the mesenteries. A single siphonoglyphe, marking

a ventral surface, is present. It is moderately deep, and is not provided at its outer extremity with lobes forming a conchula, in this respect differing from *Peachia hastata*.

The mesenteries are twenty in number (Pl. IX, Fig. 3), and are situated at equal distances from each other, but are, nevertheless, arranged in pairs, as may be seen from the longitudinal muscles. There are two pairs of directives, one being in connection with the siphonoglyphe, and with the exception of these pairs, all the pairs have their longitudinal muscles on contiguous faces, as in the Hexactiniæ. All the mesenteries are perfect, and consequently a section through the upper part of the column does not show the relation in which the various pairs stand to each other. Lower down, however, this becomes evident. On either side of the ventral directives come a pair of narrow mesenteries (IX); then dorsal to these a pair much wider, and with the longitudinal muscles much stronger (I and V); next to these, a second pair of narrow mesenteries (VIII); then a second strong pair (VI and II); and finally the dorsal directives. The numbers with which the mesenteries are denoted indicate, so far as the directives and the strong mesenteries are concerned, their probable order of development, VIII and IX belonging to the first cycle of paired mesenteries. The arrangement of the mesenteries consequently coincides with what has been described in *Peachia hastata*.

The longitudinal muscles are well developed, and have the form shown in Figs. 3 and 4. Upon the ventral directives they only reach their full strength at a much lower level than on the other mesenteries. Well-developed mesenterial stomata occur in the upper parts of the mesenteries, and mesenterial filaments occur on all the mesenteries. I cannot make any statements regarding the distribution of the reproductive organs on the mesenteries, since in the single specimen I had for examination, they were in a very immature condition and difficult to make out. It seems probable, however, that they are present on all the mesenteries.

*H. producta* can hardly be assigned to the genus *Halcampa*, on account of the arrangement of the mesenteries; nor does it agree exactly with *Peachia*, as limited by Haddon ('89). Whether the conchula is to be regarded as an important classificatory feature or not seems uncertain. For the present I prefer to

retain Verrill's name, hoping to return to a consideration of the true relationships of this species and those of the members of Andres' family Siphonactinidæ in a forthcoming report on the Actinaria dredged by the United States Fish Commission steamer "Albatross" in 1887-8.

We have then these four forms, all showing variation in the manner of development of the first cycle of paired mesenteries. In *Scytophorus* half of the dorsal pair only is developed; in *Gonactinia* both mesenteries of the dorsal pair are developed; in *Oractis* the dorsal and lateral pairs are present; and in *Peachia* the lateral and ventral pairs. A fifth arrangement occurs in the Zoanthææ, where the ventral pair only is developed at one stage of growth, the dorsal and lateral pairs never appearing. The significance of these forms is, it seems to me, strongly in favor of the successive development of the mesenteries of the second cycle of the Hexactiniæ. It is difficult to believe that all of them have been derived from the Hexactiniæ by degeneration. If this idea be dismissed, then we must admit that in these forms portions of a complete second cycle have been developed, and this fact, taken into consideration with what the Messrs. Dixons have described ('89), points to the successive appearance phylogenetically of the second cycle mesenteries.

### III. PARACTINIÆ.

The tribe Paractiniæ was established by R. Hertwig ('82) for the reception of certain forms, in which the mesenteries are developed on the radial plan which is found in the Hexactiniæ, and have a similar association in pairs, but at the same time are not arranged hexamerously. To the two forms upon which Hertwig founded the tribe, viz. *Sicyonis crassa*, in which the mesenteries are arranged octamerously, and *Polyopis striata*, which possesses thirty-six mesenteries arranged in pairs, more recent observations have added others. G. Y. and A. F. Dixon ('89) have described a decamerous arrangement for *Tealia cras-sicornis*, and Cunningham ('89) gives an account of a similar arrangement occurring in *Tealia tuberculata*. Haddon has shown that *Peachia hastata* is also decamerous; while I have described ('89) an octamerous arrangement in the Sagartid *Aiptasia annulata*, and Danielssen ('90) has found the same arrangement in his *Sideractis glacialis*.

I have already ('89) expressed an opinion upon the value of this tribe, and my only reason for referring to it here is that Boveri, though recognizing that it cannot have any phylogenetic significance, retains it as useful for systematic purposes; and further, Van Beneden in his recent paper recognizes it in his discussion of the phylogenetic relationships of the Actiniæ. I wish to point out that not even on the ground of convenience is the tribe to be retained.

If we are to group all the forms I have mentioned above, we shall certainly have a most heterogeneous collection. *Tealia* will be separated from the other Bunodidæ, with which it shows close affinities in many particulars, and placed close to *Peachia*, with which it has only the remotest affinities. But, worst of all, *Aiptasia annulata* will be separated from the other species of that genus, and grouped with *Sideractis*, whose affinities seem to lie rather with the Paractidæ than with the Sagartidæ.

I cannot see any necessity in the formation of such a tribe, but rather much inconvenience and inconsistency. It must be concluded that such forms as *Tealia* and *Aiptasia annulata* have been derived by a modification from the typical Bunodidæ in the one case, and the typical Aiptasias in the other. But how can this modification have come about? Its origin can only be ascertained with certainty by a study of the development of the modified forms, but nevertheless possible ways readily suggest themselves. The decamerous form may have been derived by the suppression of the dorsal or ventral pair of the first cycle of paired mesenteries, the individuals passing at one time through a *Peachia* or *Oractis* condition. Should the radial development of mesenteries then proceed normally, such an arrangement as is found in *Tealia* would be produced. I do not mean to suggest that there is any direct genetic relationship between *Peachia* and *Tealia*. It is much more probable that both have been derived from a typically hexamerous form by the suppression of a pair of mesenteries. This is certainly the case with *Tealia*, and that such has also been the origin of *Peachia* I shall endeavor to show later on.

In a similar manner the octamerous forms may have been derived from closely related hexamerous species by a suppression of two pairs of the first cycle of paired mesenteries, passing through, therefore, a condition comparable to that of *Gonactinia*.

Instead of speaking of a suppression of mesenteries in this case, it may be better, perhaps, to say that the octamerous condition has been brought about by the acceleration of the development of a single pair of paired mesenteries, so that they become contemporaneous with the two *Halcampta* mesenteries (V and VI). These contemporaneous mesenteries becoming perfect at the same time, we would get an octamerous form; and the ordinary radial development of the succeeding mesenteries then coming in would bring about the arrangement found in *Aiptasia annulata* and *Sideractis*.

#### IV. ZOANTHÆ.

Our knowledge of the structure of the adult Zoanthæ has been largely added to in recent years, more especially by Von Koch ('80),<sup>1</sup> R. Hertwig ('82), and Erdmann ('85), and from the information which we possess it is easy to determine, as Erdmann has done, the relation in which the members of this group stand to the Hexactiniæ. The five pairs of dorsal mesenteries, together with the ventral directives, seem to represent the twelve mesenteries of the *Halcampta* stage, later formed mesenteries developing always in the exocoels, on either side of the ventral directives, instead of, as in the Hexactiniæ, in all the exocoels present in the stage with twelve mesenteries.

Our knowledge of larval forms is, however, as yet exceedingly scanty. Semper ('67), some years ago, described two peculiar pelagic larvæ from the region of the Cape of Good Hope, which apparently were stages in the development of an Anthozoan. One of these, usually known as Semper's larva, is a cylindrical organism, with an opening at each end, and is characterized by a longitudinal band of iridescent cilia running from one extremity to the other, along one surface. The other form was more globular in shape, though capable of elongation, and differed in possessing a circular ring of cilia. Almost nothing was ascertained regarding the internal structure of these forms, so that it was impossible to determine to what group of Anthozoa they belonged, or even to be certain that they really were Anthozoan. Very recently, however, Van Beneden ('90) has

<sup>1</sup> I regret exceedingly that in a previous paper ('89) I failed, through an oversight, to ascribe the discovery of the true arrangement of the mesenteries of the Zoanthæ to Von Koch.

been able to study some very similar larvæ, and has shown that Semper's suggestion as to their relationships was correct. He gives a detailed account of a form closely similar to Semper's larva, differing from it only in the ciliated band being relatively shorter, and in the absence of a posterior opening, and shows that it possesses twelve mesenteries arranged in the same manner as the five dorsal pairs and the ventral directives of the Zoantheæ; that is to say, it possesses a pair of perfect ventral directives, a pair of imperfect dorsal directives, and between these, two pairs, on either side, each pair consisting of a dorsal perfect and a ventral imperfect mesentery. There seem to be no good reasons for doubting that this form is the larval stage of a Zoanthid, even though no specimens were found showing the place of origin of the seventh, eighth, etc., pairs of mesenteries.

Van Beneden also announces that he has specimens agreeing closely with the forms described by Semper as possessing a circular band of cilia, but defers a detailed description of them until a future occasion, merely stating that they belong to the same Actinozoan group as do the larvæ with the longitudinal band.

I have had in my possession for several years some Actinozoan larvæ collected by the aid of the surface net at Beaufort, North Carolina, during the location there of the Marine Laboratory established by the Johns Hopkins University. They resemble the second of Semper's larvæ in the possession of a strong ring of cilia encircling the body, and, as will be seen from the following account, are without doubt larvæ of a Zoanthid. I cannot say of what species they are the young, as no Zoanthid is known to occur at Beaufort. *Epizoanthus Americanus*, Verr., has been dredged in 65 to 263 fathoms off the coast of North Carolina, but it seems improbable that the larvæ belong to this species, since they are constructed, as will be seen, upon the microtype, whereas *Epizoanthus* follows the macrotypal plan.

Four of the five specimens I possess are in the twelve-mesenteried stage, but the fifth is much older, possessing mesenteries of the ventral group, and being evidently ready to settle. I shall give a detailed description of the characters of these larvæ, inasmuch as they serve to confirm the results, as to the affinities of the Zoantheæ, arrived at from anatomical studies.

The younger ones are somewhat pyriform in shape, and have

not yet developed tentacles. The mouth is at the smaller extremity, and the oral half of the body is to a greater or less extent folded within the aboral portion in the preserved individuals, the ring of cilia lying at the bottom of the groove so formed (Fig. 5). In this contracted condition they measure about 1.4 mm. in length and 1.5 mm. in diameter. A transverse section passing through the stomatodæum of one of these is represented in Pl. IX, Fig. 6, and it will be seen that there are present in all twelve mesenteries. Of these, six, those numbered I, II, III, are perfect, while the other six, of almost equal length, are quite small. The numbers assigned to the various mesenteries indicate their probable order of appearance, the ventral directives (III) being probably the third, and the dorsal directives (IV) the fourth pair to be developed. The stomatodæum is elongated in the usual direction, and the single siphonoglyphe (*Sz*) is already evident.

The older specimen was cylindrical in shape, with a well-marked base, and its ring of cilia had disappeared. It measured about 2.5 mm. in length, and 1.3 mm. in diameter. A number of tentacles, apparently about twelve, though it was impossible to determine the exact number, had made their appearance. Unfortunately, the specimen was somewhat macerated as well as distorted, so that it was impossible to make out satisfactorily the histological details, and camera drawings of single sections do not present a clear idea of the arrangement of the mesenteries, though this can be readily ascertained by a study of several serial sections. The figure I have given (Pl. IX, Fig. 7) is slightly schematized, the section from which it was drawn having been imperfect, but it represents truly the actual relations of the parts. The stomatodæum has been considerably distorted from its proper shape, but the position of the siphonoglyphe is clearly indicated. The six pairs of mesenteries seen in the younger stage are readily recognizable (I-IV), and preserve their original relations to the stomatodæum; but in addition to these, four mesenteries, arranged in pairs (1-2), have made their appearance in the exocœls upon either side of the ventral directives. Of these new mesenteries, the dorsal pair upon the right side (1r) is somewhat more developed than the others, the ventral member of the pair having reached the stomatodæum.

There are some points in the histology of the younger larvæ which deserve mention. The ectoderm is comparatively high, and lacks as yet all trace of a definite cuticle. Its cells present the characteristic Hexactinian specialization, there being large numbers of nematocysts and gland-cells present, the latter being of the two varieties described by the Hertwigs ('79). In the upper portion of the embryo the granular cells are less numerous than towards the aboral end, where they are exceedingly abundant. Immediately external to the mesoglœa is a thin layer of coarsely granular substance, in which no cells can be distinguished; it has the position occupied by the longitudinal muscles of *Cerianthus*, but I cannot obtain any evidence of muscle fibres in it. External to it is a clear band, which seems to be a layer of nerve fibres. The cells which bear the long cilia forming the ciliary ring are markedly different from those composing the general ectoderm, being considerably lower, and lacking both gland-cells and nematocysts. Apparently, no aboral tuft of cilia is present.

A second peculiar feature is the presence of two ectodermal papillæ close to the mouth (Fig. 5, *e. p*). They are not very high, but still are well marked; the mesoglœa takes no part in their formation, but they are entirely ectodermal structures, resembling that layer elsewhere on the body in their histological details, but being characterized by a special development of gland-cells. Perhaps they represent the dentations which occur upon the margin of some forms of *Zoanthus*.

The mesoglœa of *Zoantheæ*, as is well known, is characterized by being traversed by canals containing cells, and by elongated fibril-like cells, in this respect differing from the mesoglœa of other Actinozoa, the Alcyonaria excepted. The origin of these cells is of some interest. They were discovered by Kölliker ('66), who observed that prolongations passed outwards from the canals to join the ectoderm, and the same fact has been recorded by R. Hertwig ('82), Erdmann ('85), and myself ('89), though I also obtained evidence that the endoderm in adult individuals also contributed to the formation of the mesoglœal enclosures. Near the base of each mesentery there is also a large canal imbedded in the mesoglœa, and the contents of this Hertwig is inclined to consider endodermal in origin, basing his opinion mainly upon the fact that he found *Zoöxanthellæ* in

the cavity. The larvæ here described give important evidence as to the origin of the canals of the column-wall mesogloea. The mesogloea is fairly well developed in the younger specimens, and contains a number of the canals as well as a few elongated, fibril-like cells. The canals are filled with a coarsely granular mass, which does not stain well, and in which no cell outlines can be distinguished. It resembles very closely in appearance the granular layer of the ectoderm, which has been described as lying immediately exterior to the mesogloea, and is in fact derived from that layer, portions of which can be seen in various stages of enclosure by the mesogloea. The endoderm in these young stages, on the other hand, takes no part in the formation of the canals, though my preparations of the adult *Mammillifera tuberculata* show that in later stages portions of the endoderm may be enclosed in the mesogloea, a process which we know occurs in the formation of the mesogloæal sphincters. As regards the basal canals of the mesenteries, my preparations do not permit of any certain conclusions, though appearances tend to show that their contents are also ectodermal in origin. In sections passing through the stomatodæum, the basal canal is comparatively small, producing only a slight enlargement of the base of the mesentery, or it may even be entirely absent. Below that level, however, it is very large, giving the imperfect mesenteries a pyriform shape in section (Fig. 8). The canal is occupied by a granular mass exactly resembling that found in the canals in the column wall, and it seems probable that it has been formed in exactly the same way. In the imperfect mesenteries the canal is usually situated at the distal end of the mesentery, but in the perfect ones it is found almost equidistant between the base and the free edge. In all cases a canal of varying size, but usually intermediate in size between those of the column wall and that of the mesentery, is to be found immediately at the base of the mesentery, and in many cases small masses of granular substance, evidently part of the canal contents, are to be found lying outside the canal amongst the endoderm cells. This might seem to indicate an endodermal origin for the mesenterial canal contents, but another explanation seems to me preferable, viz. that these masses are portions of the canal contents which have escaped to the exterior, since I find mesenteries in which the boundary between the canal and

the endoderm has disappeared. This dissolution of the bounding wall takes place where it is thinnest, the mesogloea being always thinner on one wall than on the other, the thick wall being that upon which the longitudinal muscles will be developed.

The disintegration of the bounding wall must later be repaired, since in the older specimen the separation between the canal and the endoderm is perfect, and both walls are equal in thickness. Furthermore, the canals have extended up into the stomatodæal region, and their section there is quite as large as it is lower down. The canals still retain the same relative distances from the base of the mesentery which they possessed previously, the increase in length of the imperfect mesenteries having been produced by the formation of new mesogloea distally to the canal, a fact that would seem to indicate that the endoderm takes part in the formation of the mesogloea. The smaller canals, which in the younger larvæ occurred at the bases of the mesenteries, are in the older specimens much larger, nearly equalling in size the mesenterial canal. The contents of the canals still present the same histological character as in the earlier stage.

Van Beneden, in his paper containing a description of Semper's larva, discusses at some length the affinities of the various tribes of Actinians. He lays great stress upon the imperfection of six of the twelve mesenteries that are developed in the Zoanthid larvæ, and believes that there can be no doubt but that "il existe dans le cours de l'évolution de notre larve un stade longtemps prolongé pendant lequel l'organisme se caractérise par la présence de six sarcoseptes primaires." I cannot see that the fact that there are only six perfect mesenteries justifies this conclusion in the least. It would have been quite as reasonable before these larval forms had been studied, to conclude from the study of adult Zoanthids with, let us say, twenty pairs of mesenteries, that in the course of their evolution they passed through a stage, persisting for a considerable time, in which they were characterized by the presence of twenty primary sarcosepta. Or, to take another case, if the larvæ of the macrotypal Zoanthids be found to possess in the twelve mesenteried stage eight perfect mesenteries (which seems quite probable), one would be justified in concluding, on the same grounds that

have afforded the distinguished Belgian naturalist a basis for his argument, that these larvæ passed through a stage of long duration, in which eight primary septa were present, these septa corresponding to those which I have indicated in my diagrams as I, II, III, and V. In other words, the macrotypal Zoanthids would have an ancestry altogether different from the microtypal forms, their fourth pair of primary mesenteries being equivalent to the pair which Van Beneden believes to be the sixth pair to develop in the microtypal forms.

The mere fact of the occurrence of macrotypal forms seems to me to indicate that the perfection of a mesentery cannot in all cases be relied upon as a sure indication of its early development, or, *vice versâ*, an imperfect mesentery is not necessarily one which is more recent in its appearance than all the perfect mesenteries present. It seems to me exceedingly probable that the imperfect condition of the dorsal directives — their position with regard to the axis of the stomatodæum and the arrangement of their musculature shows them to be equivalent to the dorsal directives of *Edwardsia* — is secondary, the mesenteries remaining in an embryonic condition so far as their size is concerned; and further, there is probably a connection between their imperfection and the absence of a dorsal siphonoglyphe.

On another point also Van Beneden has been led into error by attaching too great importance to slight variations in size. He finds that in his larvæ the mesenteries that I have indicated by VI are somewhat larger than either IV or V, and therefore concludes that they are older. He believes that pair VI of the imperfect mesenteries has developed first, then pair IV, and finally pair V. It must be noted that his conclusions are based upon the study of a single specimen, and he makes no allowance for individual variation. I do not find such a disparity in the size of the mesenteries in the larvæ which I have studied; on the contrary, all the six imperfect mesenteries are almost the same size, the exceedingly slight variations which do occur having no regularity. On the view that the fourth pair are retarded in their development, it is easy to understand how the sixth pair might surpass them slightly in size, but on account of the close similarity in the arrangement of the mesenteries to what we find in the larval stages of the Hexactiniæ, it seems reasonable to conclude that the sequence of development is the same

as in that group, especially as the dissimilarities are explicable. The fifth and sixth pairs of the Hexactiniæ appear to arise simultaneously, and it is possible that in individual cases one pair may originate a little before the other, and that the sixth pair in Van Beneden's larvæ may have been slightly older than the fifth pair; but even so, such a sequence of development could not be regarded as having any phylogenetic significance, but would merely indicate an individual variation.

It is upon the two erroneous ideas here discussed that Van Beneden bases his views as to the affinities and phylogeny of the Zoantheæ. He believes that they have never had any connection with the forms represented by the genus *Edwardsia* or with *Edwardsia*-like ancestors, but that they are a perfectly independent branch. All other groups of Actinians, however, stand in phylogenetic relation to the Edwardsiæ, and hence there is no relation between the Zoantheæ and the other Actiniaria, notwithstanding the many points which the two groups have in common. Since this idea, however, is based on an erroneous interpretation of facts, it does not require further discussion.

#### V. CERIANTHEÆ.

It has been shown by the Hertwigs ('79), Vogt ('88), and H. V. Wilson ('88) that in the later stages of *Cerianthus* new mesenteries are formed only in the chamber between the dorsal pair of mesenteries; and Boveri ('90) has demonstrated the same fact for *Arachnactis*. Concerning the sequence of development of the first eight mesenteries, however, we have no direct observations, though from Boveri's discovery of the similarity in the arrangement of the musculature of the eight primary mesenteries to what is found in the Edwardsiæ and in the Hexactiniæ, it seems probable that their order of development is the same as in the latter group.

I have been able to throw some definite light upon this point from the study of some young specimens of *Arachnactis brachiolata* obtained at Wood's Holl. A. Agassiz ('62) has given an account of the external characters of larvæ of this form and of the development of the tentacles, but has given no account of the formation of the mesenteries.

The youngest specimen I obtained was in the same stage as

that described by Agassiz, possessing only four tentacles. A figure is given (Pl. IX, Fig. 9) of the arrangement of the mesenteries in this specimen,<sup>1</sup> and from it will be seen that six mesenteries are present. Two of these (I) are much larger than the other four, and, as sections below the level of the stomatodæum show, possess mesenterial filaments. It seems probable, therefore, that they are the oldest mesenteries. The other four mesenteries do not possess filaments, and the specimen affords no evidence as to which pair is the older.

The next stage, however, gives the desired information. It possessed six tentacles and eight mesenteries (Fig. 10). Of these, those numbered I and II possessed mesenterial filaments, while in III and IV they were still lacking. It is evident that III and IV are the directive mesenteries, and the specimen has reached the *Edwardsia* stage. The ventral directives (III) have the same position and structure as in the preceding stage, but at the dorsal surface a marked change has occurred. There seems to be no room for doubt that the mesenteries marked II in Fig. 11 are identical with those which are situated at the dorsal end of the stomatodæal axis in Fig. 12. They have, however, left their original position, and migrated ventrally along the stomatodæum, while the lines of their insertion into the column wall have been pushed apart by the growth resulting in the formation of the third pair of tentacles ( $t^3$ ). The fact that they possess mesenterial filaments at this stage, and extend a greater distance down the column wall, seems to indicate that they are the second pair formed, the ventral directives being the third pair, and the dorsal directives the fourth pair. *The sequence of development of the eight primary mesenteries of Arachnactis agrees, therefore, with what has been found in Rhodactis and Manicina.*

In the youngest specimen of *A. albida*, described by Boveri, eight tentacles were present. It would seem, therefore, that the unpaired tentacle developed in the endocœl of the ventral directives did not make its appearance in that species until a later period. In *A. brachiolata* the case is different. The speci-

<sup>1</sup> The sections were not perfectly transverse, and the relations shown in the figure were ascertained only by the study of several successive sections. Consequently the figure is a composite one, and not the representation of a single section. The same remark applies also to the succeeding figure.

men, of which a section is represented in Fig. 13, possessed seven tentacles (Figs. 10 and 12); the six corresponding to those present in the preceding stage ( $t^1-t^3$ ), and the odd ventral tentacle ( $t^4$ ). This form, as will be seen from Fig. 13, had ten mesenteries, the fifth pair (5) arising in the space between the dorsal directives IV, which are undergoing a separation from each other in the same manner as was seen in the case of the second pair in the preceding stage. It seems evident that in the Ceriantheæ a region of special growth occurs at the dorsal surface, localized at the time of the formation of the dorsal directives, and persisting, perhaps, throughout the entire life of the individual.

## VI. THE PHYLOGENY OF THE ACTINOZOA.

It is now generally conceded by those authors who have had an opportunity of comparing the morphological characteristics of a number of the various groups of forms, for convenience associated under the term Actiniaria, that they have descended from ancestors which possessed an arrangement of the mesenteries similar to that occurring in existing Edwardsias. In the preceding pages I have endeavored to set forth certain facts which tend to confirm this phylogenetic deduction, and to suggest explanations of a few points which do not, at first, seem to be in harmony with it.

It is necessary now to discuss the facts at our disposal with special reference to their bearing upon the affinities of the various groups of Actinozoa to each other. As regards the relations of the Actinozoa to other Cœlenterates, there is little to be said; the majority of authors who have committed themselves upon the subject, agree in tracing the Actinozoan stem back to a form similar to the *Scyphistoma*. The evidence we have seems to point in that direction; but it must be acknowledged that it is exceedingly scanty, and there are many points of difference between any *Scyphistoma* of which we have a description and the simplest Actinozoa. It seems probable, however, that the Actinozoa are to be traced back to an ancestor possessing only four mesenteries. The occurrence of an octamerous symmetry in the simplest Actinozoa seems to point in that direction, as well as the fact that, in the development of the Hexactiniæ,

the stage with four mesenteries seems to mark an epoch, much less distinct, however, than that indicated at the close of the *Edwardsia* stage.

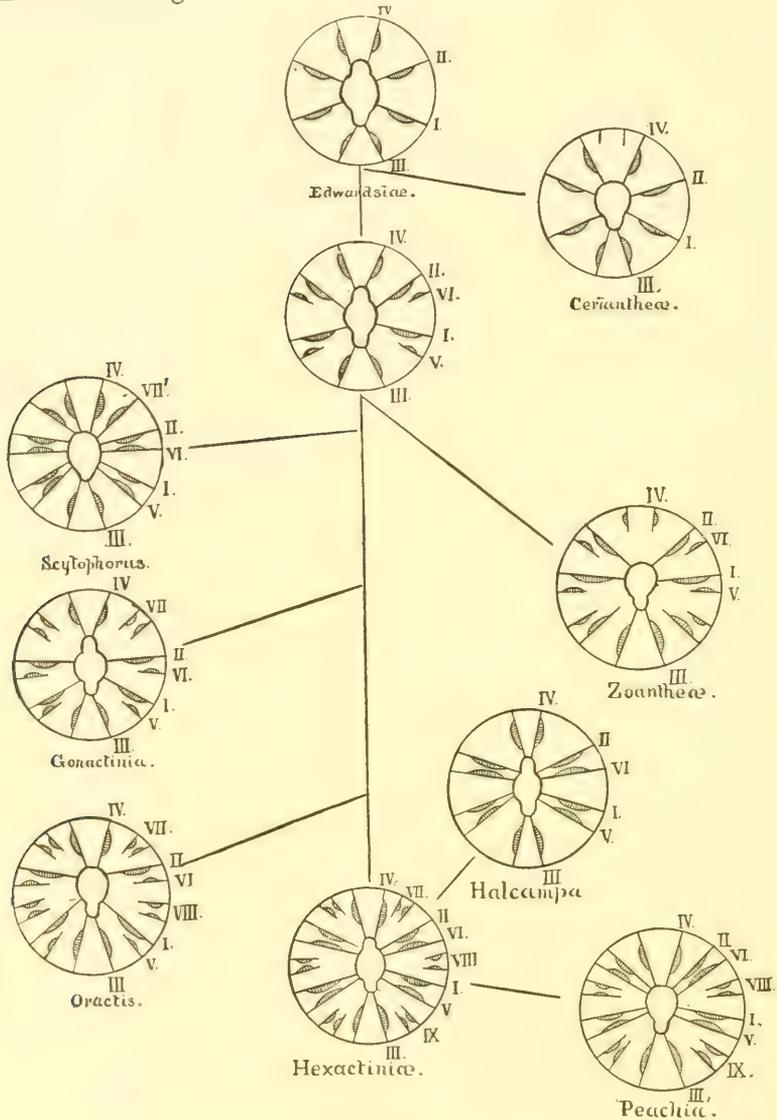


FIG. IV.

Starting, however, with the *Edwardsia* stage, we find it repeated in the ontogeny of the Ceriantheæ, the Zoantheæ, and

the Hexactiniæ, and indications of its occurrence are to be seen in the adult *Scytophorus*, *Gonactinia*, and *Oractis*.

We may imagine a line of descent running from the *Edwardsia*-like ancestors to the Hexactiniæ (see diagram, Fig. IV). As an offset from this line, a little below the point at which the Edwardsiæ stand, come the Ceriantheæ. Boveri's observations have shown clearly that this is the position which the Ceriantheæ hold with reference to the other forms. The facts which I have given in the preceding pages regarding the development of the mesenteries in *Arachnactis* indicate that they follow the same sequence that is found in the Hexactiniæ, and which, I have endeavored to show, also occurs in *Edwardsia*; and Boveri has shown that structurally the eight primary mesenteries of *Arachnactis* are equivalent to the eight mesenteries of *Edwardsia*. These two facts allow of no reasonable explanation other than that the Ceriantheæ are descended from *Edwardsia*-like ancestors.

They do not persist in this stage, but develop a large number of additional mesenteries. The formation of new mesenteries is confined to a region of growth lying on the dorsal surface, the first pair of secondary mesenteries being developed in the space between the dorsal directives. The special region of growth retains its dorsal position probably throughout the life of the individual, and appears to be mainly responsible for the increase in circumference of the body. A continual divarication of the mesenteries thus goes on, and new ones are added in the growing region between the immediately preceding pairs. It results from this that in the Ceriantheæ the eight primary mesenteries are situated in the adult on the ventral surface, the secondary mesenteries lying between them and the dorsal surface, with the more recent ones nearest the dorsal growing region.

Returning to the direct line of descent, we reach a stage in it in which twelve mesenteries are present. Eight of these are perfect and have their longitudinal muscles arranged as in *Edwardsia*. The four additional mesenteries are imperfect and arranged in two pairs, one of each pair lying on each side, between III and I, and I and II, and having their longitudinal muscles upon the dorsal face. Corresponding to this stage no adult form is known; it is a larval stage only, but seems to represent a third important epoch in the development.

A second offset arising from the main line, or even from this larval stage, gives rise to the Zoantheæ. In this group we seem to have a localization of growing regions similar to what is indicated in the Ceriantheæ; but the Zoantheæ possess two such regions, situated on each side of the ventral directives, new mesenteries continually forming at this point, and just as continually being divaricated towards the dorsal surface. We find, consequently, a very different condition as regards the relative position of the primary (including here under this term mesenteries V and VI) and secondary mesenteries from what was pointed out as occurring in the Ceriantheæ. The primaries are divided into two groups by the secondaries, the dorsal group containing ten mesenteries, and the ventral only the ventral directives. Furthermore, the youngest secondary mesenteries are situated nearest the ventral surface.

A third offset from the main line occurs soon after the development of this stage, and leads to such forms as *Scytophorus*, in which, in addition to the twelve primary mesenteries, we have a single mesentery present on each side of the dorsal directives. It is noticeable, however, that all the fourteen mesenteries of *Scytophorus* are perfect, and it may be possible that it has arisen from the main line much lower down, that is, after the *Halcampa* condition had been established. The location to which I have assigned it seems to me preferable, however, and I see no difficulty in the way of supposing that the mesenteries V, VI, and VII have become perfect since the separation from the main line.

A fourth offset leads to *Gonactinia*, which presents a stage in advance of *Scytophorus*. It retains the imperfection of V and VI, but has in the dorso-lateral intermesenterial space on each side a pair of imperfect mesenteries.

A little further down, and we reach *Oractis*, with two pairs of imperfect secondary mesenteries in the dorsal and lateral intermesenterial spaces; mesenteries V and VI being imperfect as in *Gonactinia*. In the diagram I have represented the last two groups and *Scytophorus* as far removed from the main line as the Zoantheæ. It seems probable, however, that they really stand very close to it, and indicate the gradual acquisition of new secondary mesenteries, which led to the formation of the second cycle mesenteries of the Hexactinæ. It is an interest-

ing fact that all the forms so far mentioned are strictly bilateral, both in their structure and in the formation of their secondary mesenteries. The Hexactiniæ are in reality bilateral also, so far as their structure is concerned, as was demonstrated by the discovery of the directive mesenteries by Schneider ('71), and in the early stage of their development bilaterality also prevails. At the conclusion, however, of the development of the mesenteries V and VI, a radial arrangement appears to step in, the new secondary mesenteries arising in pairs in all the mesenterial spaces. It is difficult to understand why a radial symmetry should be thus suddenly superimposed upon previous bilaterality, and I believe that such an idea is erroneous. The three forms, *Scytophorus*, *Gonactinia*, and *Oractis* seem to me to indicate that there has been a gradual development of the second cycle mesenteries of the Hexactiniæ, upon a bilateral plan. A single secondary mesentery first formed in each dorso-lateral intermesenterial space, the tendency to develop mesenteries singly and bilaterally, one on each side of the so-called dorso-ventral axis, which exists in the Edwardsiæ, Ceriantheæ, and in the larval twelve-mesenteried stage, still persisting. In the next stage a second mesentery is added in the same space on each side, forming a pair with that already present, the original single bilateral method of mesentery formation still persisting. With the formation of this pair, however, this tendency is replaced by one which leads to the formation of all future mesenteries in pairs, the bilateral arrangement, however, still persisting, and so the condition found in *Oractis* is reached. Finally, a third pair of mesenteries is added in each ventro-lateral intermesenterial space and the Hexactinian condition is reached.

If this scheme of development be correct, it is evident that the Hexactinian condition with twelve pairs of mesenteries is truly radial neither in structure nor in its phylogenetic development, and this latter fact explains the interesting observation of the Messrs. Dixon upon the embryo of *Bunodes thallia* already referred to (p. 133).

There is one point, however, in their account which needs correction, — that is, the comparison they make between a section taken about the middle of the body of the *Bunodes* embryo and a section of a *Peachia*. In both cases ten pairs of mesenteries are present, but in the *Bunodes* embryo it is the dorso-

lateral and lateral pairs of secondary mesenteries which are developed, whereas in *Peachia* the secondary mesenteries are in the ventro-lateral and lateral chambers.

It is with the completion of this first cycle of secondary mesenteries that the tendency to develop new mesenteries on a radial plan supervenes. The primary intermesenterial spaces are now all occupied by paired mesenteries, and in the formation of new mesenteries there is an endeavor to retain this symmetry; consequently, a radial symmetry becomes superimposed upon the original bilateral plan.

A difficulty, however, presents itself to this scheme of phylogenetic arrangement. Among the forms belonging to the genus *Halcampa* some present a condition in which only the twelve primary mesenteries are present, while others again possess in addition to these six pairs of imperfect secondary mesenteries. It is natural to suppose that the former, represented by such species as *H. clavus* of Hertwig ('82), *H. Kerguelensis*, Hert. ('88), *Halcampoides (Halcampa) abyssorum* of Danielssen ('90), are more primitive than the latter, represented by *H. chrysanthellum* (Peach.), *H. arenarea*, Haddon, *Halcampella maximo*, Hert. ('88), and probably *Halcampella endromitata*, Andres ('84). The members of the former group differ from the larval stage with only twelve mesenteries simply by mesenteries V and VI being perfect, and therefore stand closer to it than do *Scytophorus*, *Gonactinia*, or *Oractis*. It can hardly be supposed, however, that these forms, or ones similar to them, intervene in the line of descent between the two groups of *Halcampa*. There is too great a similarity between the forms of the two groups, and too great a dissimilarity between the members of either group and the three forms mentioned, to allow of such a supposition. It seems to me that a way out of the difficulty is to be found in a reversal of the usual way of regarding the relationships of the two groups. The possibility of a form presenting an apparently primitive structure being the descendant of a more highly specialized form, must always be kept in mind, and it seems not improbable that the simpler *Halcampa* have been derived from forms possessing secondary mesenteries, instead of *vice versa*. An analogous case is presented by the Axolotl, a form derived evidently from more highly organized Urodela, but yet becoming sexually mature, and persisting in a larval condition. The

phenomenon cannot be regarded as degeneration, but is rather an arrest of development. I imagine that the Halcampas with secondary mesenteries are phylogenetically the older, and those with only primary mesenteries have been derived from them by an arrest of the development of the secondaries.

With regard to *Peachia* I have already indicated what I believe to have been its origin (p. 139). There is a possibility, however, that the forms which are to be assigned to this genus may have arisen from the main line of descent towards the Hexactinian type, before the radial symmetry had replaced the more primitive bilaterality. I think, however, that this idea is negatived by the following consideration.

It has been shown that the pairs of secondary mesenteries which are present in *Peachia*, occupy the ventro-lateral and lateral intermesenterial spaces; that is to say, they correspond to the mesenteries of *Halcampta* which I have indicated in the diagram as IX and VIII. It seems probable that the order of appearance of the mesenteries of the second cycle in the phylogenetic development is that indicated by *Gonactinia* and *Oractis*, and this is confirmed by the observations of the Messrs. Dixon, already referred to. Consequently, it appears that the *Peachias* have arisen from forms which possessed a complete cycle of secondary mesenteries, one pair of which, namely, the dorso-lateral pair, they have lost. Their affinities seem to be with the Halcampidæ, and their ancestors are probably represented more or less closely by those Halcampas which possess a cycle of imperfect secondary mesenteries.

To complete the discussion of the phylogeny of the Actinozoa, it still remains to consider the Madreporaria, the Alcyonaria, the Rugosa, and the Antipatharia.

From the observations of Von Koch, Von Heider, Bourne, and Fowler, we now know that the Madreporaria are constructed upon essentially the same plan as the Hexactiniæ. The mesenteries are arranged in pairs, and hexamerously, and the longitudinal muscles are on the contiguous faces in each pair except in the cases of the two pairs of directives, which, however, in some species may be absent. I believe that one will not err very much in regard to the relationships of the Madreporaria in accepting the statement of R. Hertwig ('82): "Most corals will doubtless be placed later on with the Hexactiniæ; perhaps a natural

division into forms having a skeleton and forms without a skeleton, may not be possible, as even the closer limitation of the Hexactiniæ given here does not exclude the possibility of many of their families having more affinity to single families of corals than to other Hexactiniæ." The observations which have been recorded since the publication of Hertwig's paper only tend to confirm his opinion. The arrangement of the mesenteries, and their order of appearance, demonstrate conclusively that the majority, if not all, of the Hexacorallia are closely related to the Hexactiniæ.

As regards the Tetracorallia or Rugosa, however, matters are in a very unsatisfactory state. We know nothing as to their soft parts, and opinions differ as to the mode of arrangement of the septa. Some authors have been inclined to regard the Rugosa as the ancestral forms of the Hexacorallia, and have found among recent corals what they believed to be connecting links between the two groups. All such theories have, however, proved unsatisfactory, and for a discussion of their value Neumayr's recent work ('89) may be referred to. The trouble is that too much importance has been attached to adult resemblances, and too little to the essential point, the manner of formation of the mesenteries and septa.

There seems to be little room for doubt that the mesenteries of the Rugosa increased in a bilateral manner. Whether the primary plan of the organism was hexamerous or tetramerous is the doubtful point. The latter view was maintained by Kunth ('69), and is in harmony with the marked tetrameral symmetry which so many Rugosa present. According to Kunth, the formation of secondary septa was limited to four points, one on either side of the dorsal (*fossal*) septum, and one on each side immediately ventral to the lateral septa.

R. Ludwig, and later, Pourtalès ('71), maintained the other view. Pourtalès reached his conclusion from a study of *Lophophyllum*, and while he found that the formation of secondary septa was limited to four regions, he believed that six primary septa were present, and that in adult forms the arrangement was a modification of an hexamerous condition.

Whichever of these two views be accepted, it seems certain that the mode of formation of septa, and therefore of mesenteries, in the Rugosa, is entirely different from that occurring

in the Hexacorallia, and accordingly it is exceedingly unlikely that there can be any intimate relation between the two groups.

In the determination of the relations of the Rugosa to the other Actinozoa, however, the question whether their fundamental plan is tetramerous or hexamerous becomes of great importance. In the former case it may be supposed that eight primary mesenteries (sarcosepta) were present, the Rugosa agreeing in this respect with the Alcyonaria and the Edwardsiæ. They differ from these, however, in that secondary mesenteries are added in the course of development, as in the Cerianthææ; but instead of developing at one region, as in the forms of that group, they arise singly and bilaterally at four distinct regions, one mesentery corresponding to each septum of the secondary series.

If, however, the primary septa were six in number, it must be supposed that there were twelve primary mesenteries, the septa being entocœlic. Whether the secondary mesenteries developed singly or in pairs, approaching the arrangement found in *Peachia*, though not like that form derived from an Hexactinian condition, it is impossible at present to say.

Kunth's view of the development of the septa is, however, the one which seems to prevail among palæontologists at present, and is that accepted by Zittel in his Handbook, and in the recent publication by Neumayr. It is to be hoped that the question will be definitely decided in the near future by renewed and extensive observations. In the meantime, it will be most in harmony with our information on the subject if we consider the Rugosa one of the most primitive groups of Actinozoa, more primitive, perhaps, than even the Alcyonaria or Edwardsiæ.

The relative position of the Alcyonaria I have already referred to. It seems not improbable that they are phylogenetically antecedent to the Edwardsiæ. The arrangement of the mesenterial musculature is, it seems to me, simpler; and the slight development of the siphonoglyphe appears to be a point of considerable importance. The pinnate nature of the tentacles, the peculiar arrangement of the mesenterial filaments, the axis and spicules, and the simultaneous appearance in the ontogeny of all the eight mesenteries, seem to present material difficulties to the view I have advanced. It must be remembered, however, that the Alcyonaria are a very highly specialized group. There

is evidence that the colonial growth, and the development of the axis and spicules, have been acquired since the establishment of the group, since we know such simple forms as *Monoxenia*, *Hartea*, and *Haima*; and as to the development, we know practically nothing of that of these simpler forms, a study of which may, perhaps, reveal a succession of mesenteries instead of their simultaneous appearance. The peculiarities of the mesenterial filaments seem to be the greatest difficulty; but even here it seems quite possible that the difficulties may vanish or be diminished with a better knowledge of these lower forms, since Haacke ('84) states that in *Xenia* the arrangement of the filaments differs materially from what E. B. Wilson ('83) has described in *Paralcyonium*, etc., and more nearly approaches in some respects what is found in the Actiniaria, though the extent of the similarity is not fully brought out in the brief communication which is all Haacke has contributed on the subject.

The fact that Andres ('80) has stated that the respiratory portion of the mesenterial filament is absent in *E. Claparedii*, and that we have no definite information concerning its presence in any of the other forms that have been studied, might lead one to infer that the respiratory portions of the filament of the Hexactiniæ had nothing to do phylogenetically with the respiratory filaments of the Alcyonaria. This is negatived, however, by the fact that the respiratory filaments *do* occur in certain Edwardsiæ, as I have been able to find them in an undetermined species from the Pacific; and if they are absent in *E. Claparedii*, and even in other forms, this must be regarded as a secondary condition.

What is needed to determine this question is a careful and comprehensive study of the filaments of the Alcyonaria, especially of the simpler forms. In the meantime, I am inclined to consider the Alcyonaria as forms which have branched off from an Octactinian ancestor which they had in common with the Edwardsiæ, and that they approximate this ancestor in the arrangement of the mesenterial musculature, and in the nature of the siphonoglyphe more closely than do the Edwardsiæ, but in other points, such as the tentacles, the skeleton, and the mesenterial filaments, they show a marked specialization, which has occurred within the limits of the group, that is to say, since the Edwardsiæ branched off from the main line, leading from the Octactinian ancestor to the Alcyonaria, as we now know them.

Finally, as regards the Antipatharia, it must be confessed that, notwithstanding the excellent Monograph by Brook ('89), we are still far from able to estimate with any certainty their past history. We know that they possess six principal mesenteries, and a corresponding number of tentacles. In some few forms no additional mesenteries are developed, but in the majority there are in addition four other mesenteries, which attain only a slight development, and in *Leiopathes* these secondary mesenteries are six in number, making in all twelve mesenteries.

It is possible to regard *Leiopathes* as representing the most primitive arrangement in the group, upon which hypothesis affinities with the Hexactiniæ are suggested. Von Koch ('78), on the strength of his investigation of the Actinian *Gephyra Dohrnii*, believed that he had found evidence of the manner in which the Antipatharia had been derived from the Hexactiniæ, *Gephyra* being one of those Actinians which locate themselves on a relatively narrow cylindrical support (stems of Gorgonias, etc.), which they surround by the base, secreting, as many other forms do, a chitinous layer covering the support. Several Actinians are now known, however, belonging apparently to different families, which have this same habit, and the peculiarity should be regarded, as Andres ('84) endeavored to show, as physiological and not phylogenetic.

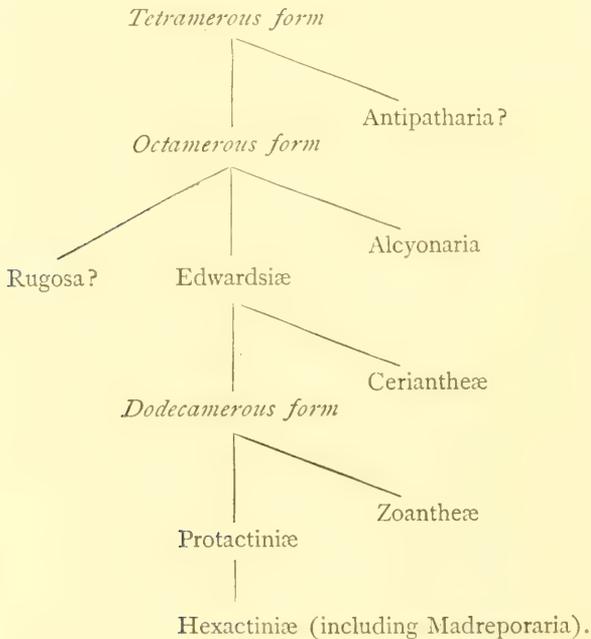
If the Hexactinian ancestry be maintained, it must be supposed, as Von Köch has done, that a decided degradation has taken place, for which there seems to be no evidence; and, furthermore, it must be shown that there is a paired arrangement of the mesenteries. This it has so far been impossible to do, since, owing to the very slight development of the longitudinal muscles, no orientation of the mesenteries has been possible. Brook endeavors, however, to make out a case for this side of the question by drawing a comparison between the degree of development of the mesenteries of *Leiopathes*, and the manner of development of the mesenteries of the Hexactiniæ, as described by Lacaze-Duthiers. I have already shown that the order of succession of the mesenteries of the *Bunodes* studied by Lacaze-Duthiers must be regarded as secondary, and it seems improbable that the Antipatharia should follow this method, instead of the more primitive one.

Instead of this manner of regarding the question, it may be

considered from the opposite side. The forms with only the six primary mesenteries may be regarded as the more primitive, additional mesenteries having been added in some forms. The fact that in all the genera only six tentacles are present, tends to support this view, and it furthermore does not necessitate any degradation theories. On this hypothesis the Antipatharia would be the descendants of an ancestor which intervened between the primitive Scyphistoma-like form and the primitive octamerous form, and would therefore be of very ancient stock. The absence of fossil Antipatharia seems to oppose this view; but on the other hand, it is probable that, as in the Alcyonaria, the colonial habit and the formation of an axial skeleton has been acquired within the limits of the group and perhaps at a geologically recent date.

However, the present evidence is too imperfect to permit of even an approximation to a solution of the question, but I am inclined to consider the six mesenteried condition to be the more primitive.

The following scheme may represent diagrammatically the line of descent which has been proposed in the preceding pages for the Actinozoa:—



The term Protactiniæ, employed in the scheme, denotes an order consisting of forms with twelve primary mesenteries ; with one, or a pair or two pairs of secondary mesenteries on each side of the sagittal axis, the increase in number of the secondary mesenteries occurring from the dorsal towards the ventral side.

The order includes *Scytophorus*, *Gonactinia*, and *Oractis*. It seems more convenient to associate these forms in a single order than to form a separate order for each one.

CLARK UNIVERSITY, WORCESTER, MASS.,  
February 21, 1891.

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## EXPLANATION OF PLATE.

The numbers I-IX denote the primary and secondary mesenteries in the order of their appearance.

FIG. 1. Diagrammatic figure of a section of *Metridium marginatum*, with only one siphonoglyphe.

FIG. 2. Transverse section of the column of *Halcampa producta* below the level of the stomatodæum.

FIG. 3. Transverse section of a primary mesentery of *Halcampa producta* to show the muscle pennon.

FIG. 4. Transverse section of the column of *Oractis diomedæa*.

FIG. 5. Longitudinal section of Zoanthid larva with twelve mesenteries. *cr* = ring of cilia.

FIG. 6. Transverse section of column of Zoanthid larva with twelve mesenteries.

FIG. 7. Transverse section of Zoanthid larva with twenty mesenteries. *1 r*, *2 r* = first and second pairs of ventro-lateral mesenteries of right side; *1 l*, *2 l* = first and second pairs of ventro-lateral mesenteries of left side.

FIG. 8. Transverse section of imperfect mesentery of Zoanthid larva with twelve mesenteries. *ec* = ectoderm; *n* = nerve tissue; *gr* = granular tissue below the nerve ring; *mg* = mesogloea; *en* = endoderm; *mc* = mesenterial canal.

FIG. 9. Transverse section of larva of *Arachnactis brachiolata* with four tentacles. *t*<sup>1</sup> = first formed tentacles; *t*<sup>2</sup> = second tentacles.

FIG. 10. Transverse section of larva of *Arachnactis brachiolata* with six tentacles. *t*<sup>1</sup>, *t*<sup>2</sup>, *t*<sup>3</sup> = first, second, and third tentacles.

FIG. 11. View of the dorsal side of larva of *Arachnactis brachiolata* with seven tentacles. *l* = lip.

FIG. 12. View of ventral side of larva of *Arachnactis brachiolata* with seven tentacles. Lettering as in preceding figure, except *t*<sup>4</sup> = unpaired ventral tentacle.

FIG. 13. Transverse section of larva of *Arachnactis brachiolata* with seven tentacles. *5* = first pair of Cerianthan mesenteries.









## DEVELOPMENT OF THE LESSER PERITONEAL CAVITY IN BIRDS AND MAMMALS.

F. MALL.

THE excellent posthumous paper of Budge,<sup>1</sup> although incomplete, adds a great deal to our knowledge of the early formation of the pleuro-peritoneal cavity. By means of injection he filled the spaces which first appear in the chick with an aqueous solution of Prussian blue. By this method he filled the various spaces forming the cœlom as they appeared, and found that they were intimately connected with the lymphatics.

The vascular layer formed between the splanchnopleur and entoderm in birds is too well known to allow further description. According to Budge, it may be split into two layers, — a dorsal or lymphatic, and a ventral or vascular. As the first blood-vessels are formed, lymph spaces appear on their dorsal side, which flow together to form networks, and accompany the primitive veins to the axial part of the germinal area. Here the lymphatics form two spaces, one on either side of the body, which are soon connected by a bridge and thus form an H. The cross-piece of the H lies oral to the sinus venosus which has just been formed.<sup>2</sup> In its further development the sinus grows to the dorsal side of the cross-piece, thus reversing the relation of the vascular to the lymphatic system. The uprights of the H fall to the outside of the body, and are swallowed up in the formation of the false amnion. The cross-piece forms mainly the pericardial cavity. Shortly before the heart is formed, two diverticula grow from the cross-piece, one on either side of the chorda, towards the tail of the body, forming the primitive pleuro-peritoneal cavities. By later anastomoses, and

<sup>1</sup> Budge, *His u. Braune's Archiv*, 1889.

<sup>2</sup> Duval, *Atlas de Embryologie*, Paris, 1889, gives on Pl. XVIII, 289 to 292, sections through the heart region before the cross-piece of the H is formed. On Pl. XX, Fig. 319, and Pl. XXI, Figs. 338, 339 to 340, the cœlomic cavities communicate on the ventral side of the heart.

finally by disappearance of the septa, the whole body-cavity is caused to communicate with the false amnion.

In this abstract I have included only what directly interests us, leaving the many interesting details regarding the development of the lymphatics.

The sprouting of the pleuro-peritoneal cavity from the pericardial places the omphalo-mesenteric veins on the ventral side of the former and on the dorsal side of the latter. After the intestinal canal is formed, it is placed on the dorsal side of the pericardial, and between the pleuro-peritoneal cavities, the septum separating the pleuro-peritoneal forming the mesentery, — a condition which remains in the adult in fishes and amphibia.

The first clear idea obtained regarding the development of the lesser peritoneal cavity and great omentum was given by Johannes Müller in 1830.<sup>1</sup> To him we owe our knowledge of the mesogastrium, and the confirmation of Meckel's description<sup>2</sup> of the relation of the omentum to the colon.

The whole subject has been thoroughly re-worked by Toldt,<sup>3</sup> beginning with human embryos of about the sixth week, — the same stage with which Müller started.

The present communication is intended to partly fill the gap between the works of Budge and of Toldt. This was made possible by a modification of Selenka's method by which "corrosion preparations" of very young embryos are obtained.<sup>4</sup> I proceed as usual to reconstruct according to the method of Born, but instead of blending the plate, the portions which are to appear in the corrosions are cut out. If the portions cut out represent spaces, the process is simple, as for instance, blood-vessels or the cœlom. The plates are now piled, and the spaces filled with Wood's metal or plaster of Paris. The former is better, if the spaces are small. After the plaster has set, the wax may be removed by boiling in water; while, if the injection has been made with Wood's metal, the plates are simply to be pulled off. For all ordinary small models, the metal is, by all odds, the most desirable. The metal cast can now easily be polished or smoothed over with wax, and the whole buried in plaster

<sup>1</sup> Müller, Meckel's *Archiv*, Bd. V.

<sup>2</sup> Meckel, Meckel's *Archiv*, Bd. III.

<sup>3</sup> Toldt, *Denkschriften d. Akademie zu Wien*, Bd. 41, 1879.

<sup>4</sup> Selenka, *Setzungsber. d. physiol. med. Soc. zu Erlangen*, 1886.

of Paris, from which the metal and wax are to be removed by boiling. The mould is now to be filled with lead or solder, and the plaster broken off. By this method any portion of an embryo can be modelled in lead or solder. The method does not cost as much labor as Born's, and in many respects exceeds it in usefulness.

#### BIRDS.

Shortly after the heart is formed, the head begins to flex upon the body, and the pharyngeal entoderm is pushed at first to the dorsal side of the heart, and then into the branchial region. At the time this peculiar rotation is taking place, the sinus venosus holds quite a stationary position, while the heart is thrown over to its ventral and aboral side. At this time a single omphalo-mesenteric vein empties into the heart, and from either side an additional branch, the ductus Cuvieri, is added. The pleuro-peritoneal cavity now breaks through on the aboral side of the ductus, thus causing the vessel to perforate the pleuro-peritoneal cavity (Fig. 1), as described by Balfour.<sup>1</sup> The union of the cavities across the median line now extends more aborally, and then communicates with the false amnion. After we have arrived at this stage, the mesentery is fully formed, the cavities on either side communicating across the median line only in the neighborhood of the heart. The pulmonary buds are forming, and the alimentary canal is almost completely closed. Just at this time two sacs, one on either side, are formed from the splanchnic wall of the pleuro-

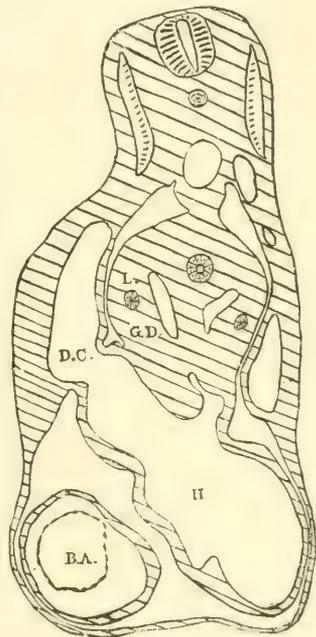


FIG. 1. Section through the region of the heart of a chick of 70 hours. Enlarged 50 times. The section strikes the oral end of the gastric diverticulum, *G. D.*, and the tips of the pulmonary buds, *L.* A few sections deeper the gastric diverticula communicate with the pleuro-peritoneal cavity. *H.*, heart; *D. C.*, ductus Cuvieri; *B. A.*, bulbus aortae.

<sup>1</sup> *Comparative Embryology*, Vol. II, p. 627, Fig. 352. See also His, *Hünschen Monograph.*, Taf. XI, Figs. I, 12, 13, 14; Duval, *Planche. XXII*, Figs. 358, 359, 360: Pl. XXV, Figs. 403-407.

peritoneal cavity. They extend between the proventriculus and the lungs, as shown in Fig. 1, *G. D.* On account of their location, I shall speak of these sacs as the gastric diverticula.<sup>1</sup> From the one on the right side the lesser peritoneal cavity of birds and mammals develops.

A few hours later, eighty-eight hours, when the body is flexed to its maximum, the gastric diverticula become more semicircular in transverse section, and also enclose the proventriculus on either side. On the right side the diverticulum is larger, markedly cup-shaped, and connects by means of a narrowed opening with the right pleuro-peritoneal cavity (Fig. 2, *F. W.*)<sup>2</sup>

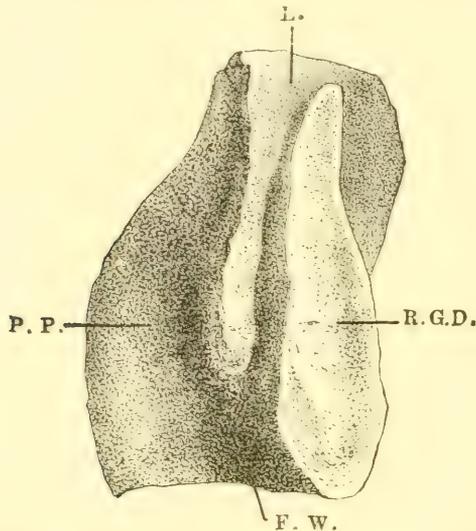


FIG. 2. Corrosion preparation of the right gastric diverticulum of a chick, 88 hours. Enlarged 44 diameters. *P.P.*, pleuro-peritoneal cavity; *R.G.D.*, right gastric diverticulum; *F.W.*, foramen of Winslow; *L.*, position of the right lung.

In this embryo the liver lies between the heart and proventriculus, the opening lying to the oral and dorsal side of the liver. The cœliac axis is already formed, and the gastric and hepatic arteries pass directly to the proventriculus and liver. On account

<sup>1</sup> Earlier stages are shown in Duval, Pl. XXV, Figs. 404 and 405. His sections are viewed from the aboral side. The communication with the pleuro-peritoneal cavity of the stage which I represent in Fig. 1, he shows on Pl. XXX, Figs. 473 to 476.

<sup>2</sup> Duval, Pl. XXX, Figs. 375, 376, shows a section of the communication of this opening with the cœlom.

of this relation, and on account of a similar arrangement in mammals, I conclude that this constriction marks the foramen of Winslow; and I shall speak of it as such.

On the left side (Fig. 3) the gastric diverticulum is much

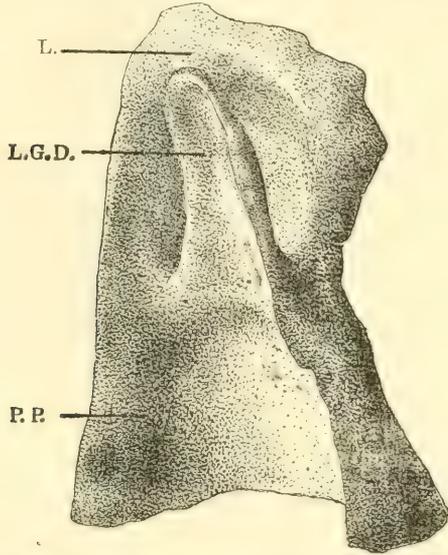


FIG. 3. Left gastric diverticulum of a chick, 88 hours. Enlarged 44 diameters. *P.P.*, pleuro-peritoneal cavity; *L.G.D.*, left gastric diverticulum; *L.*, position of left lung.

shorter and more shallow. In general, the proventriculus lies on the left side of the median line, and the spaces on either side seem to have taken on a corresponding shape and capacity.

In an embryo of five days and sixteen hours the right gastric diverticulum has about doubled all its diameters, while the embryonic foramen of Winslow has become much more sharply defined (Fig. 4). At this time the liver has greatly increased in size, the right lobe being larger than the left, both lying oral to the foramen of Winslow. The original position of the liver being aboral to the foramen, the rotation of the liver necessarily carries the hepatic artery and the portal vein around the foramen of Winslow, its adult position. With the growth of the gizzard, a space extends from the aboral end of the right gastric diverticulum along the dorsal side of this organ, and marks the beginning of the cavity of the great omentum (*o*). Nearly the whole

of the right diverticulum now lies on the left side of the body; the same position is held by the proventriculus and gizzard.<sup>1</sup>

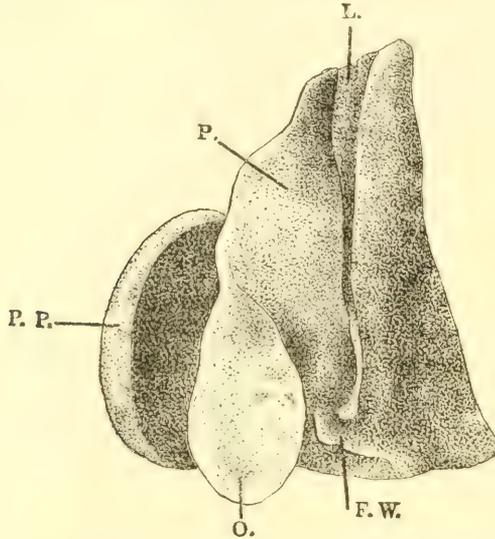


FIG. 4. Corrosion preparation of the right gastric diverticulum in a chick of 136 hours. Ventral view. Enlarged 22 times. *P. P.*, pleuro-peritoneal cavity; *F. W.*, foramen of Winslow; *L.*, position of right lung; *P.*, position of proventriculus; *O.*, omental cavity: position of gizzard.

On the left side the gastric diverticulum has become but slightly larger than in the previous stage (Fig. 5). It commu-

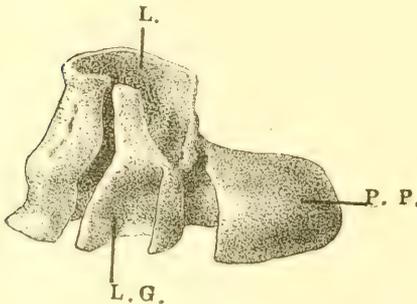


FIG. 5. Corrosion preparation of the left diverticulum in a chick of 136 hours. Ventral view. Enlarged 22 times. *P. P.*, pleuro-peritoneal cavity; *L. G.*, left gastric diverticulum; *L.*, position of left lung.

nicates on its aboral side most freely with the pleuro-peritoneal cavity, and no indication of a constriction (foramen of Winslow) is at any time present.

A day later (six days, sixteen hours) the left diverticulum has nearly disappeared, while the dimensions of the right have increased considerably in size. In general, its form is much as shown in Fig. 4. The lobus

<sup>1</sup> Duval, Pl. XXIV, Figs. 527 to 535, represents sections of this stage. The sections are all viewed from the aboral side; that is, they are negative pictures.

Spigellii now projects markedly into the oral portion of the diverticulum. The portion on the dorsal side of the gizzard has increased with the growth of this organ, and also extends markedly into the omentum which partly overhangs the intestine. The whole diverticulum measures, from lung to intestine, three millimetres; and the gizzard is one millimetre in diameter. The omental cavity is nearly a millimetre wide, and about one-half a millimetre long. It is shown as a distinct cavity, the dorso-ventricular diameter being nearly half a millimetre.

My material does not suffice to follow the fate of the embryonic omentum. A chick of ten days shows, however, that it is in no way related to the formation of the air sacs. At this stage three large air sacs project from the bronchial tubules into the abdominal cavity, representing the number present in the adult.

The domestic fowl contains three peritoneal cavities, completely separated from one another, and from one of them the lesser cavity arises. The communication is by means of a foramen of Winslow. After the anterior abdominal walls are removed, two ventral cavities are exposed, separated from each other by a vertical longitudinal septum. Into each of the cavities hangs a lobe of the liver, while into the left the ventral surface of the gizzard projects. On the dorsal side of the liver there are, on each side, three air sacs,—an anterior, a middle, and a posterior. The middle is the smallest, and the posterior the largest, and extends throughout the posterior portion of the abdominal cavity. Each sac communicates by means of a special opening directly with the lungs. By allowing the sacs to collapse, we find that a very distinct membrane extends backward from the gizzard, and cuts off the portion of the abdominal cavity containing the intestines. This is the “pseudo-epiploön” described by Weldon,<sup>1</sup> and followed more extensively by Beddard.<sup>2</sup> A similar membrane is present in crocodiles. In all respects, this membrane is situated in the same position as the epiploön in mammals, with the difference that it is adherent to the abdominal walls along its free border. On the dorsal side of the gizzard the air sacs fill all the space, thus closing off the communication between the cavity in which the intestines lie and the ventral cavities.

<sup>1</sup> Proceedings of the Zoölogical Society, 1883.

<sup>2</sup> *Ibid.*, 1885.

When the anterior and middle air sacs on the right side are separated from the posterior sac on the same side (which is quite easily done with the handle of the scalpel), a slit is shown which extends to the oral and dorsal sides of the hepatic veins. Here it communicates, by means of a round opening about one centimetre in diameter, with a large cavity lying on the median and dorsal side of the proventriculus and extending to the spleen. The cavity does not extend over the dorsal side of the gizzard. In all respects, this corresponds with the right gastric diverticulum and with the lesser peritoneal cavity in mammals.

The relation of this embryonic omentum to the "pseudo-epiploön" is as yet unknown. However, I think it probable that the one is changed into the other, and that the "pseudo-epiploön will prove to be the true epiploön, homologous with the same in mammals. We must only imagine the embryonic omentum attaching itself to the sides of the abdomen, followed by a loss of the epiploönic peritoneal cavity. A subsequent growth of the air cells back from the dorsal side of the stomach will produce the condition found in the adult.

#### MAMMALS.

The earliest stage of mammals I have to examine is an embryo of a dog, six millimetres long.<sup>1</sup> It represents about the same stages as the chick of seventy hours already described. In the chick the pericardial cavity communicated on all sides with the pleuro-peritoneal cavity, while in this specimen the communication takes place only on the aboral side of the sinus reunieus. His pictures sections of human embryos, both earlier and later than this stage;<sup>2</sup> and in all of them the communication of the pericardial cavity with the pleuro-peritoneal cavity is only on the oral side of the ductus Cuvieri. The coelom still communicates freely with the false amnion.

The stomach is still a straight, upright tube, communicating freely behind with the umbilical vesicle. The liver is just arising as two lateral spouts of epithelial cells, each of which encircles an omphalo-mesenteric vein.

<sup>1</sup> For description of this embryo, see my paper on "Branchial Clefts of the Dog," *Studies from the Biological Laboratory, Johns Hopkins University*, Vol. IV.

<sup>2</sup> *Anatomie menschlich. Embryonen, Atlas*. Earlier stages, Pl. XI, *BB* and *LR*; later stages, Pl. XII, *L*; II, *B*; IV, *A*.

On the right side a marked gastric diverticulum is present, as shown in Fig. 6. On the left side absolutely no diverticulum is present. The same holds true for all the sections pictured by Professor His in his *Atlas*. Although there are two gastric diverticula in the chick, I have found in a specimen of sixty hours a single right diverticulum, much like the one shown in Fig. 6. This may indicate that the left diverticulum is in process of degeneration.

In a human embryo seven millimetres long the gastric diverticulum is slightly larger than the dog just described. It corresponds about with His's *A*, *B*, and *B<sub>r</sub>*.<sup>1</sup> The embryo was cut into a perfect series, and I have reconstructed in wax the whole embryo. A cast of the cœlom was made with Wood's metal.

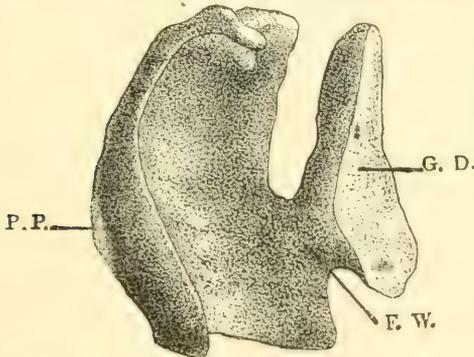


FIG. 7. Corrosion preparation of the gastric diverticulum of a human embryo 7 millimetres long. Enlarged 44 times. *P. P.*, pleuro-peritoneal cavity; *E. W.*, foramen of Winslow; *G. D.*, gastric diverticulum.

phalo-mesenteric vessels into the cord. On the ventral side of the alimentary canal, both on the oral and aboral sides of the

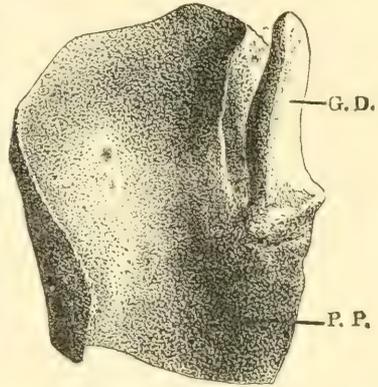


FIG. 6. Corrosion preparation of a portion of the right cœlom, including the gastric diverticulum of the dog 6 millimetres long. Ventral view. Enlarged 66 times. *G. D.*, gastric diverticulum; *P. P.*, pleuro-peritoneal cavity.

The pericardial cavity surrounds the heart with the exception of the point where the sinus reuniens enters. The bulbus aortæ is completely surrounded by a space to its origin in the ventricle. The cavity communicates on either side with the pleuro-peritoneal. It then surrounds the intestine, liver, and extends about the omphalo-mesenteric vessels into the cord. On the ventral side of the

<sup>1</sup> *Anatomie menschlich. Embryonen, and Ablandl. d. K. S. Ges. d. Wiss., Bd. XIV, 1888.*

omphalo-mesenteric vessels, the cavities on either side communicate by means of two quite large openings.<sup>1</sup>

Fig. 7 shows the gastric diverticulum somewhat more advanced than in Fig. 6, and resembling greatly Fig. 2. The marked constriction of the connection of the diverticulum with the pleuro-peritoneal cavity already marks the foramen of Winslow. A transverse section through the foramen of Winslow is shown in Fig. 8. The section strikes the coeliac axis as it arises

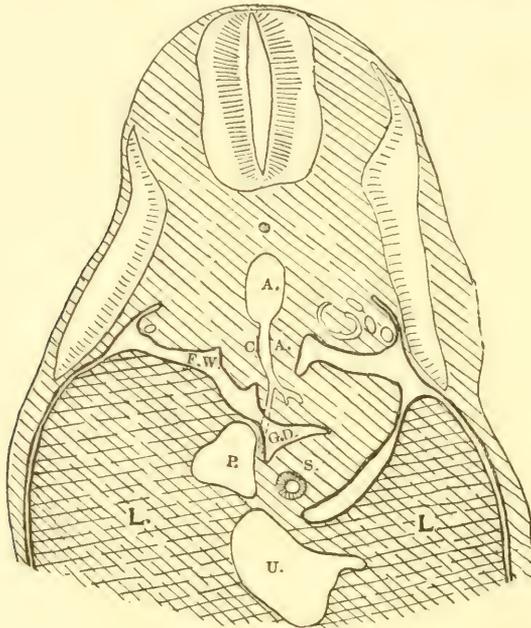


FIG. 8. Section through the foramen of Winslow of a human embryo 7 millimetres long. Enlarged 50 times. *A.*, aorta; *C. A.*, coeliac axis; *S.*, stomach; *G. D.*, gastric diverticulum; *F. W.*, foramen of Winslow; *P.*, portal vein; *U.*, umbilical vein; *L.*, liver.

from the aorta. The dotted line indicates the course of the hepatic artery a few sections deeper. It passes to the aboral side of the foramen, and on the median side of the vein the relations which are retained in the adult.

The mesentery has become considerably larger than in the dog of six millimetres or in the chick of seventy hours (Fig. 1). Accompanying the increased length of the mesentery, there is

<sup>1</sup> A description of this embryo will be given in the next number of this Journal.

a corresponding increase of the lesser peritoneal cavity, which now lies on the dorsal side of the embryonic stomach. Besides the elongation of the mesentery, there is also a gradual shifting of the stomach away from the mouth. After the liver and heart are well formed they lie in a straight line, in a transverse section, the liver being between the stomach and the heart. These three organs now lie immediately on the ventral side of the first dorsal vertebra. In the adult the stomach lies below the twelfth dorsal. In the dog six millimetres long there is as yet no artery to these organs, while in the human, seven millimetres, the artery is well formed, and arises from the aorta, just opposite the fourth dorsal. The omphalo-mesenteric artery, *i.e.* superior mesenteric, arises one segment deeper. In two dogs ten millimetres long the cœliac axis arises opposite the second and fourth dorsal segments respectively, while in a dog, 13.5 millimetres long, it lies as low as the tenth. In a cat twelve millimetres the cœliac axis lies opposite the tenth dorsal, and the omphalo-mesenteric artery opposite the eleventh dorsal. In His's embryo *M* the omphalo-mesenteric arises opposite the first dorsal,<sup>1</sup> while in embryo *B* the same vessel arises opposite the fifth dorsal.<sup>2</sup> In embryo *A* the cœliac axis arises opposite the sixth dorsal, and the omphalo-mesenteric opposite the ninth dorsal.<sup>3</sup>

These cases are sufficient to show that the stomach gradually moves away from the mouth, carrying its artery with it. Additional evidence is obtained from the study of the development of the splanchnic nerve. When the cœliac axis is opposite the first and second dorsal vertebræ, there are twigs of sympathetic nerves which surround it, coming from the first and second dorsal nerves. As the artery descends, the nerves following, third, fourth, etc., are, one after another, included, thus accounting for the high origin of the splanchnic.<sup>4</sup>

In a dog ten millimetres long the general shape of the lesser peritoneal cavity corresponds with the outline of the stomach.

<sup>1</sup> *Atlas*, Pl. VII, M 4; Pl. VI, Fig. 15.

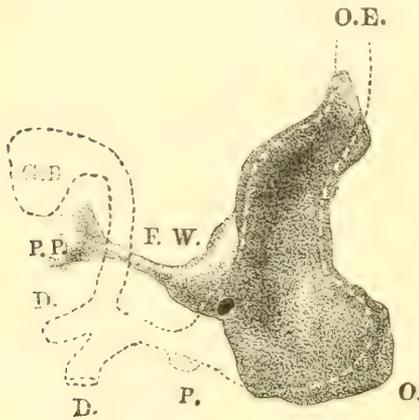
<sup>2</sup> Replace Fig. 24, Pl. III, *Atlas*, into Fig. 1, Pl. I.

<sup>3</sup> Replace Figs. 79 and 86, Pl. V, *Atlas*, into Fig. 4, Pl. I.

<sup>4</sup> Although the splanchnic is usually spoken of as arising from the eighth dorsal, it may be traced up to the third, second, or even the first dorsal. — Beck, *Phil. Trans.*, 1846.

The change of the relation of the spinal column to the heart is shown in a figure by Uskow, *Arch. für mikrosk. Anat.*, Bd. 22, S. 188.

The communication with the pleuro-peritoneal cavity has become constricted to a narrow canal, as shown in Fig. 9. The cavity



itself is still pointed on its oral side, extending up to the lung. On the aboral side it extends beyond the greater curvature of the stomach, forming the omental cavity. The liver at this stage is composed of two lobes, the right slightly larger than the left, and connected with each other by a complete band of liver tissue. A lobus Spigelii, as exists in birds, has not yet formed.

FIG. 9. Corrosion preparation of the gastric diverticulum (lesser peritoneal cavity) of a dog 10 millimetres long. Enlarged 44 diameters. The view is from the left side, and the stomach is outlined. *Æ.*, cesophagus; *G. B.*, gall bladder; *P.*, pancreas; *D.*, duodenum; *D.*, second canal to the liver; *P. P.*, pleuro-peritoneal cavity; *F. W.*, foramen of Winslow; *O.*, omental cavity.

in great part on the dorsal side. The gall bladder, which before lay in the septum transversum on the ventral side of the stomach

A stage later (Fig. 10), the stomach has twisted about, holding in great part its adult position. The liver, which before lay on the ventral side of the stomach, now lies on the aboral, and

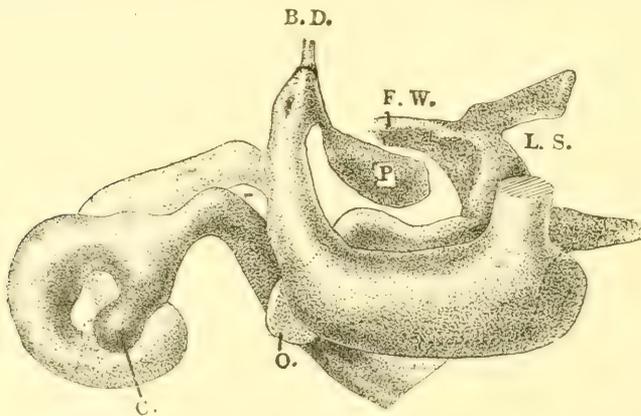


FIG. 10. Stomach, intestines, and lesser peritoneal cavity of a dog 13.5 millimetres long. Viewed from the left side. Enlarged 22 times. The lesser peritoneal cavity has been filled with metal. *B. D.*, bile duct; *P.*, pancreas; *C.*, cæcum; *O.*, omentum; *F. W.*, foramen of Winslow; *L. S.*, position of the lobus Spigelii.

and the aboral side of the liver, now lies on the aboral side of the stomach and on the ventral side of the liver. It has also shifted its position to the right of the median line. A model of these parts, from the ten-millimetre embryo, simply rotated, to throw the stomach away from the mouth, gives the condition of things as they exist in the embryo thirteen millimetres long. The intestine is composed of two loops, one from the stomach, extending into the pelvis, and the other at the cæcum, extending to the stomach, and on the left side of the first loop. The second loop is shown in Fig. 10.

The rapid growth of the large intestine has thrown the cæcum as high as the stomach, but to the right of it. The fold of

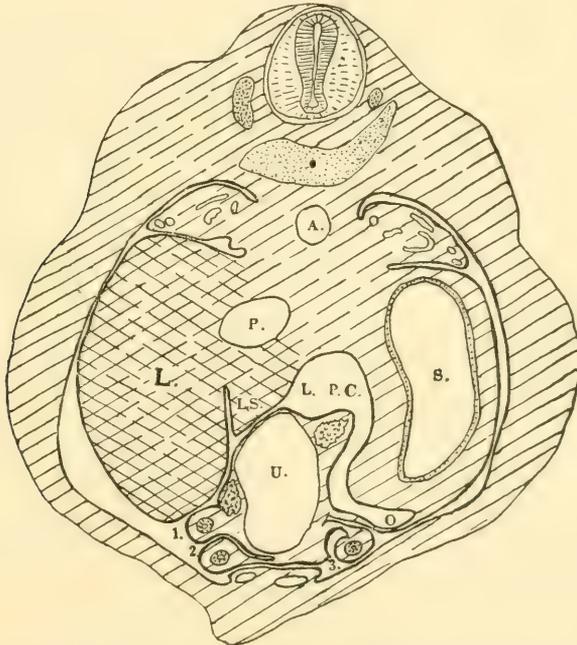


FIG. 11. Section through the foramen of Winslow and the lobus Spigelii of a dog 13.5 millimetres long. Enlarged 36 times. *A.*, aorta; *S.*, stomach; *P.*, portal vein; *U.*, umbilical vein; 1, 2, and 3, descending, ascending, and descending portions of the intestine; *L.P.C.*, lesser peritoneal cavity; *L.S.*, lobus Spigelii; *O.*, omental cavity.

omentum, coming from the dorsal side of the stomach, passes over the large intestine, as shown in the figure. The general shape of the lesser peritoneal cavity is shown in Fig. 11. The

S-shaped loop of intestine is cut across three times, and the lesser peritoneal cavity with its communication is shown throughout its whole extent. Within the foramen of Winslow, or rather the communication of the lesser with the greater peritoneal cavities, lies a triangular lobe of the liver, the lobus Spigelii. It arises from the right lobe of the liver, and is surrounded with a space, as shown in Fig. 10. In many respects, the liver of this stage represents the condition found in the adult domestic fowl.

The omentum from now on rapidly grows, covering all the intestines, but not adhering to the colon, as is the case in man. For the later development I refer the reader to the excellent papers of Müller and of Toldt.

In the lower vertebrates the alimentary canal is attached dorsally by quite a simple mesentery. The same is the case in the embryos of all vertebrates. From this simple, straight mesentery, by means of shifting, the later compartments of the coelom are formed. In the lizard the mesentery is quite simple,<sup>1</sup> and lately Ravn has shown us that on either side of the stomach there is a sack which communicates with the peritoneal cavity, the blind end extending as far forward as the heart.<sup>2</sup> On the right side the opening of the sac is related to the surrounding viscera, as is the foramen of Winslow in birds and mammals. The development of these sacs is not known, but from sections of embryos given by Orr a marked gastric diverticulum is shown.<sup>3</sup> In some specimens of adult turtles which I have examined there is a peritoneal cavity at the lesser curvature of the stomach, which does not communicate with the greater peritoneal cavity. This cavity holds the position of the lesser cavity, and no doubt will prove to be such. Fishes and amphibia probably have no such cavity.

From these observations it is seen that the lesser peritoneal cavity is present in reptiles, birds, and mammals. In certain groups of reptiles two diverticula are formed, extending from the pleuro-peritoneal cavity, on either side of the stomach, to the heart. The right is larger than the left, and communicates with the coelom around the vessels passing to the liver. This

<sup>1</sup> Pittard, Todd's *Cyclopædia of Anatomy*, Vol. III.

<sup>2</sup> Ravn, His u. Braune's *Archiv*, 1889.

<sup>3</sup> Orr, *Journal of Morphology*, Vol. I, Pl. XIV, Fig 37, c, PC.

cavity is homologous with the lesser peritoneal cavity, and the opening with the foramen of Winslow of mammals. Both right and left cavities are present in the adult.

In birds it plays a most important part, forming a distinct cavity, homologous with the lesser peritoneal cavity in mammals. At first the cavities are symmetrical, one on either side, but later in the development the left one disappears, and the right gradually enlarges to form the lesser peritoneal cavity, while the communication about the hepatic vessels with the greater cavity forms a foramen of Winslow.

In the lower mammals there are two gastric diverticula (Ravn), but the left is very insignificant and soon disappears. In the higher mammals only the right one is formed, which gradually increases in size to form the lesser peritoneal cavity.

CLARK UNIVERSITY, April 6, 1891.



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THE HABITS AND EMBRYOLOGY OF THE  
AMERICAN ALLIGATOR.

SAMUEL FESSENDEN CLARKE.

IN the fresh and brackish waters of some of the southern United States there are found two representatives of the highly organized Crocodylia or Loricata, an alligator and a crocodile. The alligators are very abundant in some of the waters of Florida and of Louisiana; they occur in less numbers in the intervening regions, and have been found as far north as the Neuse River in North Carolina,<sup>1</sup> and west to the San Antonio River in middle Texas. They live in the pools and streams where the water is almost or quite fresh, and they are also occasionally seen swimming in the nearly pure salt water of the Indian River, Florida, and other similar places.

The Indian River is not, strictly speaking, a river, but a narrow arm of the sea about one hundred miles long, and from one to several miles in width. It communicates freely by several passages with the ocean, and its fauna is mainly marine; starfishes and medusæ of several kinds, with many other marine forms, being very abundant. It receives several sluggish fresh-water affluents, the most important being the St. Lucie and the Sebastian. Near the mouth of the St. Lucie the manatee is found, and I have seen a large alligator near there, swimming at the surface in mid-stream.

Usually one finds them in the waters of the smaller streams

<sup>1</sup> And probably in Virginia.

and ponds, lying with only the tip of the nose and the eyes exposed; or lying on an exposed place on the bank where the grass and other plants are beaten down, and the black rich mud of the river bank is smoothed by the repeated movements of the alligators in climbing up and down. There they bask in the sunlight until disturbed by the hunter or the desire for food. When aroused, they make for the bottom, and I have never waited long enough to see one return, unless he were vigorously stimulated with a long pole. They frequently dig a cave for themselves in the bottom of the pond or stream, or in the bank beneath the water. Oftentimes one can start them out of the cave by using a pole; but if very obstinate, the hunters dig them out with spades. As the water decreases in the streams and ponds with the summer heat, the alligators travel to the larger bodies of water. During the breeding season, in late May, throughout June, and extending into July somewhat, the males are very active, wandering about to various ponds and rivers in search of the females. Fierce battles are said to take place during this time between the excited males; and the mutilated specimens that one sees is weighty evidence for the truth of this assertion. It is not very unusual to find a part of the tail gone, or one of the limbs mutilated, or taken off close to the body. One individual had been so bitten and lacerated on the side, that a coil of the intestine was visible through the peritoneum moving with peristaltic action. It is in the breeding season also that their bellowing is mostly heard, and more in the night than during the day. I have frequently heard them, while lying in the swamps at night, when they were in ponds fully a mile distant.

The largest specimen I saw measured twelve feet in length; and none of the many hunters and other natives of Florida I have met have seen any longer than thirteen feet. Several of the older hunters, however, were very positive that alligators sixteen and seventeen feet in length had been seen and killed by men whom they knew in the generation before them. All the hunters agree that it is only the males that acquire the great size; no one had ever seen a female that measured over eight feet, and the majority are not over seven. This agrees with my own observations. The male has a heavier, more powerful head, and, during the breeding season especially, is more

brilliantly colored. The more brilliant color occurs in patches and streaks on the sides of the head and body ; it is generally a light yellow, or even whitish, and on one large male I saw a fairly bright red spot over each eye.

The alligators are rapidly diminishing in numbers under the stimulus of the high prices offered to the hunters for their hides. Both whites and Indians make unceasing war upon them. Several thousand skins were brought into the little station of Fort Pierce last year. The pioneers and settlers always destroy the nests and eggs, because the alligators eat their pigs ; and the cleaned eggs and young alligators are sold by hundreds in the curio shops farther north.

So effective have been these various methods of destruction, that the most expert hunters at Fort Pierce were unable to get me any eggs this summer (1890). It should be stated, however, that the unusual drouth this year has driven the alligators into the remote and more inaccessible portions of the swamps. As their numbers diminish in Florida, it is noticed that the moccasin snakes increase. In Louisiana, also, the alligators are disappearing ; and there the muskrats are at the same time increasing, and are doing much damage by burrowing in the levees along the Mississippi.

While the alligator can make a very stout fight, I have never seen one offer fight if there was any chance to retreat ; and the hunters have had the same experience. They never offered to molest us, even when we waded through the ponds where they were, which we did at least a score of times.

The current statement that the armor of the alligator is bullet-proof is entirely fallacious. While it is true that a ball may very rarely glance from the head, or from the thickest, hardest covering on the back, it is also a fact that alligators are often killed with slugs or buck-shot from a shot-gun. The hunter aims for the brain, just between, or a little back of, the eyes. I did not meet any one who shoots at the eye, though it is very commonly held that the eyes are the only places on the body where a rifle bullet can force its way through to a vital part. There is no spot which is invulnerable to a buck-shot from a shot-gun, and I found no difficulty in cutting through the skin of and dissecting an eight-foot alligator with an ordinary pocket-knife. In some of the most secluded parts of the Florida

swamps, which have been frequently visited of late years by men in search of the beautiful plumage of the egrets and other birds, the alligators still occur in large numbers. This is especially true at the great breeding places of the birds known as "rookeries." I have the most reliable information from college collectors, that the waters contain so many alligators, that when a bird is shot or wounded and falls into the water, even near to the boat, the collector generally loses, and one of the many alligators gets, the bird before the light boat can reach it.

Among the oldest accounts of the alligator, that of Bartram (4), published in 1791, is especially interesting. While written with such spirit and enthusiasm as to carry the author beyond the limits of simple and accurate statement, it contains much that is undoubtedly correct concerning the alligators in Florida one hundred years ago. This is his description of a battle between two alligators, of which he was an eye-witness: "Behold him rushing forth from the flags and reeds. His enormous body swells. His plaited tail, brandished high, floats upon the lake. The waters like a cataract descend from his opening jaws. Clouds of smoke issue from his dilated nostrils. The earth trembles with his thunder. When immediately from the opposite coast of the lagoon emerges from the deep his rival champion. They suddenly dart upon each other. The boiling surface of the lake marks their rapid course, and a terrific conflict commences. They now sink to the bottom, folded together in horrid wreaths. The water becomes thick and discolored. Again they rise; their jaws clap together, re-echoing through the deep surrounding forests. Again they sink, when the contest ends at the muddy bottom of the lake, and the vanquished makes a hazardous escape, hiding himself in the muddy, turbulent waters and sedge on a distant shore."

Bartram writes as follows of their boldness in attack: "I furnished myself with a club for my defence, went on board my boat, and penetrating the first line of those which surrounded my harbor, they gave way; but being pursued by several very large ones, I kept strictly on the watch; . . . but ere I had half reached the place I was attacked on all sides, several endeavoring to upset the canoe. My situation now became precarious to the last degree; two very large ones attacked me closely, at

the same instant, rushing up with their heads and part of their bodies above the water, roaring terribly, and belching floods of water over me. They struck their jaws together so close to my ears as almost to stun me, and I expected every moment to be dragged out of the boat and instantly devoured. But I applied my weapons [clubs] so effectually about me, though at random, that I was so successful as to beat them off a little; when, finding that they designed to renew the battle, I made for the shore, as the only means left me for my preservation." Finally this from Bartram, relating to the numbers of the alligators:—

"The prodigious assemblage of crocodiles<sup>1</sup> at this place exceeded everything of the kind I ever heard of. The river in this place from shore to shore, and perhaps near half a mile above and below me, appeared to be one solid bank of fish of various kinds, pushing through the narrow pass of St. Juans into the little lake on their return down the river, and the alligators were in such incredible numbers, and so close together from shore to shore, that it would have been easy to have walked across on their heads, had the animals been harmless."

Considerable allowance must be made for the dramatic character of Bartram's style; but there is no reason to doubt that alligators were formerly more abundant in Florida, and it is highly probable that they were also less fearful of man. One other word from Bartram: "I have seen alligators twenty feet in length, and some are supposed to be twenty-two or twenty-three feet." I doubt the accuracy of this statement and believe that the largest specimens he saw were quite possibly crocodiles. It will be of interest to notice here the Florida crocodile, the only other member of the alligator group in North America.

The two species of South American crocodile, *Crocodilus acutus* and *C. rhombifer*, Cuvier, are known to range northward as far as Cuba and San Domingo.

In 1870 Dr. Jeffries Wyman (32) found a skull of a crocodile at Key Biscayne Bay, Florida, the extreme southern end of the state. Comparing this with the South American species, he failed to find any specific characteristics which would separate this from the *Crocodilus acutus* of Cuvier. The skull is now in the collection of the Boston Society of Natural History.

In January, 1875, W. T. Hornaday (11) shot a male crocodile

<sup>1</sup> He uses the term synonymously with alligators.

fourteen feet, and a female ten feet and eight inches long. Both of these were found in Arch Creek, a tributary of Biscayne Bay, Florida. He also found two skulls, and secured a small stuffed crocodile fourteen and a half inches long. H. A. Ward of Rochester, New York, had a crocodile from Lake Worth, Florida, about ninety miles north of Biscayne, which measures nine feet and ten inches. Hornaday says that the specimens from Arch Creek are between *C. acutus* and *C. rhombifer*, and proposes for them the name of *C. Floridanus*. Yarrow (33), in his check list of 1882, gives only one species of crocodile, *C. Americanus*, Seba.

I made three trips to Florida before I succeeded in getting any considerable number of eggs, obstacles, and hindrances of many kinds having been placed in my way. On the last trip I was accompanied by my friend and former student, Mr. C. C. Hayes, to whom I am indebted for many of the drawings for this paper, including nearly all those from life, and also for his faithful companionship through a long month of intense heat and other hardships, with privations of many kinds. I would gratefully acknowledge, also, my indebtedness to President Carter and the Board of Trustees, for granting me the necessary leave of absence from my college duties.

To return now to the alligator.

#### EGG-LAYING.

On the 9th of June, 1888, I found, after a long and laborious search through many miles of Florida swamp, at a point about fifteen miles from Fort Pierce, an alligator's nest containing newly laid eggs.

A second lot of eggs was gotten the next day by a hunter who was at work for me some forty miles to the northward. This second lot were taken from the oviducts of a gravid female, and were just ready for laying, as the shell was fully formed.

Old nests were to be found in abundance, and new nests were also seen partly built or completed, but not as yet containing eggs. It was evidently the beginning of the laying season, but I was obliged to return at once, carrying with me the sixty eggs which we had secured—twenty-nine from the nest and thirty-one from Madame Alligator. The journey home, made with all

possible despatch, required six days and nights, during which time the temperature was so high as to incite and continue the process of incubation. All the early stages were thus lost, and, some of the eggs proving bad, another trip to Florida was made in June, 1889. The time of nesting agreed with what we had observed the previous year, and during four weeks' stay I got, with the aid of five hunters, twelve lots of eggs, aggregating about three hundred and twenty. The latest laying that I knew of took place on June 17, and the earliest was on June 9. While it is probable that eggs are occasionally laid somewhat later than that, I doubt if they are ever laid much before the 9th.

I visited many other places farther north in Florida, but found the alligators and their nests most abundant in the swamps to the westward of Fort Pierce. Possibly farther south they are still more numerous.

#### NIDIFICATION.

The nest of the alligator is very large, and is built by the female. A great quantity of the dead leaves and twigs, together with much of the finely divided humus underlying them, is scraped together into a low mound about one metre high; this varies considerably in its other dimensions, being in some instances eight feet in diameter at the base. The nests are built on the bank of a stream or pool, and the female digs a cave under water in the bank close to the nest. Careful examination of the largest nest found showed a root of a neighboring palmetto tree, nearly an inch in diameter, running through it at about a third of a metre above the ground; there were also roots of a grape vine growing near, which extended nearly through the nest. This furnishes strong support to the statements of many of the hunters, that the nests are used for more than one season. I could get no evidence whatever that the nests are used more than once a year. The eggs are laid near the top of the nest, within twenty centimetres of the surface, are four or five layers deep, and have no regular arrangement or uniform position of their axes in relation to the nest. In the twelve lots of eggs that I have had, the number to a nest varies from twenty to thirty-one, and averages twenty-eight. I have questioned many of the alligator hunters as to the number of eggs in a nest, and the maximum given was forty-seven. This

they all stated to be unusually large. It is the common statement that the alligator lays from one to two hundred eggs, but of this I could get no evidence. I did not leave Fort Pierce until the 23d of June, and up to that time there had been but one lot of eggs deposited numbering over thirty in any of the fourteen nests found. They averaged twenty-eight eggs to a nest, and the eggs were so near the top of the nest that there was scanty room for any more, unless, perhaps, the nest should be enlarged when more eggs were laid. None of the men who spend a large part of their time hunting alligators, and who are continually in the swamps among them, knew anything of a second laying, or of such a large number as one or two hundred eggs to a nest.

It is possible that this statement grew out of what is known concerning the Egyptian crocodile, which does lay nearly one hundred eggs. Dr. A. Voeltzkow (30), writing from Lamu, East Africa, February, 1890, thus describes the egg-laying: "Ungefähr fünf bis sechs Schritt vom Ufer entfernt befand sich eine sechs Schritt im Durchmesser haltende kreisförmige, von Pflanzen entblösste kahle Stelle. Hergestellt wird dieselbe dem Anschein nach dadurch, dass sich das Thier ein paar Mal im Kreise herum dreht und mit seinem Schwanz den Boden säubert. Dadurch ist an manchen Stellen etwas Gestrüpp und Zweige angehäuft. Von Nestbau ist dabei aber absolut keine Rede. Das sogenannte Nest liegt nach dem Lande zu fast ganz offen, nur an einer Stelle finden sich ein paar spärliche Busche vor, so dass die Sonne von allen Seiten freien Zutritt hat. Die Eier fanden sich an vier Stellen, ungefähr zwei Fuss unter der Oberfläche, in Gruben, die in den harten, ziemlich trockenen Boden schräg nach unten gegraben waren. Mit den beim Ausgraben zerbrochenen Schalen, die am Nest herumlagen, betrug die Anzahl der abgelegten Eier 85-90 Stück. Nach Angabe der Eingeborenen gräbt das Crocodil, nachdem es sich einen ihm zusagenden Platz ausgewählt hat, am ersten Tag eine Grube, legt sich mit dem Bauch darüber und lässt eine Anzahl Eier, ca. 20-25 in die Grube fallen und schaufelt dieselbe dann zu, am zweiten Tag macht es die zweite Grube, etc. Vom Beginn der Eiablage verweilt das Thier den Tag über auf dem Neste und schläft daselbst bis zum Auskriechen der Jungen, so dass hier also eine richtige Brutpflege stattfinden würde. Die

Jungen schlüpfen nach ungefähr zwei Monaten, beim Eintritt der grossen Regenzeit aus. Thatsächlich war das Thier bei unserer Annäherung auf dem Nest gewesen. Die Eiablage erfolgt nur einmal im Jahre, in der Zeit von Ende Januar bis Anfang Februar."

#### THE EGG.

The eggs are white, elliptical, and vary in length from 50 to 90 mm., and in the shorter diameter from 28 to 45 mm. Generally there is only slight variation in the eggs of one nest, but occasionally a nest is found in which most of the eggs are about average size, while from two to five are very much smaller. In one such nestful I found four smaller eggs of different sizes, forming a very perfect series to the smallest, which measured only 28 by 50 mm. It is represented by the innermost outline in Pl. IX, Fig. 2. The other lines of the figure represent the outlines of four other eggs from various nests, and illustrate the differences in size. An exterior view of a medium size egg is shown in Fig. 4, and Fig. 3 is a similar view of the egg of the Florida crocodile. The shell is much rougher than that of a hen's egg and much thicker. Upon treatment with hydrochloric acid there remains a white organic matter which swells, becoming thicker than the original shell. The shell membrane is very thick, much more so than that of the hen's egg, and consists of two layers,—an inner and an outer,—in both of which the fibres are arranged spirally about the egg, but at right angles to one another. In a fresh-laid egg the shell is uniform in appearance throughout, and the same is true of the shell membrane. But there soon appears an area of a chalk-white color on the shell, which, beginning near the middle, extends gradually around the smaller diameter in the form of a median belt or zone. Upon removing the shell the cause of this change is seen to lie in the shell membrane. This has changed in appearance in just that area covered by the chalk-white zone in the shell; it has become opaque white and looks drier, with a rougher surface, while the remainder of the shell membrane is smooth and translucent: this area increases in width until it finally covers more than half of the egg. Fig. 1, Pl. IX, shows the outline of this zone on a shell membrane at three different times: the innermost line (1) was the outline

when the shell was removed; the egg was kept fully exposed to the air of the room, where the temperature was nearly 90° Fahrenheit; line 2 represents the belt as it was sixteen minutes later; and line 3 shows the increase at thirty-seven minutes after line 2 was made. The exposure to the air, then, increases the rapidity of that change in the shell membrane by which it becomes chalk-white. As this zone increases, it often becomes considerably widest at one place, and it is underneath there that the embryo is found. I would suggest that this change is produced by the gaseous interchange taking place through the membrane, and which still further adapts it to its part in the respiratory function. Certain it is that the change occurs in the region of the embryo and around the yolk, and enlarges as the embryo enlarges. Moreover, better respiratory arrangements are necessary in eggs which are buried some 40 cm. deep. Rathke (18), in his careful description of the shell membrane of *Lacerta agilis*, states that it is more complex than that of the adder and is composed of four parts; of these he reckons the shell as the first or outermost; (2) a thin, transparent layer which, fitting close to the shell, becomes uneven on its outer, but is perfectly smooth on its inner, surface; it is easily stripped off from the underlying membrane; (3) a most delicate layer, clear as glass, showing no trace of either fibres or granules, and is elastic and easily thrown into thin folds; (4) a much thicker membrane not easily torn. At each end of the egg this innermost membrane in a moderately large area forms a segment of a hollow sphere, which has quite another character than the median, very much larger part. This is non-transparent, white of color, and contains many very small granules. The end pieces, on the contrary, were transparent, colorless, without granules and thinner. This description is of the shell membrane of an egg removed from the oviduct. It is especially interesting in that a median, opaque white zone is described, like that occurring in the alligator's egg. It appears much earlier, however, if it is formed while the egg is in the oviduct. It is not stated whether this zone shows also in the shell; and as the zone will quickly grow when the membrane is exposed to the air, I cannot feel sure that the zone is normally developed in the membrane while the egg is still within the oviduct. Fig. 5, Pl. IX, is of an egg in the fifth week of incubation;

the shell is partly chipped off, showing the inside chalk-white zone.

The white of the egg has the consistency of a very thick jelly, is very clear and transparent, and is so firm that the whole egg, when perfectly fresh, may be turned out of the shell and shell membrane, and transferred from one hand to the other without breaking, and with but slight change of form. The chalazæ, as in the eggs of the other reptilia, are absent. There is, of course, no need of them in eggs which are not moved or turned, in which the yolk is surrounded by such a firm mass of white, and which are carefully buried. The white lies mostly at either end of the shell, but extends also in a thin layer between the yolk and the sides of the shell; and in this median area the white is more closely attached to the shell membrane, being after the first few days very firmly united to it at the edges of the chalk-white zone. Fig. 6, Pl. IX, represents an egg from which the yolk has been removed: the consistency of the white is shown by its hanging in heavy folds on either side. This shows the middle chalk-white zone on the upper side of the shell, and also that the white is attached to the shell membrane at the outer edges of this zone.

Fig. 48, Pl. XIII, shows the position and place of attachment of the white. The white has here been removed from one end; the stronger transverse lines in white are the lines of union with the shell membrane: a thin pellicle of white stretches across the median area.

The yolk holds a median position in the egg, is spherical, a very light pale yellow, and so large that it almost touches the shell membrane about the mid-line (see Pl. IX, Figs. 7, 8).

The germ in most of the eggs opened during the first few days of incubation was at one pole, as shown in Fig. 8, Pl. IX. About the germ is a considerable area having a more or less mottled appearance, and bounded by a sinuous white line. In some instances the germ was found upon the side of the egg, as shown in Fig. 7, Pl. IX. Somewhat later, toward the end of the first week of incubation, the germinal area is found moving from the polar region to the side, as shown in Fig. 9. Finally it comes quite to the side, as shown in Figs. 10 and 11.

The polar position at first is an advantageous one, on account of the greater protection afforded by the large mass of gelati-

nous white lying between the germ and the shell. And as growth and development proceed, it becomes essential to establish closer connection and freer communication with the exterior for respiration, excretion, etc. ; and this is secured by bringing the germ to the side, where there is comparatively little between it and the air without.

It is my purpose in the present paper to furnish a general account or outline of the forming of the alligator, as seen in the external features, as completely as my material will allow. I have been led to do this by reason of (1) the entire lack of any embryological knowledge of the alligator group,<sup>1</sup> and (2) on account of there still being something to be desired in the way of a set of general figures illustrating the development of a reptile. Later I hope to publish the results of studies of the internal development. The most complete series hitherto is that of *Lacerta agilis*, given by Strahl in his well-known papers from 1881 to 1884.

The series that I can give is at several points incomplete ; but as the eggs are each year more difficult to get, and as it is now nearly three years since I first went to Florida for them, it is perhaps wiser to publish than to wait longer.

#### THE FORMATION OF THE EMBRYO.

The youngest embryo that I received is shown in Fig. 12, Pl. X, as seen from the dorsal side. The limiting line between the opaque and the pellucid areas is clearly marked, and within the latter is a shield-shaped area connected by the narrower region of the primitive streak with the area opaca. The blastopore is already formed near the posterior end of the shield.

A ventral view of another embryo of the same age, seen from the ventral side, shows that the blastopore extends quite through the blastoderm, in an oblique direction downwards and forwards, from the dorsal to the ventral side. The thickened area of the primitive streak is here very prominent. There is, too, the beginning of a curved depression at the anterior end of the shield, the first formation of the head-fold. The head-fold rapidly increases in depth and prominence, as shown in Fig. 14,

<sup>1</sup> One must except the posthumous paper of Rathke, 1866, which deals only with a few of the later stages.

which is a ventral view a few hours later. The time cannot be given exactly, as it is found that eggs of the same nest are not equally advanced when laid, and differ in their rate of development. The lighter curve in front of the head-fold is the beginning of the anterior fold of the amnion. The notochord has been rapidly forming, and now shows very distinctly on the ventral side, when viewed by transmitted light. A dorsal view of the same embryo (Fig. 15) shows that the medullary or neural groove is appearing, and that it ends abruptly anteriorly near the large transverse head-fold. Posteriorly it terminates at the thickened area in front of the blastopore, which still remains open.

Figs. 16 and 17 are of an embryo removed, on June 18, from an egg which had been taken out of an alligator two days before. Fig. 16, a dorsal view, is of special interest in that it shows a secondary fold taking place in the head-fold. This grows posteriorly along the median dorsal line, forming a V-shaped process with the apex pointing backward toward the blastopore. There is quite a deep groove between the arms of the V. The head-fold on the ventral side, as seen in Fig. 17, made from the same embryo as Fig. 16, grows most rapidly on the mid-line, and also becomes thicker at that place. The medullary folds now begin to form on either side of the medullary groove, ending posteriorly on either side of the blastopore, and anteriorly on either side of the point of the V-shaped process in the middle of the head-fold. This is seen in Fig. 18, which is a dorsal view of an embryo from an egg three days after it was taken out of an alligator. A ventral view of the same embryo (Fig. 19) represents the thickened process on the mid-line at its greatest development. For some reason the notochord did not show in this embryo, possibly owing to particles of the yolk material adhering about the mid-line.

In an embryo a day or two older, the V-shaped fold of the head-fold is seen to have broken through at the apex; and each of the arms thus separated from one another unites with the medullary fold of its respective side. This can be seen in Fig. 20, which is a dorsal view of part of an embryo a day or two older than the one represented by Figs. 18 and 19.

This is so unexpected a method of formation for the anterior part of the medullary folds, that I have made use of both Figs.

16 and 18. They were made from very perfect specimens, and the sections of both of them, and of the specimen from which Fig. 20 was drawn, proves that the structure is what it is indicated to be in surface appearance. That is, the transverse sections posterior to the V, in the embryos shown in Figs. 16 and 18, show the medullary groove and the medullary folds: the several sections passing through the apex of the V show neither groove nor folds, but only a median thickening; and in front of the point or apex of the V the successive sections discover a gradually widening groove between the arms, which is also much deeper than the shallow groove found posterior to the V. While I have not seen, and from the nature of the conditions one cannot see, the change actually proceeding from the form of Fig. 18 to that of Fig. 20, still the explanation given appears to be the only one possible. The next pair of figures, 21, ventral, and 22, dorsal, are of an embryo out of an egg five days after it was taken from an alligator. The head-fold is increasing, and with it the amnion; three pairs of mesoblastic somites have been formed; the medullary folds are most widely separated anteriorly in the region of the brain; the blastopore still persists. The large, light-colored spots in the opaque area are produced by the separation of the germ layers from each other, forming a blister-like structure. A somewhat later stage is shown in Figs. 23, dorsal, and 24, ventral. The medullary folds are closing at the anterior extremity and in the middle region, but are widely open just in front of the mesoblastic somites, and at the posterior end, where they are surrounding the blastopore. One more pair of somites has been added. These somites are added posteriorly, as one may determine by comparing Figs. 21, 24, and 25; and in longitudinal section one finds them in process of formation immediately behind the last pair. In Figs. 25 and 26, ventral and dorsal of the same embryo, two pairs more have been added. All the figures on Plates II and III, with the exception of 27 and 28, are from alcoholic specimens. Figs. 27 and 28 are from life, and are also a dorsal and ventral view of one embryo. The parts show less clearly in the living embryo, and all the somites present were not visible from the dorsal side. The two prominent circular outlines on either side of the hind-brain and neck region in Fig. 27 are portions of the edge of the head-fold which show through from the ventral side. The

beginning of the three cerebral vesicles first indicated in Fig. 26 are more clearly seen in Fig. 27. Ten days after the fully formed eggs were removed from an alligator, the embryo had reached the stage exhibited in Figs. 29, ventral, and 30, dorsal. There is to be noted here a general increase in the development, a larger number of somites, and a further extension of the head-fold and of the amnion. Fig. 31 is an embryo from the same lot of eggs as that shown in Figs. 29 and 30, but was made four days later; consequently it was about two weeks old. I have introduced it mainly to show the beginning of the heart. It is a ventral view and this is the oldest stage in which the embryo retains its primitive position, in which the ventral side is turned toward the yolk.

The change of position begins at the anterior end of the body, first affecting the head and neck region. They are rotated about forty-five degrees on their axis, so that the head rests upon one cheek, more frequently upon the left, but often on the right. It would be strange if the head did not turn to one side, for by the growth posteriorly of the ventral wall of the body the head has come to be suspended, and being relatively very narrow, it is in an unstable position, and can very easily be swayed to either side. A movement of the body or a disturbance of the whole egg would probably effect this; and I would suggest that the pulsation of the now prominent twisted heart lying in the neck region would materially aid in bringing about this change. Once turned, it is well supported by the broad surface of the side of the head. As the body steadily increases its dimensions dorso-ventrally, becoming deep and narrow, with the heavier dorsal side adding to the instability, and as the connection with the yolk-sac is constantly decreasing, the strain exerted by the heavy head turned to one side may explain the gradual turning of the entire embryo.

The opening to the yolk-sac shows well in 34, and the outlines of the digestive tract; the position of the future mouth is clearly indicated. The most interesting feature in Fig. 33 is the apparent connection existing between the first and second pharyngeal clefts; the second being a later development, is smaller, and looks as though it might have originated from the first by an outgrowth of the latter's hinder wall. Sections prove that this appearance is due to the inner part of the throat-wall being

thinner at the point of apparent connection. It is only a thin area, however; there is no breaking through of the outer part of the wall, although it has that appearance in the very transparent living specimen. Neither of the clefts are yet open to the exterior. Fig. 34 is also from life, the precise age unknown, as the eggs had evidently been in the nest a long time — two weeks or more — when found. The caudal region is here seen to be free from the yolk; the mesoblastic somites extend to the end of the tail, and anteriorly nearly to the ear. A series of similarly appearing structures to the somites in the mesoblast are continued forward as far as the front end of the alimentary tract: they are apparently in the central nervous system, and have been described in several other forms as neuromeres. They resemble the numerous wrinkles<sup>1</sup> “which appear in that portion of the medullary canal of the chick which lies immediately behind the first cerebral vesicle.” These structures have recently acquired more importance through the labors of McClure (12). The peculiar appearance of the two pharyngeal clefts is partly due to the great transparency of certain parts of the embryo at this stage, when examined in the fresh state, and it is partly owing to the greater thickness of the epithelium lining the ventral portion of the clefts. After preservation in picric acid, or still better for external features in chromic acid, the outlines become much more distinct and clear. The first and second pharyngeal clefts at this stage are in process of formation, and their structure is given in Fig. 40. The drawing was made from a stained and mounted embryo, viewed by transmitted light. The first cleft is nearly completed and is connected by an internal groove with the rudiment of the second: this rudiment is the ventral portion of the cleft.

The clefts have increased to three with the rudiment of the fourth in the somewhat later stage of Fig. 35.

And here the fourth cleft has a similar connection with the third, which the second has to the first in Fig. 33. The embryo shown in Fig. 41 is seen when viewed by transmitted light to have three clefts formed, and in connection with the third there is an internal groove which extends backwards, and from which there appears to be forming the rudiments of the fourth and fifth clefts. The fourth and fifth are small and rudimentary,

<sup>1</sup> Foster and Balfour, *Elements of Embryology*, p. 100.

and in none of my embryos do either of them open to the exterior. It is so difficult to determine from a surface view whether a cleft is actually open to the exterior, that I have made five series of sections, upon a study of which is partly based the above statement. In all five the first cleft is open, in three the second is open, and in two the third is open.

The differences in the different specimens are due undoubtedly to the somewhat different stages of development they are in. A longitudinal, dorso-ventral section (Fig. 42) represents the five clefts; the anterior three complete, the fourth and fifth rudimentary. There exists then a groove on the inner side of the throat-wall extending from the first to the second visceral cleft, and it disappears as these clefts become complete. A similar groove extends from the second to the third, and from the third to the fourth and fifth. One may see, too, the greatly twisted form of the heart in Fig. 35, and also the nasal pits.

There is another peculiarity in the pharyngeal clefts. It is the apparent bifurcation of the dorsal end of the first, as shown in Figs. 38 and 39. The stem of the Y and the anterior arm are the true cleft, while the posterior arm is only an external groove, as is demonstrated by sections. The groove and the stem of the Y are about parallel with the remaining clefts, while the anterior arm is decidedly out of line with them. The veins for returning blood from the yolk-sac are seen entering the body immediately posterior to the heart, while the arteries to the yolk-sac leave the body much farther back. The notochord shows plainly throughout most of its length, and several neuromeres still persist anterior to the ear. The allantois has become very prominent, projecting from the posterior end of the body cavity. The rudiment of the fifth nerve has also appeared. The formation of the nasal pits is illustrated in Fig. 37. The pit is connected by a groove with the cavity of the mouth, the fronto-nasal groove. The limbs are seen developing in Figs. 43 and 44, Pl. XIII. The shape of the head is by this period very much changed, and the lower jaw is still disproportionately small. The upper jaw is noticeably hooked in Fig. 44, suggesting that of a turtle, and looking much like the upper jaw of an embryo of *Lacerta muralis* shown in Fig. 45. This latter is taken from Balfour's "Comparative Embryology," and was drawn by Professor Haddon. There is nothing peculiarly rep-

tilian as yet about the head, excepting the eyes. The wall of the body has not yet closed over the largely developed viscera, and the double tube from the body to the yolk-sac is seen in Fig. 43. This double tube, as seen in Fig. 47, proves to be portions of the intestine. They are shown in position in Fig. 46, which is of an embryo in the thirty-fifth day of incubation, measuring 53 mm. in length. This embryo, dissected, is represented in Fig. 47. Here one can trace with greatest clearness the intestine from the stomach outward to the yolk-sac; and in the same way the hind gut, starting from the rectum, proceeds outward to the same point on the yolk-sac as shown in Figs. 43 and 50. When the remnants of the yolk-sac are drawn into the body, the projecting intestine goes with it. Fig. 44 is of an older embryo than 43, and 45 and 46 are older stages than 44. The position of the head at right angles to the body still persists; it is not much longer than broad, and the mouth is scarcely larger than that of a bird at the same stage. There are, even at this late stage, only the special reptilian characters of the elongated eye and the somewhat elongated mouth, and the greater length of tail.

Figs. 48 to 51 are a series of the same egg and embryo about five weeks old. In Fig. 48 the egg-shell and membrane have been cut away, and the white of one side has been cut out up to the thickened edge, where it firmly adheres to the shell membrane. The white in the other end of the egg is in place, and also the thin pellicle of white which lies over the region of the embryo.

In Fig. 49 the shell and shell membrane, together with all the white, are cut away, showing the embryo within the amnion, lying on the yolk. The blood-vessels pass through the amnion to the vascular area of the yolk, which is clearer than the larger mottled non-vascular part.

In Fig. 50 the amnion has been cut away, and the embryo turned over to one side; this displays the arrangement of the blood-vessels, and also the two branches of the intestine, which form a long loop reaching out to the surface of the yolk. In Fig. 51 a longitudinal incision has been made in the yolk-sac, showing that the wall in the vascular area is much thinner than that in the non-vascular, and that the blood-vessels ramify for some distance in the thick walls of the latter area.

W. K. Parker has called attention to the important fact of a considerable reduction in the number of body segments that are found in the embryos of *Chelone viridis* about 15 mm. long. They have fifteen cervical, twelve dorso-lumbo-sacral, and twenty-four caudal, — fifty-one in all; while the adult has only eight cervical, a loss of seven, and twenty-one caudal, a loss of three. Thus there are fifty-one in the embryo and but forty-one in the adult. In the alligator I have found no reduction; there are thirty-five caudal and twenty-six in front of the caudal in both embryo and adult.

#### SUMMARY.

I. The eggs, to the number of about thirty, are deposited in June in large nests of dead leaves, twigs, grass, and humus, built on the ground close to a stream or pool.

II. There appears on each egg, soon after it is laid, a transverse median belt or zone of slightly different color tone from the remainder; it has a more chalk-white color than the rest. This belt increases in width with the growth of the embryo, but never extends to the ends of the egg. This change of color is mainly due to a change in the shell membrane.

III. The embryo usually lies at first toward one pole of the egg, where it has the protection of the large mass of thick white; later it moves over to a lateral position, and the chalk-white belt is developed around it. More perfect respiration is then needed, and is then readily effected in its new position. The change in the median belt of the shell membrane is apparently a drying of that part, and I suggest that it is to still farther facilitate the work of respiration.

IV. The formation of the anterior portion of the neural folds, the cephalic part, is by a median backward folding on the dorsal side, of a thickened part of the head-fold; this median fold separates at its apex, each arm uniting with the medullary fold of its respective side.

V. Tracing the intestine forward from the cloaca, it leaves the body and passes out to become attached to the yolk-sac; following the intestine backward from the stomach, it also passes out of the body, and is attached to the yolk-sac by the side of the posterior part of the intestine.

VI. The pharyngeal clefts are five in number, and the first three become open to the exterior. The anterior one appears first as an internal groove lined by thickened epithelium; this groove also extends backward and enlarges dorso-ventrally into the second cleft, and in like manner, growing backward, gives origin to the third, fourth, and rudimentary fifth. All traces of the groove between the clefts soon disappear.

The very complete series of perfectly reliable figures of the development of the bird given by Kupffer and Benecke (14) afford a most satisfactory opportunity of comparison with the reptilian type as represented by the alligator. The general appearance of the areas is at first very similar, but there is the absence of a blastopore in the bird; secondly, the primitive streak and groove are much longer in the bird; third, there is no secondary fold in the head-fold in the bird, as I have described for the alligator. As the primitive streak decreases in the bird, and the mesoblastic somites begin to form, the embryos of bird and alligator are almost indistinguishable,—the opaque and pellucid areas, the embryonic area, the head and neural folds, the primitive streak, the mesoblastic somites, and the notochord are almost identical in both.

A little later, when the mesoblastic somites have increased to ten or more, the cephalic region of the alligator becomes more opaque than that of the bird, and the entire embryo of the latter is decidedly longer in proportion to the width. The difference in length of the two embryos is just about what it was at the time of the primitive streak, when the latter area was so much longer in the birds. The close resemblance is maintained until the tail of the alligator begins to lengthen and the eyes show their elliptical outline. Even so late as the fifth week of incubation, the snout of the alligator is not much elongated, the head is still at right angles to the spinal axis, and the aspect of the whole head is much more that of a bird than a reptile. The long persistence of the general sauropsidan features is very striking.

Turning now to the other reptilian groups for comparison, one is disappointed to find that there is not a series of figures which afford a chance for careful or anything like a complete study. The best opportunity in the Lacertilia is offered by the fifteen general figures given by Strahl in his papers on *Lacerta*

*agilis*, 1882-84. Strahl's Fig. 1 (23) agrees with Fig. 12 of the alligator: the structure in the successive figures of *Lacerta* up to Fig. 7 are so similar to the corresponding stages of the alligator as to call for no special remark. In Strahl's Fig. 7, which is of the ventral surface, there is a median process just behind the head-fold, and unfortunately it is unlettered; it is similar in appearance to the thick median area on the ventral side of the head-fold in the alligator, or it might be the secondary fold on the dorsal surface of the head-fold showing through. Of Strahl's remaining figures, only 1, 2, and 3 (28) differ from the alligator. In these three there are shown very prominent wing-like sacs, one on either side of the mid-line, near the anterior end, which are described as the areas where the mesoderm has split.

There are five pharyngeal clefts in the alligator, which agrees with the number in the Lacertilia as reported by Born<sup>1</sup> for *Lacerta* and *Anguis*, by Hoffmann (10) for *Lacerta*, Van Bemelen for *Lacerta*, and Orr (16) for *Anolis sagræi*.

One finds the first four clefts open in *Anolis*; in the alligator I have never found but the first three open. Hoffmann<sup>2</sup> found only the second cleft open in one of the Ophidia, *Tropidonotus natrix*.

The connection between the first, second, and third clefts occurs also in the Lacertilia; it can be seen in Fig. 2 C., Pl. XII, of Orr's paper referred to above, which represents an embryo of *Anolis sagræi*. So far as I am aware, this connection between the pharyngeal clefts has not been mentioned before, and I do not know of any figures which show it, other than Orr's and my own.

In Orr's figure the outlines of the connection from the first to the second cleft are stronger than is the outline of the lower or ventral part of the first cleft, and the ventral line of the connecting groove is carried across the first cleft to its anterior border.

Looking to the embryology of the Chelonia, one finds the earlier stages figured by Agassiz (1) and by Mitsukuri and Ishikawa (15). Figs. 1 to 4, Pl. XI, of Agassiz I cannot harmonize with those of Mitsukuri, nor with mine of the alligator;

<sup>1</sup> Born, *Zool. Anzeiger*, Bd. VI, s. 537, 1883; and *Archiv für Mikrosk. Anat.*, Bd. XXII, s. 271, 1883.

<sup>2</sup> l.c., p. 198.

but if the part labelled "a1" in each of them be considered the posterior end of the embryo with the neural ridges developing in 3 and 4, then they all agree. It should be borne in mind that ten of the figures on this Pl. XI are monstrosities, as stated in the foot-note at page 537. One of these figures of a monstrous form is of special interest in comparison with the alligator development: it is No. 8. This dorsal view is much like Figs. 16 and 18 of the alligator, the two figures which represent the peculiar method of formation of the cephalic end of the neural tube as I have described it. This median growth of the dorsal part of the head-fold posteriorly is very clearly marked in Agassiz's figure, but it is carried much farther backward than it extends in the alligator. Such a median fold of the length there shown would be abnormal, too, for the alligator; but that there is anything abnormal in the two perfect and symmetrical embryos shown in Figs. 16 and 18 of the alligator there is no evidence for believing.

In comparison with the structure given by Mitsukuri and Ishikawa for the very early stages of *Trionyx Japonicus* there is little to be said. There is no indication of anything unusual in the method of formation of the cephalic end of the neural folds, and in so far *Trionyx* is unlike the alligator. There are no other marked differences to be discovered in the eight general figures of *Trionyx* and those of similar stages of the alligator or of *Lacerta*. The remaining figures of the turtles in Agassiz's work agree very closely with those of the alligator up to the late period when the shell and other special features of chelonian structure begin to appear.

#### METHODS.

I found it a difficult matter to remove the embryos during the earlier stages, and after many trials met with much the best success in the following way: The shell and its membrane are carefully removed from nearly half the egg in an area extending from end to end; the egg is then poured out on to the left hand, and the thick white at one end is cut off with scissors; the egg is then replaced in the shell with the germinal pole, still covered with white, uppermost; the white is now cut off from this end as completely as possible; the shell must then be placed in the corner of a deep dish where it can stand on end; a sharp-edged

lifter with moistened surface being at hand, I make two incisions with sharp-pointed scissors on opposite sides of the embryo; inserting the lifter, it is pressed upward on one side just enough to sever the lateral connections, and then the opposite side is similarly treated.

This separates a portion of the blastoderm containing the embryo, and measuring about 12 to 15 mm. on the side, from the remainder; the lifter, kept as close to the embryo as possible, so as to carry the least amount of yolk with it, is now firmly pressed upward against the opposite or distant side of the freed part of the blastoderm and gently but steadily drawn towards one: if all goes well, the embryo comes out in beautiful shape without even a wrinkle. Of course it sometimes fails, and it always requires the greatest care, patience, and steadiness. The embryo is placed on a slide and treated with Kleinenberg's picric for sections, or chromic preferably for surface study. I have found the embryos very difficult to stain, and after a long immersion in cochineal, alum, or borax carmine, I find it necessary to put them in alcoholic carmine to insure staining of the innermost parts.

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EXPLANATION OF PLATES.

REFERENCE LETTERS.

<i>a. l.</i>	Anterior limb.	<i>m.</i>	Mouth.
<i>all.</i>	Allantois.	<i>m. s.</i>	Mesoblastic somites.
<i>am.</i>	Amnion.	<i>mt.</i>	Mottled area.
<i>a. o.</i>	Area opaca.	<i>n. 5</i>	Fifth nerve.
<i>a. p.</i>	Area pellucida.	<i>ne.</i>	Neuromeres.
<i>a. t.</i>	Alimentary tract.	<i>n. f.</i>	Neural fold.
<i>aur.</i>	Auricle.	<i>n. g.</i>	Neural groove.
<i>a. y.</i>	Arteries to yolk-sac.	<i>nt.</i>	Notochord.
<i>b.</i>	Blister or place where germinal layers have separated.	<i>n. v. y.</i>	Non-vascular area of yolk.
<i>b. a.</i>	Bulbus arteriosus.	<i>v.</i>	Cesophagus.
<i>blp.</i>	Blastopore.	<i>ol.</i>	Olfactory.
<i>blt.</i>	Blastoderm.	<i>p. c. 1, 2, 3, 4, 5.</i>	Pharyngeal clefts.
<i>b. u.</i>	Region where body wall is still unclosed.	<i>p. l.</i>	Posterior limb.
<i>b. v.</i>	Blood-vessels.	<i>p. s.</i>	Primitive streak.
<i>b. w.</i>	Body wall.	<i>s. m.</i>	Shell membrane.
<i>ch.</i>	Chalk-white zone.	<i>sto.</i>	Stomach.
<i>du.</i>	Duodenum.	<i>s. f.</i>	Secondary or cephalic fold in head-fold.
<i>e. b. w.</i>	Edge of body wall.	<i>tr.</i>	Trachea.
<i>em.</i>	Embryo.	<i>t. h. f.</i>	Thickening of head-fold on median ventral line.
<i>em. s.</i>	Embryonic shield.	<i>ven.</i>	Ventricle.
<i>h. f.</i>	Head-fold.	<i>v. y.</i>	Vascular area of yolk.
<i>h. g.</i>	Hind gut.	<i>v. y. s.</i>	Veins from yolk-sac.
<i>ht.</i>	Heart.	<i>w.</i>	White or albumen of egg.
<i>i. y. s.</i>	Intestine to yolk-sac.	<i>w. l.</i>	White line bounding mottled area.
<i>l. j.</i>	Lower jaw.	<i>yk.</i>	Yolk.
<i>lu.</i>	Lung.		

## EXPLANATION OF PLATE IX.

(Figures 5 to 11, inclusive, are by Mr. C. C. Hayes; Figs. 6 and 7, by Mr. J. H. Emerton; and 1 and 2 are mine. All the figures are life size.)

FIG. 1. The lines represent the growth of the chalk-white median zone in the shell membrane at an early period of incubation. The shell had been removed; and the median enclosed area in the figure shows the beginning of the zone, not as yet extending around the egg. Lines 2 indicate the outline as it appeared sixteen minutes later, and lines 3 at thirty-seven minutes later than lines 2. The growth under natural conditions is much slower.

FIG. 2. The outlines of five eggs, the smallest two being unusually small.

FIG. 3. Egg of a Florida crocodile, *Crocodylus Americanus*, Seba.

FIG. 4. Egg of American alligator, *Alligator Mississippiensis*, Daudin.

FIG. 5. Egg with part of shell removed, showing chalk-white zone in late period of incubation.

FIG. 6. Here the shell and its membrane have been partly broken away, and the yolk taken out. This leaves the white hanging, as shown, bringing out clearly the lines of attachment of the white, at the edges of the median white zone, and also the heavy consistency of the white.

FIG. 7. An opened egg, with the blastoderm on the side.

FIG. 8. Egg opened from the end, displaying germ in mottled area, bounded by a white line.

FIG. 9. Showing the mottled area passing over to lateral surface of yolk.

FIG. 10. A much more advanced stage, the embryo on the side of the yolk, and lying almost transversely in the egg.

FIG. 11. The embryo here lies in the direction of the long axis.











## EXPLANATION OF PLATE X.

(All the figures are mine.)

- FIG. 12. Blastoderm of an egg taken out of an alligator from the dorsal surface.  
FIG. 13. View of another embryo, at the same stage, from the ventral surface.  
FIG. 14. A slightly older embryo, in dorsal view.  
FIG. 15. A ventral view of the embryo shown in Fig. 14.  
FIG. 16. A dorsal view, somewhat more advanced than Fig. 15. It shows the peculiar fold in the head, by which the cephalic end of the neural folds is made.  
FIG. 17. A ventral view of the head end of the embryo shown in the last figure.  
FIG. 18. An embryo from the dorsal side in nearly the same stage as the last embryo, a little older.  
FIG. 19. The same embryo as in Fig. 18, from the ventral surface.  
FIG. 20. This is a dorsal view after the secondary median fold at the anterior end is broken through. Compare Figs. 16 and 18 with this.





12.



*Dorsal*

15.



*Ventral*

17.



*Dorsal*

14.



*Dorsal*

15.



*Dorsal*

17.



*Vent*

*Ventral*

18.



*Dorsal*

20.



*Dorsal*

14.



*Ventral*





## EXPLANATION OF PLATE XI.

(Figures 21 to 26, inclusive, are mine. Figures 27 and 28 are from life, and by Mr. C. C. Hayes.)

- FIG. 21. Ventral side.
- FIG. 22. Dorsal side of the same embryo.
- FIG. 23. From the dorsal surface.
- FIG. 24. Ventral view of the embryo shown in Fig. 23.
- FIG. 25. The ventral surface.
- FIG. 26. The same embryo from the dorsal side.
- FIG. 27. A drawing, made from life, of the dorsal surface of an embryo.
- FIG. 28. The same embryo from the ventral side.





14

15

16

17



*Abp. ps.*

*Dorsal*

*Dorsal*

*Dorsal*

18

19

20

21



*Ventral*

*Dorsal*

*Dorsal*

*Ventral*





## EXPLANATION OF PLATE XII.

(Figures 32, 34, and 38 are from life, and were made by Mr. C. C. Hayes. The others are from preserved specimens, and are my own.)

FIG. 29. From the ventral surface.

FIG. 30. The same embryo from the dorsal side.

FIG. 31. A ventral view.

FIG. 32. A lateral and ventral view from a living specimen. The embryo is now partly turned upon its side.

FIG. 33. A little later than 32. The pharyngeal clefts are forming; also the eye and ear.

FIG. 34. This is from life, and shows especially well the neuromeres. The first and second pharyngeal clefts are developing.

FIG. 35. This shows the connection of the fourth with the third cleft; the olfactory pit is forming; several neuromeres still persist in the hind-brain; the heart is folding upon itself.

FIG. 36. The formation of the mouth region is seen here and the pharyngeal arches and clefts.

FIG. 37. The embryo is turned partly on its side, showing the nasal groove reaching to the mouth, and the outlines of the mouth; also the rudiment of the anterior limb.

FIG. 38. From life. This is not so advanced an embryo as that represented by Fig. 37, the limbs having not yet appeared. The first cleft is seen to be bifurcated dorsally; the rudiment of the fifth nerve has appeared; the allantois has become prominent; also the arteries and veins of the yolk-sac.

FIG. 39. Another embryo, showing also the bifurcated first cleft.

FIG. 40. The mode of formation of the first and second pharyngeal clefts is here shown. The drawing is made from a mounted specimen by transmitted light.

FIG. 41. Here the first three clefts are formed, and the fourth and fifth are connected with the third.

FIG. 42. A latero-longitudinal section, showing the five pharyngeal clefts.











## EXPLANATION OF PLATE XIII.

(Figures 47, 48, 49, and 50 are by Mr. S. F. Denton; the others, except 45, are my own. Figure 45 is an outline of Figure 130, Balfour's "Comparative Embryology," drawn by Professor Haddon.)

FIG. 43. The especial points in this figure are the large head, with the small lower jaw, the shape of the limbs, the elongated tail, prominent allantois, and the double attachment of the intestine to the yolk-sac.

FIG. 44. The lower jaw is still small; the upper is slightly hooked, suggesting that of a turtle, and the extremities of the limbs are changing.

FIG. 45. *Lacerta muralis*, after Haddon.

FIG. 46. An embryo about thirty-five days old. The lower jaw now equals the upper in length; the ear is formed; the digits also; the body cavity is still widely open, nearly from the pectoral to the pelvic girdle; the two portions of the intestine to the yolk-sac are shown cut off; the head is yet at right angles to the body.

FIG. 47. This is a dissection of the embryo shown in Fig. 46. It is to show the arrangement of the intestine and its connection with the yolk-sac. The two parts of the intestine have been turned to opposite sides for clearness. They lie side by side.

FIG. 48. The shell and shell membrane have been removed from one side, displaying the yolk, the embryo within the amnion, and the white at one end. At the end, to the left, the white is untouched, and it also stretches as a thin pellicle across the embryo. The heavy white ridges at either end of the embryo are the lines, along which the white closely adheres to the shell membrane. Life size.

FIG. 49. An embryo of the same age, removed from the shell. This shows more clearly the amnion, the vascular, and the non-vascular areas of the yolk. This embryo lies transversely, that of Fig. 48 longitudinally, in the egg. Life size.

FIG. 50. The same embryo as in the last figure, with the amnion cut away; the embryo turned to one side to show the vascular area of the yolk, and the two portions of the intestine that are attached to the yolk-sac. Life size.

FIG. 51. The same specimen, with a longitudinal incision through the thin-walled vascular area. The remainder of the yolk has a much thicker wall.





25



26



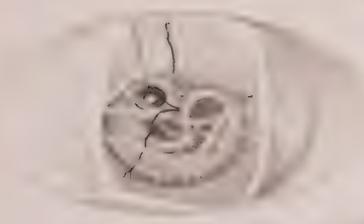
27



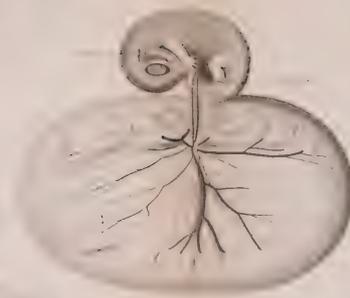
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31



32





# THE EMBRYOLOGY OF THE AMERICAN LOBSTER.

HERMON CAREY BUMPUS.

THE observations embodied in the following paper were made at intervals during the years 1889 and 1890, at the Marine Biological Laboratory, Wood's Holl, and at Clark University, Worcester, Mass.

I would express my gratitude for the many helpful suggestions and valuable assistance that the director of the Laboratories of both institutions, Dr. C. O. Whitman, has most freely offered.

At the Marine Laboratory unlimited facilities have been offered for collecting and preparing material, while the new outfit for morphological work at Clark University has proved as valuable as it is complete.

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The American lobster (*Homarus americanus*, Milne-Edwards) inhabits the Atlantic coast of North America from Labrador to Delaware, extending its bathymetrical range from low-tide mark to a depth of from fifty to eighty fathoms.

Years ago excessively abundant and not infrequently reaching a weight of twenty pounds, the inordinate demands of the market have not only rendered the animals much less abundant, but have also reduced them in size, the greater number of lobsters now caught averaging less than two pounds in weight. It was partly with the idea of intelligently coping with this serious destruction that the following observations were undertaken.

## BREEDING.

Data taken from a large number of individuals show that the females do not ordinarily bear eggs (externally) until they have reached a length of 25 cm., though it is an interesting fact that many females are impregnated at an earlier date, when

they have a length of but 20 cm., and when, I have every reason to suppose, they cannot deposit eggs until a year if not two years later.

Though the modified abdominal appendages of the male lobster have often been described, and the spermatophores of Decapods were discovered by Kölliker, and again described by Grobben ('78), the receptive apparatus of the female has, I believe, thus far escaped detection. This organ lies at the posterior end of the sternum of the female lobster, resting between the bases of the IV and V pairs of thoracic appendages. It is a highly colored, heart-shaped body, represented on Pl. XVIII, Fig. 1. On the same plate, Fig. 2, a side view is given. The openings of the oviducts (*ov. or.*) lie anteriorly, while a keel-like piece (*K*) stands as a wedge between the laterally and posteriorly directed wings (*W*). If the wings are forcibly depressed, a whitish substance is seen to ooze from between them and the keel at *Sp Or.* of Figs. 1 and 2. The microscope proves this to be the spermatic fluid. Reference to Fig. 2, which represents a longitudinal section through this region, will reveal the presence of a capsule lying inside the wings of the receptive apparatus and indicated by *Sp C*. It is mostly filled with a gelatinous cement-like substance which is quite transparent. Posteriorly, however, a whitish portion (*Sp P.*) made up of male cells, — is more fluid, and may leave the capsule through the openings already referred to. Until the male lobster has been actually observed in the act of charging this capsule, there will be some question as to the way in which he manoeuvres. Actual copulation, however, has been observed in the cray-fish, and the structure of the first abdominal appendages of the male lobster are so nicely adapted to opening the receptive orifices of the female, that there seems little reason for doubting that the ventral surfaces are applied to each other during copulation.

The spermatophores of the male may be artificially pressed from the *vasa deferentia*, and if floated in sea-water assume a characteristic shape. Gruber ('79) has shown that the spermatophores of Copepods become much more concentrated when finally within the receptive capsules of the female, and the same is true of *Homarus*.

Contrary to the inductions made by Paul Mayer in his valuable paper on the development of *Eupagurus* ('77), it seems to

me probable that the eggs of *Homarus* are fertilized as they leave the oviducts and enter the sea-water.

Several attempts to find possible canals leading from the receptive apparatus to the ovary have invariably failed, as might be expected. How the spermatozoa can leave the capsules and, at the wish of the female, enter the oviducts by way of the sea-water, is certainly not clear. We have, moreover, according to the report of Spence Bate ('80), the established fact that, at the time of oviposition in the cray-fish, spermatozoa are abundantly found mixed with the eggs; copulation having occurred some time, ten to forty-five days, previously. The presence of polar globules in the external eggs of *Homarus* would also argue in favor of external fertilization.

Data collected during the past summer go to show that the female lobster, as already noted, is charged with spermatozoa from a time long before sexual maturity, a year if not two years before the eggs are actually deposited; and from that time on, even while carrying fresh eggs or those about to hatch, she invariably has stored away in her capsule a certain quantity of male cells. Whether her supply is regularly and periodically increased, or whether she is impregnated once for all, I am unable to decide.

#### OVIPOSITION AND INCUBATION.

It is a peculiar fact that, though the lobster has been for centuries a staple article of the markets, its time of egg-laying and its period of incubation have not been definitely known. That more light might be thrown on these points, I have carried on quite an extended series of observations, the result of which I subjoin:—

The eggs are *normally* deposited during the months of July and August, and develop rapidly so long as the water is relatively warm. If the water remains unusually warm during the fall, certain precocious eggs, as, for example, those mentioned by Rathbun ('86), may possibly hatch. Such, however, is not the rule, for I have taken lobsters in October with eggs far advanced, and have exposed them to the wash of the sea from the time of capture through the winter, and even until spring, the eggs in the meantime not hatching and showing but very little advance in development. Large numbers of eggs col-

lected during the winter months, both from the colder waters of Nahant as well as from the warmer waters of Wood's Holl, were almost invariably in the same advanced stage of development — the eyes large and bright, the appendages well outlined, and the yolk occupying but a fraction, perhaps one-third, of the surface exposure.

I was not surprised, therefore, on continuing work at the United States Fish Commission Laboratory at Wood's Holl, early in May, 1890, to find that of hundreds of lobsters then "in berry," not a single one had eggs in early stages of development. Millions of eggs were kept alive in "Chester" and "McDonald" jars, but not an egg hatched until May 14, when the water had reached a temperature of 52° F. From then until the water reached a temperature of 70° the young actually swarmed in the hatchery.

The hatching period extends, then, from the middle of May to the middle of July, after which time only a few mature eggs are to be found.

The eggs are normally carried by the female from nine to ten months.

While the work of hatching was in progress it occurred to me that artificially raising the temperature of the water might yield interesting results, and certain experiments convinced me that the eggs might be taken from the female at any time during the winter or spring months, and after a few days of "artificial incubation" hatch and give rise to perfectly healthy young.

The above suggests a possible(?) solution of the problem of successfully rearing the young. For if the artificially hatched larvæ were again placed in the colder water of the ocean, they would certainly escape the attacks of many summer enemies. That the change from warmer to colder water would not prove *immediately* fatal is demonstrated by the fact that a prolonged immersion in water at 33° F. produced no visible harm to the young lobsters.

Though thousands of female lobsters were examined during the month of June, not a single fresh-laid egg could be found. It was not until July that they made their appearance, and not until the latter part of that month that they were at all abundant.

Whether the female lobsters which have just hatched their

eggs are, the same season, again afflicted with a second brood, is still questionable. The appearance of the ovaries of "egg-bearers" suggests that at times this may be the case, while the occurrence, during the winter, of many females without eggs would lead to the belief that eggs are carried only in alternate years. The time and the frequency of molting may also enter as factors in the question.

In the spring of 1890 I marked 264 small lobsters, all under 25 cm. in length, and all bearing external eggs containing almost mature embryos.<sup>1</sup> These mutilated individuals were planted on an isolated rock in Buzzard's Bay. In a communication received from Mr. Vinal N. Edwards, of the United States Fish Commission, bearing date November 13, 1890, long after the time of oviposition, I learn that four of these lobsters have been again captured, but in no case did they bear eggs.

#### THE OVARY.

The ovary of the lobster is a paired structure, of varying size and color. It extends, in the adult, from the most anterior part of the cephalo-thoracic cavity to the third abdominal ring. Above, it is covered by the heart and by certain muscles. Below, it rests on the voluminous "liver" and on the alimentary tract. While the two halves of the ovary diverge anteriorly, almost enclosing the "crop," posteriorly they run parallel to each other, though quite separate. Immediately back of the "crop," a transverse portion connects the right half with the left, though this portion, so considerable in *Astacus*, is relatively small, having a lesser diameter than the longitudinal portions.

On either side, and immediately under the heart, the oviducts are seen leading outwards and downwards to their openings at the base of the third pair of thoracic feet (Pl. XVIII, Figs. 1 and 2).

Besides the gradual increase in size that results from the normal growth of the animal, — the ovaries reaching the condition of sexual maturity when the lobster measures about 25 cm., — there is a periodic increase in size as the breeding season approaches. Immediately after oviposition the walls of the ovary

<sup>1</sup> The lobsters were marked by excision of the left eye and the removal of the terminal section of the left tail-flap.

collapse, though they may be brought back, artificially, to their full size by injecting from without into the oviduct.

The immature ovary is not only small in size, but lacks the pigment of the adult, being almost colorless. Later it becomes bright yellow, and still later minute dots of green appear in its substance. The green finally predominates, and in the fully mature ovary deep green is the prevailing color, though dots of yellow, possibly the same as those found by Lereboullet ('62) in *Astacus*, are to be seen.

After the extrusion of the eggs the ovary loses its color in the main, though here and there dark spots may be seen which on investigation prove to be eggs which were not extruded with their fellows.

So indicative of the condition of the eggs is the color of the ovary that I have been able to predict with certainty the condition of the ovarian eggs, without opening the female, by simply looking down through the transparent tissues between the posterior end of the carapax and the tergum of the first abdominal segment.

As compared with the ovaries of *Atyephira* described by Ishikawa ('85), the genital organ of *Homarus* is much more elongated and the eggs relatively smaller, — points of difference which might be made equally well for *Astacus* as described by Rathke ('29) and Huxley ('80). A further difference between the ovary of *Homarus* and that of *Atyephira* is to be found in the "germogen," which in the former Decapod is not distinguishable externally from the "vitellogen." In this respect *Homarus* resembles *Eupagurus*.

The ovary of the young female throws light on the more complex structure of the adult. It is shown in cross-section, Pl. XVI, Fig. 12. Enclosing the whole ovary is a dense but transparent layer of muscle and connective tissue which includes certain openings, the blood-sinuses. At about equal distances from each other these sinuses dip deeply into the substance of the ovary, and send ramifying prolongations between the developing egg-cells (Fig. 10, *b.s.*). The sinuses and prolongations are invariably limited at their peripheries, and all contain blood-cells. A glance at Fig. 12 shows that the older egg-cells occupy the outer portion of the ovary, while the younger occupy the central portion. The germogenal portion is

then within, while the outer portion of the ovary represents the vitellogen, as described by Herrick ('86). The figure, moreover, shows that the present is a secondary condition. The inner blood-sinuses represent localities of invagination, and sections show that they occur at varying points throughout the entire ovary.

Instead, then, of having a single germogenal line, as has been described in many Decapods, there are as many germogens as there are deep invaginations.

If one of the blood-sinuses is examined in detail, the lining membrane (Pl. XVI, Fig. 10) will be found to be, in the main, structureless and to contain varying numbers of blood-cells (Fig. 10, *Cor.*). At its deepest portion the membrane frequently presents a pitted appearance, which under a high power seems to be due to the presence of a single series of appressed cells (Fig. 10, *pt.*). Connective tissue fibres stretch from the lining membrane into the substance of the ovary between and surrounding the younger developing egg-cells at the centre, but losing their prominence as they approach the periphery.

Around the more mature eggs of the periphery a distinct layer of cells, the follicular epithelium (Pl. XVI, Fig. 10, *fe.*), presents itself, and as we pass from the periphery towards the centre these cells become less numerous and less columnar, and finally, at the very centre are not distinguishable from the cells that are finally to develop into eggs.

The primitive egg-cells are arranged in bunches around the distal ends of the sinus invaginations (Pl. XVI, Fig. 10). They are more or less irregular in shape, but betray their point of attachment by the direction of their major axes. A distinct cell-wall is not present, and frequently two or more cells seem to be in a process of fusion.

On following the lining membrane of the blood-sinus to the outside of the ovary, it is found to lead into lacunæ of the muscular layer, which, in turn, probably communicate with blood-vessels.

Passing now to the more mature ovary, the outer muscular covering is found to be much thicker, though in life quite transparent, and to exhibit the large, ripe eggs below as a surface of polygonal areas of varying shades of green. The younger eggs are crowded from the surface, to find their positions below

and between the older. If the walls of an ovary at this stage are cut with a pair of scissors, the egg-cells, old and young, ooze from the opening, though held together by the connective and epithelial tissue of the interior of the organ. The mature cells present the appearance of a bunch of grapes, while the young appear as small white patches.

If the ovary, slit open, is allowed to remain for a few hours in weak acid, additional features are brought out. The mature egg-cells become bright red, while the young cells assume an opaque white color. The distal portion of the mature eggs, however, is lighter in shade, and perhaps contains more protoplasm than the smaller, tapering, proximal ends where the enveloping tissue acts as a stem or peduncle.

If the enveloping tissue, the follicular membrane, is carefully ruptured by the use of needles, the enclosed egg will drop out. This egg is surrounded by a definite structureless membrane which in places, in prepared specimens, will be found to stand off in blisters from the enclosed yolk, and after brief maceration in water will swell up to twice its normal size, leaving the yolk, within, a naked ball.

Eggs having the above-described membrane, which, with Ishikawa, I may call the "primary egg membrane," were sometimes found lying free in the ovaries of the females that had recently deposited their eggs.

Such mature eggs as have been dropped from their follicles into the lumen of the ovary, before extrusion, are more or less irregular from mutual pressure, and cling together in masses, not, evidently, from the presence of any specially sticky fluid, but rather from a natural cohesion.

While the eggs are passing through the oviduct, they are probably covered with a varnish-like coat secreted by the elongated cells of the columnar epithelium. This coat adheres to the primary membrane, renders it more impervious to water, and also forms the funiculus by which the eggs are attached to the hairs of the lower side of the abdomen and swimmerets.

Let us now examine a section of a more mature ovary, a figure of a portion of which is shown in Pl. XVI, Fig. 11. It is drawn on the same scale as the much younger Fig. 12. The organ has a diameter of nearly ten times that of the young ovary described above. The enveloping walls are much thicker, and

clearly show the interlacing bands of muscle fibre. The greatly enlarged egg-cells have crowded the smaller into the interstices, and many have been driven from periphery to centre by the growth of their fellows. The cells of the follicular epithelium are seen in cross-section (Fig. 11) as nucleated bands of tissue enclosing the egg-cells. In places where the knife has cut tangentially across these bands, a higher power shows innumerable pavement epithelial cells and traces of connective tissue and blood-cells. The thick-walled blood-sinuses of the early ovary are no longer prominent, and the primitively radiate structure has become entirely obliterated.

Immediately after oviposition the ovary presents a torn and tattered condition. The shreds of connective tissue and follicular epithelium extend out into the lumen of the organ, giving cross-sections a spongy appearance very different from that presented at other times. The eggs to be next deposited are opaque white in color, and do not acquire the green shade until two or three weeks after oviposition.

#### THE OVARIAN EGG.

The ovary of a small female lobster presents the youngest ovarian eggs. These are in groups and clusters not clearly defined (Pl. XVI, Fig. 10, *E-c*<sup>1</sup>). The elongated and more or less homogeneous nucleus occupies nearly the entire cell. In sections a plasmodium-like appearance is often presented, and cases of apparent fusion of cells, as already stated, are not infrequent. The egg-cells are at this time indistinguishable from the cells which may ultimately form follicular epithelium. Small particles of chromatin, or at least particles that absorb the stain, are often scattered over and around the nuclei and between the cells.

Associated with the above-described elements are cells slightly older, which have taken on structures that foreshadow their ultimate condition. The nucleus is more clearly defined, it is distinctly granular, and a surrounding layer of homogeneous protoplasm is evident. Such a cell is figured on Pl. XVI, Fig. 10, *E-c*<sup>2</sup>. As the earlier cells may fuse, so these are at times found flowing together. A slightly older egg-cell is found at *E-c*<sup>3</sup>. The layer of protoplasm has become deeper, but the

most characteristic feature is the presence of a nucleolus, though granules are still present and continue to exist for some time. Cases of possible fusion are not difficult to find.

When the egg-cells have reached the condition shown in Fig. 10,  $E-c^4$ , the nucleus has become most prominent. Its contents is seen to consist of a clear fluid in which is extended a reticulum, holding in suspension one, or at times several, deeply stained, spherical nucleoli. In this respect the early egg-cells of *Homarus* resemble those of *Astacus*, but differ from those of *Eupagurus*, since Mayer ('77) claims for the latter a single nucleolus in all stages. In *Homarus* when there is but a single nucleolus this is relatively larger than when several are clustered in the same nucleus. The cytoplasm is fine-grained, with scattered dots of pigment, and is slightly different in color immediately around the nucleus, fading away like a halo towards the periphery.

When the egg-cells have reached the size of  $E-c^5$ , the halo-like layer of protoplasm around the nucleus is still more prominent, and in specimens stained with lithium picro-carmin an interesting structure is exhibited: the peripheral portion of the egg is found to abound in minute vesicles of varying size and of two kinds, fat and plasmic. The fat vesicles, which are present in many crustacean ova, are abundantly distributed throughout the more peripheral portion of the egg-cell, but take on no color. The plasmic vesicles are, in the present case, almost equally abundant, but differ from the first in selecting, to a limited extent, the color of the stain. The plasmic vesicles are oval, spherical, and at times multipolar. They may be homologous with the "transparent vesicles" of Lereboullet ('62), and in many respects answer to the description of the "yolk-cells" of *Agelena* as described by Balfour ('80); though in the latter case they were not considered in stages earlier than the blastula. Ishikawa ('85) has described very similar bodies as occurring in the "yolk segments" of *Atycephira*, though appearing *later*, during the segmentation stages. It is his opinion that they arise from the segmentation nuclei. The "secondary mesoderm" of Reichenbach ('86), and the "spores" described by Herrick ('86) as occurring in *Alpheus*, are probably related to the structures under discussion.

Though the nucleus [primordial vesicle],  $E-c^5$ , is consid-

erably larger than that of the immediately preceding stage, it has not otherwise materially changed, save that it ordinarily contains only one nucleolus. The nucleolus, moreover, is thick walled, appearing in section as a deeply stained ring, with its centre often relatively free from chromophilous substance. In the section Fig. 11, it is interesting to note that the nucleoli occupy an eccentric position, each being confined to the left half of its respective nucleus.

When the egg-cells are about one-half grown, as on Pl. XVI, Fig. 11, the protoplasmic halo becomes still more prominent, and, in some cases, minute particles of pigment are found immediately surrounding the nucleus, the signification of which I will not attempt to give. The nucleus has several times the volume of that of the preceding stage. The outer portion of the cell has become densely filled with fat and plasma vacuoles, or vesicles, which may be more clearly seen in the considerably enlarged drawing, Fig. 7, *Ft.vs* and *P.vs*. The fat vacuoles are of varying size. At the right, a smaller one will be seen in the act of emptying itself, probably the result of the action of hardening reagents. The plasma vacuoles now show nuclei, though not in all cases; and in larger vacuoles, nucleoli are to be found. We have then *cellular* (?) bodies within the so-called egg-cell, though the "plasma cells" do not take up stain so intensely as do the cells of the follicular epithelium. Two nuclei of the latter cells are to be seen at *fe*.

At the present stage in the development of the egg-cell, the primary egg membrane may be distinguished. At *pe-m*, Fig. 11, it is seen to enclose a fat vesicle or globule that is leaving the egg.

As growth continues, the perinuclear halo—in early stages never a network as it is in *Eupagurus*—leaves its primary position, and, working through the yolk, increases its extent, while approaching the periphery of the egg.

A very marked change now comes over the yolk. Heretofore made up of more or less homogeneous masses of varying size, it now becomes broken up into small spheres which are not visibly bound together. As in younger eggs, the fat vacuoles abound; but the plasma vacuoles have become altered. The latter are represented by interstitially lying chromatin bodies, probably suspended in a network of protoplasm and confined to

the outer portion of the egg-cell. The yolk spheres lying immediately under the vitelline membrane are considerably smaller than those lying deeper. They are embedded in a clear substance, which is soon found to form a distinct peripheral covering.

#### THE MATURE OVARIAN EGG.

As has been already noted, eggs which I consider to be mature were found lying free in the ripened ovary. These, though only enclosed by the primary egg-membrane, closely resembled young external eggs; and many, when viewed with a low-power lens, show most clearly that they are made up of two unequal or subequal masses. The smaller of these often appears as a cap, separated from the larger by a distinct groove (Pl. XIV, Fig. A). In certain eggs, however, the smaller portion seems to be submerged in the larger, which almost encloses it. This double structure may occasionally be found in eggs that have been but a short time extruded. Such eggs do not develop as do their fellows. I conclude that outside the ovary the retention of the double structure is abnormal.

A second feature of the adult ovarian egg, and one that may also be observed in eggs immediately after oviposition, is the gathering of a clearer layer, quite devoid of yolk matter, at one pole, as shown on Pl. XIV, Fig. B. No definite relation in position, or otherwise, seems to be borne by this clear layer to the accessory cap-shaped portion described above. Several eggs which I have examined show the two at varying positions, sometimes associated, sometimes quite apart.

A cross-section of an egg at this stage is given on Pl. XVI, Fig. 1. The nucleus, not materially changed, is seen to occupy a central position. Nor is the perinuclear halo materially different from that shown in Fig. 11. The yolk is finely granular, that of the accessory yolk-bearing portion being not essentially different from the rest, though a central mass of protoplasm is to be seen in certain examples. The line of demarcation, moreover, between the larger and smaller portions is clearly shown. My conclusion is that we have here simply a case of fusion of two egg-cells.

A reference to the above-mentioned figure will show the presence of chromatin granules, elements of the plasma vacuoles.

They are most abundant around the periphery, and when viewed under a high power (Pl. XVI, Fig. 8) are found to be embodied in amœboid masses of protoplasm.

The clear layer already noted is in section found to form a lenticular mass (Fig. 1, *l.m.*), which, by the use of high powers, may be resolved into fine grains. Its edges are seen to pass into the peripheral layer of the remainder of the egg. The delicate primary egg membrane encloses the whole.

Before considering the egg after extrusion, it may be well to compare further the ovarian egg of *Homarus* with that of related crustacea:—

Waldeyer ('70), describing the ovary of *Astacus*, speaks in a general way of the epithelial origin of the egg, a view that is now most universally adopted. He also calls attention to the follicles; to the "vitelline membrane"; to the clear, fine-grained perivitelline layer; to the increase in size of the yolk spheres towards the centre; to the large germinal vesicle, and to the germinal spot.

The origin of the egg of *Atyephira* from indifferent ovarian cells is almost precisely like that of *Homarus*; and Ishikawa ('85) also describes the presence of more than one germinal spot in the youngest egg-cells, and the presence of vacuoles—which, however, are larger, and appear earlier, than in *Homarus*. As regards structure and relative size, the germinal vesicles of *Atyephira*, *Eupagurus*, and *Homarus* are almost identical, as is also the final excess of yolk matter over protoplasmic.

The radiating strands of protoplasm described by Mayer, though absent in the younger egg-cells, are present at ovarian maturity.

There is nothing to show that the yolk does not originate endogenously.

Though in *Atyephira* and *Eupagurus* the primordial vesicle is said to disappear while the eggs are still within the ovary, leaving the egg a "cytode," I have examined many eggs lying free in the ovary, and have not yet found a single one without a nucleus. The earliest external eggs that I have been able to find, though invariably nucleated, have the much smaller nuclei of segmentation. Absolutely fresh eggs I have been unable to secure; for a lobster in the act of ovipositing has yet to be found.

## THE EGG SOON AFTER OVIPOSITION.

Though many efforts were made to secure absolutely fresh-laid eggs, I succeeded in finding nothing earlier than what is represented on Pl. XIV, Fig. B. The female bearing these eggs was captured on the morning of July 22, 1890, off the island of Cuttyhunk. The eggs were very dark in color, closely packed together, and were much more irregular in shape than when examined a few days later, many being almost triangular in outline.

When examined under a lens, the yolk was found to be flattened upon one side, in some cases becoming even concave. A clear fluid was collected at this region, possibly the same as that described for the ovarian egg.

Relatively small vesicles, the polar globules, are seen at *R-k*. They are present in many eggs, and appear to be attached at no special point of the vitellus, so far as the flattened area is concerned; being sometimes within it, and sometimes without. It may be, however, that I have only seen them in secondary positions; for in some cases they seemed to move freely about within the egg membrane. They were not observed in process of formation, nor were they invariably present. Before the blastula is formed, they disappear.

Attention has already been called to the secretion of the columnar cells of the oviduct, which in *Homarus* forms a varnish-like layer immediately over the primary egg-membrane, becoming inseparably united with it. It may be that a similar secretion on the part of the female of *Eupagurus* produces the change in the texture of the egg-membrane which Mayer ('77) has described for that form. It certainly renders the primary covering much more impervious to water and to reagents, besides making it very much tougher.

The primary egg-membrane with its outer coating I shall call by the indifferent term, *capsule*. Though a delicate layer of protoplasm covers the egg within the capsule, no distinct investing membrane comparable with a true vitelline membrane can be said to exist.

In *Atyephira* a "secondary membrane" is formed by the cells of the oviduct in much the same way as is probable in *Homarus*, but later on in the former the two become separated and a fluid

gathers between them. I have observed much the same in *Libinia*. In *Crangon* a vitelline membrane is not present.

Rathke ('36) claimed that the egg of *Astacus* had a "vitelline membrane" separated from the "chorion" by a fluid, and Dohrn claimed the same for the egg of *Palimurus*. Mayer ('77) has called attention to the fact, however, that both Rathke and Dohrn may have been considering a "Blastodermhaut," which latter certainly does occur in *Homarus*, but at a little later stage.

#### CLEAVAGE STAGES.

Sections were made through eggs similar to those just described. They show that up to the so-called "eight-cell stage" the nuclei exert no apparent influence on the external portion of the yolk-laden egg, there being no early cleavage stages, so far as the entire egg is concerned.

The earliest stage which I have found represents an egg with two nuclei. Fortunately the knife passed through both of these, as shown on Pl. XIX, Fig. 2.

The nuclei, as would be expected, are individually very much smaller than was the mature primordial vesicle and relatively minute when compared with the egg of *Crangon*, Kingsley ('87). Each is surrounded by a clearly radiate mass of protoplasm, the rays extruding out between the yolk masses. Oil vacuoles are abundantly found, except in the immediate neighborhood of the nuclei, where the investing protoplasm is quite homogeneous. The peripheral portion of the egg is still granular, as was the later ovarian egg, the yolk spheres being more closely juxtaposed as the centre of the egg is approached. Though a delicate layer of protoplasm invests the egg, no distinct membrane, other than the "capsule," can be demonstrated. The plasma cells are still represented by chromatin grains, extremely minute, which are abundantly found in favorable preparations scattered in the interstices between the yolk spheres. They are no longer confined to the periphery, however, but have advanced towards the centre and formed an indefinite ring, as figured on Pl. XIX, Fig. 2. The ring marks the dividing line between the peripheral granular yolk and the central less granular portion.

Sections made through eggs of the next following day show

that active division of the nuclei has been going on, and karyokinetic figures are not uncommon. Not only have the nuclei divided, but they have also approached the periphery and more rapidly towards the flattened, the animal pole, than towards the convex, vegetative pole.

The division of the several nuclei is not contemporaneous, odd numbers of nuclei resulting, but when division has taken place *about* three times, from eight to twelve nuclei occupying the egg, the animal pole begins to show some effects of the disturbances going on below. Elevations and furrows appear which are shown in Pl. XIV, Fig. C, and somewhat schematically on Pl. XVI, Fig. 9, which represents a very thick transverse section. The furrows are for the most part shallow and not present on the opposite, vegetative, side of the egg.

A meniscoid layer of fluid still extends over that portion of the egg that is now seen to be the animal pole, though the further stages of segmentation seem to bring about its obliteration.

Comparing these furrows with those observed in *Atyephira*, I have not seen a rhythmic appearance and disappearance as described by Ishikawa. Much variety is exhibited in the arrangement of these blastomeres. In no case were there suggestions of bilateral symmetry.

The egg of *Homarus*, then, as Kingsley has clearly shown for many other crustacea, is primarily "ectolecithal," the cells dividing independently of the yolk. Finally the egg becomes somewhat telolecithal, differing in this latter respect from the eggs of many higher crustacea so far as such have been observed.

The yolk, as the dividing nuclei leave its centre, becomes more granular, like that of the periphery, and there is no differentiated central mass of any kind whatever. "Belated" cells comparable with those found in *Crangon* by Kingsley ('87) were not found in *Homarus*.

#### THE MORULA STAGE.

A view of this stage is shown on Pl. XIV. The animal pole is shown in Fig. D, while the vegetative pole of the same egg is represented by Fig. E. The blastomeres of the former are somewhat smaller than those of the latter, and at no time is

there difficulty in distinguishing the two portions of the segmenting egg. The furrows between the blastomeres now extend deep down into the substance of the egg, though there is always a central mass of yolk which remains undivided. Careful observation will show that some of the blastomeres are in a process of still further subdivision though the nuclei have not yet reached the surface so that they can be seen in the living egg: they may, however, be clearly brought out by the action of reagents.

Polar globules are to be seen at *R-k*, Fig. D. A cross-section (Pl. XIX, Fig. 3) shows that all the nuclei have reached the outer portion of the egg, and a careful examination of complete series through several eggs failed to show any different position for these nuclei, or rather cells, since each nucleus is surrounded by an amœboid mass of protoplasm. The centre and periphery seem to take the stain more readily than intermediate portions of the egg.

Though the morula stage just described is adopted by the majority of eggs, some pass over it in a most irregular manner. Fig. F, (Pl. XIV) represents a case where the cells of the animal pole have divided very rapidly and are enclosing the vegetative cells as by a process of epibole. The nuclei have in both cases reached the surface, and are surrounded in living eggs by whitish clouds.

#### THE GASTRULA.

On the third or fourth day after oviposition, the blastoderm is found to be invaginated as shown in Pl. XIV, Fig. G. The blastopore is generally elongated, though I have found it quite circular and at times triangular. It also presents considerable variation in size. A view of the opposite pole shows that the blastoderm cells are there larger, and through their transparent bodies the yolk balls may be seen within.

The next following day shows the blastoderm cells smaller and more numerous, and the addition of weak nitric acid to the sea-water shows the blastopore to be the probable centre of activity of the developing egg.

#### STAGE H.

Seen from above, the blastopore at this stage normally appears as an oval depression, of which the major axis extends from left

to right, the anterior border curving considerably less than the posterior (Pl. XIV, H; Pl. XV, 4). From the side it appears as a considerable re-entrant of the even contour, giving a more or less reniform outline. The coagulating effect of nitric acid beautifully shows the disposition of the neighboring protoplasm. It is, in the first place, as will be seen by reference to the figure (Pl. XIV, H), abundant around the blastopore. It forms an isosceles triangle, the acute angle of which extends posteriorly from the inverted base, which is the straightened anterior border of the gastrula mouth. Extending laterally from this base two lines of thickened protoplasm are seen to diverge, and, as it bends anteriorly, each becomes wider until about one-third of the circumference has been traversed (Pl. XIV, Fig. H *Pcl.*). Ultimately each enlarges until the clouds almost fuse in the median line. A large U is thus formed, the enclosed portion of which is relatively poor in protoplasm. Other portions of the surface show no peculiar protoplasmic accumulations.

If eggs at this stage, as well as those somewhat earlier or later, are allowed to remain in alcohol for several days, especially if they have been previously hardened in hot picrosulphuric acid (Kleinenberg's), the capsule swells and the enclosed egg contracts. The space thus formed is at first filled with a cloudy fluid which finally clears in eggs of long standing. When the capsule is ruptured, the enclosed egg rolls out. The surface of the naked egg appears smooth and shining, and if not punctured will remain in stains for hours without being affected. The surface, in fact, appears to be cuticularized, a point which bears on the formation of the blastodermhaut. Extending posteriorly from the blastopore is a small whitish cloud which appears to be beneath the surface. It will be shown by sections to be the entoderm.

Pl. XV, Figs. 3 and 4, represents an egg which has been stained and rendered semi-transparent. The blastopore (Fig. 4 *Gm*) is by all odds the most prominent feature. Crowding about it are innumerable cells, the lips of the blastopore and its cavity actually swarming with nuclei, many of which are in the process of indirect division. Extending a short distance posteriorly, the nuclei are found most abundantly in the bounds of the triangle already described. The curves of the U-shaped protoplasmic clouds are also thickly nucleated, as are their ter-

minial enlargements, the procephalic lobes (*Pcl.*). At other portions of the egg the nuclei are less numerous, and on the opposite side (Fig. 3) they stand far apart, and their surrounding cells are so thin that the deeper yolk spheres become visible.

The ectoderm cells are arranged in a continuous pavement-like layer over the entire egg, their polygonal outlines appearing as a faint reticulum, and their lower, deeper walls often marked by irregularities of the finer or coarser yolk masses upon which they rest. These cells are of course largest upon the dorsal side of the egg, and smallest in superficial area where the nuclei are most abundant. Where the egg has been crushed (Pl. XV, Fig. 2), the broken edges show that each cell has immediately below it a small mass of yolk material which it seems to grasp. We then have a condition comparable with the "yolk pyramids" described for related forms. The nuclei are oval in outline, contain a reticulum and a central nucleolus, which latter often shows tendencies towards division. Karyokinetic figures are to be seen at different localities, most abundant where most rapid growth is going on (Figs. 2 and 4, *K.f.*).

The plasma vacuoles are represented by chromatin nebulæ, which generally underlie the triangular and U-shaped areas already mentioned, though they are to be found as small clouds between and also outside the limbs of the embryonal tract. They are even found in the dorsal portion of the egg. In Figs. 3 and 4 they are represented by the minute dots, shown especially at *C.n.*

Surface comparison shows this stage to be somewhat similar to stage A of *Astacus* as described by Reichenbach ('86). It also closely resembles Kingsley's figure of *Crangon*. In *Astacus*, however, the U-shaped tract has become more differentiated, so that a procephalic portion is separated from the two isolated halves of the thoracico-abdominal plate. In no case could I follow the beautiful curves of Reichenbach for more than a short distance, though the smaller size and the greater number of nuclei in *Homarus* may account for this lack of definite, regular arrangement. My figures (Pl. XV, 3 and 4) have all the nuclei, except those at the extreme periphery, placed by means of a camera.

*Astacus* and *Homarus* are externally quite similar in that the invaginated cells form a considerable depression, the "Ento-

dermhügel" of Reichenbach. In *Crangon*, at this stage, the blastopore is closed.

Suggestive is the line of nuclei extending posteriorly from the blastopore (Pl. XV, Fig. 4), a feature not mentioned by Reichenbach nor by Kingsley.

A median longitudinal section at this stage (Pl. XV, Fig. 7) shows more clearly the exact amount of invagination at the blastopore. Immediately posterior to it, in many specimens a second shallow depression is to be noticed, which may be comparable with the "oval depression" of *Atyephira*. The ectodermal cells will be found to be more crowded, smaller, and deeper in the region of the procephalic lobes (*Pcl.*). Extending into the yolk from the depression of the blastopore are the rapidly proliferating elements of the entoderm, a mass of large thin-walled cells with deeply colored nuclei. They are apparently digesting the yolk (Pl. XV, Fig. 7, *Ent.*). These entodermal cells, which are directly comparable with those found in *Atyephira*, *Astacus*, and *Crangon*, have evidently been proliferated from the ectoderm, though actual karyokinetic figures were not observed. Extending out into the yolk from the entodermal mass are pseudopodia-like prolongations, which worm their way between the masses of food yolk.

The chromatin nebulae are, as surface views showed, abundant under the U-shaped embryonic tract; and a few are seen deeper in the yolk, around the entodermal mass (*C.n.*). A few from the anterior portion of the egg are highly magnified ( $\times 1400$ ) (Pl. XV, Fig. 1). They rest between the masses of food yolk, and range in size and structure from the smallest homogeneous dot to bodies almost equalling the ectodermal nuclei in size, and containing one or more deeply colored masses which I have called nucleoli.

The food yolk is often broken up into polygonal masses, probably the result in part of the action of reagents, and is punctured with circular openings, the site of now dissolved oil globules. A distinct line separating yolk from ectoderm cannot be drawn, the ectodermal cells (*Ect.*) actually grasping the yolk granules. The entoderm is not free from yolk. The cells, indeed, seem to form a reticulum that holds a quantity of yolk grains in its meshes.

A transverse section through the blastopore (Pl. XV, Fig. 5)

confirms our former conception of the shape of the unmodified ectodermal cells, and offers strong evidence in favor of the origin of the entoderm from the proliferating ectodermal cells of the blastoporic depression. These latter cells (*Ect.*) deepen as they approach the median line, and the nuclei are seen not infrequently to occupy the deeper portion of the cell. The karyokinetic figures (*K.f.*) show that the division of the nuclei of the entodermal mass results in growth towards the centre of the ovum, while the same figures in the ectodermal nuclei (Fig. 6, *K.f.*) give rise to surface expansion.

A section through the procephalic lobes (Fig. 6) shows that the nuclei are less abundant in the median region, that there is but a single layer of ectodermal cells, and that these have their longer diameter parallel with the surface. Chromatin grains, as was seen in the surface view, are most abundant where ectodermal cells are most numerous.

At this stage in *Astacus* mesodermal cells are present in considerable number, and form tissue several layers in thickness. The ectoderm is also, for some little distance anterior to the blastopore, made up of two layers of cells. Structures comparable with the chromatin grains of the plasma cells are neither mentioned nor figured by Reichenbach, though the so-called "serum" may represent the region of their activity. In *Cran- gon* also, at this stage, mesodermal and entodermal elements are already formed, but the latter do not remain in a single mass as they do in *Homarus*, but early migrate into the yolk. Possibly, however, even while thus distributed, protoplasmic filaments hold them in communication with one another. In later stages of *Homarus* the protoplasmic continuity of the entodermal cells is often beautifully shown.

#### STAGE I.

This is one of the more important stages (Pl. XIV, Fig. I). The areas of special growth are now laid out, the blastopore closes, and the germ layers are differentiated.

The fresh egg that has been subjected to the action of dilute nitric acid shows the blastopore as it disappears between the converging limbs of the telson (Fig. I, *G.m.* and *T.*). Other preparations were made before closure had been so far effected.

The apex of the posteriorly directed triangle, which was described for the previous stage, has now become a broadened patch, while the base of the triangle has given place to the re-entrant formed by the disappearing blastoporic rim. Anterior to the just described region of important events is spread a very faint cloud with more or less irregular boundaries. Its outline is deeply bifurcated anteriorly (*Pcl.*), and laterally two extensions are to be observed (*An.*<sup>1</sup>, *An.*<sup>2</sup>) on either side. The large U-shaped cloud of the previous stage has thus been compressed towards the median line, as Reichenbach has described for *Astacus*. Its free ends, though somewhat reduced in area, still preserve their enlargements. Other portions of the egg show at present no remarkable characters.

After the hardened eggs have remained some time in alcohol, the capsule, as usual, may be easily removed; but there now appears, for the first time, a second egg membrane, the "Blastodermhaut." This membrane appears in irregular blisters, being at first only partially sloughed from the underlying ectodermal cells, of which it has hitherto formed a cuticle. The condition of the "Blastodermhaut" at this time made the securing of stained preparations extremely difficult, though a sufficient number of fragmentary preparations were made to demonstrate satisfactorily the general arrangement of the nuclei and the method of closure of the blastopore (Pl. XVI, Figs. 2 and 3).

Compared with the immediately preceding stage the surface nuclei are much more abundant, and certain definite centres of aggregation are to be noted which follow, in the main, the outlines of the cloud-like mass already described.

The nuclei are most abundant around the contracted lips of the blastopore (Pl. XVI, Fig. 2, *G.m.* and Fig. 3, *G.m.*), which in typical cases closes by the incurving of its hitherto somewhat straightened anterior edge. The lateral edges of the opening now approach each other, and become thickened at their inner edge, where they are also more highly nucleated (Fig. 2, *L.G.m.*). Externally they are separated from the surrounding ectoderm by a slight depression.

The first appearance of the third pair of cephalic appendages, the jaws, is represented at Pl. XVI, Fig. 3, *J*, anterior to which no remarkably differentiated portion of the ectoderm is found until the procephalic lobes are reached, where two

shallow divergent furrows extend anteriorly and laterally, enclosing the more highly nucleated procephalic portion. It is in the neighborhood of these furrows that the protoplasm of the fresh egg, on treatment with nitric acid, yields the whitish indefinite ends of the U-shaped cloud.

A longitudinal section through the median line shows the blastopore to be deeper and more constricted than in the previous stage. The ectodermal cells have again increased in number, especially in the region of the head folds (Fig. 13, *Pcl.*), where even in the middle line the juxtaposed columnar cells attract the eye. Midway between the head folds and the blastopore, as has been observed for earlier stages, the ectodermal nuclei are far apart, though immediately in front of the invagination, — in the thoracico-abdominal portion, — they are again aggregated. Chromatin grains are still present as nebulæ (*C.n.*), most abundant under the portions of the ectoderm that have been noted as areas of special growth. A few grains are noticed near the entoderm.

The entoderm cells (*Ent.*) have increased in number with the increase of the ectoderm cells. They extend deep into the yolk, as Herrick ('90) has already stated, as a "flask-shaped" mass. At places pseudopodia-like prolongations are seen extending out between the yolk bodies.

That which specially characterizes the present stage, however, is the appearance of mesodermal elements. In the longitudinal section at *Mes.* is to be seen a small group of lighter colored nuclei which tend anteriorly.

The mesoderm nuclei are at this stage lighter in color and generally more oval in outline than the darker more angular entoderm elements. They closely resemble the ectoderm nuclei, and their origin is clearly seen to be from the point where the latter layer fuses with the entoderm, though the sections do not show, what Ishikawa and Reichenbach have figured: cells migrating from the ectoderm into the mesoderm. A few mesoderm cells are to be seen at *Mes.* just in front of the blastopore and beneath the ectoderm. In the lower, deeper portions of the entodermic mass no such cells, nor even nuclei, are to be found. The greater number of chromatin grains will be found to accompany the growing mesoderm.

A cross-section through the blastopore is shown at Fig. 6,

and in every way agrees with the longitudinal: the mesoderm cells extend in a sheet to the right and to the left of the median line. Reference to Fig. 5, which represents a cross-section, will show the thickenings of ectoderm where the elevations of the jaws are soon to appear. Karyokinetic figures in the entoderm prove that cell multiplication is there rapidly going on, and at *K.f.*, Fig. 6, give us some idea of the limits of an entoderm cell. The section (Fig. 4) passes at right angles through the procephalic mass. It shows the forward extension of the chromatin nebulae and of the mesoderm, the nuclei of the latter appearing in a fine-grained mass recalling the "serum" of Reichenbach ('86). The curve of the section is seen to be abruptly broken at \*—\*, which are the early depressions lateral to the procephalic lobes. The position of the equatorial plate at *K.f.* proves that the ectoderm cells are still multiplying horizontally. In not a single instance have I found these bands placed otherwise in ectoderm cells.

So far as the surface is concerned the present stage of *Homarus* combines the stages B, C, and D of Reichenbach. At no stage, however, does the lobster show the regular nuclear curves of *Astacus*, nor is it possible to demonstrate any difference between the several cells of the procephalic lobes comparable to the primitive "Krystallkegelzellen" of Reichenbach. The irregularities in methods of closure of the blastopore of the lobster are duplicated in the cray-fish. In stage B of Reichenbach the so-called secondary mesodermal elements are introduced. Future comparison may prove these to be the same as the plasma vacuoles and their chromatin grains. The invagination that results in the formation of entoderm in *Astacus* is somewhat different from the proliferating mass described for *Homarus*, though certain sections which I have made show that not infrequently the entoderm of *Homarus* may contain an indistinct lumen, though I have found no continuation of this entodermal cavity to the surface of the egg. (This structure has already been noted by Herrick, '90, in his preliminary paper on the development of the present type.) The entoderm of the cray-fish is inclined anteriorly, while in the lobster it tends most generally towards the posterior, and in certain cases is actually elevated so that it reaches the ectoderm behind the blastopore. Fig. 13 represents the entoderm in its most normal condition.

## STAGE J.

Changes from the preceding condition are striking, and take place very rapidly. Indeed, I have found but few eggs that show an intermediate stage of development. The appendages, earlier seen as irregular clouds, are now more clearly outlined, and the thoraco-abdominal fold is (Pl. XIV, Fig. *J*, *Th. Abd.*) considerably elevated, the place of the future anus being indicated at *A*. The stomodæum has also appeared (*St.*), and occupies a position midway between the first pair of antennæ (*An.*<sup>1</sup>). Lying immediately posterior are the diverging second antennæ (*An.*<sup>2</sup>). The mandibles, the origin of which was noted in I, are seen to occupy a position between the second antennæ and the thoraco-abdominal plate. All the so-called "nauplius appendages" are, then, present in outline.

If alcoholic eggs are examined, the annoying condition of the "Blastodermhaut" of the previous stage is found to exist no longer, but the membrane lies entirely free from the enclosed egg. The nuclei of the embryo are now free to select the stain, and most beautiful preparations are easily made (Pl. XVII, Fig. 1).

Each procephalic lobe is abruptly elevated above the surface of the egg by the furrows (*fur.*) already noted for the previous stage, and its anterior portion (*Ce.*), more highly nucleated and slightly concave, represents the rudimentary compound eye. A slight diagonal depression separates it from the more central portion, the ganglionic elevations (*G.*<sup>1</sup>, *G.*<sup>2</sup>). At the posterior outer corner of the eye triangle a small pit is to be noticed. Its signification I cannot give. Within the ganglionic portion just mentioned, and anterior to the stomodæum, the slight elevation of the upper lip can be seen.

At the base of the antennæ, and lying on either side of the stomodæum, are the ganglia of the first antennal segment (*G.*<sup>3</sup>). Immediately posterior to them are the connecting lines of nuclei which unite them with the corresponding elevations of the second antennæ (*G.*<sup>4</sup>). The antennæ are abruptly elevated along their anterior border and exhibit a tendency to form joints. The groove that separates the antennæ from the posterior and lateral edges of the procephalic lobes, in favorable specimens, shows the presence of an elongated crescentic eleva-

tion (*Seg.*<sup>2</sup>), which, it seems to me, may have considerable morphological importance. The ganglionic mass at the base of the primitive compound eye is divided into an anterior and a posterior portion (*G.*<sup>1</sup>, *G.*<sup>2</sup>). The anterior is more directly implicated in the optic tract, while the posterior, which probably answers to the cerebrum of the adult, is possibly primarily associated with the crescentic elevations already noted. Though these lateral elevations soon disappear, the cerebral lobes increase in size with the developing embryo.

If we allow the compound eyes to occupy the position of a pair of pre-oral appendages (and their development, thus far, is not different from that of the antennæ, though I am well aware of the position held by many morphologists upon this mooted point), and if moreover the crescentic folds represent a second pair of pre-oral appendages, no longer present in the adult, the stage under consideration is most suggestive, since five pairs of ganglionic swellings are then present, each presiding over a distinct segment, while the ganglia of either side are united as shown in the figure by a longitudinal connective (*Nc.*). The stage is strikingly annelidan and, when taken in connection with the approach of the two divergent halves towards the median line, it would seem that we have a case of condescence comparable with that presented by *Lumbricus* (Wilson, '89), and by *Clepsine* as described by Whitman ('78). The part played by the U-shaped mesoderm is further evidence of condescence of *Homarus*.

The second antennæ are not as yet elevated to any considerable extent above the general surface of the egg, and their slightly smaller ganglia would point to a somewhat tardy development. Suggestions of the definitive joints are present.

The jaws, or mandibles, are somewhat smaller than the "second" pair of appendages. A longitudinal elevation or ridge (*Nc.*) marks the connective joining the mandibular ganglion with the ganglion of the appendage just described, while at the posterior edge occurs an abrupt concavity which surrounds the elevated thoracico-abdominal fold. The formation of this fold from the immediately preceding stage is as follows: The pinching together of the lateral lips of the blastopore results in the formation of two parallel nucleated masses (Pl. XVI, Fig. 3) which finally meet in the middle line over the still slightly open blasto-

pore. The lateral pressure which brought them together seems to continue for some little time, and finally results in a central elevation; which continues to be a feature of this and the next succeeding stage. As growth in this region continues, the blastopore, occupying in relation to the fold a more or less posterior position, is actually closed, though the arrangement of its nuclei makes it possible, for one to follow it into the later stages. In the present stage the blastopore may be seen in both longitudinal and transverse sections.

A groove in certain eggs passes from between the ganglia of the jaws far forward and almost to the mouth. At times, too, the nuclei behind the blastopore arrange themselves in parallel median lines. In Pl. XVII, Fig. 1, the entoderm is seen below the surface at *Ent.* Although the elaborate system of curves described by Reichenbach is at times suggested, continuous lines of nuclei are generally very short.

The present stage in *Homarus* is more directly comparable with E and F of *Astacus*, but the internal structure combines many features of D and E. The surface development of *Astacus* is, when compared with the interior growth, retarded. Whereas the nauplius appendages of *Homarus* are now present, though of varying size, in *Astacus* they are not as yet differentiated. The procephalic region is quite similar in both forms, though the optic ganglia in *Astacus* are farther removed from the cerebral or supra-œsophageal. The anus has already made its appearance in *Astacus*.

A longitudinal section shows the even contour of the younger embryos to be more or less broken (though normally less than figured Pl. XVII, Fig. 5, where the reagents have contracted the embryonic surface). The blastopore is no longer a depression, and in longitudinal sections is difficult to find, though indicated in Fig. 5 at *G.M.* Passing anteriorly, a considerable thickening of the ectoderm occurs at *G.<sup>5</sup>*, marking the position of the associated ganglia of the jaws. Though the cells are deep, but a single line of nuclei is present. Below this point chromatin grains are especially abundant. A few mesodermal cells are also shown (*Mes.*). Behind the mouth (*St.*) the ectoderm is relatively thin, though at the stomodæum it thickens again and is covered below by a number of mesodermal cells. Chromatin granules are very abundant under the procephalic

lobes. The entodermal mass has undergone considerable increase in size, and the *contained* yolk is manifestly different from that without. It is as if the corners had been digested off, the granules appearing quite spherical. The entoderm cells, or nuclei — for limiting cell walls are extremely difficult to resolve — are often in pairs, as if undergoing division. Immediately under *Gm.* (Pl. XVII, Fig. 5) are seen larger mesodermal cells. From these other cells are seen to extend anteriorly, and, to a slight extent, posteriorly. Chromatin grains are associated with the mesodermal elements.

In the transverse section through the closed blastopore (Fig. 6), which is somewhat more highly magnified, the arrangement of the germinal layers is clearly seen. The ectodermal cells (*Ect.*) form a layer one or two cells in thickness, which, at the base of the blastoporic scar (*Gm.*), give place to the larger, turgid mother-cells (?) of the mesoderm (*Mes.*). Extending laterally from these, the mesoderm forms a somewhat broken tissue, lying immediately under the ectoderm. The entodermal cells (*Ent.*) are generally slightly different from those of the other layers, though they cannot always be separated with absolute certainty.

A cross-section drawn through the egg (Fig. 4) shows the evenly disposed ectodermal cells, which are beginning to thicken at the ganglia (*G.*<sup>4</sup>). The median groove is clearly presented at *Mg.*, while the mesoderm forms a single, unbroken layer on either side the median line. Though the chromatin elements are much less abundant here than farther forward, they are irregularly aggregated in the median line and in two lateral masses.

A section through the stomodæum (Fig. 3) shows the elevations of ectoderm at the ganglionic centres as well as at the insertion of the appendages. The mesoderm is still an evenly disposed band, while the chromatin grains are almost absent. At Fig. 2, however, the chromatin is again abundantly found, while but one or two mesodermal nuclei are present. At *Seg.*<sup>2</sup> is a thickening of the ectoderm, which I consider to be the section of the intercalated, crescentic appendage.

Before leaving this stage, a comparison with *Astacus* may prove valuable. The cray-fish now has a lumen in the centre of the entodermal mass, the cells having actually devoured the

yolk. A lumen free from yolk does not occur in the lobster, though the more amœboid cells certainly attack the yolk. *Homarus* and *Astacus* agree in having the mesodermal nuclei in the neighborhood of the blastopore, considerably larger than elsewhere. Reichenbach claims for the anus a position anterior to the blastopore. In *Homarus* it does not occupy, *always*, the same position. It may arise from the anterior, middle, or posterior portion of the scar that is left after the closure of the blastopore. In both forms, it at first leads into a mass of mesoderm, and only later reaches the entoderm sac. I have been unable to find, in *Homarus*, preparations that throw any direct light on the so-called "secondary mesoderm."

#### STAGE K.

A surface view of fresh eggs that have been treated with ten per cent nitric acid shows that the cloud-like tracts of *J* have now assumed the form of definitely and abruptly elevated ridges and hills. These are considerably smaller in superficial area than the earlier tracts, because of the tucking under of the ectoderm to elevate the appendages. The antennæ, in relation to the stomodæum, have moved slightly anteriorly. Though the procephalic lobes have become considerably contracted, their former bounds are still marked by the action of the acid. A broad cloud extends backward from the thoracico-abdominal plate.

The stained egg is shown on Pl. XVIII, Fig. 3. The outlines of the appendages have become more definite and the nuclei more abundant. The contraction of the embryonic area is most striking, and the procephalic lobes no longer show the generalized condition noted in the preceding stage. The structure of the anterior portion of the embryo is with difficulty demonstrated. From examination of many preparations I conclude that the optic ganglia (*G.*<sup>1</sup>) are in close contact with the optic tract (*Ce.*), while the cerebral ganglia (*G.*<sup>2</sup>) have retained their more primitive condition, and are connected with the optic ganglia by a band of larger nuclei (*Nc.*).

All traces of the crescentic appendages have disappeared.

The ganglia of the antennæ are still prominent hemispherical swellings, but they now occupy a somewhat pre-oral position, and are closely associated with the supra-œsophageal swellings. The antennæ, curiously enough, point anteriorly, and a break

seems to occur between them and the second antennæ. An elevated ridge represents the connective joining the ganglia of the antennæ and second antennæ.

The second antennæ now show a marked tendency towards segmentation and division. Very soon they will become biramous. Their ganglia are clearly connected with the ganglia of the jaws by a continuation of the elevated connectives already noted. This elevation may be continued even to the thoraco-abdominal plate, which has now lost its earlier elevation, and has become quite flush with the surface of the egg in certain preparations. This depression of the tract is quite different from the condition of *Astacus*.

A median longitudinal section (Fig. 8) has a relatively even contour, the inpushing of the mouth being the most considerable break. The ectoderm is still made up of a single layer of cells, though in places—for example, under the upper lip—a thickening is seen. In the neighborhood of the now closed blastopore the ectoderm is considerably thicker. Mesoderm is not much more abundant than in the previous stage, though the number of chromatin grains is truly surprising. A thick layer extends from the anterior portion of the procephalic lobes to the deeply projecting entodermal mass, thinning out only in the neighborhood of the stomodæum. The grains are often of considerable size, and seem to float in a serum. The entoderm shows little change, though in certain central portions bands of clear protoplasm are to be seen. These bands are arranged longitudinally with the entodermal mass, and are bordered by closely associated nuclei. In a few instances the yolk enclosed by the peripheral entodermal cells seems to show a tendency towards the formation of entodermal yolk pyramids, as described for *Astacus*. The proctodæum has not yet reached proportions that make it a prominent object.

Fig. 4 represents a transverse section through the procephalic lobes, the thickenings for the compound eye being shown at *Ce*. The absence of mesodermal cells from the median portion and the median mass of chromatin grains may be noted.

The section passing through the mouth (Fig. 5) shows the invagination of the ectoderm, and also demonstrates the ganglia of the first antennæ (*G.*<sup>3</sup>) as thickening tracts of ectoderm. The section through the antennæ shows that they are being actually

lifted from the surface by the lateral tucking under of the ectoderm (\*\*). The position of the mesoderm cells within the cavity of the appendage is interesting. In several places the ectoderm may be seen to present more than a single layer of nuclei. Chromatin elements are not specially abundant.

The section (Fig. 6) through 6 of Fig. 3, shows the second antennæ actually cut off from the underlying mesoderm, though not separate from the ectoderm.

In Fig. 7, a section through the proctodæum, is shown the very slight elevation of the thoracico-abdominal plate. The ectodermal cells are clearly invaginated at *A*. The mesodermal and entodermal elements are seen, as in the previous stage.

#### STAGE L.

The figure of this stage on Pl. XIV shows the increased contraction of the embryonic tract, and the forward migration of the second antennæ.

#### STAGE M.

Perhaps the most interesting feature of this stage (Pl. XIV, Fig. *M*) lies in the fact that the embryonic area, which early occupied nearly one-half the surface of the egg, has now contracted until it has reached its greatest point of concentration. This embryonic contraction has been observed to characterize the early developmental stages of several crustacea. Surface views of fresh and alcoholic eggs show the embryo to be provided with well-rounded appendages (Pl. XIV, Fig. 1).

The antennæ have, in relation to the mouth, passed still farther forward. The second antennæ are clearly biramous, and have also advanced considerably towards the head end. The "third" pair of appendages is still rudimentary. The upper lip has covered the stomodæum, while the proctodæum is now quite evident, between the two halves of the telson flap, or terminal portion of the thoracico-abdominal fold. The region of the eyes has been somewhat changed. Anteriorly and laterally are to be seen two somewhat specialized tracts, one on either side (Fig. 1, *Ce.*), from each of which there passes towards the median line a very slightly elevated ridge, terminating in a pair of anteriorly placed elevations (*G.*<sup>2</sup>). I am inclined to

assign to the outer area the peripheral portion of the compound eye, to the converging ridges the primitive nervous tract or optic lobes, while the median swellings will probably turn out to be the cerebral lobes, though I have as yet been unable to trace the structures actually into the stages which are so ably worked out by Parker ('90).

It will be observed that the striking triangular masses of nuclei, heretofore called the procephalic lobes, have quite disappeared, the nuclei in their former site now being no more closely arranged than they are on other portions of the surface of the egg equally distant from the embryo. An examination shows that their earlier arrangement has been given up. They may have disappeared completely. There has also been a local ecdysis. A heart-shaped piece of cuticle elevates itself from this portion of the egg, and splits away anteriorly and laterally, following the outline shown in Plate XIV, Fig. M. Posteriorly, the flap is connected with the first antennæ, and so closely that it is with considerable difficulty that the piece can be removed, without at the same time removing the antennæ. The anterior point of the flap is, moreover, in every case connected with the investing "Blastodermhaut." On removing the heart-shaped flap of cuticle, two large bowl-shaped depressions (Pl. XIX, Fig. 1, *B.D.*) are revealed. These are, in favorable specimens, quite as deep as they are wide, and are symmetrically placed. Their signification I am at a loss to surmise, though I have been at times inclined to think that they may arise from the action of reagents upon the underlying "serum." It is possible that they may represent a "dorsal organ."

A median line of approximated nuclei now extends from the anterior and posterior portions of the embryo nearly around the egg, in nitric acid preparations appearing as an encircling white band.

The sections of this egg are specially instructive. Fig. 13 shows that the stomodæum (*St.*) is no longer a depression, but has become a tube, and, bending anteriorly, reaches well into the yolk. The upper lip has become thickened, and has closed down over the primitive mouth. In the neighborhood are many mesodermal cells and chromatin grains. The hind-gut is clearly seen at *Hd.*, though there is no lumen, this portion of the primitive alimentary tract being only marked out by the parallel rows

of nuclei, as shown in the drawing. Within, the hind-gut passes into the mass of diffused entodermal cells, which are now traversing the yolk, but keeping, in a rough way, a definite order, all tending towards the periphery. The true mesoderm cells (*Mes.*) surround the proximal portion of the hind-gut. Chromatin elements are less abundant than in the immediately preceding stage.

A section parallel to 13 (Fig. 12), drawn through Fig. 1 at 12, shows at *G.*<sup>2</sup> the invagination at the base of the optic tract, the cerebral lobe or ganglion. Just behind it lie the ganglia of the antennæ (*G.*<sup>3</sup>) and second antennæ (*G.*<sup>4</sup>). A section through the jaw, which contains mesodermal elements in its lumen, is also shown at *J.* At several places in these sections the mesodermal nuclei seem to be breaking down into chromatin granules. I am still in doubt, however, whether such is the case.

A transverse section (Fig. 4) through 4 of Fig. 1 passes through the procephalic depressions. One or two mesodermal cells are to be noted, as well as collections of chromatin grains. Fig. 5 is drawn through the ganglionic region noted in Fig. 12 at *G.*<sup>2</sup> An appearance of invagination is given, which is even more clearly shown when we examine sections of the remaining pairs of ganglia. Beneath the ectoderm mesodermal cells are seen and chromatin grains are present, exhibiting, in the main, general symmetry, though isolated nebulae may be observed at varying points. The median elevation, below which several mesodermal cells are shown, is the ridge which passes anteriorly from the upper lip.

Section No. 6 passes through the anterior portion of the fore-gut, as well as through the first pair of appendages. The position of the fore-gut is slightly eccentric, while the cavities of the appendages appear to contain yolk grains surrounded by chromatin granules. The mesodermal cells which fill in the *body* of the upper lip are still associated with yolk grains. Many of the cells have pseudopodial prolongations. The next section (Fig. 7) passes directly through the ganglionic swellings at the base of the first pair of antennæ. The arrows indicate the direction of invagination. Chromatin granules are abundant near the yolk. Six sections back, the knife passes through the free tips of the first pair of antennæ (Fig. 8), and through the body of the second pair, the internal boundaries of which

latter extend as a chain of nuclei almost down to the yolk. The ganglia (*G.*<sup>4</sup>) appear as two elevations separated from each other by a median depression. Each is seen to have its cells arranged as if in obedience to an invagination following the direction of the arrows. Though chromatin grains are abundant in the median portion, mesodermal cells are found only at the outer margins of the section. In the next following section, not figured, there are no traces of ganglionic invaginations. In Fig. 9, which passes through the ganglia of the "third" pair of appendages, the invaginations again occur, as shown by the arrows. The cavity of the second antennæ is not different from the cavities of the other appendages. Fig. 10 is drawn through the body of the pair of jaws, which seem to be elevated from the general surface by lateral pressure. The single layer of ectodermal cells is quite in contrast with the previously described sections through ganglionic areas. The last section figured (Fig. 11) passes through the biramous tips of the second antennæ, and cuts the proctodæum longitudinally. The latter ends blindly, and below it are many feeding entodermal cells. Mesodermal cells are grouped in the neighborhood, several extending out under the ectoderm. Chromatin granules are not specially abundant. At *Ent.* several entodermal cells are seen devouring the yolk.

#### STAGE N.

This is most characteristically the nauplius stage of the developing lobster. The appendages are tipped with spines. The second pair is not only biramous, but also clearly jointed. The stomodæum is covered by the upper lip, which extends posteriorly until it almost touches the tip of the anteriorly directed tail. A cuticle, which in the next stage proves to be a true ecdysis, is seen to be lifted from the embryo in the region of the compound eyes. In certain cases a whitish band extends anteriorly, as figured Pl. XIV. Sections of this and the following stages have not yet been made.

#### STAGE O.

The sloughed cuticle is clearly seen as a delicate line surrounding the embryo and its appendages. A pair of pigmented

dots, midway between the compound eyes, are the two halves of the ocellus, which has been described for several of the higher crustacea. Its absence in *Astacus* is of interest. The tip of the thoracico-abdominal fold is being constricted off from the proximal portion to form the telson, and the rudiments of thoracic appendages have made their appearance.

#### STAGE P.

The compound eyes have become pigmented, the ocellus is a single median spot, the sloughed cuticle is still present, and the thoracico-abdominal portion is much elongated.

The presence of terminal telson spines, of additional appendages, and of the clearly outlined posterior edge of the carapace should be noted. The latter appears as a crescent encircling the posterior portion of the embryo. It fades away insensibly at a little distance from the embryonic tract.

#### STAGE Q.

The tip of the telson has now reached a point even with the ocellus. Additional appendages are to be seen, which are growing over the flexed abdomen.

#### STAGE R.

The embryo has now reached a considerable size. The telson extends anteriorly, in front of the head. The thoracic appendages have grown over and partially covered the abdomen. The most characteristic feature, however, is the presence of clearly defined areas which encircle the yolk and partially hide underlying structures. The embryo has now reached a stage which may be compared with the earliest stage figured by Smith ('73).

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### EXPLANATION OF PLATES.

#### *Reference Letters.*

<i>A.</i> Proctodæum.	<i>L.Gm.</i> Lip of blastopore.
<i>Abd.</i> Abdominal appendage.	<i>lm.</i> Lenticular mass.
<i>an.</i> <sup>1</sup> First antenna.	<i>Mes.</i> Mesoderm.
<i>an.</i> <sup>2</sup> Second antenna.	<i>m.g.</i> Median groove.
<i>B.D.</i> Bowl-shaped depression.	<i>Nc.</i> Connective.
<i>b.s.</i> Blood sinus.	<i>Ov.Or.</i> Openings of oviducts.
<i>Ce.</i> Compound eye.	<i>Pb.</i> Plasma body.
<i>Cor.</i> Blood corpuscles.	<i>Pcl.</i> Procephalic lobes.
<i>C.N.</i> Chromatin nebule.	<i>p.e-m.</i> Primary egg-membrane.
<i>Cut.</i> Cuticular line.	<i>Ps.</i> Protoplasmic tract.
<i>E-c.</i> <sup>1-5</sup> Egg-cells.	<i>Pt.</i> Ovarian wall.
<i>Ect.</i> Ectoderm.	<i>P.Vs.</i> Plasma vesicles.
<i>Ent.</i> Entoderm.	<i>R-k.</i> Polar globules.
<i>fe.</i> Follicular epithelium.	<i>Seg.</i> <sup>2</sup> Second segment.
<i>Ft. vs.</i> Fat-vesicles.	<i>Sp.C.</i> Spermatophoric capsule.
<i>Fun.</i> Funiculus.	<i>Sp.Or.</i> Spermatophoric orifice.
<i>fur.</i> Furrow.	<i>Sp.p.</i> Spermatophore.
<i>G.m.</i> Blastopore.	<i>St.</i> Stomodæum.
<i>G.</i> <sup>1-5</sup> Ganglia.	<i>Th.Abd.</i> Thoracico-abdominal fold.
<i>Hd.</i> Hind-gut.	<i>T.</i> Telson.
<i>Ÿ.</i> Mandible.	<i>V.D.</i> Fore-gut.
<i>K.</i> Keel.	<i>W.</i> "Wings" of receptive apparatus.
<i>Kf.</i> Karyokinetic figures.	<i>Yc.</i> Yolk-laden cells.

## EXPLANATION OF PLATE XIV.

The figures are enlarged about thirty-five diameters, and represent fresh eggs that have been treated with dilute nitric acid.

FIG. *A*. Surface view of an egg that is not infrequently found associated with eggs similar to *B*, *C*, and *D*. Certain ovarian eggs present a similar structure (Pl. XVI., Fig. 1).

FIG. *B*. An egg before segmentation. The funiculus is represented by the whitish patch outside the egg-membrane.

FIG. *C*. Surface view of an egg undergoing segmentation. (The lithographer has represented the blastomeres incorrectly. They are but *slight* elevations, and are not so clearly separated by *deep* furrows.)

FIGS. *D* and *E*. "Morula stage." Two views of the same egg. The polar globules at *R-k* are not sufficiently distinct.

FIG. *F*. Egg in blastula stage. Deeper colored yolk-laden cells are shown at *Yc*.

FIG. *G*. Surface view of egg in process of gastrulation.

FIG. *H*. First appearance of the embryonic area.

FIG. *I*. The lithographer has failed to give the extremely delicate and indefinite outline that is presented by the embryonic area of eggs in this stage. The region posterior to the blastopore is, in reality, but little more distinct than in Fig. *H*. The formative centres of the second antennæ are represented by the lateral extensions lying in a plane immediately in front of, and lateral to, the telson, *T*.

FIG. *J*. Surface view of an egg, showing the details of the embryo more clearly outlined. Compare Pl. XVII., Fig. 1.

FIGS. *K* and *L*. Stages showing the contraction of the embryonic area.

FIG. *M*. Stage of greatest embryonic contraction. The outline of the heart-shaped cuticular flap is clearly shown.

FIG. *N*. The "egg-nauplius" stage.

FIG. *O.-R.* Successive stages in the development of the embryo.











## EXPLANATION OF PLATE XV.

FIG. 1. Chromatin granules from the "nebulæ" in the region of the procephalic lobes.  $\times 1400$ .

FIG. 2. Surface and side view of ectoderm cells, showing the relation of the ectoderm to the "yolk-pyramids."  $\times 200$ .

FIG. 3. Surface view of egg in stage *H*, seen from the dorsal side.  $\times 60$ . The deeper lying yolk masses may be seen through the transparent ectoderm. Chromatin nebulæ are shown at *Cn*.

FIG. 4. Same as Fig. 3, seen from the ventral side. In Figs. 3 and 4 the nuclei have been placed by means of a camera.

FIG. 5. Transverse section through blastopore as shown in Fig. 4, 5-5.  $\times 200$ . The entodermal cells are colored a lighter shade of gray.

FIG. 6. Transverse section through the plane 6-6 of Fig. 4.  $\times 200$ . The ectodermal cells are of a deep gray color. The yolk is represented in yellow.

FIG. 7. Longitudinal section through the median plane of Fig. 4.  $\times 200$ . Ectoderm represented in gray. The dark-colored patches extending to the left of the entodermal mass are too deeply shaded, and their limits are too definite.











## EXPLANATION OF PLATE XVI.

FIG. 1. A median cross-section through an ovarian egg. The stage is comparable with *A*, Pl. XIV. A protoplasmic mass is shown at *l.m.*, while on the right of the figure is seen a section of the smaller division of the egg.

FIGS. 2, 3. Surface views of the closing blastopore.  $\times 60$ .

FIGS. 4-6. Cross-sections through planes represented on Fig. 13.  $\times 200$ . The ectoderm is colored deep gray, while the entoderm is represented in a lighter shade, extending indefinitely into the yolk.

FIGS. 7, 8. Highly magnified sections through the ovarian egg.

FIG. 9. A diagram illustrating the migration of the segmentation nuclei towards the surface, and the formation of the blastomeric "hills." Five nuclei are shown in the upper part of the egg, while in the lower portion only a single nucleus is represented.

FIG. 10. Enlarged figure of the portion of the ovary represented in Fig. 12.  $\times 200$ .

FIG. 11. Section through an older ovary.  $\times 55$ .

FIG. 12. Cross-section through an immature ovary.  $\times 55$ . Fig. 10 represents a portion of same considerably enlarged.

FIG. 13. Longitudinal section through egg of same stage as represented in Pl. XIV., Figs. *H-I*.  $\times 200$ .











## EXPLANATION OF PLATE XVII.

FIG. 1. Surface view of egg in same stage as represented on Pl. XIV., Fig. 7.  $\times 60$ .

FIGS. 2-4. Transverse sections through the egg along the lines similarly designated in Fig. 1.  $\times 200$ . The ectoderm is represented in gray. The mesoderm is represented by the single layer of elongated nuclei which extends, immediately under the ectoderm, from the median line to near the lateral limits of the section.

FIG. 5. A longitudinal section through the median line of Fig. 1. The contour, due probably to the action of reagents, is somewhat too irregular.  $\times 200$ . (The lithographer has given too much shading to the yolk spheres in the lower, deeper portion of the entodermal mass.)

FIG. 6. A transverse section through the blastopore.  $\times 400$ .











## EXPLANATION OF PLATE XVIII.

FIG. 1. Ventral view of hinder part of thorax of a female lobster. The Roman numerals indicate the third, fourth, and fifth ambulatory appendages. Natural size.

FIG. 2. Receptive apparatus as seen from the right side, the right half having been removed. Natural size.

FIG. 3. Surface view of egg in stage represented on Pl. XIV., Fig. *L*.  $\times 60$ .

FIGS. 4-7. Transverse sections made through embryo, as indicated by the horizontal lines in Fig. 3 (4-7).  $\times 200$ . The ectoderm is colored deep gray. In Fig. 7 the entoderm is seen working its way into the yolk.

FIG. 8. Longitudinal section through median line of same stage as Figs. 3-7.  $\times 200$ . The entoderm extends deep into the yolk as a nucleated reticulum. The cells arranged in an irregular oval, around the end of the line *Pb*, enclose a peculiar plasma-like tract, which was unfortunately omitted by the lithographer.











## EXPLANATION OF PLATE XIX.

FIG. 1. Surface view of egg in stage represented on Pl. XIV., Fig. *M*.  $\times 60$ .

FIG. 2. Portion of a section through a segmenting egg which contained but two nuclei.  $\times 50$ .

FIG. 3. Section of an egg in stage represented on Pl. XIV., Figs. *D* and *E*.  $\times 50$ .

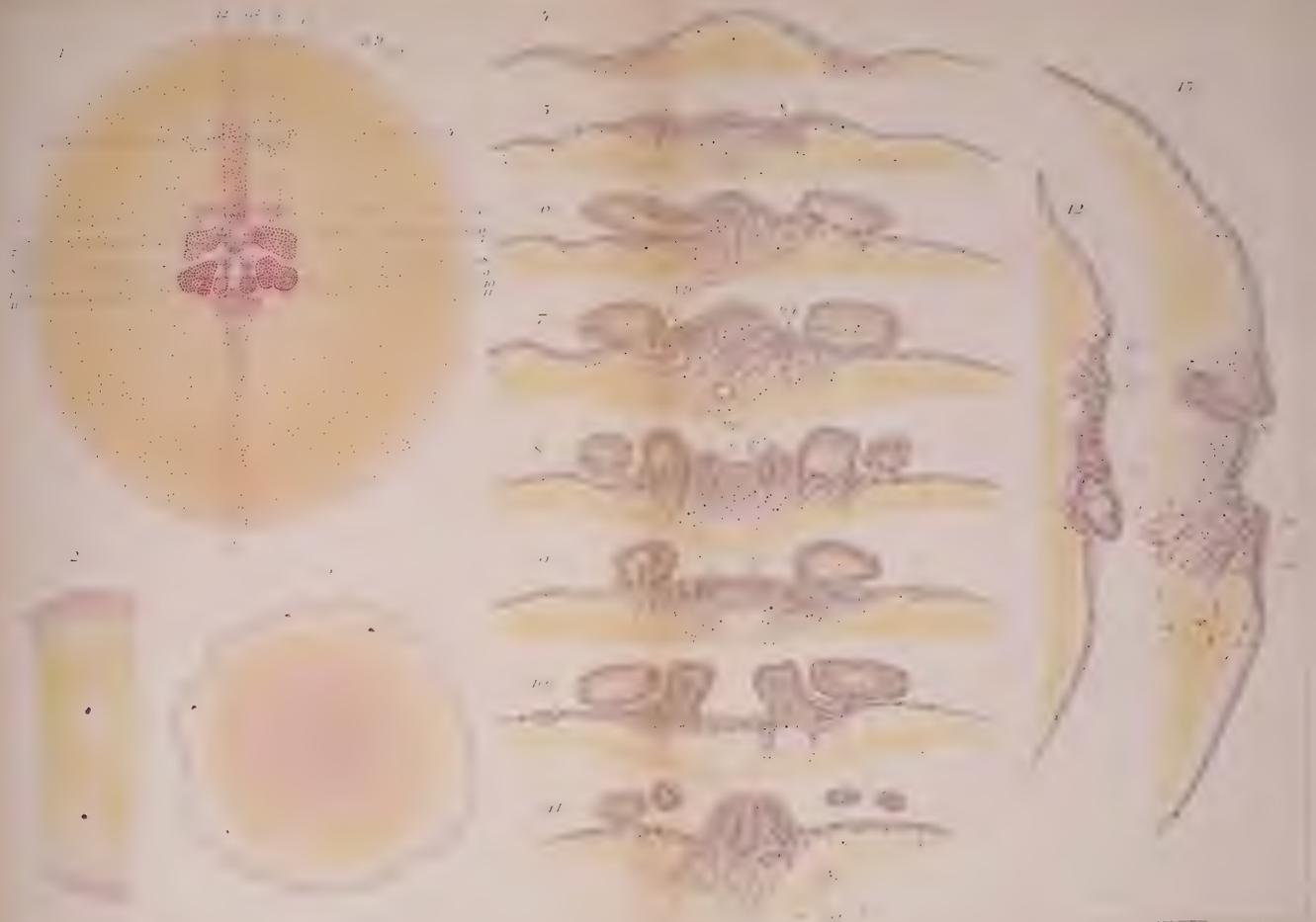
FIGS. 4-11. Transverse sections made through embryo, as indicated by horizontal lines in Fig. 1 (5-5 to 11-11).  $\times 200$ . The ectoderm is represented in a deeper and the entoderm in a lighter shade of gray. Fig. 11 represents, in the median line, a section through the anus.

FIG. 12. Longitudinal section through the embryo, as indicated by the line 12-12 in Fig. 1.  $\times 200$ .

FIG. 13. Longitudinal section through median line of Fig. 1.









## THE SPERMATOPHORES OF DIEMYCTYLUS.

EDWIN O. JORDAN.

SINCE several months will probably elapse before I shall have fully ready for publication my study of the habits and development of the newt (*Diemyctylus viridescens*, Raf.), I here describe in advance some of the more remarkable features in the process of fertilization. Although the process in its main outlines has been recently observed by Zeller,<sup>1</sup> it seems pardonable briefly to supplement his description, both because I observed the process independently while still in ignorance of Zeller's observations, and because, working as I was with the advantage of abundant material, I was able to discover several interesting facts that appear to have escaped Zeller completely.

The fertilization of the Urodela has been until lately very imperfectly understood, and this lack of positive knowledge is the more surprising now that it has been demonstrated by the fine observations of Gasco and Zeller that a few days of ordinarily careful observation at the suitable time of year are all that is required in order to obtain a comprehensive knowledge of the process. F. Gasco has been the pioneer in this field. He was the first to describe the method of fertilization in the European triton (*Triton alpestris*), and a year later he followed this with a minute and spirited account of the amours of the Axolotl, worthy of the highest praise.<sup>2</sup> As pointed out by Zeller, however, Gasco's discoveries have not as yet received due recognition, and in the recent text-books of zoölogy the old view of direct cloacal contact is still adhered to. Nearly a hundred years before Gasco, in 1785, Spallanzani had proved that, at least in the case of several European aquatic salamanders, the fertilization of the eggs is internal, and that there

<sup>1</sup> E. Zeller, Ueber die Befruchtung bei den Urodelen. *Zeitschr. f. wiss. Zool.*, Bd. XLIX., 1890, p. 583.

<sup>2</sup> F. Gasco, Gli amori del tritone alpestre, Geneva, 1880; Les amours des Axolotls, *Zool. Anz.*, IV., 1881, pp. 313, 328.

is no direct cloacal contact between the sexes. Spallanzani was in ignorance, however, of the way in which the spermatozoa entered the cloaca of the female, and believed that the spermatozoa discharged by the male were diffused in the water and thence found their way to the genital opening of the female.

Up to about ten years ago there had been few important advances on the facts established by Spallanzani, and there had been serious retrogression in one respect; namely, that of assuming — in the face of Spallanzani's distinct proof to the contrary — a direct cloacal contact. This retrograde step was hastened by v. Siebold's significant discovery of an accumulation of spermatozoa in the cloaca of the female salamander (*Salamandra maculosa*) in a sort of, "*Receptaculum seminis*." V. Siebold<sup>1</sup> was led to believe that this "receptacle" could be filled with spermatozoa only by means of a true copulation, and this has been until very recently the generally received opinion.

As regards the American newt, the more obvious phenomena of the breeding season have been long known and commented upon. As spring approaches, a crest appears on the tail of the male, already broader than that of the female, the cloacal regions in both sexes appear somewhat enlarged, and both male and female shine in rather livelier colors. All these external features have been greatly exaggerated by some writers; the general appearance of newts captured in April is not strikingly different from that of those captured in October. In one respect, however, the male has added materially to his attractions. All the way up and down the inside of the hind legs, as well as on the adjoining parts of the body, are developed round, black, wart-like elevations. These warts are hard and rough, and undoubtedly aid the male in clasping the female more firmly. They grow yellow and soft and lose their distinctive character soon after the breeding season is past. These black prominences were, I believe, first carefully described by Braun,<sup>2</sup> although they had been noticed by different observers long before his time. The hind limbs of the male are throughout the year much larger and stouter than the corresponding limbs of the

<sup>1</sup> C. T. v. Siebold, Ueber das Receptaculum seminis der weiblichen Urodelen. *Zeitschr. f. wiss. Zool.*, IX., 1858, p. 463.

<sup>2</sup> M. Braun, Ueber äussere Hilfsorgane bei der Begattung von Triton viridescens. *Zool. Anz.*, I., 1878, p. 124.

female, and thus afford a ready means of distinguishing between the sexes. They are also much larger than the fore limbs of both sexes.

It has been suspected by most writers on the subject that the fertilization of *Diemyctylus* is internal, and this has been recently demonstrated to be the case by Gage.<sup>1</sup> The demonstration of internal fertilization is by no means difficult; one has only to isolate any female freshly captured, say between April 15 and June 15, to be convinced that internal fertilization is the normal procedure in this species. Almost every female so isolated will for at least several days after her capture continue to lay fertilized eggs. In one instance an isolated female under my observation laid fertilized eggs for nineteen days after her separation from a male. I shall describe the egg-laying of this species more in detail in my coming paper.<sup>2</sup>

I have found, furthermore, spermatozoa in the cloaca of the female in nearly all the specimens examined between the first of May and the first of July. These spermatozoa are not inside the mouth of the oviduct, as might be expected, but are closely packed in the ducts of two groups of gland-like structures situated in the cloacal wall just below the entrance of the oviducts. These ducts are undoubtedly identical with the "Samentaschen" described long ago by v. Siebold (*loc. cit.*) in the European salamanders and tritons. Blanchard,<sup>3</sup> who has recently investigated the structure of the pelvic and cloacal glands of the Urodela, makes on this point the following statement: "La glande que v. Siebold a décrite dans la cloaque de *Salamandra*

<sup>1</sup> *American Naturalist*, April, 1891, p. 380.

<sup>2</sup> The possibilities of mal-observation may be estimated perhaps by a quotation from a recent paper ("Notes on the Life-History of the Common Newt," Colonel Nicolas Pike, *American Naturalist*, XX., 1886, p. 17): "The males dart about, gyrating round their chosen mates, heading them off in their endeavors to escape, and when they have at last won the victory they seize the females round the lumbar region and remain thus often for hours. The milt and ova pass simultaneously, and the operation takes some time, but it is generally accomplished under cover of darkness. The older females often deposit 150 to 300 eggs at a time, which they attach to twigs in the water or long grass. The eggs are very small at first, but rapidly swell." The eggs, so described, were undoubtedly the eggs of some species of *Amblystoma*. That the "milt and ova" do not pass "simultaneously" is abundantly evident from the observations recorded in my paper.

<sup>3</sup> R. Blanchard, Sur les glands cloacale et pelvienne et sur la papille cloacale des Batraciens urodèles. *Zool. Anz.*, IV., 1881, pp. 9, 34.

*maculosa* femelle, et qu'il a désignée sous le nom de *Receptaculum seminis*, a une situation anatomique et une structure identiques à celles de la glande pelvienne du mâle. . . . Je ne crois pas exacte l'opinion de v. Siebold relativement au rôle physiologique de cette glande chez la femelle, car je n'ai vu dans aucun cas de spermatozoides engagés dans les tubes de cette glande." V. Siebold's careful descriptions and figures would seem, notwithstanding, to leave no doubt as to the presence of spermatozoa in all the species of female Urodela examined by him, and it is certain that in *Diemyctylus*, spermatozoa ensconced in these ducts may be detected without difficulty.

The question as to how the spermatozoa find their way to these snug resting-places is one of considerable interest. Why should they enter these small ducts and there lie dormant, in preference to passing *en masse* up the oviducts, or to entering the alimentary canal, or even to issuing from the mouth of the cloaca? It appears to me probable that the explanation lies in what Pfeffer has called "positive chemotaxis." Pfeffer found, as is well known, that certain chemical substances, as malic acid, attract spermatozoa (positive chemotaxis), and that others, as chloroform, repel them (negative chemotaxis). For example, the mucilage in the central canal of the archegonia of *Pteris* contains a trace of malic acid, and Pfeffer has shown that this amount is sufficient to attract spermatozoa to the mouth of the canal. A similar explanation has been given by some bacteriologists to account for the gathering of leucocytes at inflammatory foci. It is supposed that the leucocytes have been drawn thither in virtue of their chemotactic properties which were brought into play by the metabolic bacterial poisons, or, as now seems more likely, by the freed albuminoid constituents of the bacterial cell.

It seems highly probable that the pelvic gland of the female newt may secrete a substance — proteid or otherwise — with a positively chemotactic effect and thus draw the spermatozoa into its ducts. At all events, such a supposition may serve for a provisional hypothesis. I shall reserve a further consideration of the structure and significance of this gland until my later paper.

The most favorable time to watch the process of copulation is between the first of April and the middle of May. After

about May 15th there is a perceptible slackening in the "Liebesspiel," and spermatophores are rarely discharged after the first of June. The male, heretofore amorous to an extraordinary degree, has by the latter date become comparatively quiescent and unsusceptible.

If at any time during the month of April several pairs of newts are freshly captured from the ponds, and the sexes kept apart over night, the phenomena of copulation may be observed on bringing the animals together in pairs on the following morning. In many cases an interesting courtship precedes the actual clasping of the female. As soon as the male becomes aware of the presence of the female in his neighborhood, he becomes somewhat agitated, and usually begins to move stealthily towards the female with an air of exaggerated caution. It not infrequently happens that the latter, on perceiving his approach, darts away in a state of great excitement, and has to be patiently approached again and again by her unwearied suitor. When the male is finally allowed to come into the immediate neighborhood of the then passive female, he usually enters upon a series of contortions resembling those witnessed at the time of the discharge of the spermatophores. After a few seconds of this suggestive "Vorspiel" the male vaults quickly upon the back of the female and clasps her tightly around the body with his strong hind legs. When the animals have been for some time in captivity, or a number of individuals of both sexes are together in one aquarium, this deliberate courtship is not observed, and the male clasps the female without any ceremonious preliminary. It often happens that he first catches the female by the hinder part of the body, but if he retains his hold for longer than a few minutes, he invariably moves forward until he has the female securely clasped under her throat, either directly before or directly behind her fore legs. Once in this position no attempt of the female can dislodge him, and he may cling there for hours. On a number of occasions I have seen females appear much the worse for this rough usage, and on one occasion an apparently robust female lay as if dead for several hours after the male had left her, although she eventually revived.

When the male is thus mounted, a period of comparative quiet ensues, lasting from thirty minutes to several hours in individual

cases. During this period the animals remain on the floor of the aquarium in almost exactly the same spot, and the male is not, as incorrectly stated by most observers, "jerking the female unmercifully around during the whole time." On the contrary, both animals are well-nigh motionless, with the exception of the often-described fanning movement of the tail of the male. This half-stroking, half-fanning motion is kept up with more or less rhythmical regularity, first on one side and then on the other, and probably serves to excite both animals, although heretofore it has been not unnaturally regarded by many observers as for the purpose of diffusing the spermatozoa throughout the water. The female responds by slowly raising her tail until it forms an angle of  $45^\circ$ , or even a right angle, with her body, and occasionally repeats in her turn the slow fanning movement.

From this condition the male passes gradually into a more violent stage, which has been wrongly stated by some writers to extend over the whole of the foregoing period. This more violent stage usually lasts for only about ten minutes, and during this time the unhappy female is dragged, jerked, and pulled over the whole floor of the aquarium, the entire body of the male meanwhile quivering with intense excitement. The cloaca of the male at the same time begins to swell and to show a few whitish papillæ projecting from the sides. At the climax of his agitation the male, after a few rapid bendings of his body from side to side, leaves the female, and with his tail slightly raised, his cloaca widely distended with numerous white protruding papillæ, throws his whole body into a series of rapid and strenuous undulations, and waits for the female to follow him. If she does this and presses her head lightly against his tail and cloacal region, the male soon deposits a spermatophore and then creeps on to a distance of a few centimeters, where, if the female still continues to follow him, he soon deposits another. I have often seen one male discharge as many as three spermatophores in this way, but have never seen one individual discharge at one time more than this number.

The spermatophore consists, broadly speaking, of three parts: a thick, irregular gelatinous mass about six millimeters in diameter which adheres to the bottom of the aquarium; a tough elastic spine projecting upwards from this base; and, borne on

this spine, an approximately spherical mass of spermatozoa about one and one-half millimeters in diameter, this mass being a sort of concretion of small balls of spermatozoa. The whole structure is very simple as compared with the elaborate bell-shaped spermatophore of *Triton alpestris* described and figured by Zeller (*loc. cit.*).

After the male has deposited his first spermatophore in the manner above recorded, he moves ahead a few centimeters with the female closely following him. In this forward movement of the female she quite naturally brushes over the spermatophore, and, if all goes well, the mass of spermatozoa adheres to the cloacal lips, and thence passes, in part at least, into the cloacal chamber. More frequently the spermatozoa adhere to the rough skin in the neighborhood of the cloaca, and do not come into close relations with the opening itself. A considerable number of the spermatophores, moreover, are not touched at all by the female, but are passed by on one side or the other. I should think that in my aquaria about one spermatophore in five fulfilled its mission, but it is possible that in the ponds the number of failures is not so large.

As to the way in which the spermatozoa actually enter the cloaca of the female there has been some difference of opinion. Gasco has described the female Axolotl as holding the spermatophore firmly with her hind legs and pressing the mass of spermatozoa into her cloaca, but Zeller has been unable to confirm this observation. Zeller at first thought that the European triton took up the spermatozoa actively by means of the widely opened lips of her cloaca, but he has very lately<sup>1</sup> abandoned this view, and now holds that the spermatozoa, by virtue of their own activity, pass up between the *tightly closed* cloacal lips. Zeller attempts no explanation of the fact that the spermatozoa choose to pass into the female cloaca rather than into the surrounding water. Indeed, it is difficult to understand just why this movement in precisely the right direction should occur, unless we suppose a positively chemotactic influence to attract the spermatozoa into the cloaca. It is not improbable that the pelvic gland of the female may be stimu-

<sup>1</sup> Ernst Zeller, Berichtigung betreffend die Samenaufnahme der weiblichen Tritonen. *Zeitschr. f. wiss. Zool.*, LI., 1891, p. 737.

lated to secretion during the "Liebesspiel," but I do not care to enter at present into a full consideration of that question.

In *Diemyctylus* the pointed spine above described sometimes plays an important part in the entrance of the spermatozoa. I have in several cases, in females watched from below, seen the tip of the spine covered with spermatozoa actually pass directly between the closed cloacal lips. The elastic spine, easily bent down by the passage of the female over it, and as easily springing up when the entrance to the cloaca is reached, functioning thus as a sort of penis, would seem admirably adapted for effecting the entrance of the spermatozoa, but I do not think that the spermatozoa obtain an entrance only in this way. The springing up of the spine is apparently of rather infrequent occurrence, and I am constrained to think that this is not the sole and invariable mode of entrance. It much more frequently happens that the cloacal lips and the surrounding skin are thickly smeared with spermatozoa, and I am inclined to believe that, as in the European form, the spermatozoa then find their way to the "Samentaschen" by virtue of their own activity.

CLARK UNIVERSITY, WORCESTER, MASS.,  
June, 1891.

## COMPOUND EYES OF ANNELIDS.

E. A. ANDREWS.

### I. POTAMILLA.

THINKING the peculiar pigmental organs upon the branchiæ of certain tubicolous, sedentary Polychætæ would repay investigation, as being apparently compound eyes entirely different from anything in the higher Annelids, and as possibly giving aid in the interpretation of Arthropod eyes, I availed myself of the opportunities offered at the United States Fish Commission Laboratory in Wood's Holl, Massachusetts, to study several specimens of *Potamilla* obtained there in the summer of 1889, and again in 1890.

The species examined is undoubtedly *Potamilla reniformis*, of Malmgren, though the number of eyes may be as many as seven or eight upon each branchia, while Malmgren figures only three: small individuals have, however, as few as three, or even one or two; and others a variable number, even different branchiæ of the same individual presenting considerable variations in this respect. Though this New England form was at first referred to a new species, *P. oculifera*, by Professor Verrill, its identity with the European is recognized by him in more recent publications.

This Annelid lives in a leathery tube projecting somewhat from holes in gasteropod and bivalve shells, etc. From the end of this tube the cephalic branchial plumes are expanded as a circular series of radiating stems, each bearing two rows of branchial filaments, all directed anteriorly in the fully expanded condition, when the whole apparatus stands about at right angles to the long axis of the body. In this state the eyes are upon the posterior or outer sides of the main stems of the branchiæ, a row of three to eight upon each of the twenty stems. They are not arranged with much symmetry, but yet tend to lie in concentric rows upon all the branchiæ collectively, since the proximal ones occur at about the same distance out upon all.

The branchiæ are marked by transverse bands of dark red pigment, not extending on to the outer side of the main stems where the eyes are; yet these frequently lie in the general areas of such pigmented bands.

Each eye is a convex, hemispherical protuberance upon the outer or convex side of the main branchial stem; not, however, upon the median line, but to one side, as best seen in transverse sections (Fig. 14). The diameter of an eye is about  $92 \mu$ ., but varies much, smaller eyes being often found toward the tip, or even interpolated between larger ones along the branchia. The color is uniformly dark red, as usually seen, but in strong sunlight (Fig. 1) the reflected light is of a golden yellow color over the surface. Here, also, it is seen that, though the surface is uniformly convex and homogeneous, yet when the microscope is focussed a little beneath the surface, there are conspicuous rounded areas of dark red scattered irregularly through the reflecting pigment, and each appearing like a limpid, liquid mass, transmitting red light from below. These small, clear areas represent what has been known as the component elements of the so-called compound eye, and which I will speak of as the refracting cells.

The histological structure of these eyes was first studied by maceration and disassociation. Macerated in Bela Haller's liquid, the eye is readily broken up into a number of elements roughly corresponding to the above dark red areas of the surface preparation. Each element has the form of an elongated cone, the base peripheral in the eye, the prolonged apex central; each is a clear mass covered over by red pigment, and having its basal part easily separable from the surrounding pigment. In potassium bichromate macerations the elements are isolable as large, conical cells (Fig. 2) covered by red pigment granules, but showing the clear, axial portions in places, shimmering through the thin pigment envelope. This clear, axial part of the cell stains with methyl green, as does also a long process extending from the apex of the cell, the central end in the eye, and covered by separate red pigment granules. Some of these cells have bluntly rounded bases, as in the figure; others, obliquely pointed bases with no pigment over them. In addition to these large cells, refracting cells, there are also much more slender cells (Fig. 3), having a clear, nucleus-like body within the thick

pigment, and a less evident process from the apical or central end.

With little pressure and percussion much of the pigment may be removed from the outside of the refracting cell, and then the axial part is seen to contain a nucleus about the middle of its length, and to present in the basal, peripheral part a peculiar refracting body staining dark blue in the methyl green.

The most intelligible views of the axial part of these refracting cells were obtained after maceration in sea-water containing a small amount of sulphuric acid, — a method suggested to me by Professor Patten. The pigment, now of a bright red color, is no longer firmly attached to the cell, but readily falls off, revealing the clear, non-pigmental, axial parts. In the central part of the cell the conspicuous nucleus (Fig. 4) stains dark red with Mayer's acid carmine, or lavender color with Czokor's cochineal, or faintly bluish in methyl green, just as do the nuclei of the ordinary epithelial cells of the branchiæ. The large, peripheral end of the cell is sharply defined, refracting, and very noticeable, as containing a clear, highly refracting, vase-shaped body, nearly filling this end of the cell. This body or inclusion stains very dark blue in methyl green, and dull red, less intense than the nucleus, in Mayer's acid carmine. The peripheral end of this inclusion is a cylindrical projection passing to the centre of the basal or peripheral end of the cell, while the central end is abruptly truncated, and forms the base of the vase itself, and coincides with a sudden transition from this peripheral part of the cell to that next to be described. The axis of the cell in this last region, between the above inclusion and the nucleus, presents a series of rounded disks, or parts of the cell, differing in refractive effect from the rest, and slightly differentiated when stained in methyl green. Finally, the apical part of the cell beyond the nucleus is homogeneous, and passes over into a slender process usually broken off in these preparations.

This refracting cell thus has within its protoplasm a nucleus, a remarkable, very highly refracting body of peculiar shape, and between these an axial series of faintly differentiated parts.

The whole is covered by pigment, and has often adhering to it smaller pigmented cells with a single nucleus, but with neither of the above unusual parts characteristic of the large refracting cells.

Such of the refracting cells as have oblique, clear bases are now seen to have also a vase-shaped inclusion asymmetrically encased in the peripheral base of the cell, as shown in Fig. 5.

The peripheral portion of one of these refracting cells may be readily separated from the rest, and then, by pressure, the contained vase-shaped inclusion forced out of it. In this process a circular, cup-shaped, slightly granular disk, with a central hole or depression, is pulled off from the neck and shoulders of the vase, leaving it naked and clear. This cup is especially well seen after gold chloride staining, its central opening or deep depression corresponding to the small, cylindrical neck or process of the vase. In this way we remove the softer base of the cell from the more resisting, highly refracting inclusion, the above vase-shaped body.

When strong potash is used after the last-mentioned maceration, the broken-off basal ends of the cells appear very plainly as vase-shaped bodies (Fig. 6) enclosed in faintly granular material, the cell body, especially noticeable at the peripheral end of the cell, as a circular region of the cell representing the above-described broken-off disk. The action of potash upon the axial part peripheral to the nucleus of the cell is to produce rows of drop-like areas, evidently artificial products.

Using the same maceration, but applying strong nitric acid, the vase-shaped bodies turn bright yellow and become swollen out of shape, the color turning brighter upon the addition of ammonia; this same reaction is seen in the case of the "cartilage cells" of the branchiæ, which turn more intensely yellow on the addition of ammonia.

When the isolated basal ends of the cells are treated with hydrochloric acid, the pigment becomes diffused through the vase, giving it a dark red-brown color, with certain oil-like drops or granules in its centre, though the general shape and consistency are retained.

The result of this examination by maceration, as regards the structure of any one of the refracting cells, may be expressed by the accompanying diagram (Fig. 1 in text). The axial part differs from the vase-like inclusion in being less refracting, much less resisting and definite in outline, as if merely clear protoplasm with less clear interpolations.

The pigment of this cell is confined to a thin, ensheathing

layer, which, in fact, might be regarded as outside the cell, from the definiteness of the apparent cell outlines when deprived of pigment.

Such macerated eyes before disassociation show the clear, refracting cells, radiating out from the central region of the eye towards the cuticle that covers the entire organ, the small process of each vase-shaped inclusion coming, apparently, into contact with that cuticle. These cells are now seen to be imbedded irregularly in a mass of pigment cells, such as seen in Fig. 3, each refracting cell being one of the clear, red areas seen in Fig. 1, where we are to suppose the red light transmitted through the clear, axial parts of the cell comes to the observer as different from that reflected from the more peripheral, similarly pigmented parts. On the addition of strong potash the pigment is removed, and the twenty to forty refracting cells seen in optical section are distinctly recognizable as the same made out in maceration, each being now somewhat shrunken away from its fellows, and from the smaller cells; pigment cells.

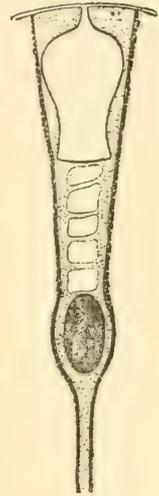


FIG. 1.

Branchiæ depigmented and macerated in ten per cent nitric acid show that the eye is the end of a gradual thickening of the epidermis, an elongated ridge rising gradually, to end suddenly at the distal edge of the eye. Hence longitudinal optical sections show the epidermal cells becoming gradually longer as the eye is approached from the proximal side, longest in the eye itself, and finally suddenly returning at the distal side of the eye to the usual cuboidal epidermis of the rest of the branchial surface. Transverse sections, on the other hand, show this ridge passing off gradually and equally on each side into the common cuboidal epithelium. The eye is thus, as it were, at the tip of a rudimentary external process, a mere ridge, however. The structure of the eye, as now seen, is evidently merely a modification of the general epithelium of the branchia, an elevation in which many cells have nuclei near the outer, peripheral ends; others, the large, refracting cells, their nuclei much nearer to the central part of the eye, remote from the cuticle. The arrangement of the two sets of cells is not definite; the pigment cells sur-

round the refracting cells usually, but not in any precise number or positions.

This formation of the eye from a hemispherical thickening of the epidermis covered by the ordinary thin cuticle, having the cells thickened at the large, peripheral surface, and drawn out into fibre-like processes where crowded at the central part of the eye, as well as the irregular arrangement of the variable number of refracting cells packed in amongst the ordinary pigment cells, may be easily seen also in preserved branchiæ that are overstained in picro-carmin, depigmented in Grenacher's liquid, and mounted in glycerine.

It is to be noted, in addition, that the longitudinal bands of cilia found along the branchial stem at the junction of the outer and lateral faces, are interrupted where eyes occur, so that the eye itself is not ciliated: this is shown in transverse sections (Fig. 14).

In examining fresh, living branchiæ, however, I saw, upon one occasion, what appeared to be stiff, seta-like projections from the eye; but these were then disregarded, as being only appearances produced by the adjoining cilia of the branchia.

To supplement the knowledge of the eye obtained as above, actual sections were resorted to; these confirm all the above points in the structure of these so-called compound eyes. Longitudinal sections, stained in Kleinenberg's hæmatoxylin (Fig. 7), show the elongated, epithelial cells proximally, and the short, cuboidal ones distally; the unmodified, thin cuticle over the eye; the oblique, radiating position of the cells that make up the pigmented eye; the presence of cells with peripheral nuclei, and of those with more centrally placed nuclei; the occurrence of clear, refracting inclusions, of which the above section happens to show only a very small number, two; and finally the passage of the elongated, central ends of the cells underneath the proximal epithelium as a band of nerve-processes containing a nucleus here and there, one only shown in this section.

This nerve may be followed through several transverse sections as a rounded cord of fibrils (Fig. 13) lying imbedded in the epidermis proximal to the eye and at the bases of these cells. Farther down it seems to be resolved into smaller branches, or a network, perhaps, and could not be followed into any direct connection with the two large, longitudinal nerves of the bran-

chia (Fig. 14). These latter nerves, however, are seen to give off branches, at certain places, into the epidermis, and so, if there be an epithelial network of nerves, there may be a connection between the eye and the two large trunks. In gold chlorid and other surface preparations, however, I have not been able to find these optic nerves at all, nor to discover any such epithelial nervous system.

Transverse sections of the eye show its component cells radiating out, fan-like, from a central point, so as to present symmetrical right and left sides, and showing usually several, often a considerable number of the refracting cells distinguishable from the smaller pigment cells by the possession of the peripheral, clear inclusion, as well as by the fact that their nuclei are situated centrally as compared with the more peripheral nuclei of the ordinary pigment cell.

Tangential sections (Figs. 8, 9, 10) taken successively nearer the central part of the eye show the relative positions of the simply pigmented and the refracting cells, as well as the position of nuclei and the structure of these latter cells at different levels. Just within the cuticle (Fig. 8) the stained inclusions of the refracting cells are surrounded each by the clear part of the base of the cell. Each refracting cell is imbedded in the red pigment, in which are irregularly scattered the nuclei of small pigment cells. The boundaries of the cells are not seen, but some pigment more densely aggregated about the clear cells is probably to be regarded as belonging to the surface of these refracting cells. The refracting cells, traced into sections nearer the central part of the eye (Fig. 9), show as clear, stained areas the peculiar nodulated or roughly lamellated axial part of the cell seen in Fig. 5, between nucleus and inclusion. No nuclei are seen at this level, but large masses of pigment between the above cells. Still farther down (Fig. 10), sections show the nuclei of the refracting cells, each surrounded by a little clear protoplasm and by much pigment belonging to these and to the smaller pigment cells.

Sections still nearer the central area of the eye show only transversely cut, filament-like, pigmented ends of cells, seen best where shrunk from one another, as in material hardened in Merkel's liquid.

When the eyes are depigmented in Grenacher's liquid, either

*in toto* for twenty-four hours or on the slide for about two hours, all that was made out in macerations regarding the structure of the refracting cells may be seen again in sections, as also the relative arrangement of these cells and the smaller pigment cells. Thus transverse sections, such as Fig. 11, show the transition of the ordinary epithelium into that forming the eye, the peripheral position of nuclei of small pigment cells, the more central position of the larger nuclei of the refracting cells, as well as the structure of these latter identical with that seen in isolated cells.

The inclusions have often a clearer, very highly refracting central part, that may be exposed by a section cutting one side tangentially, as in one case in the above figure. In many preparations, both sections and surface views, this central or interior part of the inclusion contains a number of minute drops or vacuole-like spherules seen in Fig. 12. The basal end of these refracting cells, their cup-like part separated in macerations, is clear and somewhat vacuolated in sections, as if having a watery consistency readily acted upon by shrinkage, etc., in the process of preparation. The axial part between the nucleus and inclusion is sometimes made of alternating areas, as in macerations; more often, however, granular, and even entirely clear, so that one is led to suppose this region easily changed by different reagents.

The cell outlines are faintly marked, in various methods of staining, and show the necessarily radiating arrangement of the cells in fitting into the hemispherical eye mass. The marked difference in shape, diameter, and position of the nuclei of the two sorts of cells is especially noticeable; many sections show those of the refracting cells arranged very uniformly in a circular arc, while those of the simple pigment cells have no constant distance from the cuticular surface of the eye.

The cuticle over the eye is very thin and delicate, as elsewhere, and neither in sections nor in any other mode of preparation could any apertures in it be seen corresponding to the projections of the inclusions, yet such may exist.

In tangential sections the same appearances are met with as in preparations having pigment, except that the nuclei are much clearer and their positions more definitely determinable. As seen in a section (Fig. 12) near the surface of the eye, the nuclei

of the small pigment cells are not definitely arranged about the refracting cells, but so that their cells are to be regarded as filling in the spaces left amongst the large refracting cells. In the inclusions of these refracting cells granules or spherical droplets are often seen, as already noticed.

In connection with these eyes of *Potamilla*, the common pigmented, epithelial cells of the branchiæ may be noticed. As indicated in Fig. 1, the pigment of the large, transverse, colored areas of each branchia is arranged in a reticulated fashion, as seen magnified; in fact, these reticulated pigment lines correspond to the cell boundaries. That is, the ordinary pigmented, epithelial cells often have their pigment granules aggregated about their lateral surfaces as well as towards their cuticular, outer ends, so that surface views frequently show the axial part of each cell more nearly free from pigment, though this is quite dense as seen from a side view. A surface view, or an optical, transverse section, thus may present an appearance similar to that shown in Fig. 9 for a tangential section of the eye, only the pigment is much less, lighter, obviously confined to the parts of the cells near their boundaries, and the clearer, central parts are not as definite nor as refracting as in the eye.

## II. SABELLA.

The reputed eyes upon the branchiæ of several other Annelids have also been examined, though less thoroughly than in *Potamilla*. Of these, *Sabella microphthalmia*, Verrill, is very abundant at Wood's Holl, living in tubes, and having transverse bands of pigment upon the branchiæ, much as in *Potamilla*. The so-called "eye spots" are not by any means confined to the regions having pigmented filaments, the transverse bands, but occur all along the outer side of each branchial stem in indefinite numbers. These dark spots or blotches present no regularity, but form series right and left of the median line of the branchia, varying much in size, shape, position, and intensity of color. Some spots may be as broad as  $70 \mu$ ., others merely single pigment cells, with intermediate conditions.

In a very young specimen, obtained in 1885 at Beaufort, North Carolina, and about 5 mm. long, inclusive of branchiæ,

there are but six or seven spots upon a branchia, each a collection of about as many pigment cells.

Macerations show only simple pigment cells, much like the small pigment cells of the eye of *Potamilla*. Surface views also fail to indicate any refracting bodies whatever.

In sections the spots occur here and there, and are often only one or a few cells with pigment granules in them, and nothing else to distinguish them from the ordinary epithelium over the branchia. In some cases, as seen in the transverse section, Fig. 15, the pigmented cells are club-shaped, larger at the outer ends, and hence crowded into a triangular arc in the section. The outer, swollen ends may also contain less pigment, appearing vacuolated and somewhat clear, but showing no trace of any special refracting body.

It will be noticed that the epithelial cells are much elongated and are slender, with the nucleus near the base, where the cell is in contact with the heavy basement membrane; occasionally a nucleus appears high up near the outer end of the cells, apparently in a filamentous cell body, this occurring both in pigmented areas and in non-pigmented areas of the epithelium. Now when the spot is depigmented, as in *Potamilla*, only these elongated cylindrical cells and their nuclei are seen, no inclusions, nor refractive bodies, nor even cuticle, for the cells seem to have an exceeding delicate cuticle, if any at all.

In some tangential sections, however, certain larger, clear cells are seen, many times wider than the common epithelial cells, and irregularly scattered amongst them, as in Fig. 16.

These clear areas appear to be merely non-pigmented, watery, or vacuole-like parts of the protoplasm in the swollen, outer ends of a few cells, and certainly have no such appearance as the refractive parts in *Potamilla*.

The "eye spots" of this Annelid are thus scarcely comparable to those of *Potamilla*, but are to be regarded as mere areas of pigmented, epithelial cells, in which a few may be somewhat clearer at the outer end.

The case stands quite differently with a large *Sabella* very common along the shores of Green Turtle Cay, Bahamas.

This fine species is undoubtedly *S. melanostigma*, of Schmarida (14), as more fully described by Ehlers (8), supposing that both had only small, immature specimens. However, I find two rows

of uncini which would refer it to the genus *Sabella*, as restricted by Malmgren (15). As Ehlers has noted, there are here four or five pairs of conspicuous dark red eyes upon the outer side of each branchial stem, the pairs separated by a very long interval, and the two eyes in a pair not usually exactly opposite, but one more distal, the other more proximal. Each organ has about the same size as that of *Potamilla*, and has a similar position at the union of the lateral and outer faces of the branchia, but more upon the outer face (Fig. 17). Moreover, each is less prominent, more elongated longitudinally, though in this section across its distal end it appears more prominent. Here, again, these organs occur upon parts of the stem bearing the pigmented filaments; that is, in the general regions of the transverse color bands.

As the material was not especially prepared for this work, these eyes could not be as satisfactorily examined as in the above cases, but surface views and sections, pigmented and depigmented, give the following results.

The eye has the same structure as that of *Potamilla*, with but few minor differences.

The cuticle is very thick, compared to the above case, and sometimes presents slight pits, as seen in surface view or on section, which are due to the fact that the refracting inclusions are not only firmly attached to but even continuous with the cuticle, so that a depression may occur at the centre of the base of each inclusion. Presumably, this is due to shrinkage in preparation, but may possibly exist in the living eye. The attachment does not extend over the entire base of the conical inclusion, but leaves a peripheral protoplasmic area, as in *Potamilla*, though but a very thin one indeed (Fig. 18) between part of the base and the cuticle.

Macerations of this hardened material leave no doubt as to this continuity of inclusion and cuticle (Fig. 19), the conical mass being frequently obtained *firmly* attached to the cuticle, or torn off and showing a distinct scar.

As far as could be made out without the aid of fresh material for maceration, the refracting cells have otherwise the same structure as in *Potamilla*, the axial portion, however, presenting more numerous and fainter transverse areas of clearer and less refracting material. Hence the idea of this cell would be diagrammatically expressed somewhat as in the accompanying

figure (Fig. 2 in text). Here it must be noted, however, that the relations of the pigment in the cell cannot be made out satisfactorily from sections, and are hence put into the diagram as they probably exist, judging from successive tangential sections.



FIG. 2.

In sections that are not stained the pigment of each refracting cell has a decidedly golden yellow tinge as compared with the dark red granules in the other cells of the eye. Some common epithelial cells have this same yellow pigment; others, dark pigment.

The characteristic dark red spots, 2 to 4 mm. in size, upon the body of this animal, one on each side, both dorsal and ventral to the parapodial region of each somite, were also examined in surface views and sections, but proved to be merely special aggregates of the epidermal glands, each surrounded by pigmented, epidermal cells, so that a surface view may present a reticulum of pigment with clear interstices. This was seen by Schmarda, who suggested they might be eyes.

A much smaller Annelid found with the last has equally interesting branchial eyes. This species seems to be Ehler's *Dasychone conspersa* (8), and is perhaps the same as the *Sabella melania* of Schmarda (14), while having many resemblances also to *S. (Dasychone) cingulata*, Grube (6).

Along the outer face of the branchia is a series of filamentous processes in pairs, and usually, not always, in the interval between two successive pairs, but on the lateral faces of the branchial stem, there is also a pair of eyes, one eye on the right, one on the left lateral face. On each face, then, the eyes occur at somewhat regular intervals of about 7 mm.

Each is about 70  $\mu$ . wide, a prominent hemispherical elevation much as in *Potamilla*. Here, however, the general appearance is very markedly different, owing to the fact that the pigment is drawn away from the surface for a distance of 16  $\mu$ ., leaving thus an outer, clear, refracting layer of that thickness. This layer is noticeably made up chiefly of forty or more radiating, pear-shaped, very highly refracting bodies, the inclusions, with only their inner tips buried in the central pigment mass.

The general position of the eyes and this division into central pigmented and peripheral, clear zones is well seen in transverse sections of the branchia (Fig. 20).

Whether this position of the pigment is normal or constant in life, or perhaps varying with the illumination, or withdrawn in process of preparation, remains an open question. In maceration the pear-shaped inclusions are each seen inside a clear cell with the pigment as if shrunk towards the conical tip of the inclusion, which it partly surrounds.

The structure is the same here as in the last Annelid examined (Fig. 21), and here also the isolated inclusions may still adhere to the cuticle (Fig. 22), yet not as firmly as in *S. melanostigma*, for the evident reason that the point of union is much reduced, often eccentric, and usually broken in preparation.

Though the axial part of the refracting cells shows no transverse striation, I judge this is due to the poor preservation of the material as compared with that used in the above cases, and that probably the structure is here also much as indicated in the diagram (Fig. 2).

A beautiful yellow *Sabella* taken with the preceding two has branchial organs, presenting a most unexpected structure, at first sight entirely different from the branchial eyes previously described.

This Annelid may be put into the genus *Hypsicomus* of Grube (19), but does not agree with any described species known to me.

The eye spots form a row of about thirty-four to forty red-brown, elongated, quadrangular areas on each lateral face of a branchial stem, extending, however, from the base to about the middle of the length only, and there gradually ending as smaller, less crowded specks. Each spot is about  $37 \mu$ . by  $15 \mu$ ., and separated from the adjacent members of the row by a somewhat constant interval, varying from  $30 \mu$ . to  $60 \mu$ .; being thus at places nearly as numerous as the pairs of branchial filaments there. Irregularity in the degree of separation is accompanied by irregularity in direction of the long axes of these areas, most being elongated in the axis of the branchia, others set diagonally and even at right angles to that axis, but not with the regularity mentioned by Ehlers in *H. circumspiciens*. Closer observation of an eye shows that it is an elongated mass of pigment buried beneath the surface, not projecting as in the previous animals,

yet bearing at one end what from surface views appears as a single ellipsoidal, highly refracting body, very slightly protruding above the general level of the cuticle. This body is free from pigment for about 30  $\mu$ ., and then is buried in the pigment mass: in most eyes it lies at the end towards the base of the branchia, but in oblique eyes it faces towards the inner or outer side, never towards the top of the branchia.

There is thus but a single refracting body for each eye.

Besides the pigment of the eyes similar pigment is scattered in a few epidermal cells separate, or aggregated in small patches at places, and then resembling eyes. Moreover, there are transverse bands due to the presence of pigment in certain sets of branchial filaments.

Sections show the relation of the single refracting body and the pigment cells of the eye to be as follows: The refracting body projects inwards obliquely, and is surrounded beneath the cuticle by epidermal cells bearing pigment in their outer ends where adjacent to the side surfaces of this refracting ingrowth; hence the appearances shown in a transverse section such as Fig. 23, while a section parallel to the long axis of this ingrowth (Fig. 24) shows also a peculiar pigmented cell applied to the abruptly truncated end of this ingrowth, and containing a spherical, highly refracting, and very faintly granular body that does not stain with hæmatoxylin. The pigment is most abundant in the cells about the apex of the refracting body and less so towards its base, not appearing at all in any of the cells that come out to the cuticle; hence the appearance the organ presents of lying beneath the cuticle. The oblique position of the refracting body renders it possible to be completely enveloped by an epidermis not as thick as the body is long, while making the line of vision very far from vertical to the branchial surface.

A similar section depigmented in Grenacher's liquid and double stained in hæmatoxylin, followed by borax carmine, gives a well-differentiated result in which cuticle, refracting ingrowth, and the abundant connective tissue matrix are all bright red, while the nuclei are blue, and the pigmented parts of the epidermal cells faint yellow. Such a section of the apical or innermost part of an eye is represented in Fig. 25, showing clearly the pear-shaped terminal cell containing the

spheroidal refracting body, and pigmented like the adjacent cells that apply their inbent ends against the lateral sides of the cuticular ingrowth: the nucleus of this cell, also, has a characteristic triangular section.

A series of sections at right angles to the long axis of an eye leaves no doubt as to its structure. In one series there were twelve sections, each  $5 \mu$ . thick; of these, beginning at the outer end of the eye, the first four or five cut only the common epidermal cells and the oblique base of the refracting body where still continuous with the cuticle: passing inward, this body is next represented by a series of perfectly circular disks, separating more and more from the cuticular surface, diminishing rapidly in diameter, and entirely surrounded by epidermal cells applied to its circumference, and becoming more and more pigmented towards the apex of this body. Thus, in the 8th and 9th section we find the apex (Fig. 26) far removed from the cuticle, and surrounded by three pigment cells. The next two sections do not cut the refracting ingrowth, but the terminal pigment cell and its spherical refracting body, which is circular in transverse section and much larger than the truncated apex of the above ingrowth. Finally, the nucleus of this section is cut, forming the end of the long axis of the eye.

The conical shape of the long refracting body deduced from the above section is evident in macerations (Fig. 27), where its enlarged base is entirely continuous with the cuticle, and its apex as abruptly truncated as in the inclusions of *Potamilla* and *Sabella*, which it essentially resembles.

A brief reference to the branchiæ of the only member of the Serpulidæ examined, *Hydroides dianthus*, Verrill, so common at Wood's Holl, will show that there are here no eyes such as above described, nor, in fact, any obvious organs of sense.

Though the branchiæ are usually most brilliantly colored and variously banded, yet all the pigment is readily soluble in alcohol, and leaves no dark spots of any kind as indications of possible sense organs. Moreover, careful examination and sectioning shows only the structure indicated in Fig. 28, where the thick cuticle and elongated epidermal cells present no discovered eye-like modification; the two peculiar structures occurring in the angles of the section being longitudinal nerves cut

across. These nerves lie in, or at the boundary of, the epidermis, in a groove, and send numerous large and small branches towards the filamented side of the branchia.

### III. HISTORICAL.

Before discussing the preceding facts concerning the so-called compound eyes of certain sedentary Annelids it seems advisable to review the literature upon this subject, at least as far as the published figures and the less superficial descriptions of the eyes are concerned.

The existence of pigment spots, or pigmented organs, upon the branchiæ of certain tubicolous Annelids was too patent a fact to be long overlooked, and figures of them recur frequently in systematic works.

They are plainly shown by Dalyell (1) as red spots, occurring in seven or eight regular, transverse rows upon the branchial apparatus of an Annelid he speaks of as *Amphitrite ventralabrum*, and in more numerous pairs in *A. bombyx*. No careful examination of them, however, seems to have been made till Kölliker (2) studied them both in an Annelid obtained at Naples, and in the one previously known to Dalyell, in Scotland; nor was any subsequent investigation of their minute structure attempted for several decades. He found in the former species one "compound eye" upon each of the eight branchiæ, near its base. The eye is composed of fifty to sixty elementary eyes, each with a cuticle, special refracting, pear-shaped body, and a crystalline cone surrounded by brown-red pigment. The other form, studied some years later, he calls *Branchiomma Dalyelli*, and in this finds eighteen to twenty pairs of hemispherical, projecting, compound eyes, arranged at regular intervals on the outer side of each branchia.

In each eye there are fifteen to eighteen clear, glass-like, pear-shaped, crystalline cones, imbedded in granular, brown pigment.

The blunt base of each cone projects somewhat from the main mass of pigment, yet some of the latter extends up to the cuticle.

The cuticle presents a depression at the centre of each lens, or area, over a cone, and into this fits a small projection of the

cone itself. From this a central canal extends in some cases into the centre of the cone.

He states that the consistency and chemical nature of these crystalline cones forbids any idea of glandular structure.

Near each eye is a lid-like, projecting structure.

A few years later Claparède (3) figures a large organ at the end of the branchia in *Protula Dysteri*, Huxley, "hanging like a fruit from a tree," and composed of compressed, pear-shaped, clear cells, 9  $\mu$ . in diameter, arranged about a central cavity. Though he knows no function for this organ, I am inclined to regard it as undoubtedly belonging to the same category as the so-called compound eyes, though Huxley (18) had described it as a collection of granular cells, and so that one would infer a glandular rather than a sensory function. In a later work (4) he gives surface views and descriptions of compound eyes in *Branchiomma Köllikeri* and *Br. vesciculosum*, and observes that the former is very sensitive to changes in the amount of illumination, for a slight movement of the hand in the air, at the distance of a metre from the aquarium, causes all the animals to withdraw into their tubes as soon as the shadow falls upon them. Yet Sabellas, having no eyes, remain, he finds, perfectly immobile and unaffected.

Dalyell had already (1) noted that *Amphitrite bombyx* is "impatient of light," and upon the interception of light instantly retreats into its tube.

In the first species the eye is a pyriform mass adnate to the branchia on its concave side near the tip, and presents in section about thirty crystalline cones, each a pyramidal body 13  $\mu$ . thick, with its apex imbedded in the central mass of violet pigment. The cuticle over this compound eye is 4  $\mu$ . thick.

In the second species the eye is a hemispherical mass, about 190  $\mu$ . thick, near the tip of the branchia, contains crystalline cones, and is covered by a cuticle of the same thickness as in the former species.

In *Protula intestinum* there are four pairs of compound eyes, or rather collections of ocelli, upon each branchia, each ocellus being a spherical lens surrounded by a mass of reddish pigment.

In the Supplement to the above work, published in 1870, the author describes and figures the compound eye of *Branchiomma vigilans*, in which the branchia is embraced near its tip by the

large, spherical eye, only one side of this eye being free from the very numerous crystalline cones. The pigment ensheathing the cones is violet. In the figure we note each element of the eye is a radiating, dark red-brown, cell-like body, bearing a yellow, clear mass in its peripheral end next the cuticle; these elements are separated by considerable intervals. Here, also, experiment proved the animal very sensitive to light and shadow, as in the above case.

In *Vermilia infundibulum* there are at least 220 separate ocelli upon the outer side of each branchia, about 11,000 eyes in all! Each is a pear-shaped, crystalline body 20  $\mu$ . long, imbedded in red pigment, which appears to adhere especially to its centrally placed apex.

Some eight years later J. Chatin (5) gave figures and descriptions of the eyes of several of these Annelids, and attempted to compare them closely with the compound eyes of Arthropods.

In *Psygnobranchus protensis*, Phil., he finds an elongated, pyramidal mass of red-orange color, having a clear, crystalline body in its outer, basal end, next the cuticle.

In *Protula intestinum*, Lamb., the eye is made up of two such elements, with bright red pigment, while several species of *Eupomatus* have ten or twelve such in each eye. In *Dasychone bombyx*, Dalyell, the animal first mentioned by Dalyell, as above stated, there are three or four elements in each eye; each is separable as a pigmented, pyramidal mass, with a clear, crystalline body at its outer, basal end. Kölliker, it is to be remembered, found fifteen to eighteen clear bodies in the eye of this animal, but Chatin appears to indicate only the number seen in section.

The pigmented spots upon the body are found by Chatin to contain no refractive bodies, and hence are not to be regarded as eyes.

In *D. lucullana* Delle Chiaje, however, there are two pigment spots upon each somite, covered by a modified cuticle, and containing a number of elements having a prismatic, refracting part set in a sheath of pigment, and drawn out into a filament at the apex.

The branchial eyes of this species have as many as eight elements, such as were described for *D. bombyx*.

Finally, in *Vermilia clavigera*, Phil., the branchial eyes present the bright, shining appearance of the eyes of *Pecten*, and are

figured as having one or two clear bodies imbedded in pigment. In all the figures the refracting bodies are simply spheroidal or somewhat elongated structures, projecting somewhat from a pyramidal mass of pigment.

Such compound eyes, or simple eye specks of unknown structure, occur upon the branchiæ of many Annelids, but not always upon closely related forms, judging from the figures and accounts of systematists. Thus Grube (6) finds protuberant eyes in a row upon the branchia of *Sabella* (*Potamilla*) *polyophthalmus*, a species closely related to *P. reniformis*, Malmg.; yet they are said to be absent in *P. neglecta*, Malmg., and *P. Torelli*, Malmg.

Again, *Serpula chrysogyrus*, Gr., has seven or eight eyes on each branchia, the eye having twenty-seven round lenses covering a circular area without pigment (in preserved specimens), but sending a conical streak towards the centre of the eye from each lens.

Most *Sabellas* with dorsal processes upon the branchia are said to have eyes, but *S. decora*, Sars., has none. Eyes are figured in *Sabella* (*Dasychone*) *cingulata*, Gr.; *S. oligophthalmus*, Gr., has only two eyes on a branchia; *S. acrophthalmus*, Gr., has but one, at the end; *S. serratibranchis*, Gr., has only black spots not regarded as eyes. Moreover, in *Myxicola ommatophora*, Gr., though not occurring elsewhere in this genus, there is a pair of eyes near the tip of the branchia.

Fortunately, Semper had made notes upon this species, in the Philippines, from which it appears that these compound eyes may be regarded as special collections of red pigment spots found separate elsewhere upon the branchiæ. Each eye contains crystalline cones with spheroidal bases and elongated, conical apices, surrounded by red-brown pigment, and ending as delicate threads borne by the cartilaginous skeleton.

Although the branchiæ are ciliated, the convex surface of the eye is not, "ist dafur mit eigenthümlichen langen, wie es scheint starren Borsten dicht besetzt, welche wohl als besondere Tastorgane aufzufassen sein werden!"

As the tissue changed so quickly, nothing could be made out as to the connections of these hairs.

In the systematic work of Ehlers (8), also, we meet with figures and notices of the general anatomy of such compound eyes.

Thus the eyes of *Branchiomma bioculatum* and *Br. lobifera*,

cleared in glycerine, show rounded lenses or cones, and conical, pigmented central parts, much more numerous in the latter species than in the former, and also unusual in having the pigment blue-black.

*Dasychone conspersa* has numerous eye-like, branchial specks, while in *Hypsicomus circumspiciens* there are paired eyes, the long axes of which point, as I may say, away from some imaginary point at the centre of the whole branchial system. Each eye has one conical, refractive body, somewhat projecting above the general surface and enveloped in pigment, especially at its inner apical end.

At the tip of the branchia in *Filigrana Huxleyi* there is a peculiar organ, intermediate, it seems to me, between that shown in figures of *Salmacina incrustans*, Clap., by Langerhans (16), or the presumably similar eye-like spots of *S. ædificatrix* of Claparède's Supplement (4), on the one hand, and the more complex structure already noted in *Filigrana (Protula) Dysteri*, Huxley, as given by Claparède in (3), on the other hand.

Ehlers describes these organs as club-shaped collections of modified epithelial cells surrounding a cavity. These cells are club-shaped, the large ends at the surface, and appear to be gland cells, as the peripheral part is sometimes full of granulations. Irregularly scattered over the surface of the organ, and far apart, are stiff, straight, hair-like structures, thought to belong to small cells indicated by nuclei between the above large, club-shaped cells.

The author has found Nauplii enclosed in the branchial filaments, and thinks these terminal organs may prove to be sensory and at the same time secretory, discharging an adhesive substance reflexly to catch prey. He recognizes their resemblance to the terminal eyes of Branchiomma, with which they might prove to be homologous, assuming a change of function.

A somewhat similar organ is found as a quadrangular area on each ventro-lateral face of the buccal somite in *Placostegus incomptus*. Each has very many conical, highly refracting bodies buried with apices inward and rounded bases next the cuticle. A cell nucleus is present for each of these bodies, apparently. The entire animal is colorless, in preserved specimens; yet in *P. tridentatus* and *P. tricuspидatus*, Hansen (20) and Langerhans (17) describe similar areas on the buccal somite having red pig-

ment between the separate lenses, and regarded as eyes by Langerhans, who emphasizes the fact that both these species live in transparent tubes. The tube is transparent in Ehlers' species also, but whether these organs are eyes or glands, he regards as not determined yet.

Finally, Brunotte (9) applied modern methods of technique to the study of these compound eyes in a species of *Branchiomma*. The eye is here at the tip of the branchia, variable in size, spheroidal except for a colorless furrow on one side, where it does not surround the skeletal axis of the branchia, and is covered by the usual unmodified branchial cuticle. The eye is composed of numerous separate eyes or elements, each a pyramid embedded in pigment, with the broad base next the cuticle, the attenuated apex continuous with the nucleated filaments of the branchial nerve. In the base, next the cuticle, is a spheroidal, generally homogeneous lens that stains darkly and may be reticulated in some preparations.

Next this lens is a clear, cup-shaped cavity, sharply set off from the rest of the eye, and containing a nucleus. In the elongated central part of each eye element is a series of transverse disks or lamellæ, alternatingly clear and more opaque, but not visible in balsam. A second nucleus is found in the eye between this last lamellated "striated spindle" and the first-mentioned outer nucleus. The whole element is thus to be regarded as made up of two cells, an inner or central optic cell and an outer or peripheral, lentigerous cell. No pigment occurs in either of the above two cells, but is found in many small, attenuated, surrounding cells, arranged in circles at different levels along the outside of the above apparatus, and each having a nucleus, as seen when depigmented in strong nitric acid.

The eye is thus two-layered and the visual cells are non-pigmented. Illustrations of these peculiar eyes and comparisons with those of Arthropods are given in a later paper (10), but these may be considered in the final part of this article.

The last notice of such compound eyes that has come under my notice is that of Beddard (11), who figures a somewhat mushroom-shaped eye borne upon a stalk projecting from the inner face, near the tip, of the branchia of *Branchiomma intermedium*, a new species from the Mergui Archipelago.

Certain unusual ventral eyes of the "Palolo worm" may, I think, be also regarded as having much of the structure found in various branchial eyes, at least so I would interpret the figures given by Ehlers (8).

These organs are figured as *dorsal* pigmented spots by Macdonald (13) and regarded as *dorsal glands* by Ehlers; yet Spengel (12, p. 43) states they are undoubtedly eyes, and situated as a median series, one for each somite, upon the ventral nerve ganglia.

Such an important extension of these compound eyes from the lowest tubicolous Annelids to the Eunicidæ is, however, scarcely to be ventured upon without further knowledge of the structure in question.

#### IV. CONCLUSIONS.

The eyes of *Potamilla* are numerous areas of modified epithelium of the main stems of the cephalic branchiæ. Each is composed of elongated, pigmented cells, a few of which are characterized by the possession of peculiar refracting bodies in their outer ends and modified axial parts. These latter cells are presumably the sensory cells, and have pigment only in the superficial part of the protoplasm, as shown in the diagram (Fig. 1). The eye is compound, since each such sensory element is separated from its neighbors by intervening pigment cells.

In a species of *Sabella* and of *Dasychone* the eyes have essentially this same structure. As represented in diagram (Fig. 2) the pigment is found deeper in the substance of the cell, and the refracting body is actually continuous with the cuticle.

In a species of *Hypsicomus* the branchial eyes are not compound, but comparable to one of the elements of the above eyes.

The single refracting, cuticular ingrowth resembles one of the numerous inclusions of *Sabella*, but is not contained within its cell. This cell may be regarded as sunk beneath the surface, and shortened in proportion to the elongation of the refracting cone. Thus the axial part of such diagrams as 1 and 2 would be shortened also, and be represented in *Hypsicomus* by the single spherical body found in the cell between its nucleus

and the refracting cone. Along with this retreat of the sensory or refracting cell, away from the surface, there has taken place a bending, and also a sinking in, of the surrounding pigment cells.

If this comparison be correct, the eye of *Hypsicomus* has much in common with a single element or ommatidium-like collection of cells in the compound eyes of the other Annelids examined; at the same time it presents interesting resemblances to the common eyes found upon the heads of higher Annelids, as I hope to illustrate in another paper.

The clear spherule compared above to the shortened axial region of the refracting cells of *Sabella*, etc., also suggests the phæospheres of certain scorpions.

A review of the literature shows that eyes such as those described in the present paper are widely distributed through the Sabellidæ and Serpulidæ. Excepting a few doubtful organs that may prove to have structure and function different from that of true branchial eyes, all but one of the organs referred to in the historical review may be readily reduced, either to the type of *Potamilla* or to that of *Hypsicomus*. Most of the observations are, however, of too superficial a character to admit of detailed comparisons as regards cellular structure.

The one exceptional organ, the eye of a species of *Branchiomma*, is very important, since it is about the only one that has been studied by the aid of sections and depigmentation. Although the general anatomy of this eye is identical with that of *Sabella*, etc., yet the arrangement of the cells, according to Brunotte (8, 9), is fundamentally different. While the eyes of the Annelids described in this present paper are composed of a single layer of epithelium, those of *Branchiomma* are of two layers, each element having an outer corneagen cell and an inner sensory cell, both surrounded by small pigment cells. There is, moreover, no pigment in the sensory cells.

If, however, it were permissible to interpret the figures given in Brunotte's monograph (9) in the light of experience gained in studying *Potamilla* and *Sabella*, one could readily explain them as being representatives of what is sometimes observed in these latter animals, but not representing the true structure. Thus if sections are cut obliquely, or not thin enough to prevent superposition of cells, or if strong nitric acid produces such

changes as some reagents do in *Potamilla*, we could suggest an interpretation of these figures that would show the eye of *Branchiomma* to be closely similar to that of *Sabella*, etc. The outer nucleus (9, N. 30, Fig. 11, *n.*) and surrounding clear space would thus represent an artificial product; the second nucleus (Fig. 13, *n.*) could readily be one of the pigment cell nuclei projected out of its proper plane, while the peculiar circular space left in Fig. 11, central to the striated body, would exactly correspond to the only nucleus found in the refracting cell of *Potamilla* and *Sabella*.

If some such suggestions should prove to be true, we would have essential agreement in all the compound branchial eyes of Annelids; all are then monostichous.

These compound eyes are not confined to the branchia, but may occur upon the anterior part of the body, where, as in some species of *Placostegus*, there may be pigmented areas, right and left, upon six or seven somites. These areas in this case present the same structure as the branchial eyes, as shown evidently enough by the figure of Hansen (20).

The central eyes occurring in one of the *Eunicidæ* may, as has been conjectured above, prove to be compound eyes of this same type.

These compound Annelid eyes are areas of pigmented epithelium, and frequently correspond somewhat in position to areas of pigment upon the branchial filaments. The ordinary pigment cells of the branchiæ have the pigment granules more densely aggregated in their superficial parts, so that in surface view such pigmented epithelium frequently presents a mosaic of pigment granules outlining the adjacent cells. Clearer, vacuole-like parts of the protoplasm may be present in the axial or interior parts of these cells. In *Sabella microphthalmia* special regions of such pigment cells, forming so-called "eye spots," have some larger, club-shaped pigment cells, with noticeable, swollen, included parts of the protoplasm, suggesting the inclusions of *Potamilla*, etc., though not at all refracting and resistant. These eye-like, pigment spots thus offer a possible transition from common pigmented epithelium to the special, true compound eye.

The increase in the clear part of the cell, and limitation of the pigment to the periphery, seems to have reached a maxi-

num in *Potamilla*, where it is difficult to decide if the granules are really in the cell, in neighboring pigment cells, or also in some intercellular matrix.

These compound eyes are found to be too simple in structure to admit of any direct comparison with the eyes of Arthropods. If the eye of *Hypsicomus* may be homologized with one element of *Sabella*, as above suggested, that is, if we assume the formation of an elongated, cuticular, lens-like body by the gradual sinking down of an epidermal cell, we would have a method of formation different from those open, pit-like depressions of many cells assumed in the explanation of the Arthropod ommatidium.

When compared with certain members of the Mollusca, however, we find quite close agreement. The peculiar, protuberant mantle organs of the Lamellibranchs *Arca* and *Pectunculus* have quite the same structure as in these Annelids, as may be seen from the figures of Rawitz (23), Carrière (22), and Patten (24). However, the sense cell or refracting cell in these molluscs is quite different from the Annelid cells represented in Figs. 1 and 2 above. The refractive cuticular body has no such shape as found in the Annelids, the nucleus of the cell is in its outer part, there appears to be no specialized axial region external to the nucleus, but a peculiar conical body occupies the apical part of the cell.

This sensory cell is also not pigmented, thus agreeing with the sensory cell of *Branchiomma* as described by Brunotte.

Though this similarity is too general to point to definite morphological conclusions, being merely the agreement of pigmented epithelial regions having sense cells surrounded by pigment cells; yet taken with the fact of linear arrangement of the organs, of their occurrence in large numbers, and of the like responses of the animals to light, it will, I think, furnish evidence as to these functions in both animals.

In both cases the animals respond very quickly to slight sudden changes in the intensity of illumination, bivalves seeking safety by retreat within the hard shell, the Annelid withdrawing into firm tubes.

Though the structure of these organs is such as to justify our interpretation of them as undoubted eyes in the common morphological sense, yet the following considerations show the need of physiological experimentation here.

The occurrence of stiff, hair-like processes upon these organs as observed by Semper (6), by Ehlers (8) in *Myxicola* and *Filigrana*, and their possible existence in *Potamilla* and others, raises a suspicion that some other sense organ in addition to or in place of an eye may be here concerned.

The great number and position of these organs suggest doubts as to their usefulness as eyes: the same that have been made to the like organs of *Arca*.

Finally, a much more important fact is the dubiousness of our present evidence. In *Potamilla*, as in so many other cases observed by others, the animals are exceedingly sensitive to sudden passage of very slight shadows over their branchiæ. Almost always, but with striking exceptions, they instantly withdraw into their tubes. The natural assumption that the peculiar branchial organs are here concerned is no proof. In fact, *Hydroïdes dianthus* is found to respond fully as well, though, as we have seen, it has no such branchial organs nor any other special sense organs as far as known.

Here the seat of sensation is also in the branchiæ; when these are cut off more and more, the animal still reacts till nothing but the bases of the branchial stems remain.

As the sensitiveness attributed to the branchial organs may be thus present in other undetermined parts of the branchiæ, we must fall back for the present upon the structural evidence and upon comparison with other groups to support our belief in the existence of functional, compound Annelid eyes.<sup>1</sup>

BALTIMORE, Feb. 12, 1891.

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<sup>1</sup> Experiment with *Potamilla* with reference to the possible phosphorescent nature of the branchial eyes gave a negative result.

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## EXPLANATION OF PLATES XX AND XXI.

All the figures are from camera-lucida drawings made with use of Zeiss lenses, and reduced in reproduction.<sup>1</sup>

FIGS. 1-14. *Potamilla reniformis*.

FIG. 1. Side view of portion of branchia, preserved, showing one eye by reflected light and filaments in a pigmented area. 2·D.

FIG. 2. Sensory cell isolated in potassium bichromate and methyl green. 4·F.

FIG. 3. Small pigment cells as above. 8·4.

FIG. 4. Sensory cell macerated in H<sub>2</sub>SO<sub>4</sub> sea-water, stained in methyl green and Mayer's acid carmine. 4·F.

FIG. 5. A similar cell, not stained. 8·4.

FIG. 6. Separated inclusions of three sensory cells, macerated as above, but cleared in KOH. 4·F.

FIG. 7. Longitudinal section of entire eye, showing entrance of nerve and two inclusions. Hæmatoxylin. 8·4.

FIG. 8. Tangential section near outer surface, showing inclusions and nuclei of pigment cells. 8·4.

FIG. 9. Tangential section through the axial parts of several sensory cells. 8·4.

FIG. 10. Tangential section across the nuclei of several sensory cells. 8·4.

FIG. 11. Transverse section of depigmented eye. 8·4.

FIG. 12. Tangential surface near-surface of depigmented eye. 8·4.

FIG. 13. Transverse section of lateral epithelial surface of branchia, proximal to eye; to show the optic nerve. 8·4.

FIG. 14. Transverse section of branchial stem and bases of two filaments, showing one eye cut across, skeleton, blood-vessels, and nerves: the muscles are omitted. 2·D.

FIGS. 15, 16. *Sabella microphthalmia*.

FIG. 15. Transverse section of outer part of a branchial stem, showing pigment cells in a cluster. 2·D.

FIG. 16. Tangential section of half of a pigment spot, with a few swollen, clear cells. 8·4.

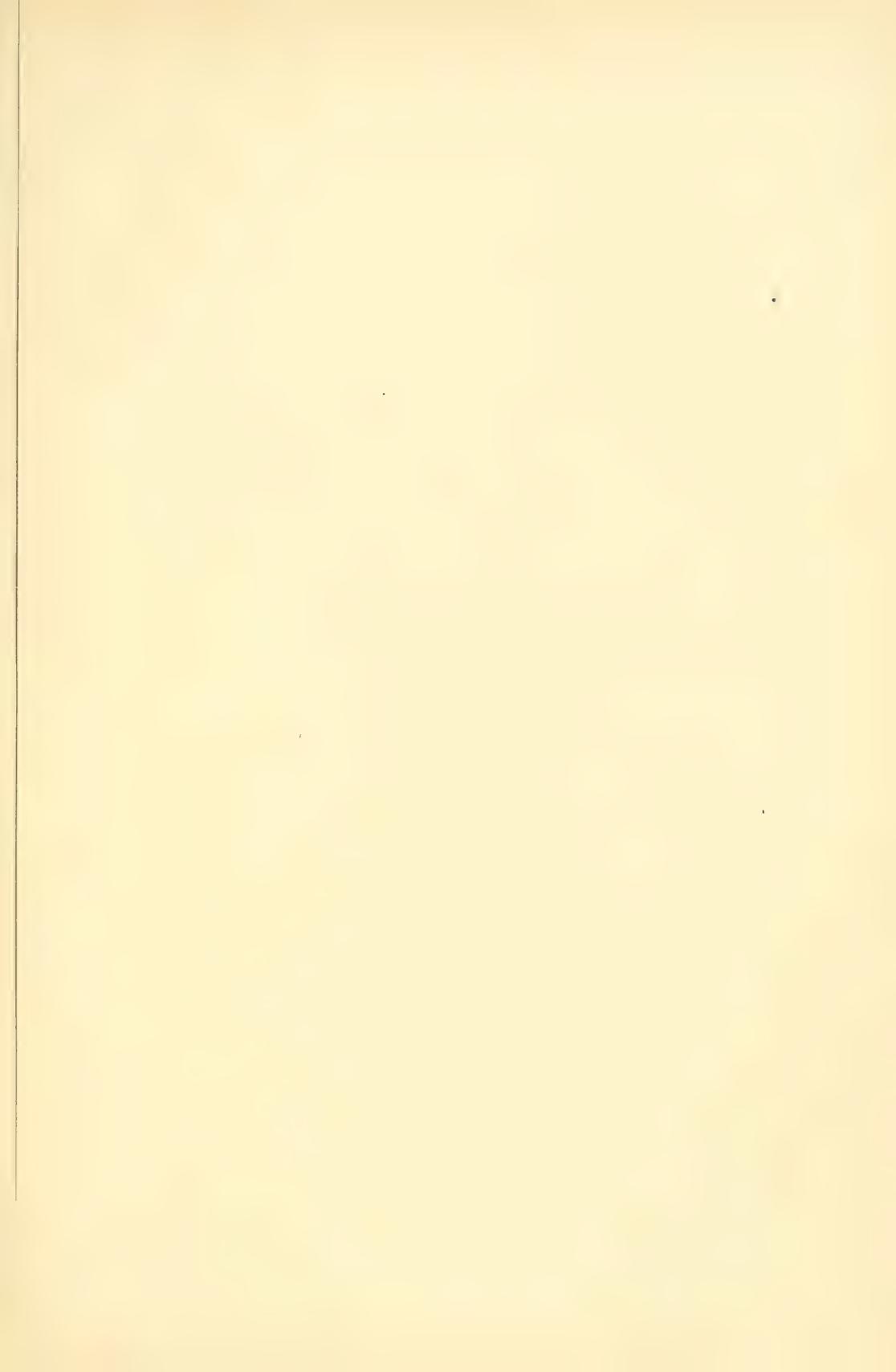
FIGS. 17-19. *Sabella melanostigma*.

FIG. 17. Transverse section of outer part of a branchial stem, showing a pair of eyes cut across. 2·D.

FIG. 18. Part of such a section of an eye enlarged. Three refracting bodies in contact with the cuticle; the axial parts of the sensory cells and large nuclei probably belonging to such cells. 8·4.

FIG. 19. Isolated refracting bodies of sensory cells, showing continuity with the cuticle and adherence to the axial pronuclear portion of the cell in one case. 8·4.

<sup>1</sup> Figures on Plate XX multiplied by  $\frac{1}{2}$ , except Fig. 1, that by  $\frac{1}{4}$ . Figures on Plate XXI multiplied by  $\frac{8}{13}$ .









FIGS. 20-22. *Dasychone conspersa*.

FIG. 20. Transverse section of outer part of a branchial stem cutting across a pair of eyes. 2·D.

FIG. 21. Portion of radial section of depigmented eye, inclusions or cuticular ingrowths, axial parts and nuclei of sensory cells, with nuclei of pigment cells. 8·4.

FIG. 22. Isolated refracting bodies or cuticular ingrowths, in two cases attached to cuticle. 8·4.

FIGS. 23-27. *Hypsicomus*.

FIG. 23. Transverse section of outer part of a branchial stem, an eye cut where in contact with cuticle on one side, and where buried amongst epidermal cells on the other side. 2·D.

FIG. 24. Section vertical to epidermis and parallel to long axis of an eye. Hæmatoxylin. 8·4.

FIG. 25. Inner end of such a section as Fig. 24, but depigmented. A single terminal cell, pigmented, contains the clear refracting spherule, and abuts against the truncated end of the refracting cuticular cone. 8·4.

FIG. 26. Section at right angles to the above, and passing across the apex of the conical, cuticular, refracting body and the three surrounding pigmented cells. 8·4.

FIG. 27. One of the refracting cones isolated with a fragment of cuticle continuous with its base. 8·4.

FIG. 28. *Hydroides dianthus*; transverse section of outer part of branchial stem, showing two nerves in the angles, but no eyes. 2·D.







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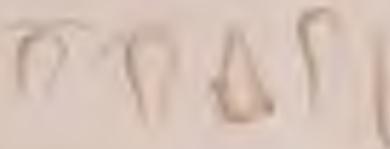
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ON THE OSTEOLOGY OF *MESOHIPPUS* AND  
*LEPTOMERYX*, WITH OBSERVATIONS ON  
THE MODES AND FACTORS OF EVO-  
LUTION IN THE MAMMALIA

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THE genus *Mesohippus* stands about midway in the line of equine descent, so far as that line is known, and is itself, very probably, an actual ancestor of the modern horses, or at all events is so closely allied to such ancestor as to answer all the purposes of this study. Although the horse series is perhaps the most complete of any that have yet been made out among mammalian phylogenies, yet it is not my design to attempt a description of all the members of this series, as that would require a very extended and voluminous account, and is, besides, quite unnecessary for the main object in view. This object is to ascertain, so far as is yet possible, the mode or law of evolution in a mammalian phylum, and as the place of *Mesohippus* in the equine phylum seems to be fairly well established, a comparison with existing forms will yield instructive results.

The very number of well-preserved fossil equine genera is a source of embarrassment, and renders the systematic position of some of these forms a matter of grave doubt. Thus the relation of the European genera *Anchilophus*, *Anchitherium*, and *Hipparion* to their American contemporaries and to existing species, is very far from clear, and to assume, as has been done,

that the genus *Equus* has had a dual origin, on the one hand from *Hipparion*, and on the other from *Protohippus*, involves a degree of convergence which cannot be admitted in the present state of our knowledge. It follows, therefore, that results drawn from such a doubtful phylum can be of little service, and on that ground these genera of uncertain position will not be taken into consideration.

I have chosen *Mesohippus* as the subject of the following description for a twofold reason: in the first place, because its ancestral relation to the modern genus is extremely probable; and secondly, because its structure is the least fully known of almost any of the horse series, and we may thus avoid the repetition of well understood facts. The description is founded chiefly upon a series of specimens obtained by the Princeton expeditions of '82 and '90. I am also indebted to the kindness of Professor Cope for the loan of some of his beautiful material from Colorado.

The typical American species, *M. Bairdi*, was first described by Leidy as belonging to *Palæotherium*, (No. 32, p. 122), but shortly afterwards referred by him to *Anchitherium*, under which name it is described in all of Leidy's subsequent publications on the subject. In 1875, Marsh erected it into the type of a new genus, *Mesohippus*, with the following definition: "This genus presents characters intermediate between *Orohippus* Marsh, and *Anchitherium* von Meyer. The skull and teeth are very similar to those of the latter genus and the dental formula is the same. In the feet, however, the lateral digits are larger, the fifth metacarpal is represented by an elongated splint bone; and the second and third cuneiform bones of the pes are not co-ossified. The type of the genus is *Mesohippus Bairdi*—*Anchitherium Bairdi*, Leidy." (No. 34, p. 248.)

With regard to this description it may be noted that the fifth metacarpal is present in *Anchitherium*, as is demonstrated by the facet for it upon the unciform, but nothing is known as to its shape. The other distinctions are obviously not of generic, but only of specific value, and consequently the new genus has not been generally accepted as such. I have shown elsewhere, however, that the characters of the incisor teeth are sufficient to generically separate the European form from that of the American White River beds. (No. 49.) In the former they

have broad crowns with distinct pits or invaginations of the enamel, while in the latter the crowns are sharp and chisel-shaped, very much as in *Hyracotherium*, without any trace of such invagination. (Cf. Cope, No. 9, Pl. XLIX. *a*, Fig. 3; and Kowalevsky, No. 25, Pl. III., Fig. 57.)

There are, besides, not unimportant differences in the construction of the molars and of various parts of the skeleton, which show that *Mesohippus* is a more primitive form than *Anchitherium*, and indeed it may be doubted whether the European type is in the line of equine descent at all, but does not rather form a side-branch.

It is not necessary for our purpose to enter into the question whether the equines of the John Day Miocene should be referred to *Anchitherium* or not.

Though the White River species has so long been known, our knowledge has been chiefly confined to the structure of the skull and the dentition, which have been described and figured by Leidy. Cope has published some valuable notes on the skeleton (No. 11), as has also Marsh (No. 35), but these are too brief for the object of this paper. Kowalevsky's excellent memoir upon *Anchitherium* (No. 25) was never completed, and is to some extent vitiated by the supposition, now abandoned, that *Palæotherium* is the primitive horse-type.

## I. THE DENTITION.

The dentition has been so fully described by Leidy (No. 33), Osborn (No. 42, p. 88), and others, that a brief summary is all that is necessary here.

1. *Upper Jaw.* The superior incisors and canines are not preserved in any of the specimens which I have seen, but the alveoli for them show that they were present in unreduced number, and that they were of small size. The first premolar is a small, compressed, and simple cone, with a rather strong cingulum developed on the inner side of the crown. The other premolars are almost exactly like the molars in construction, with very slight differences of detail; thus the posterior pillar is less developed and sometimes altogether absent; the posterior transverse crest is more completely divided from the postero-internal cusp. In other respects the transformation is complete. The second pre-

molar shows a beginning of the peculiar shape seen in the horse, not being quadrate in outline, but narrower in front than behind, and having a forward extension of the antero-external angle.

Although the premolars have thus entirely assumed the molar pattern, yet the development of them as presented by the Eocene genera, shows that, just as in the Artiodactyls, the functionally similar parts of the crown are not homologous in the two series.

The molars of *Anchitherium* differ very slightly from those of *Mesohippus*, the median ribs of the external lobes are less distinctly shown, the transverse crests, which in the American form do not quite reach the outer wall of the crown, are connate with the ectoloph; the median cusps, para- and metaconules, are relatively smaller, and the posterior pillar larger. In both genera the teeth are typically brachyodont.

2. *Lower Jaw.* The incisors of *Mesohippus* are small, with narrow crowns, and simple, sharp cutting edges, which are abruptly truncated. The canine is also small and erect. The first premolar is a minute compressed conical tooth, implanted by a single fang, and not separated by a diastema from the second. The second premolar is not quite molariform, the posterior crescent only being developed, the anterior portion of the tooth being compressed and somewhat trenchant. The third and fourth premolars and the true molars are composed of two crescents; the anterior pillar is well developed, forming with the metaconid the twin cusps (*aa* of Rüttimeyer); the posterior pillar which rises from the cingulum behind the entoconid is present, but less advanced. The third molar has quite a large fifth lobe or talon.

In the recent *Equidæ*, the most important change to be noticed is that the teeth have become very long and prismatic, and covered with cement. The incisors have deep pits of enamel, and the pattern of the molars has become very complex, through the sinuous folding of the enamel crests; nevertheless, this complicated hypsodont molar is plainly derived from the simple tooth of *Mesohippus*. "By tracing back the rise of the eleven elements which compose the upper *Equus* molar, we find that six belong to the primitive sextubercular bunodont crown. Two elements of the ectoloph, the anterior pillar and median pillar, rise from the simple primitive basal cingulum of the

*Hyracotherium* molar : the same mode of development, we have just seen, is true of the posterior pillar. The eleventh element, the fold of the postero-external angle of the crown, is not prominent until we reach *Equus*." (Osborn, No. 42, p. 89.)

Wide as appears to be the interval between the molar pattern of *Mesohippus* and that of the recent forms of *Equidæ*, it is completely bridged over by the teeth of such intermediate forms as *Merychippus*, *Protohippus*, etc.

## II. THE SKULL. (Pl. XXII., Figs. 1, 2; Pl. XXIII., Fig. 17.)

The skull of *Mesohippus* has been well described and figured by Leidy (No. 33), but his specimens were not very complete, and we need to examine this portion of the skeleton from a somewhat different point of view.

The cranium is long, narrow, and low, the face deeper, but short and tapering rapidly forward, the orbits are placed far forward, their anterior rim being over the first molar. The cranio-facial axis is straight and the occipital surface high and narrow.

The basi-occipital is broad, stout, and strongly convex, with a faintly marked median keel. The condyles are rather small, not strongly projecting, and in contact in the median line below; the articular surfaces are continued forward some distance upon the inferior surface of the basi-occipital; but these surfaces are narrow and nearly flat, not concave from before backward, and not having the elevated anterior borders which occur in the horse. The exoccipitals are rather low and broad, and form a very strong convex prominence in the median line, which lodges the large vermis of the cerebellum. This prominence is not thickened and diploëtic, as in *Equus*, but has very thin walls. The superior margin of the foramen magnum is notched in the median line, and on each side of the median line there is a small protuberance. The paroccipital processes are long, slender, and compressed. The supra-occipital is quite high and narrow, concave in the median line, and with acute margins, forming the lambdoid crest; it extends but a little way upon the roof of the cranium. The occiput as a whole is proportionately higher and narrower than in the horse, and the surfaces for ligamentous and muscular attachment are much less prominent and rugose. The foramen magnum is narrower and more circular in outline.

The basi-sphenoid is shorter and more slender and tapering than the basi-occipital, but otherwise like it in shape. The pre-sphenoid is so covered by the expanded vomer that little of it can be seen. The alisphenoid is of peculiar shape; the ascending portion is divided by an angulation into two portions, of which the anterior is high, narrow, and nearly vertical; and the posterior forms a broad, flat, and nearly horizontal surface, rising gently to the glenoid cavity. The much more elevated position of the latter in the horse gives to this part of the alisphenoid a very different appearance. The orbito-sphenoid is high, but rather narrow, not forming nearly so much of the wall of the orbit as in the horse.

The periotic has a high, but very narrow mastoid portion, which is exposed between the squamosal and the exoccipital, and forms a large part of the wall of the cerebellar fossa, as is plain in a longitudinally bisected skull. The tympanic is not ankylosed with the periotic, and in most specimens has become detached and lost. It is very small and forms a minute bulla with an elongated tubular meatus, and ending in front in a short, sharp styloform process; it encircles and apparently is co-ossified with the tympanohyal. The periotic is in contact with the basi-occipital, so that the large lacerated foramina are not continuous, nor so extensive as in the horse.

The squamosal is large, forming much of the side walls of the cranium, but not rising so high relatively as in the horse; the zygomatic process is quite long and slender, and as in the horse, extends forward so as to form part of the inferior rim of the orbit. The peculiar and exceptional construction of the horse's orbit is thus already indicated. The glenoid cavity is likewise characteristically equine in structure; its articular portion is very narrow, slightly concave from side to side, and convex from before backward; its external portion is raised, and when viewed from the side forms a prominent tubercle, which, however, is not so broad, nor so conspicuous as in the horse. The post-glenoid process is quite high, massive, and rugose; between the post-glenoid process and the articular surface there is a broad, shallow depression. The post-tympanic process is short and inconspicuous, and is closely applied to the mastoid portion of the periotic. The deep notch between the post-tympanic and post-glenoid processes lodges the tubular auditory meatus.

The jugal is quite long and slender, its posterior portion reaching back nearly to the glenoid cavity: it extends, however, but little upon the face, very much less than in the horse, and the masseter surface is but feebly developed. As a whole, the zygomatic arch is decidedly different from that of *Equus*, being longer, much more slender and compressed. These differences are due in part to the changed position of the orbits, and in part to the increased relative importance of the masseter muscle in the modern species.

The parietals are long, but narrow; anteriorly they diverge strongly to receive the posterior projections of the frontals; the sagittal crest is short and inconspicuous, but longer and more prominent than in the horse; anteriorly the ridges diverge and form a narrow triangular area. Near the posterior portion of the suture with the squamosal, the parietal is perforated by a number of large venous foramina: in the horse these foramina are situated in the squamosal, are more scattered, and extend farther forward.

The frontals are very long, but rather narrow; their shape is much as in the horse, but the forehead is narrower and slightly concave. The frontal sinus is but little developed, and does not extend over the brain at all. The fronto-nasal suture is nearly straight, but in the median line the frontals send forward a narrow tongue, which is wedged in between the diverging nasals. The cranium is quite sharply constricted behind the orbits. The post-orbital processes are long and slender, with rugose edges; there is no trace of any corresponding process from the zygomatic arch. The superior rim of the orbit is more prominently projecting in some specimens than in others, and in the former there are two small supra-orbital foramina; in the latter the foramen is represented by a notch at the anterior base of the post-orbital process.

The lachrymal is quite large, and though smaller than in the existing genus, extends well up on the face and articulates superiorly with the nasal as well as the frontal; in front of the orbit there is a pit or depression, which is partly upon the lachrymal, but more extensively upon the maxillary. This pit is very much deeper in some specimens than in others, though this difference may be a sexual one, as I have reason to believe is the case in *Oreodon*. There is an obscure lachrymal spine

upon the rim of the orbit, and the foramen is single and placed well within the orbit.

The nasals are very long and narrow, and in general appearance resemble those of the horse, but with some differences. Posteriorly they are quite broad, reaching nearly to the antero-superior margin of the orbit, and diverging so as to receive between them the short and sharp nasal processes of the frontals. In front of this expansion the nasals become very narrow, but their sides are bent down nearly at right angles to the horizontal portion, very much as in the horse. The free ends extend far beyond the suture with the premaxillaries, and taper much less rapidly than in *Equus*, their tips being rounded and blunt, not sharp points.

In correspondence with the small size of the incisor teeth, the alveolar portion of the premaxillaries in *Mesohippus* is but feebly developed and is conspicuously smaller transversely, and more especially in the vertical diameter than in *Equus*: the ascending ramus is much shorter and less obliquely directed than in the horse; it forms a thin and narrow plate and has a short contact with the nasal. The anterior nares are much lower and narrower than in the horse. The palatine plates of the premaxillaries are very small, and the spines much more slender and very much shorter than in the horse, as are also the anterior palatine foramina.

The maxillaries are chiefly remarkable for their small extent vertically, especially of the alveolar portion, which is very low, so that the inferior rim of the orbit is brought very near to the molars; but even the portion which is applied to the formation of the nasal chamber is much less extended vertically than in the existing species. There is a short diastema between the canine and the first premolar, and just in front of the latter the face is slightly constricted. The maxillary is also much shorter, proportionately, than in the modern forms, in correlation with the much smaller size of the molars. The alveolus is extended some distance behind the last molar, but less than in *Equus*, and there is a well marked notch between the palatine and this portion of the alveolus. The palatine processes of the maxillaries are narrow and quite short, which is brought about by the position of the posterior nares, which extend as far forward as the first molar, and thus have a much more anterior situation than in the

existing type. The masseter crest is very feebly developed, and does not extend at all in advance of the jugal suture.

The palatines form very little of the hard palate and are chiefly confined to enclosing the posterior nares laterally. This opening is decidedly horseshoe-shaped, broad and rounded in front, and much contracted behind. The palatines are in contact with the maxillaries throughout, the inner wall of the orbit being formed in its postero-inferior portion by the outer wall of the narial opening, giving to this region of the skull an entirely different appearance from that which occurs in the horse. The pterygoids are very small and inconspicuous, and do not form distinct hamular processes. The vomer, so far as it can be made out, agrees with that of *Equus*.

The inferior maxillary has a slender and compressed horizontal ramus, which tapers rapidly forward, and is very sharply constricted at the diastema, expanding again slightly to form the incisor alveolus. The two rami are firmly co-ossified, and the symphysis is quite long. The symphyisial region is directed quite sharply upward and forward, thus forming an angle with the remainder of the horizontal ramus, while in *Equus* the symphysis is flattened, procumbent, and in the same straight line as the molar-bearing region. These differences are no doubt due to the changes in the character and especially the size of the incisor teeth. The angle is regularly rounded and has a thickened border; it is more extended antero-posteriorly than in the horse. The ascending ramus, on the other hand, is decidedly lower, and the condyle less elevated above the level of the molars. The coronoid process is regularly recurved and pointed, and resembles that of the ruminants rather than that of *Equus*. The condyle is extended transversely, but very narrow antero-posteriorly.

The cranial foramina of *Mesohippus* have attained very nearly the modern arrangement. The anterior palatine foramina are much shorter than in the horse, and the posterior palatine foramina are farther forward, opposite the first molar. The infra-orbital is over *pm.* 3, as in *Equus*, but much lower down than in that genus, and it is separated from the orbit by a much shorter interval. The supra-orbital foramen is sometimes present, sometimes indicated by a notch. The optic foramen is placed in front of the foramen lacerum anterius, and not above it. There is an

alisphenoid canal. The large space surrounding the small tympanic bone includes the Eustachian canal, foramen lacerum medium and posterius, and the carotid canal; in none of the fossils which I have seen can these foramina be distinguished.

The numerous venous foramina which perforate the parietal, are in the horse shifted to the squamosal. In the mandible there are three small mental foramina, extending from *pm.* 3 to the diastema.

When viewed in longitudinal section, the skull of *Mesohippus* (Pl. XXIII., Fig. 17) presents many important differences from that of *Equus*. Especially striking is the small size of the nasal chamber and the large size of the brain cavity, especially in the antero-posterior direction. The cerebellar fossa is decidedly larger in proportion, and is less overlapped by the cerebral fossa. There is very little thickening or diploëtic structure in the posterior parietal and supra-occipital regions, and the alisphenoids and orbito-sphenoids are excessively thin. The frontal sinus is exceedingly small, and does not extend over the hemispheres. The nasal chamber is low and narrow, and the maxillary sinus much smaller than in *Equus*. Unfortunately the specimen gives us no information as to the condition of the vomer or of the maxillo- and ethmoturbinals.

I have not been able to see a well-preserved skull of the European *Anchitherium*, nor, so far as I am aware, has any such specimen been figured. Kowalevsky's drawings (No. 25, Pl. III., Figs. 50-52, 56, and 57) show some differences from *Mesohippus*, especially in the increased thickness and width of the alveolar portion of the premaxillaries and of the *symphysis mandibuli*, corresponding to the development of the incisor teeth. *Anchitherium* appears to agree with *Mesohippus* in having a well-marked pre-orbital depression.

In the skull of *Equus* the principal changes are as follows: (1) The face has become greatly elongated and increased both in vertical and transverse diameters. (2) The alveolar portion of the maxillaries and premaxillaries has become very much higher, in correspondence with the development of prismatic teeth. (3) The anterior nares are much higher and wider, the nasals longer and tapering anteriorly to sharp points. (4) There is no pre-orbital depression. (5) The jugal and lachrymal are much more extended upon the face, and the masseter crest

has become very prominent, extending far forward upon the maxillary. (6) The maxillary alveolus extends farther behind the last molar. (7) The posterior nares are placed far back, and the posterior part of the palatines is not in contact with the alveoli. (8) The orbits are completely enclosed, much elevated in position, and pushed back of the molar series. This shifting causes important changes in the shape of the alisphenoids. (9) The zygomatic arch is shorter and more massive. (10) The cranial cavity is broader and more rounded, and the cerebral fossa overlaps the cerebellar. (11) The tympanic is ankylosed with the periotic. (12) Large sinuses are developed in the frontals and diploëtic thickenings in the median line of the parietals and occipitals. (13) In the lower jaw the symphysis is broadened, procumbent, and in the same line with the rest of the horizontal ramus; the ascending ramus is higher and narrower, the coronoid straighter and less pointed, and the condyle higher above the level of the molars.

### III. THE BRAIN.

The brain of *Mesohippus* has been described and figured by Osborn (No. 42, p. 87), who says of it: "*Mesohippus* had a large and well-convoluted brain. The length and breadth indicate that it weighed about one-third as much as the brain of the recent horse, while if we estimate the body weights of the fossil and recent animals by the relative size of the humeri, the brain of the Miocene species was proportionally heavier. The cerebrum of the horse is, however, much more highly convoluted, and the frontal lobes are relatively broader. The *Mesohippus* brain is distinguished in a marked manner by the longitudinal direction of the parietal and occipital sulci, and by the deep transverse frontal sulci, from the oblique sulci of all recent ungulates. In fact, in this respect it bears a marked general resemblance to the brain type of recent Carnivora, and conforms with the higher Ungulata of the Eocene." To this may be added that the hemispheres are narrower and less capacious in the fossil, and as in all the lower members of the ungulate series, they taper much anteriorly. This brain shows in the parietal and occipital region very close agreement with the principal fissures of the equine brain as figured by Krueg (No. 27, Taf. XXIII.), but in the frontal region the agreement is much less close, owing to the transverse direction of the frontal sulci.

Another well-preserved specimen of a *Mesohippus* brain-cast was obtained by the Princeton Expedition of 1890, which presents some differences from the one figured by Osborn. This brain was of a larger animal (perhaps species), and is more modern in appearance, the frontal lobes being decidedly broader, and the convolutions richer and more sinuous. In the frontal region the sulci tend to become less exactly transverse, and in the parietal region a slight tendency to obliquity of the sulci is observable. The olfactory lobes are large, and the cerebellum is not overlapped by the hemispheres to the same degree as in the recent species.

#### IV. THE VERTEBRAL COLUMN.

1. *Cervical Vertebrae.* The atlas (Pl. XXII., Fig. 3) is rather long antero-posteriorly in proportion to its breadth. The anterior cotyli for the occipital condyles are deeply concave and are notched, sometimes more and sometimes less deeply, on their outer margins. Inferiorly they are almost in contact, but above are widely separated by a deep and broad notch of semi-circular outline. The neural arch is rather broad and low, and the neural spine is represented by a low rugose ridge; on each side of this there is another similar ridge which runs obliquely forward and outward, ending above the foramen for the first spinal nerve. The inferior arch is strongly convex, and constricted in the middle by the deep fossæ into which the vertebrarterial canals open; there is a small but very distinct hypapophysial tubercle. The posterior cotyli for the centrum of the axis are rather high and narrow, and face obliquely backward and inward; the articular surface for the odontoid process is in some cases separated from the cotyli by deep grooves, either partially or completely; in others the two are continuous. The transverse processes are very short, but extended from before backwards, with regularly curved and slightly thickened free margins. When viewed from the side, the process presents a slight sigmoid curvature, and runs obliquely downward and backward. At the anterior root of the transverse process there is a deep notch for the first spinal nerve which is not converted into a foramen. The posterior opening of the vertebrarterial canal is on the dorsal side of the transverse process. In advance of its anterior opening there is a small vascular opening, which enters but does not perforate

the side of the atlas. The characters of the atlas of *Mesohippus* are thus obviously equine.

The atlas of *Anchitherium* figured by Kowalevsky (No. 25, Pl. I., Fig. 40), so far as it is preserved, closely resembles that of *Mesohippus*. The notch which separates the anterior cotyli above is not so broad or deep; the posterior cotyli face more directly backward, and the foramina for the dorsal branches of the first pair of spinal nerves are continued forward as deep grooves. In other respects the two are alike.

In the modern *Equidæ* the atlas has become broader and more rugose and massive in construction; the transverse processes are extended forward, converting the notches at their bases into foramina, and the posterior openings of the vertebrarterial canals are considerably enlarged.

The axis (Pl. XXII., Figs. 5-9) of *Mesohippus* presents many more differences from the modern type than does the atlas, and is also subject to an unusual degree of individual variation. The centrum is long, very much depressed and quite broad in front, becoming narrower and deeper behind, ending in a nearly circular and deeply concave posterior face. On the posterior half there is a thin but prominent hypapophysial keel, terminating in a small tubercle. The articular surfaces for the atlas are usually high and narrow, rising far up on the sides of the neural canal, but their shape varies much in different individuals; ordinarily they are nearly flat, or very slightly concave from side to side, the medial margin standing somewhat in advance of the external, and slightly convex from above downward; but sometimes the medial margins are far in advance of the external, giving the surfaces a curiously warped appearance. Sometimes the surfaces project down below the general level of the centrum, producing a deep notch between the two; in other cases they do not so project, and there is no notch. The odontoid process varies much in shape, being in some specimens short, broad, and straight, with truncated free margin; in others longer, narrower, curved upward, and pointed; but in all cases it is peg-like, and either flat or convex on the dorsal side, very different from the broad spout-like odontoid of the horse. The facet upon its inferior surface is usually separated from the articular faces of the centrum, but is sometimes continuous with them, as is the case in the corresponding surfaces of the atlas.

The neural arch is not very high, and is much broader in some specimens than in others; the pedicels are perforated near the anterior edge for the passage of the second pair of spinal nerves. The neural spine is very peculiar, being a long, high, hatchet-shaped, thin, and very much compressed plate, which terminates behind in an obtuse point, projecting considerably beyond the postzygapophyses and raised much above them; altogether very different in shape and appearance from the structure seen in the horse. The postzygapophyses are large and very prominent; in some specimens they are directed nearly straight outward, in others more obliquely outward and backward. Sometimes they are quite concave from side to side, but again they are as strongly convex. Transverse processes are not preserved in any of the specimens which I have seen.

The axis of *Anchitherium*, so far as known, is, according to Kowalevsky (No. 25, p. 69, Pl. I., Fig. 46), entirely like that of the horse; it differs from the axis of *Mesohippus* in the much greater outward projection of the anterior part of the centrum with the atlanteal facets. A more important difference is in the shape of the odontoid, which, though still relatively short, is completely spout-like in shape.

In the horse the anterior articular surfaces project outward and also downward, as in some specimens of *Mesohippus*; the odontoid process is spout-shaped, though not so deeply concave as in the ruminants; its facet for the atlas is continuous with those on the anterior face of the centrum, the medial margins of which stand far in advance of the external. The neural spine is relatively low but very massive, and with a thickened rugose margin, which posteriorly bifurcates into two ridges, one of which passes into and dies away upon the postzygapophyses; the latter form, therefore, the hindermost projection of the vertebra. The neural canal is proportionately low and narrow. The centrum is very strongly opisthocœlous, and the posterior face is obliquely placed, slanting upward and forward.

It will be observed that the numerous individual variations of the axis of *Mesohippus* consist chiefly in approximations to the condition found in the horse, now in one respect, now in another.

The third, fourth, and fifth cervical vertebræ of *Mesohippus* (Pl. XXII., Fig. 10) are very much alike; they all have elongate

centra, which are strongly keeled inferiorly, and have faces set obliquely to the long axis; the anterior face is hemispherical, and the posterior deeply concave. In these three vertebræ the centra are of nearly equal length. The neural arches are low and very broad on top; the zygapophyses are large, strongly projecting, and present nearly vertically. The neural spine is represented by a faint ridge on the third, which becomes a small tubercle on the fourth, and a distinct spine on the fifth. The transverse processes have considerable antero-posterior extension and become successively shorter and stouter as we pass backward; at the same time the inferior lamella, which is rudimentary on the third, steadily enlarges on the succeeding vertebræ.

The sixth cervical (Pl. XXII., Figs. 11 and 12) is shorter than the preceding ones, and has no hypapophysial keel or tubercle; instead, the lower edge of the posterior face is emarginated in the median line. The neural spine is quite high and inclined strongly forward. The transverse process is a short, stout hook, curved upward at the extremity, and the inferior lamella has greatly increased in size, attached to the centrum throughout its length, and projecting considerably both in front and behind it.

The seventh cervical is still shorter than the sixth; it has a broad, flat, and depressed centrum, which, in advance of the transverse processes, is somewhat suddenly constricted to form the small, nearly hemispherical, and obliquely placed head; the posterior face is quite broad, and displays on each side of the rounded pit for the head of the first dorsal a facet for the head of the first rib. The transverse processes are quite stout and simple, and are not perforated by the vertebrarterial canal. The prezygapophyses are nearly flat, very prominent, and obliquely set, facing more inward than upward; the postzygapophyses are less conspicuous, as they do not project behind the neural spine. The latter is stout, strongly inclined backward, and occupies the whole antero-posterior extent of the neural arch, but unfortunately none of the specimens is sufficiently complete to enable us to estimate its height.

Comparing the posterior five cervical vertebræ of the horse with those of *Mesohippus*, we find many important differences. The centra have been much elongated, so that the neck as a whole is much longer than in the Miocene genus; all of the

processes for muscular and ligamentous attachments are much more prominent and massive, in correlation with the increased size and power of the animal. The faces of the centra are more decidedly concave behind and convex in front, and are set more obliquely to the long axis of the vertebræ, so that the neck exhibits a more decided sigmoid curvature, as well as being longer. Neural spines have disappeared from all but the seventh, where the spine is much lower proportionately than in *Mesohippus*. In *Equus asinus*, however, there is a very short spine on the sixth also, and the inferior lamella on this vertebra is less developed than in the Miocene form.

The number of dorsal vertebræ which *Mesohippus* (Pl. XXII., Figs. 13-15) possessed is uncertain, though it can hardly have been less than eighteen. The first vertebra of the series has a centrum very similar in character to that of the seventh cervical, but shorter, and less strongly opisthocœlous. The transverse processes are quite long, and have very large, crescent-shaped and deeply excavated facets for the tubercles of the first pair of ribs. The prezygapophyses are very large and prominent, the postzygapophyses much smaller, but projecting strongly behind and to the sides of the neural spine; the latter is stout, especially on the posterior edge. The succeeding dorsals gradually lose these characters, the centra becoming less opisthocœlous, the transverse processes shorter and with more flattened facets; the zygapophyses on the third dorsal are developed on the anterior and posterior faces of the neural arch. Metapophyses appear quite early in the series and on the ninth (?) vertebra they are very prominent. In the middle region the transverse processes are very short and are placed above the centrum. The spines are long, but very thin and much compressed; in the anterior region they have expanded tips. The posterior dorsals become longer and have trihedral, sharply keeled, and slightly opisthocœlous centra, with faces set obliquely to the long axis. The spines are quite high, but very thin and inclined forward; the zygapophyses are more lateral in position and slightly concave and convex respectively, thus being of a somewhat interlocking character.

The anterior lumbar vertebræ have elongate trihedral and sharply keeled centra, which are slightly opisthocœlous and have oblique faces; in these vertebræ the transverse diameter

but little exceeds the vertical; posteriorly the centra become much broader and more depressed. The spines appear to be thin and compressed, the transverse processes quite stout and with considerable antero-posterior extent; on the last (Pl. XXII., Fig. 16) and penultimate vertebræ the transverse processes have articular surfaces for contact with those of the succeeding vertebræ. The zygapophyses are interlocking in a moderate degree. The obliquity of the faces of the dorsal and lumbar vertebræ show that the back was decidedly arched.

In the horse the back is nearly straight and the dorso-lumbar vertebræ vary less in length in the different regions; the lumbar vertebræ in particular are shorter in proportion than those of *Mesohippus*. The spines are much more massive and more nearly straight, and the zygapophyses of the posterior dorsal and lumbar regions are much more decidedly of the interlocking type.

The first sacral vertebræ of *Mesohippus* has a very much depressed centrum; the pleurapophyses are greatly expanded and form the large iliac surfaces, the second vertebræ not contributing to their formation. On the anterior edge of the pleurapophysis is a very large convex facet for the transverse process of the last lumbar.

No caudal vertebræ are preserved in the specimens.

Nothing is known of the sternum, and the few fragments preserved indicate that the ribs were more slender in proportion than are those of the recent horses.

## V. THE FORE LIMB.

The *scapula* is not well preserved in any of the specimens, but enough remains to indicate its chief characters. The glenoid cavity is nearly circular and quite shallow, and is slightly notched at its antero-internal border by the synovial incision. The coracoid process is very large, both in the vertical and antero-posterior directions, but is thin and plate-like, and is not recurved at the free end. The neck is very narrow and long; the spine rises somewhat nearer to the glenoid cavity than in the horse, and is not median in position, but nearer to the coracoid border, thus making the postscapular fossa larger than the prescapular. None of the specimens has a sufficiently well-

preserved spine to show whether a metacromion was present. The glenoid border is much thickened, and the coracoid border, so far as preserved, is quite thin and sharp. The course of the former indicates that the blade of the scapula was proportionately broader than in the horse, and the neck is much more contracted.

The fragment of *Anchitherium* scapula which Kowalevsky figures (Pl. I., Fig. 37), agrees very closely with that of *Mesohippus*, the only observable difference being that the coracoid is somewhat more massive. "La *spina scapulæ* commence plus loin du bord glenoïdale que dans les Paléothériums et monte presque perpendiculairement, avec une légère inclinaison en dehors ou en arrière; cette inclinaison de la *spina scapulæ* en dehors est très caractéristique pour tous les imparidigités, elle s'explique par le fait que cette portion de l'omoplate sert d'insertion aux grands muscles qui aide à tourner le bras (*M. cucullaris*, ce muscle est insignifiant chez le cheval). Chez les rhinocéros cette partie de la *spina* donne encore un processus en arrière pour augmenter la superficie de l'insertion musculaire. Avec la réduction des mouvements latéraux ce caractère commence à se perdre, et chez le cheval tous les mouvements latéraux des extrémités sont réduits à leur minimum, la *spina scapulæ* perd les caractères périssodactyles et fait un pas vers les ruminants; elle s'incline dans sa partie antérieure en dedans" (No. 25, p. 5).

It is of interest to observe that the scapula of *E. caballus* differs from that of *E. asinus* in very much the same way as does the scapula of the camel from that of the llama.

The humerus (Pl. XXIII., Figs. 19-22) of *Mesohippus* is relatively short; the head is flattened and projects very strongly backward; when the bone is placed in the vertical position, the head presents more posteriorly than superiorly. The external tuberosity is very large, extending across nearly the entire anterior face of the bone and ending in a stout, blunt hook, which overhangs the bicipital groove. This tuberosity is divided into two portions, a smaller external one with smooth surface, and a larger rugose internal one. The inner tuberosity is well developed, and incloses, with the outer, a very deep and narrow bicipital groove, which is situated at the antero-internal angle of the head. In none of the specimens which I have examined is

there any indication of the bicipital tubercle at the bottom of the groove. The shaft is slender and slightly curved in a sigmoid shape; in the middle it is of nearly circular section, below this transversely oval, and proximally it is also oval, with the long axis directed from before backward. The deltoid ridge is prominent and rugose and runs far down on the shaft, forming, however, no projecting hook; the supinator ridge is distinctly marked, but short. The anconeal fossa is very small, but deep, and penetrates the shaft to form the supra-trochlear foramen. The distal end is but little expanded transversely, and the trochlea is set obliquely to the long axis of the shaft; it is also of considerably greater vertical height internally than externally. The inner condyle is broad on the anterior face, but becomes much narrower on the distal and posterior sides; the intercondylar ridge forms a broad and thick rounded prominence. The external condyle is almost confined to the anterior face, hardly descending at all upon the distal surface; its outer portion projects laterally and is flared in a peculiar manner, forming with the corresponding surface on the radius a joint which allows an extraordinary degree of flexion. The obliquity of the trochlea has the effect of throwing the radius outward during flexion; otherwise the arrangement of facets is such that the two bones could be brought into contact through almost their whole length without dislocation.

The epicondyles are but feebly developed, the external one being hardly indicated, the internal one somewhat larger and more prominent. The inner side of the distal end has a considerably greater antero-posterior depth than the outer, so that when the bone is viewed from the side the internal margin of the anconeal fossa is seen to project behind the outer margin, but much less decidedly than in *Equus*.

The humerus of *Anchitherium* is very similar to that of *Mesohippus*, but more equine in construction. The shaft is rather stouter, and the deltoid ridge more prominent, an incipient hook being plainly indicated. The external tuberosity is considerably reduced in size, not extending so far toward the medial line. The internal tuberosity is also smaller, and the bicipital groove much wider and shallower, and has moved toward the outer side; the beginning of the bicipital tubercle is likewise clearly shown. The distal end is, according to Kowalevsky, thoroughly hippoid in character, and so far as can be judged from his

figure, it has not the peculiar flaring external condyle which is so characteristic of *Mesohippus*.

In the horse, the shaft has become much stouter and straighter, as well as longer than in the Miocene genus, and the ridges for muscular attachment, especially the deltoid hook, much better developed. The external tuberosity is little, if any, larger than the internal, and does not project over the bicipital groove, which, in its turn, has become very broad, and is divided into two portions by the large bicipital tubercle. The latter is now as prominent as either of the tuberosities. The distal trochlea is broad, set nearly at right angles with the long axis of the shaft, and of uniform height. The inner condyle is proportionately more extended than in *Mesohippus*, and the intercondylar ridge more thickened. The external condyle has not the peculiar facet above described, and there is no supra-trochlear foramen. The inner margin of the anconeal fossa projects far behind the outer.

The humerus of *Mesohippus* is in many ways like that of *Pæbrotherium*, while that of *Equus* is very similar to that of the camel, especially in the construction of the proximal end.

The ulna (Pl. XXIII., Fig. 23) of *Mesohippus*, though much reduced, is usually distinct from the radius throughout; in some specimens, however, the distal ends of the two bones are co-ossified for a short distance. The olecranon is quite high, but thin and compressed, with a thick end and abruptly truncated superior margin; it is continued upward in a vertical line with the shaft, hardly projecting at all backward. The sigmoid notch is shallow, and the articular facets for the humerus are confined to its superior and anterior faces, and are obliquely placed with reference to the long axis of the shaft. The radial facets are two, of which the outer one is decidedly the larger and more prominent. The shaft is very slender and compressed, but not interrupted, and the distal end is but slightly expanded and bears a small saddle-shaped facet for the cuneiform.

The radius (Pl. XXIII., Figs. 23-25) is short and has a shaft which is arched forward and quite slender, though in the latter respect there is considerable variation, some specimens being decidedly stouter than others. The shaft is much flattened antero-posteriorly, and is of transversely oval section and nearly uniform diameter, except at the extremities. The proximal end

is quite broad, the increase being chiefly upon the external side. There are three clearly demarcated facets for the humerus, of which the internal is the broadest, and is separated from the external by the broad and deep intercondylar notch, which, however, emarginates the anterior edge but slightly. The external facet projects strongly beyond the line of the shaft; it is nearly flat and descends steeply from behind forward, somewhat as in *Oreodon*. The very unusual amount of flexion which this arrangement permits has been already mentioned. Distally the radius is thickened, but not much expanded transversely; the anterior face has broad, not very deep sulci for the extensor tendons, and on the external side there is a deep groove for the distal end of the ulna. There are two carpal facets, for the scaphoid and the lunar; the former is concave in front, and behind forms a stout convex projection which extends much posteriorly to the lunar facet and is reflected up upon the hinder face of the bone. The surface for the lunar is simply oval and concave; its greatest diameter is transverse, in which dimension it somewhat exceeds the scaphoid, but is much less extended antero-posteriorly. The tubercle for the insertion of the biceps and brachialis internus muscles is on the inner side of the proximal end. The ulna and radius of *Anchitherium* present no important differences from those of the American genus.

In *Equus* the ulna and radius have completely coalesced and the shaft of the former is interrupted. The olecranon is longer and projects more strongly backward than in *Mesohippus*, and its free end is more regularly rounded. The shaft of the radius is much stouter and more expanded at the extremities; the facet for the internal humeral condyle is decidedly broader in proportion, and the intercondylar groove notches the anterior margin quite deeply. The rugosity for the biceps and brachialis internus is on the anterior face.

The carpus of *Mesohippus* (Pl. XXIII., Figs. 26-28) is in general appearance and construction very much like that of the horse, but with many differences of detail, and on the whole decidedly more primitive. The carpus of *Anchitherium* is distinctly nearer to the modern condition, which is partly due to its greater size, partly to the more pronounced enlargement of the median digit, and reduction of the lateral ones.

The scaphoid is rather narrow transversely, but high and of

considerable antero-posterior depth. The internal side is rugose and marked by a deep oblique groove, which, however, does not appear to be a tendinal sulcus; the posterior face is also rugose, but less transversely extended than in the horse, where this face forms a hook projecting toward the ulnar side. The proximal facet for the radius has a greater antero-posterior extent than that of the lunar or cuneiform; it is broader and slightly convex in front, narrower and concave behind. On the ulnar side of the scaphoid there are two facets for the lunar, of which the inferior is less distinct than in the horse, and the interval between the scaphoid and lunar not so large as in that animal. The distal surface of the scaphoid exhibits three articular facets, arranged one behind the other; of these the anterior and largest one is for the magnum, which is nearly plane; behind and slightly internal to it is the concave facet for the trapezoid, and on the postero-internal angle a minute facet for the trapezium. There is no posterior facet for the head of the magnum. The scaphoid of *Anchitherium* is very similar to that of *Mesohippus*, but is relatively lower and broader and more cubical in shape, and the trapezoid facet more entirely posterior to that for the magnum. Both of these features are exaggerated in the horse, and the palmar face of the scaphoid much widened and inflected towards the ulnar side. Usually there is no facet for the trapezium in *Equus*, but according to Kowalevsky it very often is present (No. 25, p. 20).

The lunar is high and narrow, with the proximal end considerably broader than the distal. The radial facet is slightly convex in front, concave behind, and on the internal side descends somewhat upon the anterior face of the bone. The lunar is in contact with the scaphoid only at the superior and inferior borders, being elsewhere separated by a considerable interval, but it is closely applied to the cuneiform throughout. The distal end, when seen from the front, is unevenly divided between the magnum and unciform, the former surface being usually much the wider; in one specimen the proportion is 1 : 1½; in another, the magnum facet is but slightly broader than that for the unciform. The latter facet has a smaller antero-posterior extent than the former, the projection from the palmar side covering only the magnum.

The cuneiform is very narrow transversely, its principal diameter being the antero-posterior, caused by a prominent and

massive projection from the palmar face. The proximal surface is small, slightly concave, and occupied by the ulna; there is a small facet also for the radius, but this is not apparent in all specimens. Distally there is a concave facet for the unciform, which is broader behind than in front. The pisiform facet is narrow, but long, and but little oblique in position, presenting nearly directly upwards. The cuneiform of the horse is relatively broader and more massive, but lower; the posterior projection is much less prominent, and the pisiform facet is nearly vertical, presenting backward, and but very slightly upward.

The pisiform is of entirely different shape from that seen in the horse; it is quite long and compressed, with a somewhat contracted neck and expanded free end, which is slightly inflected at the tip. The cuneiform facet is long and narrow and entirely on the inferior surface, forming nearly a right angle with the ulnar facet, with which it is continuous (though in some specimens it is separated from it by a short interval); the latter is of triangular shape, and slightly concave. In the horse, the pisiform has a much greater vertical diameter and no neck; the ulnar and cuneiform facets are both on the proximal end, on nearly the same plane, and separated from each other by a deep notch.

The trapezium is a very small nodular bone, with its vertical diameter the principal one; proximally it has a minute contact with the scaphoid, and distally it presents an oblique facet for the posterior side of the head of the second metacarpal, projecting below the level of the distal face of the trapezoid.

The trapezoid is rather low, and very narrow in front, broader behind. Its position is rather more lateral than in the horse, and more of it is visible when the manus is viewed from the front. The proximal surface is somewhat convex, the distal nearly plane, and there is a small posterior facet for the trapezium. The trapezoid supports only metacarpal II., and there is no separate posterior facet for the magnum such as occurs in the horse.

The magnum is relatively high and narrow, in correlation with the moderate degree of expansion which the median digit has undergone. The proximal surface is in front divided, nearly equally, between the facets for the scaphoid and the lunar, the former slightly the broader, the latter more oblique in position, and the two meeting in an open angle, and forming a sharp ridge. Posteriorly the magnum is covered only by the lunar,

into a concave facet of which the narrow, elevated "head" of the magnum fits. The distal surface of the magnum is nearly plane, broad in front and narrow behind, and is occupied entirely by the third metacarpal, but on the radial side is a small facet for metacarpal II. The magnum of *Anchitherium*, as figured by Kowalevsky (No. 25, Pl. II., Fig. 1), is very different from that of *Mesohippus*, being low and very broad, and the lunar facet is relatively very wide; on the ulnar face there is in front but a single facet for the unciform, which occupies the whole height of the magnum, while in the horse this facet is divided into superior and inferior portions. Some specimens of *Mesohippus* agree with *Anchitherium* in this respect, others with *Equus*. In the latter genus, the magnum has become extremely broad and low, which especially affects the radial side, so that the scaphoidal facet is now much broader than the lunar. In particular, the posterior portion of the magnum, which is very narrow in *Anchitherium*, and still more so in *Mesohippus*, has become very wide in the horse.

The unciform is narrow and compressed, but very high, having nearly twice the vertical diameter of the magnum, and in consequence projecting far below the distal face of the latter. The proximal end exhibits a small facet for the lunar, and a much larger one for the cuneiform, which is reflected well down upon the postero-external face. Distally there is a large facet for metacarpal IV. and a much smaller one for metacarpal V. The facet for metacarpal III. is vertical and entirely lateral in position, being placed upon the radial side of the bone, and not at all distal. In *Anchitherium* (Kowalevsky, Pl. II., Figs. 1 and 9), the unciform is lower, and the distal portion much more produced posteriorly; the facet for metacarpal III. is very oblique in position. The unciform of the horse is very different from that of the Miocene genera; it is much lower, hardly projecting at all below the level of the magnum, which it exceeds but little in height; the lunar facet has become somewhat broader, and the facet for metacarpal III. almost entirely distal in position, forming a gently curved outline with the facet for metacarpal IV.; of course, there is no facet for a fifth digit; posteriorly the unciform is seen to rest upon the third metacarpal: in *Mesohippus* this is not the case.

The *metacarpus* (Pl. XXIII., Figs. 26-28, 30) consists of three

functional members, the second, third, and fourth, and one rudimentary, the fifth. Metacarpal II. is very slender, compressed, and elongated, with a much flattened shaft which is closely applied to that of the median digit, and which is arched forward. The proximal end is somewhat thickened antero-posteriorly, but very little wider than the shaft; it exhibits three well-marked facets,—a small one on the posterior or radial edge, for the trapezium; a larger, slightly concave, and truly proximal one for the trapezoid; and on the ulnar side a small facet for the magnum. The distal trochlea is very much compressed laterally and narrower than the inferior end of the shaft; the carina is very nearly median in position, not at all prominent, and entirely confined to the palmar side.

Metacarpal III. is by far the largest of the series, though it is relatively much narrower and more slender than in the later genera of the equine phylum. The shaft is flattened antero-posteriorly, and of transversely oval section; it is narrowest and deepest above, becoming broader and shallower distally. The proximal surface is nearly plane, but is not placed so nearly at a right angle with the long axis of the shaft as in the horse, rising gently toward the ulnar side. This facet for the magnum is broader in front than behind,—a difference which is more marked than in *Equus*, and is suddenly constricted in the middle. The proximal surface displays no facets for the trapezoid or unciform. The unciform facet is on the ulnar side of the head and presents altogether laterally; this facet is divided by a deep groove into anterior and posterior portions. The distal end is expanded laterally just above the trochlea, which is narrower; the carina is much stouter and more prominent than in the lateral digits, and extends farther upon the anterior face, but not so far as in *Anchitherium*.

Metacarpal IV. is more slender than No. III. and has a narrower and less thickened head. The unciform facet is nearly plane and of triangular shape, with the apex directed posteriorly. Upon the radial side there is a small facet for the overlapping projection of metacarpal III., and on the ulnar side another for the head of No. V.

The fifth metacarpal is represented by a rudiment which carries no phalanges. The head is as large as in No. IV., but the shaft is very slender and tapers rapidly to a point. The

unciform facet is narrow and slightly concave from side to side, the ulnar border rising somewhat higher than the radial.

The metacarpus of *Anchitherium* exhibits no very important differences from that of *Mesohippus*. The median digit is much broader relatively and appears also to be longer in proportion; the unciform facet is more obliquely placed, so as to present upward as well as laterally; the carina of the distal trochlea is somewhat more prominent, and continued farther up upon the anterior face of the bone. The second and fourth metacarpals are very much as in the American genus, but judging from the facet upon the unciform, metacarpal V. is still further reduced, and must have been concealed from view by No. IV., when seen from the front; in *Mesohippus* it is plainly visible in the anterior aspect. The carpo-metacarpal articulations have undergone no important modification from the condition found in the latter.

The metacarpus of the horse (see Fig. B, p. 336), on the other hand, presents some very important changes. The fifth digit has entirely disappeared, the second and fourth reduced to mere splint bones without phalanges. The median metacarpal has greatly increased in breadth and thickness, especially toward the radial side, and the distal carina has become very stout and encircles the entire trochlea, dorsal as well as palmar. The anterior unciform facet has become almost entirely proximal instead of lateral in position. Seen from the front, the carpo-metacarpal articulations seem to have undergone little change, but the great increase in breadth of the posterior portion of the head has brought the median metacarpal into contact with the trapezoid and unciform, thus supporting it on all of the distal carpals.

The phalanges of *Mesohippus* are very like those of *Anchitherium*. Those of the lateral digits are short, slender, and much compressed laterally; the unguals narrow and pointed. Those of the median digit are longer, very much broader, and more symmetrical in shape. The proximal one is relatively much shorter than in the horse; the groove for the metacarpal carina is confined to the palmar half, and the distal articular surface does not extend so far upon the dorsal side. The ungual phalanx is long, broad, flattened from above downwards, and pointed. It is not so much elongated as in *Anchitherium*, but very different in shape from the characteristic ungual of the existing *Equidæ*.

## VI. THE HIND LIMB.

The pelvis (Pl. XXIII., Fig. 31) of *Mesohippus* is very like that of the horse, with some differences of detail. The neck of the ilium is much longer and more slender, when viewed from the side, but rather broader when viewed from below, owing to the prominence of the pubic border, upon which a small rugose spine is developed. The plate is too much injured in the only specimen at my disposal to allow an accurate determination of its shape, but it is plain that it expands much less abruptly than in *Equus*, and apparently it is relatively much smaller than in that genus. The acetabulum is deep, with prominent edges, and the pit for the round ligament is smaller and more median in position than in the modern forms.

The ischium is long and quite straight; for most of its length it is much more slender and rod-like, and less curved upward than in *Equus*. The posterior portion is expanded and depressed, sending off from its outer side a long and sharp but low tuberosity. Above the acetabulum the border of the ischium is very slightly elevated into a crest, which terminates behind in a shallow groove for the internal obturator tendon. The obturator foramen is very much larger proportionately than in the living forms, and consequently the posterior expansion of the ischium much smaller.

Kowalevsky states that in *Anchitherium* the crest of the ischium is more rounded and thickened than in the horses, and that the sulcus for the internal obturator tendon, which is wanting in the horses, is profound (p. 15).

The femur of *Mesohippus* (Fig. A) is characteristically equine in appearance. The shaft is quite long and stout, in comparison with the other long bones, but slender as compared with the modern type. When viewed from the side, it presents a decided sigmoid curve. The head is small and nearly sessile, but rises somewhat above the bridge connecting it with the great trochanter: the pit for the round ligament is deep, but narrow and

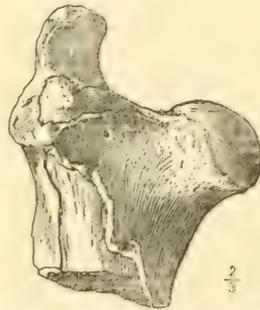


FIG. A. — Right femur of *Mesohippus*; anterior view.  $\times \frac{2}{3}$ .

short. The great trochanter is low, massive, and rugose in front, behind it rises into a high, stout hook, which projects far above the head; the digital fossa does not invade the shaft, but is formed by the recurved edge of the trochanter. The second trochanter is a long, rugose, and prominent ridge, and the third is moderately developed. The distal condyles, of which the outer is considerably the larger, are rather small and do not project strongly backward; the groove separating them is wide but shallow. The rotular trochlea is broad and shallow, with edges which are sharp and of nearly equal height. A long depression runs up the shaft above the trochlea. Above the external condyle, on the posterior side of the shaft, there is a deep pit for the plantaris muscle. In *Anchitherium* (de Blainville, *Palæotherium*, Pl. VII.) the femur is very like that of the American genus, but is somewhat stouter and straighter, and more equine in the details of construction.

In the horse, the femur has become very much stouter, and all the processes for muscular attachment more massive. The head is sessile, and the great trochanter approaches nearer to it, and the pit for the round ligament is much larger. These changes, as Kowalevsky has pointed out, involve to a considerable degree the loss of rotatory movements, and the confining of the motion of the femur to the vertical plane. The condyles are much more massive and prominent; the trochlea is oblique to the long axis of the shaft, and its inner border greatly elevated and enormously thickened.

The tibia (Pl. XXIII., Figs. 32, 33) of *Mesohippus* is long and very slender, and the shaft has a slight sigmoid curvature. The femoral facets are slightly concave and are placed obliquely to the long axis of the bone, inclining downward and backward. The cnemial crest is long and massive, and has the usual deep tendinal sulcus on its outer edge. The distal end is quite narrow, and the astragalar facets are deep and very oblique in position, with a high intercondylar ridge, which is more prominent behind than in front; the inner malleolus is only moderately developed.

The proximal end of the *fibula* is not preserved in any of the specimens; the distal end is sometimes co-ossified with the tibia, as is also a considerable portion of the shaft; in other specimens it is free. This end is expanded to form a stout

external malleolus, which exhibits two facets, — an internal one for the astragalus, and on the posterior side of the distal surface a small one for the calcaneum.

In *Anchitherium*, the tibia and fibula are very much as in the American form, but the former is straighter and decidedly more massive.

In the horse, the tibia has become nearly straight and very heavy; the femoral facets are nearly at right angles to the long axis of the shaft; the cnemial crest is very massive, but does not extend so far down the shaft as in *Mesohippus*; the distal end of the fibula is indistinguishably fused with the tibia, but preserves its facet for the calcaneum, at least in some cases.

The tarsus of *Mesohippus* (Pl. XXIII., Figs. 34, 36–38) is very equine in appearance and construction. The calcaneum is rather long and quite slender and compressed, the dorso-plantar diameter being conspicuously small; the two borders are straight and nearly parallel. This is true also of *Equus*, but in this genus the short, massive, and deep tuber has a very different appearance. The distance from the superior or “ectal” astragalar facet to the distal end is very considerable; this facet forms a high crest, descending obliquely toward the tibial side, and on its posterior aspect there is, as Osborn has pointed out (No. 41, p. 546), a very distinct fibular facet. This ectal astragalar facet is slightly prolonged at its infero-external angle. The sustentaculum is very prominent and massive, but has only a proportionately narrow facet for the astragalus. The inferior astragalar facet is narrow and of limited antero-posterior extent. The cuboidal facet is narrow, slightly concave, and obliquely placed with reference to the long axis of the bone, descending downwards and forwards. Posteriorly it is very little recurved or inflected toward the tibial side.

The calcaneum of *Anchitherium* is more equine in shape, as is especially marked in the increased dorso-plantar diameter of the tuber calcis and the more pronounced beginning of the “facette surnuméraire” by a prolongation of the infero-external angle of the ectal astragalar facet. The inferior astragalar facet, on the other hand, is less equine, being much more extended antero-posteriorly than in *Mesohippus*. The sustentaculum is more prominent and massive than in the latter genus, and the cuboidal facet but little recurved posteriorly.

In *Equus* the calcaneum has become relatively shorter and stouter, the dorso-plantar diameter being especially increased; the sustentaculum is very prominent and enlarged both transversely and from above downwards. There are two ectal astragalar surfaces, the supernumerary facet being completely separated from the principal one. The cuboidal facet is divided into two portions by a ridge, the smaller anterior one running from before backwards, and the larger posterior one directed nearly transversely. This curvature and transverse extension of the distal end, together with the enlarged sustentaculum, give to the posterior aspect of the horse's calcaneum a very different appearance from that seen in *Mesohippus*, though an indication of the modern arrangement is clearly apparent in the older genus.

The astragalus of *Mesohippus* has a narrow, deeply incised, and obliquely directed trochlea, the condyles running downward and outward. The internal condyle is longer than the external, extending beyond it both above and below, and inferiorly reaching to the navicular facet, while the external condyle is separated from this facet by a considerable interval. The surface for the external malleolus is narrow and in some specimens quite strongly everted as a distinct process at its lower end; the facet for the internal malleolus is very much broader, and terminates inferiorly in a pit, into which the tip of the malleolus fits in extreme flexion. Internal to this is a prominent tubercle for the attachment of the astragalo-metatarsal ligament. On the plantar side of the astragalus three calcaneal facets are visible; the ectal is very deeply concave, and at its infero-external angle there is a small, plane facet, the beginning of the supernumerary facet. The ectal facet is separated by only a narrow interval from the sustentacular, and in some specimens, notably those of the larger animals, the two are in contact. The sustentacular facet is long, narrow, and nearly flat; distally it forms a projection of the posterior margin of the navicular surface. The inferior calcaneal facet is very small and elongate oval in shape. The distal surface for articulation with the navicular is relatively narrow, and of irregular shape. It is slightly concave from side to side, and the external margin projects strongly downward; a similar projection is formed on the posterior margin. As Osborn has pointed out (No. 41, p. 546), the fossa in the navicular surface

varies much in depth and distinctness. The cuboidal surface is very small, and abruptly truncates the projection of the external margin already mentioned.

The astragalus of *Anchitherium* is very much like that of *Mesohippus*, but is relatively broader, especially the distal end, and the neck is shorter, so that the external condyle projects downwards as far as the navicular surface. The projection of the external margin of the latter surface is less pronounced than in *Mesohippus*; that from the plantar margin rather more so. According to Kowalevsky, there is no fossa in the navicular facet: "J'ai examiné plus de quarante astragales de l'*Anchitherium* sans pouvoir trouver un seul qui présenterait cette échancrure caractéristique, toute la surface tarsienne est invariablement d'un poli uniforme. Sur deux astragales seulement j'ai pu remarquer à l'endroit où se trouve l'échancrure chez les chevaux une légère rugosité" (No. 25, p. 39).

The astragalus of the horse has become decidedly broader, the trochlea more widely open, and the condyles thicker; the neck is shorter, and the condyles overhang so far as to project below the navicular surface. The supernumerary calcaneal facet is quite widely separated from the ectal. The surface for the external malleolus is broader. The anterior margin of the navicular facet forms a nearly straight line, there being no projection of the outer edge, but the posterior projection is very strongly developed. The fossa of the navicular facet is very distinct. The cuboidal facet is more completely distal than in the earlier forms.

The cuboid of *Mesohippus* is high and narrow, but deep antero-posteriorly, and with a short but broad and rugose posterior hook. The proximal surface is somewhat oblique to the vertical axis of the bone, descending anteriorly; it is obscurely divided into two portions, of which the anterior is the broader, but there is no such difference as in *Anchitherium*; the two are in the same antero-posterior line. The astragalal facet is very small and placed on the tibial side of the cuboid. There is no antero-superior facet for the navicular, the two bones being separated at this point by the downward projection of the astragalus, but there is a well-marked antero-inferior facet. Posteriorly there is a small projecting process, which carries two facets, a superior one for the navicular and

an inferior one for the ectocuneiform. The distal surface is much smaller than the proximal and bears a slightly convex, rounded facet for the fourth metatarsal; on the tibial side there is a very small, entirely lateral facet for the third metatarsal, which is enabled to touch the cuboid laterally, because the latter projects below the ectocuneiform, having a height greater than that bone and the navicular combined.

In the cuboid of *Anchitherium* the calcaneal facet is more distinctly divided into anterior and posterior portions, the latter being very much narrower and somewhat recurved. The facet for metatarsal III. is of very different shape, being broader in front and narrower behind, and that for metatarsal IV. is more oblique in position, presenting downward as well as inward. The whole bone is more massive and thickened, and the posterior projection longer and more rugose.

In the horse, the cuboid has become very different. The calcaneal facet is now very distinctly divided into anterior and posterior portions, though the two are still continuous, and the latter is strongly incurved. There is a large antero-superior facet for the navicular, the astragalus no longer intervening between the two; the posterior facet for the navicular and ectocuneiform is much more prominent than in *Mesohippus*. The distal surface also exhibits important changes. The facet for metatarsal III. is very much larger and altogether distal in position, while that for metatarsal IV. has become very oblique and rather more lateral than distal; an additional facet for this metatarsal appears on the postero-internal angle. The cuboid does not descend below the ectocuneiform.

The navicular of *Mesohippus* is low and broad, though relatively higher and narrower than in the existing genus. The proximal surface is concave and the posterior margin considerably elevated at its inner and outer angles; between the two is the wide depression for the corresponding process from the astragalus. There is a small triangular space in the navicular facet, which extends toward, but does not reach, the fibular margin; this represents the fossa which occurs in the horse and is more clearly shown than the corresponding structure on the astragalus. There is no anterior facet for the cuboid: when the two bones are placed in position, they divaricate anteriorly; the posterior cuboidal facet is quite large and is continuous

with that of the ectocuneiform. The distal surface has two facets, for the ectocuneiform and the coalesced meso- and entocuneiforms respectively. The former is broad, and sends out a narrow posterior prolongation. The latter is much smaller and regularly convex from before backwards, and does not show any definite separation into facets for the two elements of the compound cuneiform.

The navicular of *Anchitherium* is broader and lower, and the antero-external angle is very much produced, encircling the cuboid in a curious way (Kowalevsky, Pl. III., Fig. 17). The posterior prolongation of the facet for the ectocuneiform is curved sharply toward the fibular side, and the facet for the first and second cuneiforms are in contact, though their limits are defined by a ridge. There is no fossa in the astragalar surface.

In *Equus* the navicular is still broader and lower; it has quite a large anterior facet for the cuboid, and the posterior facet has become more prominent. The elevations of the posterior proximal margins and the depression between them are hardly more marked than in *Mesohippus*, but have become decidedly more massive and rugose. The fossa in the astragalar surface is deep and conspicuous and continuous over the fibular margin. The facet for the coalesced cuneiforms, especially for the entocuneiform portion, has become decidedly larger; but the principal increase in the breadth of the navicular is, as Kowalevsky has suggested, in that portion of it which supports the ectocuneiform.

In *Mesohippus*, the ento- and mesocuneiforms have coalesced. The disposition of the equine tarsus to become reduced in breadth, but increased in depth, and to close behind so as to form a circle, has been pointed out by Rüttimeyer (No. 46, p. 17), and is already very apparent in the White River genus. The entocuneiform is high and compressed, and sharply everted so as to be in contact with the cuboid; it greatly exceeds the mesocuneiform in vertical height, rising much above it on the navicular and descending much below it distally. The navicular facets of the two elements are confluent, but the distal facets are very distinctly separated; of the latter there are two only, one on the distal surface of the mesocuneiform for the head of the second metatarsal, and one on the anterior face of the entocuneiform for the hinder edge of the same metatarsal. There

is no connection with the median digit. The ectocuneiform is high and narrow proportionately; its proximal and distal surfaces are D-shaped, with the curve directed anteriorly, and a short, narrow tongue directed posteriorly from the hinder edge. The navicular surface is emarginated by a small fossa on the fibular edge; the distal facet also shows a very shallow oval fossa, but the articular surface of the tongue, or posterior prolongation, is continuous with that of the body of the bone, nor is its free end transversely extended. There is a small and sessile antero-inferior facet for the cuboid, and a larger postero-superior one. There is also on the tibial side of the posterior prolongation a small facet for the second metatarsal.

In *Anchitherium*, the ecto- and mesocuneiforms are co-ossified, and the entocuneiform is free. The former is broader and lower than in the American genus, and of very different shape, as is especially shown in the fact that the posterior tongue or beak is directed toward the fibular side, instead of backward (cf. Pl. XXIII., Fig. 36, with Kowalevsky,\*Pl. II., Fig. 23). There is on this beak no facet for the second metatarsal.

In the horse, the ento- and mesocuneiforms are co-ossified, as in *Mesohippus*, though in some specimens all three of the bones are distinct, and Forsyth Major states that, as a rare exception, the ecto- and mesocuneiforms unite (No. 18, p. 62). The ectocuneiform is greatly increased in breadth and is very low; the beak is very much wider, and bears at its posterior end a distinct broad facet for metatarsal III., which is separated by a wide fossa from the anterior one; the latter is reduced in antero-posterior extent, as compared with that of *Mesohippus*. There is normally no facet on cu. 3 for the second metatarsal; but Kowalevsky reports finding it rarely, and then associated with a reduction in width of the facet for metatarsal III. upon the beak (No 25, p. 45). The mesocuneiform presents two distal facets, for the second and third metatarsals respectively. As a whole, the tarsus of *Equus*, compared with that of *Mesohippus*, has decreased in height and increased in breadth and depth, and is especially modified by the connection of the median metatarsal with all three of the distal tarsal elements.

The metatarsus of *Mesohippus* (Pl. XXIII., Fig. 39) consists of the second, third, and fourth metatarsals, the fifth having completely disappeared. Metatarsal II. is very much compressed

laterally, and has a long, very slender shaft. The head is expanded antero-posteriorly and bears two facets, one proximal for the mesocuneiform, the other oblique and posterior for the entocuneiform: there is also a small lateral facet for the tongue of the ectocuneiform, but there appears to be no anterior contact with the latter in some specimens, though there clearly is in others. Connection with the median metatarsal is by means of ill-defined facets. The distal end is much compressed and slightly recurved, with a sharp keel on the plantar side of the trochlea; the portion of the trochlea medial to the keel is decidedly more prominent than the external portion.

The third metatarsal is very long and slender; proximally it is narrow and deep, distally it becomes broader and flattened antero-posteriorly. The head bears a facet for the ectocuneiform, which is broad, with a rounded anterior margin and a narrow posterior tongue or beak. The articular surface is continuous over the proximal end, being only slightly interrupted by a small fossa. The facet for the cuboid is small and somewhat oblique, but more lateral than proximal in position. There are two small facets for the fourth metatarsal, which are placed very near together. The distal end of the shaft is quite broad and has two lateral tubercles for ligamentous attachments; the trochlea is narrower and is terminated above by a deep pit. The carina is more prominent than on the median metacarpal, and there is a very obscure indication of it upon the anterior face. The proportions of this digit vary considerably in the different specimens, being decidedly stouter in some than in others.

The second metatarsal rises higher than the third, and the third higher than the fourth. The latter is slightly stouter than the second and has a more thickened and rugose head; it bears a single facet for the cuboid, but there is in some individuals a posterior prolongation of this, which may be regarded as the beginning of a second one.

In the metatarsus of *Anchitherium* the median digit is decidedly larger proportionately than in the American form, and in particular the head is transversely extended; its articulations are also different, in that the cuboidal facet shows a stronger tendency to become proximal, and a small connection with the mesocuneiform is established. Distally the shaft is still broader

than the trochlea, but there is no pit above the latter. The head of metatarsal IV. is decidedly more massive, and the difference in the shape and size of the shaft between this and metatarsal II. much more marked (see Kowalevsky, No. 25, Pl. II., Fig. 28).

In *Equus* there are very important changes aside from the great development of the median digit, and the reduction of the lateral ones to splint bones, accompanied by the loss of their phalanges. The head of metatarsal II. now has the facet for the entocuneiform proximal, and that for the mesocuneiform oblique and anterior.

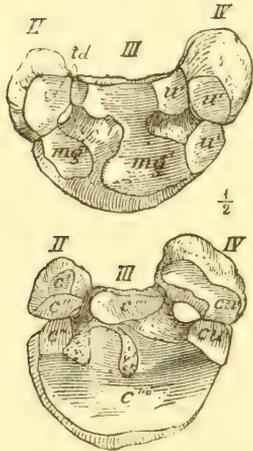


FIG. B.—*Equus Burchelli*. Proximal end of left metacarpus and metatarsus (after Kowalevsky).  $\times \frac{1}{2}$ . *td*<sup>d</sup>, facet for the trapezoid; *mg*<sup>d</sup>, for the magnum; *u*<sup>d</sup>, for the unciform; *c'*, for the ento-; *c''*, for the meso- and *c'''*, for the ectocuneiform; *cu*<sup>d</sup>, for the cuboid.

The head of metatarsal III. has four distinct facets, three anterior for the meso- and ectocuneiforms and cuboid respectively, the latter altogether proximal in position; the fourth facet is posterior and for the beak of the ectocuneiform, and is separated by a large fossa from the anterior surface for that bone. The transverse breadth of the posterior facet is very striking as compared with the same structure in *Mesohippus*. The head of metatarsal IV. is provided with two distinct facets for the cuboid. The distal end of the shaft of the median metatarsal is not produced laterally beyond the trochlea, and there is no pit above the latter.

The phalanges of the pes in *Mesohippus* appear to be somewhat more massive than those of the manus; whether they are shorter the available material does not enable me to decide.

## VII. RESTORATION OF MESOHIPPUS (Fig. C).

The successive genera of the horse series show for the most part a steady increase in size from the tiny *Hyracotherium* of the Wasatch Eocene to the great animals of Post-Pliocene times. *Mesohippus*, however, has not reached a large stature, advancing

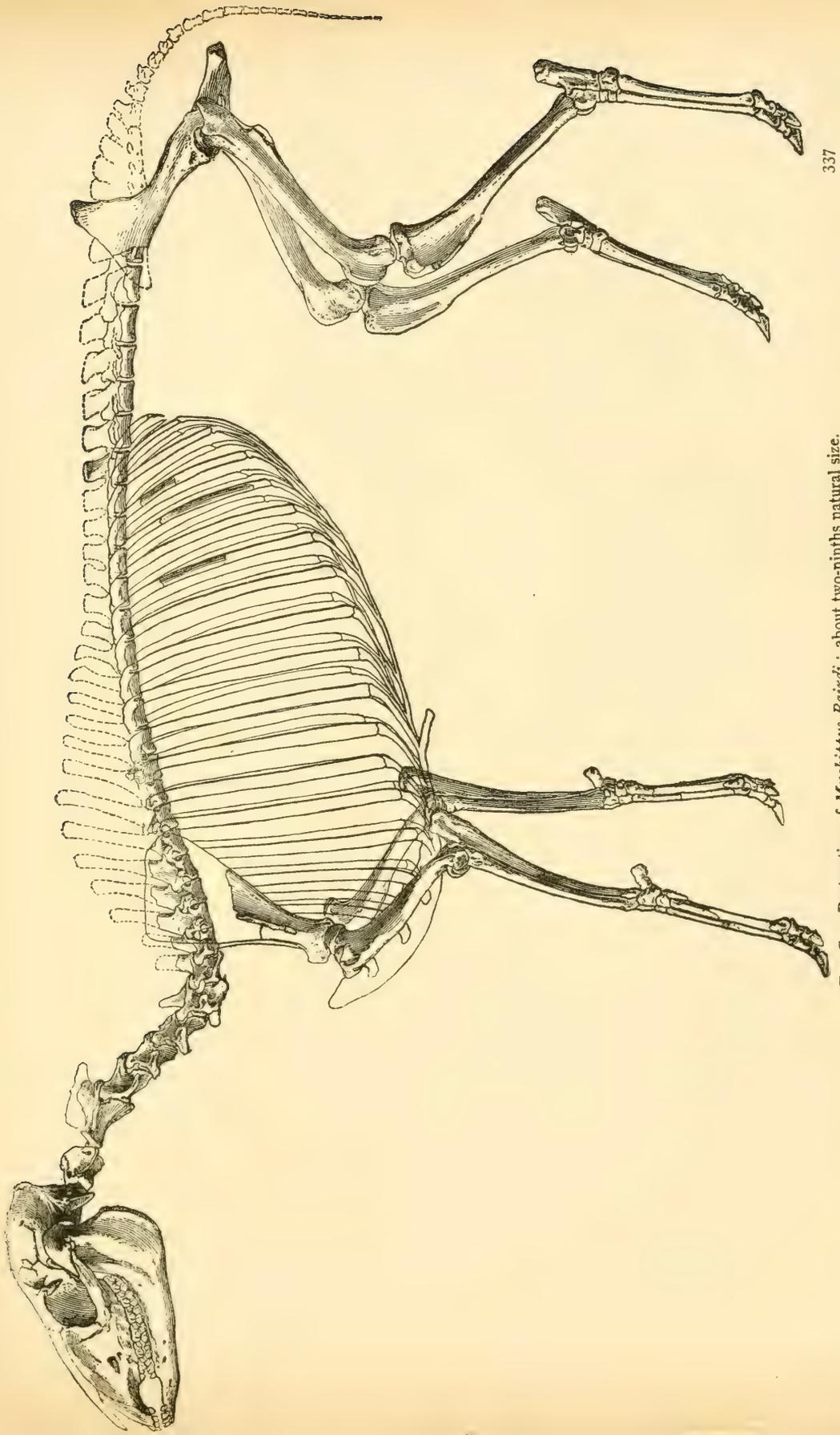


FIG. C.—Restoration of *Meshiphus Bairai*; about two-ninths natural size.



beyond its Bridger predecessor, *Pachynolophus*, much less in regard to size than in morphological differentiation; the larger species of the Bridger genus are but little inferior in this respect to the smaller species of the White River form. In spite of its comparatively high degree of differentiation, *Mesohippus* was a very small animal compared with the recent horses, about the size of a Newfoundland dog. The skeleton is essentially like that of existing *Equidæ* in character and appearance, but presents many striking points of difference.

The skull is much smaller, and in particular the facial region is shorter, shallower, and more tapering. The orbit is relatively very large, not enclosed behind, and situated very far forward and low down in the face. This position of the orbit brings about other noticeable differences in the character of the skull, as for example the great elongation of the zygomatic arch, and especially of the malar or jugal portion of it. The arch is also quite slender and the masseteric crest is but slightly developed and does not extend forward upon the maxillary. The short-crowned molars render the alveolar portion of the maxillary very low and contracted, in sharp contrast to the alveolus in those genera which have prismatic teeth, and owing to the very small size of the canine and incisor teeth, the premaxillaries and the symphysis of the lower jaw are short and slender, which in its turn modifies the shape and size of the anterior narial opening. The ascending ramus of the mandible is relatively low and of quite a different shape from that seen in *Equus*, and the condyle is not placed nearly so far above the level of the molars.

The neck is quite long, but the vertebræ are much less massive, not so decidedly opisthocelous, and with less strongly developed processes than in *Equus*. The neural spine and odontoid process of the axis are of entirely different shape in the two genera, and in the Miocene form the spines on the fifth and sixth vertebræ are much higher. The back is long, and, as appears from the faces of the posterior dorsal and lumbar vertebræ, much more arched than in the horse; the spines, so far as they are preserved, are more slender and compressed. If we may judge from the comparatively few fragments which have been preserved, the ribs were more slender, rounded, and less flattened than in the horse, — a peculiarity which is common to nearly all of the earlier ungulates.

The limbs would appear to be quite as long as in the horse, or even somewhat longer, in proportion to the size of the body ; but the relative lengths of the constituent parts are quite different in the two genera. The scapula seems to have been rather broad, somewhat as in *E. asinus*, and has but a small coracoid process. The humerus is rather long, but with a slender shaft, and with the tuberosities and deltoid ridge and hook not strongly developed. The conformation of the proximal end of the humerus is entirely different from that which occurs in the true *Equidæ*, and is closely similar to that of the White River camel, *Pæbrotherium*. The ulna and radius are likewise rather long and slender ; the shaft of the former is complete and uninterrupted, though much reduced in diameter ; the two bones are only slightly co-ossified at the distal end. The carpus is decidedly higher, but narrower than in the recent forms, and the arrangement of its component parts quite different, in correlation with the greater number of functional digits. I have seen no complete specimens of the metacarpals, and so their length is conjectural. In width and antero-posterior depth, the third metacarpal is much inferior to that of *Equus*, and its carpal articulations quite different. On the other hand, the splint bones of the horse are represented by the second and fourth functional digits in *Mesohippus*, while the fifth digit of the latter is a splint bone. The phalanges are much shorter and very much less massive, and in particular the ungual phalanx of the third digit is very small when compared with the massive bone of recent forms, though its shape is very suggestive of equine affinities.

The pelvis is in general very like that of the horse, but with some marked differences ; the sacral plate of the ilium is somewhat more expanded vertically and less everted horizontally ; the crest above the acetabulum is more prominent ; the ischium is somewhat shorter and nearly straight, the posterior end curving upward very much less. The femur has a stout shaft, as compared with that of the humerus, but very slender in proportion to the horse's femur ; it is quite long relatively to that of the latter animal ; the trochanters are much less massive, and the condyles smaller and project backward less strongly ; the rotular trochlea is wider, shallower, and less prominent, and has its two margins of nearly equal height,

while in the recent type the trochlea is massive, very prominent, and obliquely directed, the inner margin being much higher than the outer. The tibia is long, but very slender, except in the upper portion, which is deepened antero-posteriorly by the large cnemial crest. The fibula may have been complete; at all events, the distal end is quite large, and in several of the specimens a considerable length of the very slender shaft is attached to it. In some individuals the distal ends of the tibia and fibula are co-ossified, in others they are separate, and this does not appear to be altogether a matter of age, but rather of individual variability. The tarsus is relatively higher and narrower, and of less antero-posterior extent than in the recent forms; the calcaneum longer and less massive. The metatarsus is of nearly the same length proportionately as in the horse, but the third digit is very much less enlarged, while the second and fourth, as in the manus, are functional and of nearly the same length as the third. The enlargement of the median metatarsal has proceeded somewhat farther than in the case of the corresponding metacarpal.

As the restoration is drawn from several individual specimens, reduced to a common average standard, it is impossible to give the relative dimensions of the parts with any great accuracy, but, on looking over a large number of specimens, it is clear that the hind limbs are decidedly longer, in proportion to the fore limbs, than in the recent species. In the figure this is compensated by the degree of flexion given to the posterior extremities, though very possibly the hind quarters were much more elevated, in somewhat the same fashion as in the tragulines, though of course in a less marked degree.

There are thus many points of difference, as regards the proportionate development of the various parts of the skeleton, between *Mesohippus* and *Equus*, and these divergences, more especially the smaller and differently shaped head and the very slender tridactyl feet, give to the older type quite another physiognomy than that of the recent representatives of the group, even without taking into consideration its very much smaller size. Nevertheless, no one can examine the skeleton of the Miocene genus without being struck by its essentially equine nature; in the teeth alone is the fundamental similarity of plan not apparent at the first glance, though even here a careful

examination reveals the connection very clearly. This similarity extends also to the earlier members of the equine series, for *Hyracotherium* from the lower Eocene belongs as unmistakably to this line as do any of the later genera. Indeed, one of the most striking features of this phylum is the way in which its essential features, and even many apparently insignificant details, are, as it were, sketched out in very early times and then gradually elaborated, without deviation and without retrogression, until the final term of the series is reached.

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#### THE OSTEOLOGY OF *LEPTOMERYX EVANSI* LEIDY.

This problematical little selenodont is very abundantly represented in the White River beds by fragments of jaws and teeth; but owing to their small size and extreme fragility, well preserved skulls and parts of the skeleton are very rare. However, by combining the material contained in the Princeton Museum with that in the Academy of Sciences in Philadelphia, and some beautifully preserved specimens which Professor Cope has most kindly placed at my disposal, I am enabled to give a fairly complete account of the structure of this genus.

#### I. THE DENTITION.

1. *Upper Jaw.* The skulls of all the specimens which I have examined are broken away anteriorly, so that the premaxillary region is lost, and it is therefore impossible to say whether *Leptomeryx* had any remains of upper incisors, but from the character of the lower incisors it seems probable that the superior set had vanished. From the analogy of *Amphitragulus* and the tragulines, it might seem likely that the upper canine, at least in the males, was a long, recurved blade. But, on the other hand, no such tooth has ever been found associated with *Leptomeryx* remains. None of the specimens shows any trace of the first upper premolar, and if present at all, it must have been separated by a considerable diastema from the second. *Pm. 2* is a sharp, compressed, cutting blade, which seen from the outside has a considerable resemblance to the corresponding tooth of

*Tragulus*, but the median ridge is much more pronounced and the depressions in front of and behind it much deeper. A more important difference is in the large internal cusp (deuterocone) which in *Tragulus* is a mere rudiment. *Pm. 3* is similar, but the deuterocone is still larger, and from its anterior edge there passes a ridge to the outer wall of the crown enclosing a small valley. In some specimens, however, which agree exactly with the typical *Leptomeryx* in size and in the construction of the upper molars, the premolars are quite as simple as in the tragulines. *Pm. 4* is of the typical ruminant pattern, consisting of an internal and an external crescent; the horns of the inner crescent are separated from the outer wall and are connected with it only at an advanced stage of wear.

The outer side of the tooth resembles that of the preceding premolars.

The molars are composed of four crescents and closely resemble those of the smaller deer. They differ from the molars of *Tragulus* in the greater thinness and compression of the crescents, and in the presence of well-developed basal pillars between the internal lobes; the median and anterior external pillars are also very prominent, while in *Tragulus* the anterior one is but feebly developed, and the median one is absent. In *Dorcatherium* (*Hyæmoschus*), on the other hand, the external pillars are very well marked, but here there is no internal pillar and the lobes of the tooth are more massive and conical, less completely crescentoid than in *Leptomeryx*. In the latter the internal crescents are separated from each other in the unworn tooth by a considerable interval. The valleys are perfectly simple, and not complicated by any projections from the walls. The inner side of the crown is covered with a very finely wrinkled enamel, but the external side is smooth and polished. The cingulum is confined to the anterior and posterior faces of the crown.

2. *Lower Jaw.* The incisors are somewhat peculiar and not at all traguline in character. The median incisor is procumbent, long, straight, and narrow; in shape it is more like that of *Moschus* than that of the deer or chevrotains, but is very much narrower, more elongate, and very different from the corresponding tooth in *Tragulus*. The second and third incisors are shorter, somewhat more spatulate, and are curved toward

the outer side of the jaw. They are less procumbent than the median, and project slightly upward. They are much like the corresponding teeth in *Coassus*. The third is somewhat shorter and broader than the second. The crown of the canine is not preserved in any of the specimens, but its fang shows that it had taken on the functions of an incisor, and that it was slightly larger than the external member of that series.

The first premolar is a very small tooth, which is separated by a considerable diastema from the canine, and by a shorter one from the second premolar. The crown is a perfectly simple, erect, and compressed cone, and were it not for its position in the jaw, might easily be taken for a small canine. This tooth is inserted by a single fang.

The succeeding premolars increase successively in size and complexity from the second to the fourth. When looked at from the external side, they are all very much alike except in size, and are composed of a high, compressed, and very acute cone, with sharp-pointed anterior and posterior basal cusps, except that in *pm.* 2 the anterior cusp is wanting. On the inner side, however, there are more important differences. In *pm.* 4, there is a thin crest which runs back from the median apex of the tooth parallel to its external wall and enclosing a deep valley with the latter; an indication of this same structure, but not nearly so marked, is visible on *pm.* 3. Compared with the premolars of *Tragulus*, those of *Leptomeryx*, both upper and lower, are in most specimens very much more complicated.

The inferior molars are at first sight much like those of *Tragulus*, but there are some important differences. Schlosser has pointed out a peculiarity which occurs in all tragulines: "Die unteren Molaren sind ausserordentlich charakteristisch. Sie haben in der vorderen Hälfte auf jedem Monde eine starke, von der Spitze nach hinten zu herablaufende kammförmige Leiste" (No. 47, p. 73). These characteristic crests are usually, but not invariably, present in *Leptomeryx*, and often occur on the posterior crescents as well. In this genus also the valleys are wider and deeper than in *Tragulus*, and the talon of the last molar decidedly larger; it consists of two distinct cusps, of which the external one is the larger, and is separated from its fellow by a deep cleft. There are no basal pillars on the lower molars. All of the inferior molars and premolars

are covered with a finely wrinkled and minutely tuberculated enamel.

The milk dentition is decidedly traguline in character.  $\underline{D}^4$  is molariform, but very small, and the median internal and external pillars feebly marked;  $\underline{d}^3$  consists of three external cusps, of which the anterior is very long, compressed, and trenchant, which is much larger than in *Tragulus*, and a small postero-internal crescent, from which a faint ridge runs forward; this ridge is also better developed than in *Tragulus*.  $\overline{D}^4$  is composed of three pairs of crescents, of which the anterior pair are quite small and much like the talon of  $\overline{m}^3$ .  $\overline{D}^3$  is much like the premolar which succeeds it in the permanent set.

The dentition of *Leptomeryx* is on the whole most like that of the tragulines, especially in the construction of the molars and the milk dentition; on the other hand, the incisors are very different, and the premolars much more complex, though less so than in the *Cervidae*.

## II. THE SKULL.

The skull of *Leptomeryx* is peculiar in several respects, and with many points of resemblance to that of the chevrotains, presents almost as many differences. As in the primitive ungulates generally, the cranium is long, narrow, and low, the eye very far forward in the face. The occiput is low, and the upper contour of the skull curves regularly upward and forward to a point just behind the orbits and thence downward to the face. The orbits are rather smaller than in *Tragulus*, are situated higher in the face, and project somewhat more strongly outward. As in that genus, they are very deep and are posteriorly separated only by a thin interorbital septum, so that the optic foramina are nearly or quite confluent—a peculiarity which is shared by some of the small antelopes and by *Pæbrotherium*.

There appear to be two types of skull represented among the specimens: in one, that figured by Leidy (No. 33, Pl. XIV.), the occiput is low and rather broad, and the sagittal crest is very short, hardly longer than in *Tragulus*. The second type, which perhaps belongs to a species as yet unnamed, has a higher, narrower occiput, and a much longer sagittal crest with narrower forehead and less abruptly diverging supraciliary ridges.

In other respects it is not necessary to distinguish between the two.

Examining the skull more in detail, the following structures present themselves. The basi-occipital is broader and flatter than in *Tragulus* and tapers more regularly forward; in the chevrotains the enormous size of the tympanic bullæ reduces the basi-occipital and basi-sphenoid to a mere rod, which is keeled in the median line. In *Leptomeryx* this keel is not present, but we find a pair of small surfaces for muscular attachments, much as in the deer. The condyles are small, sessile, and less widely separated than in the tragulines. The exoccipitals are low and rather narrow, and are flat or even concave from side to side, in sharp contrast to the very convex surface of the smaller tragulines. The supra-occipital is, in one type of *Leptomeryx* skull, quite high; in the other much lower; in both it extends well over upon the sides of the cranial cavity and is terminated by a projection which is the hindermost part of the skull, whereas in *Tragulus* the upper margin of the foramen magnum projects further back. The lambdoidal crest is much more prominent than in the tragulines. The foramen magnum is also higher and somewhat narrower than in the latter. The paroccipital processes are small, but are relatively longer, stouter, and less compressed than in *Tragulus*; they stand but very little in advance of the condyles, from which they are separated by deep but narrow fossæ.

The basi-sphenoid is broader than in *Tragulus*, but does not extend so far forward between the pterygoids. The alisphenoid is directed nearly horizontally, but there is a curious angulation or ridge in it, from which a portion of the bone passes upward, bounding the anterior edge of the temporo-sphenoidal lobe of the cerebrum; the pterygoid plates of the alisphenoids are, unfortunately, broken away in all of the specimens. The horizontal portion is much longer than in the tragulines and much more distinctly separated from the glenoid cavity. The orbito-sphenoids are much as in the tragulines, and form a thin and fragile interorbital septum.

The tympanic bullæ differ from those of the tragulines in a very important and characteristic way; they are very much smaller in every dimension, but especially in the vertical direction; they are not filled with cancellated tissue, but are hollow,

and the walls are composed of very dense, flinty-looking bone. The meatus auditorius is a long tube, with relatively very large diameter, which extends more decidedly backward and less upward than in the tragulines. The postero-external angle of the bulla shows a rather wide and shallow styloid groove. So far as I can interpret the sutures, there appears to be a broad surface of the petiotic exposed between the squamosal and the occipital; but if so, it lies entirely in the occipital plane and not on the side.

The parietals are very long and form almost the entire roof of the cranium; they are much longer and narrower than in *Tragulus*. This narrowing is partly due to the fact that the brain itself is narrower, and partly that the squamosals encroach much more upon them. In front of the latter, the parietals send down descending processes to the sphenoids. The sagittal crest varies in length, but is always longer than in the tragulines. Anteriorly the parietals diverge somewhat to receive the frontals and are thus rather longer on the sides than in the median line.

The squamosals are very long and high proportionately, and form most of the side walls of the cranial cavity. The root of the zygomatic process is stouter, but less extended antero-posteriorly, and the process itself is longer and heavier than in *Tragulus*; the zygoma rises slightly forward, whereas in the recent genus it descends anteriorly. The glenoid cavity is very different in the two forms; in the existing type, it is a broad, flat surface, with nothing deserving the name of a post-glenoid process; in *Leptomeryx* "its fore part is nearly straight transversely, and inclines slightly outward from its inner extremity, and slopes convexly backward and outward into a comparatively deep concavity, bounded behind by a post-glenoid tubercle proportionately stronger than in the deer" (Leidy). The post-tympanic process is also more distinctly developed than in *Tragulus*. The jugal has a nearly straight course, and is relatively a very large bone, with much greater vertical diameter than in *Tragulus*; the masseteric crest occupies nearly the same position as in that genus, but is not nearly so well developed. There is quite a long post-orbital process, but it is shorter than in the existing genus, and does not quite reach the corresponding process of the frontal. The lachrymal, on the

other hand, is distinctly smaller than in the tragulines, and has no pit; it articulates with the frontal, maxillary, and jugal, but is separated from the nasal by a small vacuity which is developed at this point, as in the deer and many other ruminants. There is a single large lachrymal foramen placed within the rim of the orbit. The frontals are shorter and broader than in the tragulines. They extend farther behind the orbits, but not so far in front of them as in those animals, and thus are concerned more in roofing the cranial cavity and less in covering the nasal cavity. Except for their smaller size and greater elevation in the face, the orbits have very much the same position that they occupy in *Tragulus*, their anterior rim being over the first molar.

The nasals are not preserved in any of the specimens which I have seen. The maxillaries are long and low, especially the alveolar part, which, however, is higher than in *Tragulus*, and the facial portion which forms the side of the nasal cavity is also higher than in that genus. The palatine processes of the maxillaries are narrow and slightly concave from side to side. The molars are arranged in gently curved lines, which give the hard palate its greatest width at about the first true molar.

Unfortunately the premaxillaries are broken away in all of the available specimens, so that those very characteristic parts of the skull cannot be described. The posterior nares are situated far back, and the roof is formed by the palatines for some distance behind the last molar, as in the tragulines, but the lateral palatal notches are shallower and wider than in those animals, and the palatines are continued farther forward in the roof of the mouth; the pterygoids do not extend so far back and are more widely separated from the tympanic bullæ.

The lower jaw is very peculiar, especially for the great breadth of the ascending ramus; the angle is strongly prominent, giving to this region of the jaw a very different appearance from that of *Tragulus*, and somewhat like *Cainotherium*, but differing from the latter in being regularly curved and not notched; its margin is also somewhat inflected. The masseteric fossa is deep and placed high up, as in *Pæbrotherium*. The coronoid process is stout and apparently vertical in position. The condyle is shaped very much as in the chevrotains, but

rises much higher above the level of the teeth and projects more directly vertically and less posteriorly. The horizontal ramus is slender and shallow, with a nearly straight inferior border. The symphysis is quite long and differs from that of *Tragulus* in being much less sharply compressed inferiorly, and in having its superior margins erect, not flaring and everted.

The *foramina* of the skull of *Leptomeryx* are, on the whole, most like those of the tragulines, but not without some important differences. The optic foramina are confluent and situated far forward; the foramen lacerum anterius is relatively small; the foramen rotundum has not coalesced with the foramen lacerum anterius, as it has in *Tragulus*, but is situated close to the foramen ovale. Owing to the small size of the auditory bulla, the foramina in this region are very different from those of the chevrotains, the foramina lacerum medius and posterius being large, and the carotid canal not grooving the side of the bulla. Post-glenoid, stylo-mastoid, and condylar foramina are present. At least one large venous foramen pierces the parietal near the sagittal crest. The infra-orbital foramen is placed very low down, just above *p. 2*. The foramina in the anterior part of the orbit are very characteristic in the tragulines, and are thus described by Rüttimeyer: "Von einer Fossa sphenomaxillaris, wie sie sonst den Wiederkäuern zukommt, ist eigentlich bei Tragulina nicht zu reden, da der Alveolartheil des Oberkiefers so niedrig ist, dass er nur als Boden der Augenhöhle dient, ohne dieselbe zu verengen. Nur der trichterförmige Eingang des Infraorbitalcanals bleibt als Rest einer Fossa sphenomaxillaris übrig, während das Foramen sphenopalatinum, und zwar von rundlicher Form, vollkommen frei an der Innenwand der Augenhöhle liegt. Unter ihm führt das For. palatinum superius nach abwärts, um sich in das auffallend weite und ungefähr in der Mitte der Gaumenbeine liegende Gaumenloch zu öffnen" (No. 45, p. 19). This description applies almost exactly to *Leptomeryx*, except that the opening of the infra-orbital canal is divided into two parts, as it shows a tendency to be in *Tragulus*; the lachrymal foramen is placed much higher up than in that genus, and the supra-orbital canal has the same position and relative size, but the groove which runs forward from it is shorter and less distinctly marked.

## III. THE BRAIN.

The museum of the Academy of Natural Sciences in Philadelphia contains a brain-cast which appears to belong to *Leptomeryx*, although it is smaller than the skull figured by Leidy (No. 33, Pl. XIV.). In shape and in the character of the convolutions this specimen is very like the intracranial cast of *Tragulus* figured by Milne-Edwards (No. 37, Pl. VI., Fig. 2). The olfactory lobes are decidedly larger than in the modern form, the hemispheres narrower, and the cerebellum and cerebrum not in contact, so that the corpora quadrigemina were probably partly uncovered. The hemispheres are very narrow anteriorly; the constriction is more sudden than in *Tragulus* and the portion in front of it much smaller. The splenial fissure does not appear to show upon the dorsal surface, as it does in the chevrotains and the small deer, though this is not quite certain. The lateral fissure is longer and better marked than in *Tragulus*; the suprasylvian fissure follows very much the same course as in that genus, but the coronal sulcus, with which it is continuous, is more oblique and approaches nearer to the median line. The occipital lobes are broad and the temporo-sphenoidal lobes deep.

The cerebellum is large, with very prominent and convoluted vermis; the posterior surface of the latter is strongly projecting, is vertically placed, and forms nearly a right angle with the dorsal surface. The top of the cerebellum is nearly in the same plane as the top of the cerebrum, agreeing in this respect with *Cainotherium* rather than with *Tragulus*. The lateral lobes of the cerebellum are apparently smooth and the flocculi are small. The medulla oblongata is very thick.

## IV. THE VERTEBRÆ.

Of the spinal column we have preserved the neck and first two dorsal vertebræ of one specimen, and several scattered dorsal and lumbar vertebral centra of other individuals. The cervicals are very much indeed like those of *Tragulus*. The atlas is short and broad, with transverse processes of only moderate extent, very different from those of the Pecora. The axis has

a broad, much depressed, and opisthocœlous centrum; the condyles for the atlas rise higher upon the sides of the neural canal than in the modern genus. The odontoid process is short and peg-shaped, not in the least like the spout which occurs among the true ruminants. In the Cope collection, however, there is a small axis with a broad depressed odontoid, much as in *Oreodon*, but this may belong to *Hypisodus*. The transverse processes of the axis are short and slender and perforated by the vertebrarterial canal. The neural spine is developed into a great hatchet-shaped plate; the upper margin of this spine is nearly straight and the posterior edge almost vertical, while the anterior one curves gently downward and forward. In spite of its great size, the spine overhangs the third vertebra hardly at all. This spine differs strongly from the corresponding ones of *Cainotherium* and *Tragulus*. The third cervical has a rather long opisthocœlous centrum with a slight keel; the spine is a low ridge. The fourth vertebra is somewhat shorter than the third, but has a more distinct keel, ending posteriorly in a stout tubercle; the neural spine is short, slender, and inclined distinctly forward. The fifth vertebra is like the fourth, except that it has no keel on the centrum and that the neural spine is considerably higher. On the sixth the spine is still higher, much better developed, indeed, than in *Tragulus*, and as in that genus, the transverse process has a large pleurapophysial plate. The seventh cervical is decidedly the shortest vertebra of the series, but has the same depressed, opisthocœlous shape as the others; the spine is very much stouter than that of the preceding vertebræ and much heavier than in the modern genus.

The anterior dorsals are very small; they have short and simple transverse processes, terminating in concave facets for the tubercles of the ribs. The spines are proportionately stouter than in *Tragulus*, and incline strongly backward.

The lumbar vertebræ are relatively shorter than in the tragulines and indicate a less strongly arched back, which is also borne out by the fact that the disproportion between the length of the fore and hind limbs is not so great as in *Tragulus*.

The rib fragments which are preserved indicate a thorax similar to that of the modern genus. Nothing is known of the sternum.

## V. THE FORE LIMB.

The scapula is very similar to that of the tragulines. The glenoid cavity is small and rounded. The coracoid process small, slender, and strongly recurved. The neck is very slender and contracted, and continues for some distance upward; the coracoid border curves gently forward for most of its length,

while the glenoid border is nearly straight. The spine does not arise so near to the glenoid cavity as in *Tragulus*, but rises higher. The acromion is more prominent, and projects more strongly downward than in that genus. As in most of the ruminants, the spine is placed much nearer to the coracoid than to the glenoid border, thus making the post-scapular fossa very much larger than the prescapular, which, indeed, is extremely narrow.



FIG. D. — Left humerus and radius of *Leptomeryx Evansi*; natural size. Cope collection.

The humerus is a stouter bone than that of *Tragulus*, though constructed very much like it; the head is somewhat larger and heavier, the external tuberosity higher and more massive, but less hook-like and overhanging the bicipital groove less; the internal tuberosity is heavier but less compressed and prominent, and consequently the bicipital groove is

not so deep. The shaft is slender, but of greater antero-posterior diameter, and relatively longer. The distal end is very much alike in the two genera, the trochlea oblique to the long axis of the shaft, with large internal and small external condyle, separated by the prominent intercondylar ridge.

The radius and ulna are entirely separate throughout their length, and show no tendency to co-ossification. The former is decidedly longer than in *Tragulus* and proportionately more slender. The proximal end is very much alike in the two genera, except that the groove for the intercondylar ridge of the

humerus is not so deep in *Leptomeryx*. The shaft is flattened and nearly straight. The distal end is much less expanded than in *Tragulus*. The ulna is much reduced and has a very slender shaft; the olecranon is higher than in the modern genus, but of less antero-posterior diameter.

The manus, which has been described by Cope (No. 10), is very traguline in character, both in general appearance and in details of structure. The scaphoid is not preserved in any of the specimens, nor is the trapezium; not improbably the latter was altogether wanting. The proximal end of the lunar is shaped very much as in the Pecora, but the distal end is very different, in that the lunar rests almost wholly upon the unciform and has only a lateral contact with the magnum—a traguline character upon which Cope has laid much stress. The cuneiform is very small, and is not in contact with the radius; its ulnar surface is saddle-shaped and extends well down upon the external surface of the bone. The trapezoid and magnum have coalesced; the compound bone is low, rising slightly behind; it is supported almost exclusively by the scaphoid. Distally it presents facets for the second and third metacarpals. The unciform is the largest bone in the carpus, but is not so high proportionately as in *Tragulus*.

The metacarpus consists of four digits, none of which shows any tendency to coalesce with another. The lateral digits are very slender, though not so much so as in the chevrotains; the median digits are of about the same relative length, but decidedly more slender. Metacarpal II. articulates with a downward projection from the trapezoid element of the trapezomagnum. Metacarpal III. articulates medially with the side of this same projection, proximally with the magnum, and laterally with the unciform, sending out a process which overlaps the head of No. IV. Metacarpals IV. and V. articulate only with the unciform. The manus is thus of the "adaptive type." The carinæ of the metacarpals are entirely confined to the palmar surface.

The phalanges of the manus do not differ appreciably from those of *Tragulus*.

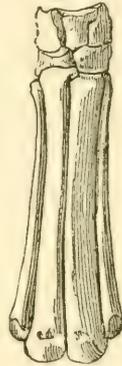


FIG. E.—Left manus of *Leptomeryx Evansi*; natural size. Cope collection.

## VI. THE HIND LIMB.

Of the pelvis, only the ilium is preserved, but this is very different from the ilium of *Tragulus*; the neck is much shorter, less compressed, and more trihedral in shape; the plate is broader, more everted, and more suddenly expanded; the crest above the acetabulum is higher and thicker. What is preserved of the pelvis, therefore, rather resembles that of the true ruminants than of the tragulines.

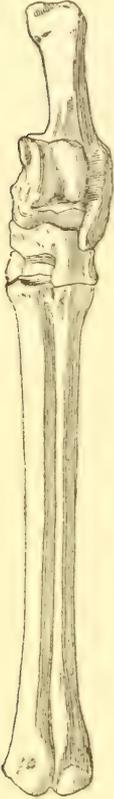


FIG. F. — Left pes of *Leptomeryx Evansi*; natural size. Cope collection.

The proximal end of the femur is also very different from that of *Tragulus*; the neck is much longer and more constricted, and the head relatively smaller; the great trochanter is higher and more massive, and the bridge connecting this process with the head is more constricted, the digital fossa is much deeper, and the second trochanter more massive and prominent. The shaft appears to be rather more slender. The distal end is very much like that of the modern genus. The rotular trochlea is broad and shallow, with margins of nearly equal height; it is very long vertically, and but little arched antero-posteriorly. The condyles have but a small fore and aft diameter; they are of nearly equal size and quite widely separated. Above the external condyle there is sometimes a pit, sometimes a rugosity, for the plantaris muscle.

The patella is long, narrow, and pointed, resembling that of *Tragulus*, except for the much diminished thickness of its proximal portion.

The tibia is of about the same relative length as in the modern type, but the cnemial crest is more prominent; the outer condyle projects considerably beyond the line of the shaft. The astragalar surface is not very deeply grooved and the internal malleolus of only moderate length. The fibula is completely

reduced ; its proximal end forms a short, sharp spine, co-ossified with the tibia ; the distal end is generally free, and in this case forms a nodule wedged in between the distal end of the tibia and the calcaneum. In one specimen, however, which may possibly belong to a different but closely allied form, the distal end of the fibula is co-ossified with the tibia, forming an external malleolus, just as in the chevrotains. A similar variability in the fibula is to be found in *Dorcathe-rium* (Flower, No. 17, p. 180).

The pes, as Cope has shown, is more like that of the Pecora than of the Tragulina. The astragalus is higher and narrower than in *Tragulus* ; the calcaneum is rather shorter. The cuboid and navicular have coalesced, as have also the meso- and ecto-cuneiforms. Cope states that "the ecto- and meso-cuneiforms are distinct, and there is no ento-cuneiform" (No. 10, p. 405), but this is a mistake. The ento-cuneiform is present, and the other two are co-ossified, just as in the ordinary ruminants.

The third and fourth metatarsals have coalesced into a cannon-bone, which is extremely like that of *Tragulus* in appearance and relative length, but is decidedly more slender, and as in that genus the carinæ appear only on the plantar side. The lateral digits, however, are very different, as only the proximal ends are preserved, and these have coalesced with the cannon-bone, just as in the true ruminants. The limits of metatarsals II. and V. are still plainly visible in the compound bone. Except for the position of the distal carinæ of the cannon-bone, therefore, the tarsus and metatarsus of *Leptomeryx* show all the characteristics of the Pecora. The contrast between the condition of the manus and that of the pes in this genus is, as Cope has remarked, quite unparalleled.

The phalanges resemble those of the fore foot, but, as in *Tragulus*, they are considerably larger than the latter.



FIG. G. — Right cannon-bone of *Leptomeryx Evansi* ; showing the rudimentary mt. II: natural size. Cope collection.



FIG. H. — Proximal and ungual phalanges of the pes of *Leptomeryx Evansi* ; natural size. Cope collection.

## VII. RESTORATION.

With many differences of detail, the skeleton of *Leptomeryx* is exceedingly like that of *Tragulus* in general character and appearance. If we compare the restoration (Fig. I) with the skeleton of *T. stanleyanus*, the following differences are apparent. The head is rather smaller and, with its long cranium, small open orbit, and curiously formed lower jaw, is strikingly different from that of the modern genus. The neck is rather longer, the lumbar region shorter, and the back much less strongly arched, owing to the greater relative length of the fore limb. Except for this increased length, the less reduction of the lateral digits, the smaller size and separation of the median digits, the fore limb of *Leptomeryx* is almost a reproduction of that of *Tragulus*.

Although the disproportionate length of the posterior limbs, as compared with the anterior ones, is less in *Leptomeryx* than in the existing genus, it is still very great and striking, and the appearance of the hind limbs in the two genera is very similar. Such differences as do occur — and, as we have seen, there are some very important ones — are hardly apparent in a general glance at the skeleton. The entire absence of the lateral digits in the pes, and the shorter and differently shaped pelvis, are the only divergences which call for mention.

## VIII. THE SYSTEMATIC POSITION OF LEPTOMERYX.

Very different opinions have been expressed by various writers upon the position of this remarkable genus. Leidy (No. 33) placed it among the *Moschidæ* (in which family he appears to have included the chevrotains) and considered that it combined characters of the tragulines and the deer. Schlosser has adopted substantially the same view. "Näher kommt den Traguliden die Gattung *Leptomeryx* aus dem Miocän von Nebraska . . . *Leptomeryx* selbst ist auf jeden Fall nur der Überrest gewisser Mittelformen zwischen den Traguliden und Cerviden" (No. 47, p. 75).

Rütimeyer takes a very different view of the matter. "Die Merkmale des Schädels mit Einschluss namentlich des Unterkiefers scheinen weit eher auf eine nahe Beziehung von *Lepto-*

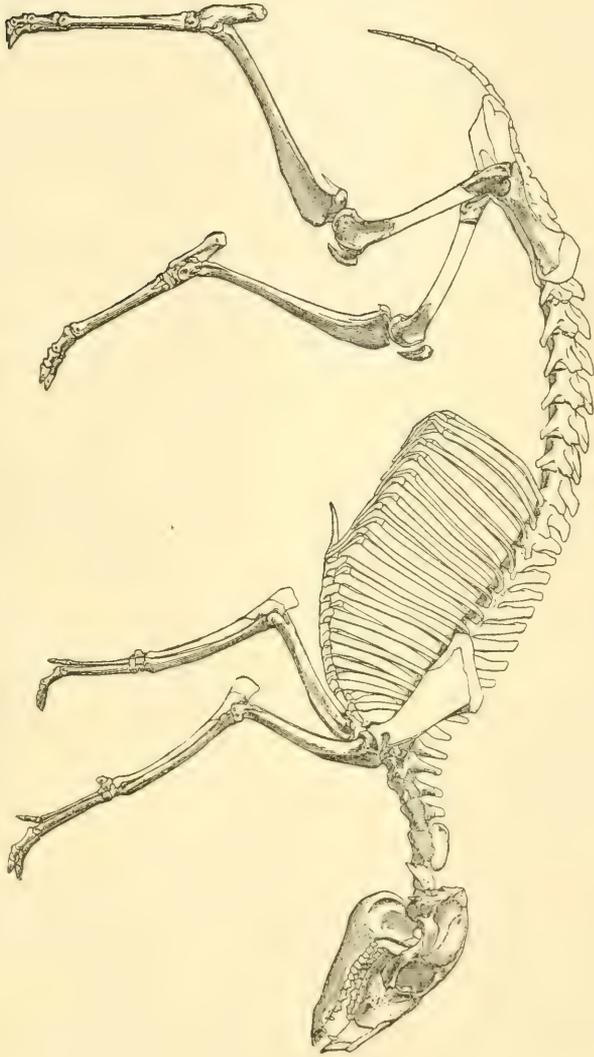


FIG. I.—Restoration of *Leptomeryx Evansi*; one-fourth natural size.

*meryx* zu den in Nordamerika so stark vertretenen Vorläufern der *Camelina* (*Oreodon*, *Procamelus*, *Leptauchenia*, etc.) hinzu- deuten und denjenigen von *Tragulina* und *Cervina* sehr fern zu stehen. Zu demselben Schluss scheint mir das fast vollständig erhaltene Gebiss zu führen. Von vorn herein ist es bemerklich durch die den Kameelen so eigenthümliche Unregelmässigkeit der Ausführung des selenodonten Baues von obern und untern Molaren, aber auch die Praemolaren stehen vor allem denjenigen von *Tragulina* sehr fern; eher liessen sie sich — mindestens für diejenigen des Unterkiefers — in dem stark abgetragenen Zustand, den die Abbildung darstellt, mit solchen von *Coassina* vergleichen. Aber weit näher scheinen sich wieder denjenigen von *Procamelus* und ähnlichen kleinen *Prodromal*-Formen anzuschliessen. Nach jeder Richtung scheint mir also *Leptomeryx* den hornlosen Wiederkäuern des europäischen Miocens sehr ferne zu stehen" (No. 45, pp. 98, 99).

Though we now know pretty nearly all parts of the skeleton of *Leptomeryx*, the proper reference of the genus is by no means easy. As a preliminary to the discussion of this problem, it may be useful to point out some of the peculiarities which separate the Pecora from the *Tragulina*. It will not be necessary to consider the Tylopoda in this connection, for it must be obvious from the foregoing description that *Leptomeryx* can have nothing to do with this group, such resemblances as do occur being merely primitive characters common to all the early selenodonts, which the Tylopoda have retained.

The salient characters of the traguline skull are, according to Rüttimeyer the following: (1) Very small size. (2) The cranio-facial axis is straight. (3) The orbits are very large, median in position, and separated by a thin septum, but they do not project much beyond the sides of the skull; the optic foramina are confluent. (4) The cranium is long, narrow, and low, and the parietal zone is correspondingly long. (5) The occipital surface is unusually high, narrow, and convex, and the supra-occipital is extended upon the side walls of the cranium. (6) The alæ orbitales are extraordinarily extended, reaching to the roof of the skull. (7) A short sagittal crest is formed. (8) The frontal zone is limited to the roof of the orbits and nasal cavity. To these should be added (9) the large size of the auditory bullæ, which are filled with cancellous tissue.

In the dentition the characteristic points are: (10) the peculiar spatulate form of the lower incisors; (11) the great simplicity of the premolars; (12) the presence of crests upon the anterior crescents of the lower molars (this Schlosser regards as the most important character of all); (13) the character of the milk molars.

In the vertebral column we observe: (14) the shape of the atlas; (15) the peg-like odontoid process of the axis; (16) well-developed neural spines on the cervical vertebræ; (17) the long, curved, dorso-lumbar region.

In the limbs we have: (18) the great length of the hind limbs as compared with the fore limbs; (19) the ulna and radius are not coalesced; (20) the lunar rests almost entirely upon the scaphoid; (21) the median metacarpals may coalesce into a cannon-bone or not; (22) the lateral metacarpals are complete; (23) the lower end of the fibula fuses with the tibia, except sometimes in *Dorcatherium*; (24) the cuboid, navicular, and cuneiforms fuse into one compound bone; (25) the median metatarsals form a cannon-bone; (26) the lateral metatarsals are complete, though very slender; (27) the keels on the distal ends of the metapodials are confined to the palmar and plantar side.

It is obvious that *Leptomeryx* agrees with the tragulines as regards much the greater number of these characters. The skull is that of the chevrotains with most of the primitive features emphasized. To this statement two exceptions must be made: (1) the occiput is flattened or even concave, and (2) the auditory bullæ are small and not filled with cancellous tissue.

In the dentition, we see that *Leptomeryx* agrees with the tragulines in the characters 12 and 13, and differs from them as to numbers 10 and 11. Some specimens, however, have premolars as simple as those of *Tragulus*, which shows that this character is not a constant one. We may add here that the brain is also very traguline, but little weight can be given to this fact, as there is the same resemblance between *Moschus* and *Tragulus*. "In other respects, the brain of *Tragulus*, as far as its surface markings are concerned, is a simplified miniature of that of the *Cervidæ*" (Flower, No. 17, p. 176). All the traguline characters in the vertebral column recur in that of *Leptomeryx*.

In the fore limb there are no important differences between *Leptomeryx* and the tragulines, even in matters of such detail as the mutual relations of the carpal bones. In the hind limb, the differences are more important. The lower end of the fibula appears usually to remain free, though sometimes it fuses with the tibia; the cuneiforms do not coalesce with the cubo-navicular, and only the proximal ends of the second and fifth metatarsals are preserved, and they coalesce with the cannon-bone. But even in the pes, the distal keels occur only on the plantar side of the metatarsals. Thus in the twenty-seven characters enumerated above as distinguishing the tragulines, *Leptomeryx* agrees with that group more or less completely in twenty-one.

On the other hand, there are the following points of agreement with the Pecora: (1) The character of the occiput; (2) of the auditory bulla; (3) the form of the lower incisors; (4) the complexity of the premolars; (5) the character of the tarsus, and (6) of the metatarsus, except for the shape of the distal end. If the more primitive extinct members of the Pecora be included in the comparison, the number of correspondences with *Leptomeryx* would be much increased.

To those who accept the position of Boas, that the tragulines are a group of simplified ruminants which have been derived from typical members of that series, and not to be regarded as a primitive group (No. 3, p. 522), the apparently intermediate character of *Leptomeryx* would be just what we should expect, and this genus would then be considered as one of the direct ancestors of the tragulines. For reasons into which the limitations of space forbid my entering here, I cannot agree with this view, and therefore cannot adopt such an explanation of the position of the genus before us.

It seems clear to me that the probable interpretation of the problem is this. *Leptomeryx* is a side branch of the traguline stem, given off before the extreme concentration of the tarsus characteristic of existing members of that stem had been acquired, and which has paralleled more or less exactly the characters of the Pecora in certain particulars; e.g. the condition of the auditory bullæ and the constitution of the posterior cannon-bone. There is every reason to suppose that the character of the tarsus in *Leptomeryx* is nearly what it was in the ancestral tragulines. Such a conclusion may seem highly

improbable, and yet when the list of unmistakable parallelisms to be given in the next section is examined, it will appear less unlikely. Nor will the difficulty be diminished by assuming that the resemblances to the Pecora are due to genetic affinity, because then we should have to account for an even greater number of resemblances to the tragulines, which could not have occurred in the ancestor common to this group and the Pecora. If we agree with Rüttimeyer, and refer *Leptomeryx* to the fore-runners of the camels, then the difficulties become all the greater.

Obviously, the final solution of the question can only be reached when we have learned more of the selenodonts of the Uinta formation, and are enabled to trace the ancestry of *Leptomeryx* back to the Eocene forms. From the evidence at present available, I cannot doubt that the genus has a real relationship to the tragulines, with certain independently acquired resemblances to the Pecora, resemblances which appear to be carried even further in the curious little genus *Hypisodus*, with its prismatic molars and highly specialized inferior incisor series.

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#### ON THE MODE OF EVOLUTION IN THE MAMMALIA.

We may now attempt to apply the results gained from the history of the fossil mammals, discussed in this and the preceding paper, to the problems which were stated in the paper on the Tylopoda (No. 52, pp. 2-9). In the discussion which follows I shall not undertake to go over the whole vast field which these questions open up, but shall confine myself as far as possible to the mammals, using other groups of organisms only occasionally as a means of comparison and illustration. To do more than this would require a volume.

1) The first question propounded, viz. that as to the single or multiple origin of genera, is at bottom rather a question about words than about things, and the answer which we make to it will to a great extent depend upon the view taken as to the definition of the word *genus*. If we make classification an expression of real relationship, and not of mere similarity of structure, as should certainly be the end proposed, then it is obvious that all the species of a genus must be more nearly allied

to each other than they are to those of any other genus, recent or extinct. But as genera are at present employed and in the existing state of knowledge, such an exact expression of relationship is impracticable, as that would necessitate a minute knowledge of the phylogeny of each species, such as we are very far from possessing. In the current usage, a genus is a group of nearly allied species agreeing among themselves and differing from all others in the possession of some common character. But if the various species of the ancestral genus may acquire the new character independently of each other (parallelism), or if the species of widely different genera may gradually assume a common likeness (convergence), then it is plain that such a genus is an artificial assemblage of forms of polyphyletic origin. That such parallelism of development does occur, we shall see in the next section, and there are good reasons for believing that convergence is not so rare a phenomenon as it is generally assumed to be; from which it follows with great probability that many generic groups are not real expressions of relationship, but artificial assemblages of similar forms.

While it is easy to make these distinctions theoretically, in practice it is a matter of extreme difficulty, even under the most favorable circumstances, at least so far as cases of parallel development are concerned. Many of the known cases of convergence show that this process is more apparent than real, and may generally be unmasked upon careful examination, though even here the cases of the Ammonites, presently to be mentioned, show the need of extreme caution. The mutual relationships of the various species of two successive genera are usually very obscure. In a given case each of the five species of genus *A* may seem to have been derived from a different species of genus *B*, and yet the assumption of such a mode of derivation may prove to be altogether erroneous, because of the tendency so frequently to be observed for each member of a descending series to develop a similar cycle of variations. Neumayr (No. 40, p. 61) has observed this among invertebrates: "Ein anderer bisweilen beobachteter Fall von grosser Wichtigkeit ist der, dass die verschiedenen Glieder einer Reihe Variationen derselben Art zeigen; während also ein Theil die Merkmale gleichmässig nach einer Richtung im Laufe der Zeit mutirt, zeigen andere Charaktere regellose Abänderungen und

jede Mutation entwickelt denselben Varietätenkreis." In spite of this source of difficulty, many of the facts of palæontology render it extremely probable that many genera, *as now constructed*, are of multiple origin, as was long ago suggested by Cope (No. 5), but our present knowledge is insufficient to enable us to point out the particular cases. Mivart goes so far as to argue that genetic relationship should have but a subordinate place in deciding questions of classification. "Real genetic affinity must exist, and when it can be securely detected must be most important. But the response of organization to need being such as it is (structure and function manifesting themselves so simultaneously), the discrimination between genetic and adaptive families must long, if not ever, continue a work of extreme delicacy and difficulty. . . . On this view, the classification of existing and extinct animals can never, at any future time, be constructed on a purely genetic basis; but surely it need not therefore be a purely arbitrary and artificial system" (No. 38, p. 510).

2) The problems of parallelism and convergence, of which that as to the origin of genera is merely a special case, open up a discussion of far-reaching extent and importance, which can only be briefly touched upon here, though the facts of palæontology are perhaps the most instructive in this connection. The distinction between the two classes of phenomena is obviously one of degree rather than of kind, and it will therefore be convenient to consider them together. What we may call negatively parallel development, *i.e.* the independent suppression of similar parts in different phyletic series, is a very well-recognized phenomenon. Thus, nearly all the known mammals from the Puerco Eocene agree in having an entepicondylar foramen in the humerus, the third trochanter on the femur, a perforated astragalus, an alisphenoid canal, and, probably, interlocking cylindrical zygapophyses on the posterior dorsal and lumbar vertebræ. In existing groups of mammals these characters are scattered and combined in the most heterogeneous fashion, suppression or retention of one or more of them being carried out in widely separated orders. The edentates of the Old and New Worlds are for the most part united by merely negative characters and very probably represent a polyphyletic group. In the same manner, reduction in the number of digits, of teeth,

of vertebræ and ribs, may be similarly brought about in very different groups.

When we come to examine positive differentiation, the same parallelism is abundantly proven. The prismatic, cement-covered molar, has been independently developed in many forms; *e.g.* several of the ruminants, certain pigs, the horses, one of the rhinoceroses (*Elasmotherium*), the elephants, many rodents, etc. The resemblance of the molar of *Elasmotherium* to that of the horse is very striking, but its fundamental plan is rhinocerotid and not equine. The scalpriform incisor, growing from a persistent pulp, is repeated in many very different orders of mammals. Within narrower limits, the selenodont molar-pattern has been several times independently evolved: 1) in the true ruminants; 2) in the camels; 3) in the oreodonts, not to mention the somewhat aberrant types of dentition exhibited by *Anoplotherium*, *Xiphodon*, *Cainotherium*, and the like. The rhinoceros form of molar has been independently acquired at least twice; namely, in the rhinoceros and hyracodont lines. In a great many different series of perissodactyls, as well as in *Hyrax*, the premolars have become molariform; the dentition of certain creodonts has become extremely cat-like, and that in forms which can have no direct connection with the true cats. There is a wonderful similarity in the mode of development of cerebral convolutions in many different lines of ungulates, a similarity which the fossil series show to have been independently acquired, and which are plainly the necessary outcome of mechanical principles. In the same way we find that the milk dentition of all the primitive selenodonts agrees in character, as does that of all existing members of the group, except the tragulines, which still retain the ancient structure, but the history of the various ruminant lines proves that the modern type has been independently acquired at least three times, in the Pecora, the Tylopoda, and the later *Oreodontidæ*, such as *Merychius* (No. 51, p. 370). The spout-shaped odontoid process of the axis has arisen in the true ruminants, the horses, the camels, and, to a certain degree, in the later oreodonts, such as *Merychius*. The proximal end of the humerus in the modern Tylopoda is extremely like that of the horse, and the lower Miocene representatives of these two series, *Pæbrotherium* and *Mesohippus*, also agree almost exactly as to the structure of the

humerus, but in this case the bone is of a more primitive type, with single bicipital groove and no bicipital tubercle, or only a very rudimentary one.

The steps of modernization which may be observed in following out the history of many different groups of mammals are seen to keep curiously parallel, as may be noticed, for example, in the series of skulls figured by Kowalevsky (No. 26, Pl. IX.), where we find similar changes occurring in such families as the pigs, deer, antelopes, horses, elephants, etc. Indeed, one may speak with propriety of a Puerco, or Wasatch, or White River type of skull, which will be found exemplified in widely separated orders. Of course there are exceptions, some types being in advance of, and others lagging behind, the standard of their age, and others, again, attaining great peculiarities of structure which will not be perpetuated; but, on the whole, the type of skull or limbs keeps strikingly true to the standard. These facts emphasize the truth of the proposition laid down by Cope: "From these and many analogous cases, the general law may be deduced, that identical modifications of structure, constituting evolution of types, have supervened on distinct lines of descent" (No. 8, p. 343). Of similar import are the simultaneous and similar variations of different orders, according to geographical location, such as the characters of the Lepidoptera in the different Malay islands, to which Wallace has directed attention (No. 56), and which is exhibited in such a striking way by the coloring of Arctic and desert animals, and very many other well-known phenomena. All this but illustrates anew the conclusion long since universally accepted, that no natural system of classification can be founded upon the presence or absence of a single character.

Parallelism may, however, extend much further than this, and embrace, not single characters only, but whole series of them. It is this fact which renders the proper reference of such forms as *Leptomeryx* so very difficult. If the interpretation of the tylopodan phylogeny which was given in my former paper be correct, then the camels and the true ruminants have no common ancestor nearer than the *Dichobunidae*, animals with quinquetuberculate upper molars, complete dentition, short limbs, unreduced ulna and fibula, and tetradactyl feet, all the digits being free. The two series have independently acquired tetra-selen-

odont molars ; have lost all or nearly all of the superior incisors ; have developed types of skull which, with all their differences, have many features in common ; in both the limbs and especially the metapodials have greatly elongated ; the ulna and fibula are very much reduced and in precisely the same fashion ; the cannon-bones in both series are composed of just the same elements ; in both epispheial processes have been independently developed upon the zygapophyses of the lumbar vertebræ, and in both the odontoid process of the axis, which was originally peg-like, has become spout-shaped. The stomach of the camel resembles that of the typical ruminants in a way that we cannot suppose to be due to a common inheritance from the *Dichobunidæ*. In both series the final result is strikingly alike, though the parallelism is by no means complete, and as we have already noticed, the keen insight of Rüttimeyer detected the true relationship from a comparison of the modern forms alone. In one respect, however, I must venture to differ from his interpretation of the facts. Rüttimeyer regards the llama as less aberrant than the camel ; a better statement would perhaps be that its parallelism to the Pecora is more complete.

The resemblance between the creodonts and the carnivorous marsupials has been much dwelt upon, but I think that it may be shown that the relationship between the two groups is a very remote one and that the points of likeness are due partly to parallel development and partly to the retention in both series of certain primitive characteristics.

The group of reptiles presents very similar phenomena ; on the one hand there are the Dinosauria, which have developed so many ornithic peculiarities in the hind limb, while, on the other hand, the Pterosauria possess equally striking avian features in the skull, cervical vertebræ, sternum, and shoulder girdle. To assume, as has been done, that the birds are diphyletic, is to admit the principle of convergence in almost its extreme form, while if this be denied, then the bird-like structures of either the pterosaurs or the dinosaurs, or both, must be due to parallelism.

Among the invertebrates the same problems confront us. Thus Würtenberger finds well marked convergences among the ammonites. "Aus den Betrachtungen welche wir bisher über die Stammesgeschichte der Ammoniten angestellt haben, dürfte

wohl ohne weiteres schon hervorgehen, dass der Ursprung der meisten der hier berücksichtigten Gruppen sich als monophyletisch zu erkennen gibt; denn fast immer sehen wir eine bestimmte Form oder enger begrenzte Formengruppe nur als das Glied einer einzigen Entwicklungsreihe auftreten; nur einzelne wenige Fälle machten sich bemerklich, wo aus verschiedenen Formenreihen einander sehr ähnliche Endglieder hervorgingen. Es sei z. B. an die *Mutabilis*-Gruppe erinnert; hier wurden diese Endglieder einander selbst so ähnlich, dass sogar schon mehrere derselben zu einer einzigen Art vereinigt worden, und wir demnach hier sogar von einem polyphyletischen Ursprunge der *Species* sprechen könnten. Wenn nun aber die äusseren Umgänge solcher *Mutabilis*-formen einander noch so ähnlich werden, so sind dann die inneren Windungen um so verschiedener und verrathen den verschiedenartigen Ursprung der allenfalls zu einer *Species* zusammengefassten Individuen nur zu deutlich, so dass eine solche polyphyletische *Species* dann eben bloß noch als eine naturwidrige Zusammenstellung verschiedenartiger Dinge erscheint. . . . Solche Fälle wie bei der *Mutabilis*-Gruppe, wo zu verschiedenen Zeiten verschiedene Formen, ähnlichen Existenzbedingungen sich anpassend, derart sich abänderten, dass sie einander sehr ähnlich wurden, trifft man bei den Ammoniten noch mehrfach" (No. 61, pp. 106, 107).

Hyatt fully confirms these results, and adds others to them: "The evidence is very strong that *Baculites*, *Scaphites*, etc., of the Cretaceous are not necessarily species of the same genus, but probably always polyphyletic in origin. The *Baculites* of North America have so close resemblance to those of Europe that they are usually considered as allied species; but there are indications, in the peculiar nodular markings and great size of many species, which lead us to think that they originated from American stocks" (No. 23, p. 31).

Haeckel believes that the Siphonophora are of diphyletic origin, part of them being derived from trachomedusoid ancestors, and part from anthomedusoid (No. 22, p. 40).

Similar examples, drawn from a very wide range of animal groups, might be multiplied almost indefinitely, but those here given are sufficient to prove what probably few morphologists doubt, namely, that parallelism and convergence of development are very real phenomena. Much more difficult to

decide is the question as to how far these processes may be carried. In all of the cases cited, the final result is not identity, but similarity, and there is in all of them some fundamental discrepancy which exposes the deceptive character of the process. I have already quoted Rüttimeyer's opinion as to the relationship between the camels and the typical ruminants. Semper found that while the shells of certain genera of land mollusca exhibit a remarkable degree of convergence, the structure of the soft parts was sufficient to correct the improper association of these forms. Other instances might be cited to show that a careful use of the comparative method is often able to avoid these obstacles. On the other hand, one cannot doubt that great numbers of such cases have escaped detection, as the instructive instance of the *Mutabilis* group of ammonites plainly renders probable; for if the embryological stages of these shells were not preserved in the inner whorls, no palæontologist would hesitate to class them together as closely allied, or even as members of the same species. In the construction of the larger taxonomic groups, which embrace so many and such various forms, the difficulties arising from parallelism, both positive and negative, become greatly increased, and only complete and unbroken phyletic series will enable us to overcome them entirely. It is, therefore, quite impossible to determine, from our present knowledge, to what extent these processes may be carried, though probably few morphologists will follow Mivart in the extreme position which he has taken upon this question. The fixity of direction of the lines of development, which is so strikingly exemplified in nearly all well-defined series of descending forms, seems to offer some assurance that these interrelations of various groups will not prove to be so inextricably confused as to defy any attempt to unravel them.

The supposed dual origin of the horse in the Old World and the New does not offer such insuperable difficulties as one might at first imagine. In both hemispheres occur almost unbroken series, from the Eocene *Hyracotherium* to the existing *Equidæ*, and were only one of these series known, probably no one would hesitate to regard it as the true ancestral line. But several of the genera, such as *Hyracotherium*, *Pachynolophus*, *Hippotherium*, occur both in Europe and in America, and there can be little doubt that these genera originated in one continent

and reached the other by immigration. Other genera form abortive side branches which lead to no permanent results, and thus it seems altogether probable that there is only one series, at least as late as the Pliocene. That some species of *Equus* should be derived from *Protolippus* and others from *Hippotherium*, as Cope has suggested, it is by no means impossible, but cannot be admitted until the ancestral history of these species has been followed out step by step.

These considerations show how profoundly important it is that in all phylogenetic discussions the possible effects of parallelism and convergence should never be lost sight of. One of the commonest fallacies to which neglect of these factors leads is the assumption that because two allied groups possess a certain character, their common ancestor must also have possessed it. This may or may not be true in any given case. For example, it has been shown that the spout-like odontoid process of the axis has been independently developed several times, yet Boas concludes that the ancestor common to all ungulates must have possessed it: "Auch beim Pferd, beim *Anchitherium* (nach Kowalevsky) und (nach Flower) beim Tapir verhält sich der Proc. odont. ähnlich wie bei den typischen Wiederkäuern, und es ist somit wahrscheinlich dass die gemeinsamen Vorfahren *aller Ungulaten* diesen Charakter besaßen und dass auch die konische Form, etc., desselben beim Schwein sekundär erworben ist" (No. 3, p. 518). But even this conclusion involves the admission of a parallel development of the peg-like odontoid in the pigs, tragulines, rhinoceroses, etc. Flower's view is more consonant with the facts of palæontology. "The form of the odontoid process in the Tylopoda might lead to the idea that they were segregated from the ruminant stock after the Tragulina had been given off; but as it is also found in the horse, it is probably adaptive, as are the hypsodont molars" (No. 17, p. 190).

It is further evident that Huxley's dictum to the effect that in forming natural groups "it is more important that similarities should not be neglected than that differences should be overlooked," cannot be maintained. On the contrary, it is only a due consideration of the differences that enables us to distinguish artificial from natural groups. It is likewise clear, if these conclusions be sound, that no general rules can be laid

down for determining the taxonomic value of any particular structure, whether it is adaptive or inherited, positive or negative. In this respect every group must be considered by itself, neglecting nothing. Fürbringer has reached very similar results in his great work on the birds: "Unter diesen Umständen muss die Beurtheilung dieser heterogenen Kennzeichen und die Auslese unter ihnen *für jede Gruppe von Anfang an* unter den bereits angegebenen Cautelen getroffen werden und nirgends darf man vergessen dass dieses oder jenes Merkmal, das sich bei 10 Familien als ein constantes bewährte, bei einer 11<sup>ten</sup> eine ganz überraschende, seine taxonomische Anwendbarkeit sehr beeinträchtigende Flüssigkeit darbieten kann" (No. 19, p. 1134).

4. Palæontology is not well adapted to solve the fourth problem, as to whether lost structures may be regained, because we never can be sure that any case which might seem to require such an interpretation is not really due to an imperfection of the geological record. The apparent reacquisition of a digit, for example, might be due to the fact that the ancestor of the polydactyl form had not been preserved. There is, however, one case which is of interest as indicating possibilities in this direction. One of the most characteristic features of the *Oreodontidæ* is the fact that the first inferior premolar has assumed the form and function of the canine, while the latter is functionally one of the incisors. This condition is obviously a secondary one and implies a change from the ordinary relations of these teeth. On the other hand, in *Pithecistes*, one of the later and more aberrant members of the family, the caniniform premolar has disappeared and the canine has again taken on its normal functions. This is, of course, not exactly a case in point, as the canine was not lost and reacquired, but it would seem to indicate that such reacquisition is not impossible. If Weissman's interpretation of the relations of *Siredon* to *Amblystoma* be correct, then this is a clear case of a lost organ being reacquired; e.g. the gills, although these organs are normally present and functional in the larval state of *Amblystoma* (No. 58). At all events, such reacquisition, among the higher animals at least, would certainly seem to be unusual, and should not be assumed in any given case, except upon the clearest evidence.

5. So far as the series of fossil mammals which we have been considering are concerned, the developmental history appears to

be very direct, and subject to comparatively little fluctuation, advancing steadily in a definite direction, though with slight deviations. Thus in the cameline series, the size and position of the orbit, the shape and character of the posterior nares appear to change first in one direction and then in another, so that in some respects the skull of *Pæbrotherium* is more modernized and ruminant-like than that of the camel. But these fluctuations are slight and of no great importance. On the whole we are impressed by the steady march of differentiation; thus, in the equine series the premolars one by one become molariform, the molar pattern more complex, the face elongated, the digits are continually reduced in number, the median digit becomes more and more enlarged, and the carpal and tarsal bones adjusted to the new character of the strains, the limbs become more and more elongated, and the stature of the whole animal increased. In many genera the cycle of variation appears to be a singularly small one, and as Neumayr has observed in the Mollusca, the same or a very similar cycle appears in successive genera. Thus in the genera *Palæosyops*, *Diplacodon*, and *Titanotherium*, of the Bridger, Uinta, and White River formations respectively, there are curious similarities in the specific variations, which are repeated in each of the successive formations. The same thing is true of the Oreodons of the White River, and Epreodons of the John Day, though perhaps these cases are in part to be explained as belonging to genera of multiple origin, where several species of the older genus have similarly and simultaneously taken on the character of the new. Indeed, the limited plasticity of the mammals, except along certain definite lines, is very marked. In every formation the majority of species appear to die out without leaving any successors behind them, and too early a specialization would seem to be fatal to the perpetuation of a group. With rare exceptions the progenitors of permanent lines seem to be those forms which have not strayed too far in any direction from the safe middle course; every formation contains numerous examples of what from one point of view may be called premature differentiations, advantageous, no doubt, to their possessors, but not sufficiently plastic to adapt themselves readily to new conditions.

These facts are opposed to the assumption that in the evolution of a *mammalian* phylum frequent alternations of advance

and retrogression have occurred. Of course, a mammal may advance to a certain degree and then degenerate, but that is not the point under consideration. Nor is it meant that the direction of advance is something absolutely fixed; on the contrary, this direction may be followed for a certain length of time, and then changed. A very instructive example of this is given by the history of the Pecora. The lower miocene representatives of this series, which are hornless, *Amphitragulus*, *Palæomeryx*, etc., show a continually increasing size of the upper canines, which are still retained in the hornless deer, *Moschus*, *Hydropotes*, etc., as well as in the small-antlered muntjaks, while in the typical *Cervidæ* and in the *Bovidæ* the antler and the horn have been gradually substituted as weapons, and the upper canines have dwindled to mere rudiments or entirely disappeared. *Chalicotherium* is doubtless an example of the change of direction of specialization.

Obviously, this conclusion is far from certain, and may well be modified or even disproved by more extensive and complete material. Nor can we extend this result to the lower groups of animals. The facts which have been brought out with regard to the Axolotl, the experiments of Schmankevitch (No. 48) on *Artemia*, and many other facts, render it inapplicable to these forms. But it appears to be the fact that, just as the power of regeneration of lost parts diminishes as we ascend in the scale of animal life, so plasticity of organization and capacity for differentiation of structure in widely different directions diminishes also.

6. As a general rule, it certainly appears to be the case that among mammals differentiation is by reduction in the number of parts, but there are some facts which go to show that this rule is not without exceptions. Thus in the toothed whales and in certain edentates the number of the teeth has surely been increased, as has the number of the phalanges in the Cetacea and the Sirenia. Probably no one will be inclined to believe that the primitive antelopes had four horns and that *Tetraceros* is the only living form which has retained this peculiarity. On the contrary, it seems certain that in this genus an additional pair of horns has been developed, just as in certain monstrous domestic breeds of sheep. In certain breeds of dogs a double hallux has been rendered constant. Indeed, reduplication of

parts is a very common teratological occurrence, and there is no *a priori* reason to assume that such reduplication might not occasionally be selected and perpetuated. The fourth molar of *Otocyon* appears to me to be probably either a case of this sort, or of permanent reversion, as any other assumption with regard to it seems very unlikely. *a*) That all the known fossil cynoids have no direct connection with the existing dogs, can hardly be believed by any one who has examined the material, and yet all of these, with occasional individual exceptions (which still occur among the recent *Canidæ*, see Filhol, No. 16), have but three molars at most. *b*) That the *Canidæ* are of dual origin, one line through *Miacis*, *Daphænus*, *Cynodictis*, etc., to *Canis*, and the other through unknown ancestors to *Otocyon*, involves a degree of convergence which known facts do not justify us in assuming. Between the third and fourth hypotheses, that the additional molar is atavistic, or that it has been added *de novo*, it is very difficult to decide; for in the fairly complete mammalian series which we have been considering in the present and preceding papers, neither process can be shown to have taken place. Yet both are conceivable and do take place in individual cases; and if so, they might, under favorable circumstances, and provided they recurred frequently enough, be rendered permanent. In *Otocyon* the dentition is much more primitive (aside from the number of the molars) than in any other known member of the family, recent or fossil. Judging from the state of development of the skull and skeleton, this condition almost certainly implies retrogression, which may possibly have stimulated atavistic tendencies. The problem can be definitely solved, however, only by a much more complete phyletic series than we can at present command. At all events, this reacquisition or addition *de novo* can only be very exceptional in the history of the higher mammals.

7. In large groups of mammals the method which is followed in the reduction of parts is generally a very uniform one. Thus Owen's laws of the reduction of digits hold good for all artiodactyls and perissodactyls. Great uniformity is also exhibited in the order of disappearance of the teeth, but this is not without exceptions; *e.g.* in artiodactyls the first premolar is usually the first one to disappear, but in the camel this tooth is retained, while the second is lost. The Creodonta and Carnivora follow another law, but in these groups there is less uniformity, and

other exceptions might be cited. With regard to the mode of reduction of the vertebral column, fossils are not well adapted to throw light upon the question, because specimens in which the vertebral column is at all completely preserved are very rarely found. So far as the evidence goes, however, it appears to favor Fürbringer's position, that reduction is from behind forward, and that the changing numbers of the dorso-lumbar vertebræ are due to a shifting of the limb-girdles. The early forms of mammals in which the number of trunk-vertebræ is known, have, for the most part, a larger number than have their modern representatives, and a very general characteristic of these ancient forms is their very long, stout, and well-developed tails. This evidence is, however, too imperfect to be at all conclusive, and whatever may be true of the mammals, Parker's results seem to show that in the turtles, suppression of vertebræ may take place in the cervical region without affecting the position of the limb-girdles or the number of the dorso-lumbar-sacrals. Baur has recently published (No. 2) the results of his studies upon the spinal columns of certain lizards, crocodiles, and serpents, in which he comes to the conclusion that intercalation does occur. "My opinion is that in the increase of the number of segments, not only in vertebrates, but also in invertebrates, intercalation has played a much greater rôle than is generally admitted" (p. 335). The evidence adduced is not, however, altogether conclusive.

8. Increased size and weight of body of course entail increased thickness and massiveness of the bones, with much more prominent and rugose processes for the attachment of muscles and ligaments; but the effect upon the skeleton is much more profound and far-reaching than this, as will appear from a comparison of the Proboscidea, the Dinocerata, and the equally huge perissodactyl, *Titanotherium*, which are about as widely separated from one another as three ungulate lines well can be. Little is known about the phylogeny of the elephants, but so far as the other two series are concerned, their earlier members are in many respects less alike than the later ones, while in the final members of all three lines we find many and striking resemblances. The neck is shortened, the trunk very long, and the anterior dorsal vertebræ rendered very heavy, with much elongated spines to support the massive head, which is greatly en-

larged, but lightened by large sinuses or air-cells. The ribs are very long, and strongly arched, to carry the great mass of viscera. The scapula is triangular in shape, and in the Dinocerata extremely like that of the elephant, with greatly elongated suprascapular border and very large post-scapular fossa, prominent and massive acromion. The humerus also is much alike in these two groups, but that of *Titanotherium* is more rhinoceros-like. In all, the ulna is unreduced or even enlarged, and the carpus is composed of massive cubical blocks. The ilium is in all greatly everted and immensely broadened in the transverse direction. The femur is long and massive; that of *Uintatherium* is almost an exact copy of that of the elephant, having neither third trochanter nor pit for the round ligament, both of which are preserved in the earlier members of the Amblypoda, e.g. *Coryphodon*. In all, the tibia is short, and the fibula complete; the astragalus extends far over on the cuboid, though separated from it in the elephant by the navicular, and is little or not at all grooved, so that the maximum of motion is at the knee-joint. The tarsus of *Uintatherium* is in general character very much like that of the elephant, while that of *Titanotherium* does not lose its perissodactyl structure.

The metapodials are short and massive, especially so in the Dinocerata and Proboscidea, and the unguis phalanges are reduced and nodular in shape, showing that in all the foot was enveloped in a pad. It seems probable that great size and weight of body stops in most cases the process of digital reduction. In *Titanotherium* the number is, it is true, only IV. in the manus and III. in the pes; but then this degree of reduction is already reached in the Bridger genus, *Palæosyops*, which is of moderate size. The other two series are pentadactyl,<sup>1</sup> and in all the foot is nearly isodactyl; i.e. the digits are all of approximately the same length and thickness, though in *Titanotherium* there is more inequality than in the others. In all three groups there are no medullary cavities in the long bones, the interior of which is filled with cancellous tissue.

<sup>1</sup> To this statement one exception must be made. The specimens of naviculars of *Dinotherium giganteum*, from Pikermi, preserved in the Paris museum, show only a very small facet for the first cuneiform, while in the *D. Bavaricum* of the Vienna museum there is no facet for that bone. This points to a great reduction or loss of the hallux. The same statement will apply to a rather small, *Uintatherium*-like navicular in the Princeton museum.

The comparison might be extended to the larger rhinoceroses and hippopotamuses, and would show much the same state of things in a less pronounced degree. It is thus apparent that mere increase in size and body-weight may produce many remarkable convergencies in skeletal structure in animals which are but distantly related to one another. Indeed, so many and so close are the approximations of the Dinocerata to the elephants, that Cope, at one time, proposed to place them among the Proboscidea (No. 6).

The materials for determining the effects of great diminution of stature among the ungulates are much less complete and satisfactory, though probably the many points of resemblance between the tragulines and *Cainotherium*, and perhaps also *Leptomeryx*, as also between the tragulines and dwarf antelopes, are largely due to this factor.

Fürbringer has reached very similar results with regard to the influence of stature in the birds: "Im speciellen Theile dieser Arbeit konnte an zahlreichen Stellen gezeigt werden, dass bei der Ausbildung der Knochen und Muskeln die Körpergrösse der verschiedenen Vögel keinen gleichgiltigen Factor spielt, sondern vielmehr in sehr bestimmter Weise mit charakteristischen Differenzirungen des Vogelkörpers coincidirt. Luftarmuth bis Luftleere des Skeletes verbindet sich bei den kleineren Vögeln mit relativ mächtiger Entwicklung der Flugmuskulatur, während andererseits ein höherer Grad von Pneumaticität bei den grösseren Fliegern mit einer grossen Ersparniss an Muskelementen Hand in Hand geht. . . . Aber auch sonst konnten nach der Körpergrösse variirende Verhältnisse nachgewiesen werden. Mit zunehmender Grösse wächst im Allgemeinen, doch nicht ohne Ausnahmen, der Intercoracoidalwinkel, die Spannung der Clavicula, die Zahl der Halswirbel, die sternale Krümmung, etc., während andererseits die Configuration des Xiphosternum in sehr vielen Fällen eine Vereinfachung, die Crista sterni und die Crista lateralis humeri eine Verminderung ihrer Höhe darbietet. Die Configuration der Gelenke zeigen mit zunehmender Grösse auch im Ganzen eine Zunahme der Differenzirung. . . . Welche specielleren Correlationen hierbei in Frage kommen entzieht sich zunächst unseren Blicken; aber auf Grund der bisherigen Beobachtungen dürfen wir mit dem Factum rechnen, dass im Grossen und Ganzen bei

den ziemlich grossen und mässig grossen Vögeln die einfacheren und primitiveren Verhältnisse vorwiegen, während die grossen, wie auch die kleinsten Formen eine einseitige Entwicklung und eine grössere Abweichung von den als ursprüngliche zu beurtheilenden Bildungen darbieten. . . . Wie mir scheint sind es aber nicht allein die Vögel, deren grösste und sehr grosse Formen eine höhere Differenzirung und eine grössere Abweichung von primitiven Zuständen darbieten. Vielmehr scheint diese Regel eine recht weite Verbreitung zu besitzen. Ich erinnere u. A. an das Verhalten der Wirbelsäule, die z. B. bei den kleineren und primitiveren Formen der Plesiosaurier eine viel geringerer Zahl von Halswirbeln besitzt als bei den grösseren und mehr typischen Verwandten, ferner an den Brustgürtel der bei den kleineren Insectivora und Rodentia verschiedene an ursprünglichere Bildungen erinnernde Verhältnisse darbietet, welche den grösseren Thieren fehlen, dann an Carpus und Tarsus, wo ebenfalls bei den genannten Abtheilungen der Säugethiere durch Albrecht, Bardeleben, Baur und Leboucq eine im Ganzen recht primitive Anordnung nachgewiesen werden konnte" (No. 19, pp. 991-3).

The extremely important question as to whether development is always by the accumulation of minute gradations, or whether it may not, sometimes at least, be *per saltum*, is one which can never receive a conclusive answer from palæontology, because we can never be sure that what appears to be *per saltum* development is not merely due to the loss of certain links in the chain. There are, however, some facts which seem to point to the conclusion that evolution does not always proceed at a uniform rate, but that there are periods when this rate is much accelerated, and widespread changes and readjustments are carried out. While it is perfectly true that frequently the successive forms in a series of beds point "rather to substitution through migration than to transmutation," yet this is often not the case, as in those series where we may follow out the transmutation step by step. Yet even in these series it is generally found to be the case that the amount of structural change is greater in any phylum in passing from one formation to another than between the top and bottom of the same formation. To assume that the rate of development is always constant would involve the further assumption that the unrecorded gaps between

the successive horizons represent a longer time than do the formations themselves. So far, at least, as the fresh-water Tertiaries of North America are concerned, this assumption receives little support from geology, and we may fairly infer that the geographical changes which brought about the drying up of the great lakes in one region and their appearance in another were accompanied by an accelerated rate of change in the organic world.

The conclusions as to the mode or laws of evolution which thus seem to follow from the study of series of fossil mammals can make no pretensions to novelty, as they have all been repeatedly suggested before. Nor can they be regarded as entirely conclusive, for some of them, as we have already seen, may be fairly interpreted in several ways; it is not even possible, in the present state of knowledge, to entirely avoid all presuppositions in the construction of the phyletic series. But inasmuch as there is so little agreement upon these points, I have thought that it would be of service to clearly state just what the problems are and how the known facts seem to be related to them. On some of the questions the evidence speaks with no uncertain sound; thus, for example, arrange the phyletic series how we may, the occurrence of parallelism and convergence in development is clear. This conclusion can only be avoided by the assumption of complex cross and reticulated relationships, such as no one has ever ventured explicitly to defend. I venture to hope that morphologists may test and extend these tentative results by applying to them other and wider classes of facts than those from which they have been drawn.

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#### ON SOME OF THE FACTORS IN THE EVOLUTION OF THE MAMMALIA.

The question of evolutionary philosophy as to which there is at present the most dispute is undoubtedly that with regard to the causes of variation, together with the problems of heredity, which are inseparably connected with it. The brilliant essays of Weismann have done great service in calling renewed attention to these fundamental questions, for there can be no doubt that most speculations upon the subject had been taking

too much for granted, and that the foundations of one essential part of current evolutionary belief were insecurely laid. The whole subject needs, therefore, to be exhaustively re-examined and tested from every side.

For the purposes of this paper it is not necessary for me to enter into the reasons of my dissent from Weismann's theory of the continuity of the germ-plasm, nor to explain why, in my opinion, so far from rendering the phenomena of heredity more intelligible, it tends to confuse them still further and to end logically in a system very like the old preformationism. As Lloyd Morgan has very pithily put it, "I cannot but regard Weismann's doctrine of the continuity of germ-plasm as a distinctly retrograde step. His germ-plasm is an unknowable, invisible, hypothetical entity. Material though it be, it is of no more practical value than a mysterious and mythical germinal principle. By a little skilful manipulation it may be made to account for anything and everything. The fundamental assumption that whereas germ-plasm can give rise to body-plasm to any extent, body-plasm can under no circumstances give rise to germ-plasm, introduces an unnecessary mystery. Biological science should set its face against such mysteries" (No. 39, pp. 141 and 142). But into this subject we need not enter, because so far as the mammals are concerned, the difficulty of comprehending how somatic changes can affect the germ in appropriate fashion so as to reproduce these changes in the offspring, is in no way diminished by a denial, or even a complete refutation of the continuity theory. Weismann states the difficulty thus: "It is perfectly right to defer all explanation, and to hesitate before we declare a supposed phenomenon impossible, because we are unable to refer it to any of the known forces. No one can believe that we are acquainted with all the forces of nature. But, on the other hand, we must use the greatest caution in dealing with unknown forces, and clear and indubitable facts must be brought forward to prove that the supposed phenomena have a real existence, and that their acceptance is unavoidable" (No. 57, pp. 80 and 81). But does the assumption that acquired characters are transmissible involve, as a matter of fact, an appeal to unknown forces? Rather, I should say, to the as yet not well understood operation of known forces. In another connection, Weismann has himself well defended this principle, when, in

arguing against the idea of a vital force, he says: "The latter, [*i.e.* the ontogenetic vital force] is no longer admitted by anybody, now that we have turned from mere speculation to the investigation of nature's processes; nevertheless its non-existence has not been demonstrated, nor are we yet in a position to prove that all the phenomena of life must be traced to purely physico-chemical processes, to say nothing of our actually being able to so trace them" (No. 58, p. 643).

In his later papers, Weismann admits that the germ-plasm may be modified in various ways. "It must be admitted that there are cases, such as the climatic varieties of certain butterflies, which raise some difficulties against this explanation. I, myself, some years ago, experimentally investigated one such case, and even now I cannot explain the facts otherwise than by supposing the passive acquisition of characters, produced by the direct influence of climate" (No. 57, p. 99). "I am at present inclined to believe that Professor Vines is correct in questioning whether sexual reproduction is the *only* factor which maintains Metazoa and Metaphyta in a state of variability" (No. 60, p. 322). We have, indeed, abundant evidence that food, temperature, moisture, salt, and the like may have a profound influence upon the germ-plasm, and though we can form no conception of the way in which the amount of salt in the water will change *Artemia* into *Branchipus*, or the quantity of food will determine the proportion of the sexes in tadpoles, or how the change of food-plant metamorphosed the Texan species of *Saturnia* into something very different (see Moritz Wagner, No. 55, pp. 307-310), yet we are not impelled to take refuge in an appeal to unknown forces. Nor can the well-known influence of the germ-glands upon the body be explained in the sense of determining just how and why the effect is produced. If the presence of the germ-glands can so profoundly affect the soma, why should the converse influence appear so incredible? Still more mysterious is the influence exerted upon the maternal organism by the spermatozoa (or perhaps the fœtus), so that the offspring by later sires often show characters of previous sires. Virchow pronounced the stigmata of Louise Lateau to be "either fraud or miracle," but the recent investigations in hypnotism show that the case may be explained without accepting either horn of the dilemma. Whether acquired characters be transmitted or not, it is cer-

tainly inadmissible to speak of such transmission as inconceivable or as involving the operation of unknown forces.

It is extremely difficult to obtain any satisfactory evidence of the transmission of acquired characters, and this for two reasons. In the first place, it is generally well-nigh impossible to determine in any given instance whether a character is acquired or congenital (employing the latter term to designate characters due to changes in the germ-plasm itself). As a rule, it is taken for granted that those structural features with which an animal is born or hatched are altogether congenital, but nothing can be more improbable; for we know that embryos are very sensitive to changed conditions, and are easily modified, but to determine what characters are due to changes in the ovum and what to modifications in the embryo, is a difficult matter. For my own part, I am not inclined to attach much importance to the supposed cases of transmitted mutilations, as from an *a priori* standpoint they are improbable, and more especially because the long-continued mutilations practised by many savage races appear to be without result in this respect. Nevertheless, such facts as those stated by Eimer (No. 15, p. 191) and DeCandolle (No. 14, p. 94), from their own knowledge, and the experiments of Obersteiner upon guinea-pigs, are not to be dismissed with a sneer. Arbuthnot Lane has come to the conclusion "that a force which produces no obvious change in the skeleton of the antecedents, but only a tendency to change, can, acting as a developmental factor, cause the apparently spontaneous development of that change in the offspring" (No. 29, p. 215). It is also well worthy of inquiry how far the extraordinary skill and deftness of Japanese and other Oriental workmen is due to the fact that handicrafts have long been hereditary in the same families.

Dall's position is an eminently reasonable one: "The contention of Weismann, that 'not a single fact hitherto brought forward can be accepted as proof' of the transmission of acquired characters, demands attention. This reminds one of the familiar statement of twenty years ago, that the Darwinians had not brought forward a single instance of the conversion of one species into another species. If the Dynamic Evolutionist brings forward an hypothesis which explains the facts of nature without violence to sound reasoning, that hypothesis is entitled

to respect and consideration until some better one is proposed or some vitiating error detected in it" (No. 12, p. 7). When we remember that evolution is a slow process, it is hardly to be expected that dynamic influences should be immediately apparent, though the experiments on *Artemia* and on feeding caterpillars point to a different conclusion. The question must be decided, if at all, by the inductive method, by determining how the observed facts can best be interpreted.

When we turn to the hypotheses which Weismann proposes in place of what Dall calls the dynamic theory, we might naturally require the same rigid demonstration which he demands of his opponents, but of such demonstration we find little, but rather ingenious speculation. Although he has abandoned the view that sexual reproduction is the *only* factor in inducing variability, he still appears to maintain that it is by far the most important. "I am still of the opinion that the origin of sexual reproduction depends upon the advantage which it affords to the operation of natural selection; nay, I am completely convinced that only through its introduction was the higher development of the organic world possible. . . . Even if, however, from our present knowledge it is probable that sexual reproduction is not the sole radical cause of variability in the Metazoa, still no one will dispute that it is a most effective means of heightening variations, and of mingling them in favorable proportions. I believe that the important part which this method of reproduction has played in calling out the existing processes of selection, is hardly diminished, even if one grants that direct influences upon the idioplasm call forth a portion of individual variability" (No. 60, p. 323). Weismann still maintains that somatogenic characters, the effects of use and disuse, and the like, cannot be transmitted, and attempts "to elucidate the phenomena without the aid of this principle."

But as Lloyd Morgan has pointed out, "by sexual admixture alone, there can be no increase or decrease, beyond the mean of the two parental forms. If, then, the union of sperm and ovum be the source of new or more favorable variations, other than or stronger than those of either parent, this must be due to the fact that the hereditary tendencies not merely commingle, but, under favorable conditions, combine, in some way different indeed from, but perhaps analogous to, that exemplified in chem-

ical combination" (No. 39, p. 151); of course such organic combination is not vouched for by a particle of evidence.

Again, on the theory of heredity propounded by Weismann, such variations are necessarily single, and there is no probability that the same variation will arise twice, even in the same litter. Now it has never been shown that such variations can be perpetuated in spite of the swamping effects of free intercrossing, nor that such minimal differences as a slight shifting of the carpal and tarsal elements, or the presence of a tiny incipient cusp upon a tooth, can be of decisive effect in the struggle for existence. This difficulty has long been felt, and many attempts have been made to meet or to evade it. Weismann has stated the case thus: "Such calculations as those quoted by Darwin from the article in the *North British Review* of March, 1867, are extremely deceptive, since we have no means of measuring the amount of protection afforded, and we can therefore hardly compute with any certainty, in how great a percentage of individuals a change must contemporaneously occur in order to have a chance of becoming transferred to the following generation. . . .

*Variations which occur singly have but little chance of becoming predominant characters*, and this is obviously what Darwin concedes; but this is by no means equivalent to the assumption that only those variations which from the first occur in numerous individuals, have a chance of being perpetuated" (No. 58, pp. 658 and 659). But it is difficult to see, on Weismann's principles, how variations can occur other than singly (*i.e.* excluding those cases of the influence of the environment upon the germ-plasm, by which many individuals are simultaneously affected), except in the direct line in which the change first appeared, for by hypothesis every fertilized ovum is different in important respects from every other, and on the doctrine of chances there is only an infinitesimal probability that it can ever be duplicated. The argument that variations do occur in nature sufficient to give the necessary material for the operation of natural selection, does not touch the real difficulty, which is what *causes* these variations? It is taking a great deal for granted to assume that they are solely or even mainly due to sexual reproduction.

The relatively fixed direction taken by variations, which has been insisted upon by so many observers, — *e.g.* Askenasy (No. 1), Eimer, Geddes and Thompson (No. 21), Osborn (No. 43), —

comes out most clearly in the series of fossil mammals. Granting that unlimited variation is no necessary part of the selection theory, it seems strange that new facets on the bones and new cusps on the teeth should appear only in such definite ways, and that there should not be many tentative attempts and false starts before the proper development is hit upon. In the structure of the carpus and tarsus we find that in any given phylum very definite lines of evolution are early established and closely adhered to, and the changes are just those called for by the operation of dynamical influences. If Weismann's position were correct, we ought to find much greater latitude of variation.

It is thus difficult to understand how even a single variation can be established by the unaided operation of sexual reproduction and natural selection, but the difficulty is greatly increased when we take into account the phenomena of parallelism and convergence. We have seen that the selenodont type of molar tooth has been independently acquired in at least three lines, and probably in many more. The molariform premolars which occur in so many perissodactyls, in some artiodactyls, and in other groups, though copying more or less exactly the pattern of the molars, are composed of parts which are not homologous with those occupying similar positions in the molar crowns. These changes can be followed step by step and accounted for, if we admit the action of mechanical influences, but are very puzzling on the hypothesis of all round variation. The spout-shaped odontoid process of the axis occurs in the camels, the true ruminants, the horses, and other groups, and it has been shown that this structure is not due to inheritance from a common ancestor, but has been separately acquired. Still more striking is the case cited by Kowalevsky (No. 26), of the sudden and simultaneous appearance (using these terms in their geological sense) in so many different groups of the prismatic or rootless molar, with very complex enamel foldings, and the valleys filled with cement. Kowalevsky believes that the occasion of this remarkable revolution, as it may be fairly called, was the great extension of the grassy plains, and the consequent change on the part of most herbivorous animals from a diet of soft plants and leaves, to the siliceous grasses. Now what is the probability that such a series of changes in horses, rhinoceroses, pigs, ruminants, elephants, and other families, should be

due primarily to the mingling of different hereditary tendencies, especially when it is remembered that none of the ancestors of these groups possessed any such teeth? Or can it be reasonably contended that such parallel variations are due to the direct action of the climatic or other environment upon the germ-plasm? The tendency to the formation of prismatic molars appears even in the early Tertiary times, as is seen in *Paloplotherium* and *Hypisodus*, but these were premature attempts, and led to nothing. Cope has shown how clearly the skeletal peculiarities of the feet of the Tylopoda may be deduced from the mechanical effects of the cushion or pad upon which the foot rests, and I may add that the steps of the enlargement of this pad may be inferred, in the extinct forms, from the successive changes in the phalanges. The similarities between the elephants, on the one hand, and *Uintatherium*, on the other, are just those which must accompany greatly increased height and bulk, though the latter is the more important factor.

Furthermore, the facts of pathology and surgery bring clearly before us the way in which the skeleton is moulded by the pressures and strains to which it is subjected. The tendinal sulci are formed by the pressure of the tendons, and if these tendons are dislocated, the old grooves are gradually filled up and new ones formed. "After dislocations the old articular cavities will be filled up and disappear, while at the new point where the head of the bone is actually placed, a fresh articulation is formed, to which nothing will be wanting in the course of a few months, neither articular cartilages, synovial fluid, nor the ligaments which retain the bone in place" (Marey, No. 36, pp. 88, 89). The arrangement of the trabeculæ in the interior of the bones is in the direction of the line of the greatest pressure and strain, giving great strength with a minimum of material. When, by a fracture and reunion, the relation of the bone to the line of strain is changed, the direction of the trabeculæ will be correspondingly altered. The papers of Arbuthnot Lane (Nos. 28 and 30) give an admirable account of the way in which long-continued routine labor will modify the shapes and articulations of the bones. It would, however, be a mistake to suppose that the bone-structure is entirely due to influences exerted in the lifetime of the individual, for the facts of development show that these structures appear in the fœtus before such influences are exercised.

We have seen that the proximal end of the humerus is very similar in the White River representatives of the horses and camels (*Mesohippus* and *Pæbrotherium*), having the bicipital groove single, narrow, and placed at the antero-internal angle of the head, while the external tuberosity is very large, and extends across nearly the entire anterior face of the bone. In the modern forms the bicipital groove is double, being divided by the large bicipital tubercle, and the external tuberosity is reduced to the size of the internal one. If all of these changes, which are carried out in such exact accord with the mechanical exigencies of each case, are not somatogenic, how can they be accounted for? What chance is there of such occurrences repeatedly taking place in widely separated groups of animals as the result of sexual reproduction, or of changes in the germ-plasm which stand in no other causal connection with the mechanical needs of the body, than that those variations which happen to be favorable are preserved? The improbability of such an explanation is still further increased by the fact that the numerous non-mechanical variations, which on this theory ought to occur, are not to be found in the fossil series except very rarely, and then as the manifest results of disease or accident. Why should there be such a profound difference between the method in which useful changes are brought about in the individual and those which modify the species? and how can we explain the mysterious pre-established harmony between the two classes of phenomena? It seems very wonderful that an "ever-vigilant natural selection," which introduced sexuality for the very purpose of producing and combining variations, should have failed to seize and make use of somatogenic changes. This class of phenomena is by no means confined to the vertebrate skeleton. Dall has shown how the characters of the hinge and shell of the bivalve mollusks have been evolved in accordance with mechanical principles (No. 12, p. 445). He has also shown "how the initiation and development of the columellar plaits in *Voluta*, *Mitra*, and other Gasteropods, is the necessary mechanical result of certain comparatively simple physical conditions; and that the variations and peculiarities connected with those plaits perfectly harmonize with the results which follow with inorganic material subjected to analogous stresses" (No. 13, p. 9). Neumayr, in describing the transition

of *Paludina Neumayri* into *P. Hærnesi*, says: "Wenn man ein Thonmodell von *Pal. Neumayri* hätte und dasselbe auf die einfachste und kürzeste Weise in *Pal. Hærnesi* umformen wollte, man könnte es kaum anders machen als die Natur vorgegangen ist" (No. 40, p. 61). Jackson has reached very similar results in the same department of investigation (No. 24).

It must not be inferred from what has been said above, that there is no individual variation among fossil mammals; on the contrary, there is a great deal of such variation, so that it is often a matter of extreme difficulty to distinguish the species even of the same horizon from one another, and the larger the number of specimens compared, the greater does the difficulty become. Nevertheless, these variations are to a great extent those which dynamical necessities demand, besides others for which, as yet, no explanation can be given. Indeed, there is some reason to question whether individual variations, in the ordinary sense of that term, form in all cases the material with which natural selection has to operate. Neumayr has called especial attention to the distinction between "mutations" and variations, using the former phrase, which was adopted from Von Waagen, to designate the successive members of a series in geological time, while the latter is employed for contemporaneous alterations in the same horizon. "Noch andere Eigenthümlichkeiten stellen sich ein, welche die Mutationen als etwas von den Varietäten Verschiedenes bezeichnen; so in erster Linie, dass in der Regel eine bestimmte Mutationsrichtung in jeder Reihe vorhanden ist, indem durch eine längere Aufeinanderfolge von Schichten hindurch immer dieselben Charaktere in demselben Sinne von einander abweichen. Wenn man die beiden hier abgebildeten Reihen genauer betrachtet, so sieht man, dass dieselben von einem Gliede zum anderen ohne wesentliche Schwankungen und Abwege in geradester Linie sich der Endform nähern. . . . Ein anderer bisweilen beobachteter Fall von grosser Wichtigkeit ist der, dass die verschiedenen Glieder einer Reihe Variationen derselben Art zeigen; während also ein Theil die Merkmale gleichmässig nach einer Richtung im Laufe der Zeit mutirt, zeigen andere Charaktere regellose Abänderungen und jede Mutation entwickelt denselben Varietätenkreis" (No. 40, pp. 60-61). Similar facts are clearly marked in several of the mammalian series, as in the various

species of the successive genera *Palæosyops*, *Diplacodon*, and *Titanotherium*, of *Oreodon* and *Eporeodon*, and many others. On the other hand, it is by no means always the case that those genera which exhibit the greatest amount of variability at any given time, are those which in the long run have undergone the most extensive "mutation"; on the contrary, such genera frequently exist for very long periods substantially unchanged, but showing great variability at every stage in their history.

These facts at least suggest the possibility that individual variations are not incipient species, but that the causes of transformation lie deeper, and act with more or less uniformity upon large numbers of individuals. It may, perhaps, be the outcome of future investigations, that while variations are generally due to the union of changing hereditary tendencies, mutations are the effect of dynamical agencies operating long in a uniform way, and the results controlled by natural selection. While this *may* be true, a great many facts must be gathered in its support, before it can be regarded as more than a suggestion.

In particular, it is difficult to see how a new character can arise from the crossing of two forms, neither of which possess that character. Some facts are, it is true, recorded, which seem to show that new characters may thus arise, as for example in certain hybrid plants which exhibit features present in neither of the parent species. But, for the present, such facts must be received with great reserve, for the analogy of domesticated breeds shows that crossing favors reversion, and in every case the supposed new characters may be atavistic. At least, no conclusion can be safely drawn from such facts, until it is shown that reversion is excluded. To avoid this difficulty as to the production of new characters, Weismann assumes that all variations are quantitative and not qualitative. This is equivalent to saying that there are no qualitative differences in the organic world. No summation of quantitative differences can bring about chemical changes; for example, the first appearance of muscle, cartilage, and the various tissues cannot thus be accounted for, and if the principle be abandoned for these cases, its importance is at once destroyed. The only escape from this difficulty is the suggestion of Lloyd Morgan, already quoted, that impregnation represents not a mere commingling, but a combination analogous to chemical union; but for this there is no evidence, and Morgan himself is

not inclined to accept it. Many authorities attribute just the opposite influence to sexual reproduction to that which Weismann postulates. Strasburger regards it as the means of removing injurious modifications, and of keeping the species constant to its type, and a very similar position is taken by Hatschek and others. But in view of the many observations collected by Darwin upon the subject of cross and self-fertilization, and of the physiological importance of crossing to the individual, both Weismann's position, on the one hand, and Strasburger's, on the other, appear to be but a very partial and incomplete view of the matter. At all events, we are entitled to demand much fuller and more satisfactory evidence before attributing to sexual reproduction such a pre-eminent place as a factor in evolution.

In the course of development the reduction and loss of structures plays quite as important a part as differentiation and the acquisition of new organs. No one can study any large group of vertebrates without being struck by the way in which the two processes accompany and balance each other. In any advancing group of organisms the course of differentiation does not affect all organs alike; some are stationary, others are progressing towards a higher state of efficiency, and others again are retrograding and even disappearing. It is this fact which makes the natural arrangement of any group of organisms such a very difficult and puzzling problem. It is obvious, therefore, that any system of evolutionary philosophy must include an explanation of the way in which organs are reduced and suppressed, as well as the mode in which they are acquired. The current view of the matter is that the loss of organs is due to atrophy from disuse, but this view is of necessity entirely rejected by Weismann, who has examined the problem with much care in his very interesting essay, "Ueber den Rückschritt in der Natur" (No. 59). According to him the efficient cause of reduction is cessation of selection or panmixia, by which useless parts, being no longer selected, tend gradually to disappear, and a free intercrossing, as regards those particular structures, is no longer prevented. This view, however, presupposes that selection is the only power which originates and maintains structures,—a thesis which is very far from being proved, if it can even be regarded as probable. Indeed, the

whole theory of panmixia is highly problematical, supported by very few observed facts, and the very cases which Weismann cites show how unsatisfactory is his explanation. Let us examine a few of these cases. "Ein Beispiel ganz anderer Art geben uns diejenigen Thiere an die Hand, welche einen Theil ihres Körpers in Gehäusen verbergen. So stecken die Einsiedlerkrebse ihren Hinterleib in leere Schneckenschalen, die Larven der im Wasser lebenden Köcherfliegen verfertigen sich Gehäuse in denen sie ihren langgestreckten vielgliedrigen Hinterleib verbergen und dasselbe thun die Raupen gewisser kleiner Schmetterlinge aus der Gruppe der Spinner. Bei allen diesen Thieren finden wir nun, dass die Haut der durch Gehäuse geschützten Körpertheile weich ist und weisslich, d. h. ohne besonderen Farben, während die aus der Schale hervorragenden Theile den gewöhnlichen harten Hautpanzer der Gliederthiere und verschiedentliche, meist lebhaftere Farben besitzen. Nun kann man ja in einem gewissen und etwas uneigentlichen Sinn sagen, der Hautpanzer der Krebse und Insekten habe die 'Funktion' die inneren weichen Theile des Thiers vor äusseren Verletzungen zu schützen, aber im wahren Sinn ist das eben keine Funktion, weil keine Thätigkeit damit verbunden ist; die Leistung des Panzers beruht einfach auf seiner gänzlich passiven Anwesenheit. Ob das Thier durch ihn gegen Stiche oder Bisse, oder ob solche Bedrohungen gar nicht bis an ihn gelangen, das ist für den Panzer selbst und sein Gedeihen völlig gleichgültig; er verliert und gewinnt dabei nichts und am allerwenigsten hängt sein Wohlbefinden davon ab, möglichst häufig von Stichen oder Bissen getroffen zu werden. Er kann unmöglich dadurch direkt zur Rückbildung veranlasst werden, dass er durch das Gehäuse solchen Angriffen ganz entzogen ist. Wenn also der Panzer in allen den drei angeführten Fällen, sich genau so weit zurückbildet, als der Körper von dem schützenden Gehäuse bedeckt ist, so kann dies wiederum nur dadurch erklärt werden, dass für die von dem Gehäuse bedeckten Körperstellen der Panzer überflüssig und bedeutungslos wurde und dass Naturzüchtung sich deshalb nicht mehr mit seiner Erhaltung befassen konnte" (No. 59, p. 19).

The inadequacy of this account of the function of the armor is too obvious to need comment; one might as well say that the bones of the vertebrate skeleton perform their functions

merely by their passive presence, and therefore could not be affected by disuse, which we know very well is not the case. Probably no one imagines that the armor of crustaceans and insects owes its origin to "Stiche und Bisse," or that its welfare in any way depends upon them, but muscular activity, contact with the water, light, etc., are essential. On the theory of panmixia what is the probability that the reduction should reach *exactly* as far as the tube or shell in which the animal lives? It is a matter of no consequence whether the armor extends a little way into the tube or not; why, then, such superfluous accuracy? Admitting that this might happen in the case of one species, it becomes more and more improbable with every case observed. On the other hand, if the presence of the tube or shell does have a direct effect, this exact correspondence is just what might be expected. Indeed, Weismann's explanation is contradicted by a dictum which he lays down in another part of the same essay, though it should be added that this proposition refers primarily to positive differentiation. "Die Organismenwelt beweist uns, dass dem so ist, denn bis ins Einzelste hinein, sehen wir jede lebende Art sich zweckmässig gestalten, als es unumgänglich nothwendig ist, um sie existenzfähig zu machen, *nicht um ein Minimum mehr*" (p. 30).

The case of the neuter insects does, however, offer a formidable difficulty to the doctrine of the inherited effects of disuse, as, indeed, it does to any explanation. It would lead too far from the main subject of this paper to give to this problem the full and extended discussion which it requires. I can, therefore, only refer the reader to Eimer's examination of this question (No. 15, p. 286 ff.), which it seems to me is quite as probable as Weismann's, to say the least; especially if one will carefully follow out the steps of the probable process by which, for example, the worker ants have lost their wings. But even if we admit Weismann's position in regard to the neuter insects, it would merely be saying that disuse is not the only factor in the suppression of organs, an assumption which few would be bold enough to make. At all events, Darwin, who first insisted upon the difficulty presented by these insects, did not regard it as militating in any way against the assumption of the effects of disuse in other cases.

The positive evidence in favor of the theory of panmixia is

extremely scanty, and indeed what direct evidence there is, tells against it. Thus Galton's researches have brought out the law of "regression to mediocrity," by virtue of which the succeeding generations of a population resemble each other. "In each generation, individuals are found to be tall and short, heavy and light, strong and weak, dark and pale; and the proportions of those who present these several characteristics in their various degrees, tend to be constant" (No. 20, p. 116). Galton's results, which are too long to quote and cannot very well be abridged, tell strongly against attributing any importance to panmixia as a factor in transformation. Lloyd Morgan, following the same line of reasoning, points out that panmixia "can only affect a reduction from the 'survival-mean' to the 'birth-mean'" (p. 191). "Unless, therefore, some cause be shown why the negative variations should be prepotent over the positive variations, we must, I think, allow that unaided panmixia cannot affect any great amount of reduction" (p. 193). Lankester does not admit that panmixia can explain the reduction of parts, unless assisted by the principle of economy of growth (No. 31, p. 559). But the importance of this principle may be easily overrated. In the admirably thorough investigations of Tornier (No. 54) upon the calcaneo-astragalar joint, it is shown how closely the development and reduction of facets follows the manner in which the foot is used, and the consequent mechanical necessities. Now, it is incredible that economy of growth should demand the reduction of these minute facets, when such rudiments as the splint-bones of the horse or the pelvis of the whale are allowed to persist in the organism. Nor is it easy to see how the principle of economy can apply to domesticated animals, and still more to internal parasites which have such a superabundance of nutriment, and yet the latter are precisely the forms in which reduction of parts has proceeded to the greatest extremes. Among domesticated animals and plants we find that those parts which are not subject to selection are (aside from the effects of correlation and the direct action of the environment, such as too much or too little of certain foods, water, etc.) remarkably constant, which by Weismann's theory they should not be.

Another class of facts, which are very difficult to explain from the standpoint of panmixia, is furnished by certain larvæ. In another paper (No. 50) I have examined the development of

the higher sense organs of *Petromyzon*, which are subject to a remarkable degree of retardation. Thus the eye, throughout the long larval life of the creature, is extremely small and deeply buried beneath opaque tissues of the head. Even at its first appearance the optic vesicles are extremely minute, and the lens is tiny. The retina remains in a rudimentary condition throughout larval life, and only when the larva is metamorphosed into the sexual animal does the eye reach its normal size and development. Similarly, the olfactory organ during the larval period is a simple epithelial sac, which at the time of metamorphosis becomes an exceedingly complicated structure. The ear alone attains in the larva a degree of development comparable to what it has in the adult. This retarded condition of the higher sense organs has an obvious connection with the habits of life; for the larva lies buried in the mud and sand of rivers, while the adult lives in clear and swift waters. The effects of the larval habits are shown even in the embryo before hatching; for the sense organs, and especially the eye, are proportionately much smaller than they are in other vertebrates, even in the earlier stages. These facts are easily enough explained, if we admit the direct action of the environment, at first arising in the larva, and then gradually transferred to the embryonic stages, just in the way in which Hyatt and Würtenberger have shown that new characters in the shells of ammonites arise first in the fully adult shell, and then are gradually transferred to earlier and earlier stages. But to refer this retardation in the development of the sense organs of *Petromyzon*, to what in this connection may fairly be called fortuitous changes in the germ-plasm, is merely to conceal our ignorance under the guise of an explanation.

When we turn to the series of fossils, and follow out the history of disappearing organs, we find little to support the theory of panmixia. The reduction is steady and sure, if slow, exhibiting of course a certain degree of individual variation, but not the fluctuations which we should naturally expect to find, were panmixia alone the cause of the reduction. As a matter of fact, when examining an extensive series of fossils reaching through many horizons, it is difficult to escape the suspicion that individual variations are not the material with which natural selection works, so steadily does the series advance toward what seems almost like a predetermined goal. This slowness and steadiness

of reduction, together with other facts already mentioned, render the question as to whether mutilations are or are not transmissible, a matter of relatively small importance; for only those direct effects of the environment which similarly modify many individuals and are long continued can be of real significance in the work of transformation. "On the whole, even taking into consideration the effects of panmixia, of reversed selection, and the principle of economy, the reduction of organs is difficult to explain, unless we call into play 'disuse' as a co-operating factor" (Lloyd Morgan, No. 39, p. 197).

Weismann's views upon the factors of evolution are, to a great extent, deductions from his theory of heredity. If established, they will render impossible any real insight into the mechanism of development in any given case, and we shall always leave unexplained the immense series of cases in which development follows just such a course, and no other, as it would do if somatogenic influences really shaped the result; the path being followed out with neither fluctuation nor important deviation, as is apparent whenever extensive phylogenetic series can be thoroughly studied. Of course, it is no argument against the truth of these theories that such should be their outcome, but it should be clearly recognized that progress does not consist in substituting a phrase or a formula for an explanation. This has been well expressed by Claus (No. 4, pp. 27, 28), who says:—

"Wollten wir auf die Verwerthung derselben [d. h. der functionellen Anpassungen] verzichten, so würden wir mit Nägeli und Weismann auf die geheimnisvollen Vorgänge im Innern des Idioplasma und der Keimzelle beschränkt sein, die wir uns zwar als moleculär-mechanische Veränderungen theoretisch vorstellen können, deren factischer Verlauf aber unbekannt und überdies seiner wahren Ursache nach im völligen Dunkel bleibt. Das ist das Gemeinsame an den Theorien Nägeli's und Weismann's und wird nicht etwa, wie letzterer meint, durch den Umstand widerlegt, dass er zur Begründung seiner Lehre eine einfache Thatsache verwerthe. Wenn es auch eine Thatsache ist, dass bei der Befruchtung die Vererbungstendenzen, welche in der Eizelle schlummern, sich mischen, und daraus ein neuer Organismus mit einem bisher noch nicht dagewesenen Gemenge individueller erblichen Charaktere hervorgeht, so ist doch damit das Geheimnissvolle des bezüglichen Vorganges nicht minder

behaben als das Dunkel, welches in Nägeli's Vervollkommnungstendenz liegt, für deren Bestehen auch thatsächliche Verhältnisse der im Sinne der Vervollkommnung fortschreitenden Entwicklung geltend gemacht werden. . . . Denn was ist diese in das Urkeimplasma hineingelegte Entwicklungsordnung Anderes als eine ihrem Wesen nach geheimnisvolle phyletische Kraft, über deren bewirkende Ursache wir ebensowenig durch Nägeli's zweckmässig eingerichtete Vorgänge der Molecularmechanik, wie durch Weismann's Vererbungs- und Entwicklungstendenzen auch nur eine entfernte Auskunft erhalten. Auch in den von Letzterem verwertheten Variationen wird man doch nur Bedingung oder Anlass zu der besonderen Structurgestaltung des Keimplasmas und diesen entsprechenden Bewegungsvorgängen der Molecülgruppen, nicht aber die bewirkende Ursache der Erscheinung selbst erkennen. . . . Weismann täuscht sich daher selbst wenn er Nägeli's Annahme eines völlig unbekanntes Principis gegenüber die Umwandlungen der Organismen lediglich aus den *bekanntes* Kräften und Erscheinungen ableiten zu können glaubt. In Wahrheit steht derselbe mit Nägeli auf wesentlich gleichem Boden, auf der Supposition eines inneren, treibenden Entwicklungsprincipis, wenn er auch die Annahme desselben nicht zugesteht und ohne dessen Hilfe auskommen zu können vermeint."

The great difficulty in the way of the "dynamic theory" of evolution (to use Dall's phrase) is the problem of heredity, of understanding how changes in the periphery can modify the germ-plasm in such a way as to reproduce the new characters in the offspring. But, admitting this difficulty to the fullest extent, it would certainly seem that the proper method of treatment is first to determine what are the facts of heredity, and then attempt an explanation of them, not to formulate an *a priori* view, and then ascertain whether the facts can be made to support it. I am not concerned to elaborate here a theory of heredity, being strongly of the opinion that, in the present state of knowledge, nothing better than provisional working-hypotheses can be devised, which, of course, may serve a most useful and valuable purpose, but which have little chance of final establishment.

To sum up the results of our examination of certain series of fossil mammals, one sees clearly that transformation, whether

in the way of the addition of new parts or the reduction of those already present, acts just *as if* the direct action of the environment and the habits of the animal were the efficient cause of the change, and any explanation which excludes the direct action of such agencies is confronted by the difficulty of an immense number of the most striking coincidences. We must all heartily agree with Weismann in saying that "we require, not a mere formal explanation of the origin of species of the most comfortable nature, but the real and rightful explanation." Whether his theories, profound and brilliant as they are, are to give us this real and rightful explanation, the future must decide.

GEOLOGICAL MUSEUM,  
PRINCETON, N.J., July 20, 1891.

P.S. — The preceding paper was all in type before I received Lloyd Morgan's very valuable and suggestive article on "The Nature and Origin of Variations" (Proceedings of the Bristol Naturalists' Society, Vol. VI., Part III.). I regret this the more because Professor Morgan seems to have somewhat misapprehended the character of the evidence to be derived from palæontology in favor of the dynamical view of evolution. "Those American zoölogists who have studied the evolution of mammalian teeth contend that the occurrence of new points and cusps is not indeterminate, but determinate. New elements of tooth-structure appear in definite positions. There is nothing to indicate selection from among indefinite variations. Other evidence of like implication is adduced by American evolutionists; but this of tooth-structure is put forward as the strongest case. I am inclined to think that the facts of palæontology, so far as they go, point in this direction. But I question whether they can be regarded as conclusive. In criticising the position, stress may be laid on the imperfection of the geological record; and it may be urged that the number of individuals in our palæontological collections is not sufficient to constitute a truly representative sample. Furthermore, on the hypothesis of selection, the individuals possessed of teeth with points and cusps in other than these adaptive positions must have been weeded out in the early stages of life. In view of these objections the evidence

cannot be said to be convincing, though in my opinion it affords some presumption in favor of determinate variation" (p. 5).

"We have seen that the American school of biologists contend that variations, for example in tooth-structure, are determinate and not indeterminate. They also contend that these variations are largely due to the inherited effects of use and disuse. They tell us that in a large percentage of cases the new elements of tooth-structure appear in regions of ancestral wear and abrasion. Granting the determinate variations, we may perhaps inquire whether the abrasion may not be due to the presence of incipient points rather than the development of points to increased abrasion. It is admitted that the new points do not always occur where there has been previous abrasion. Granting the determinate variations, therefore, it does not appear to be satisfactorily proved that they are due to the effects of inherited use and disuse. Seeing the nature of tooth-growth and development, one needs very cogent evidence of the production of new points or cusps at regions of marked ancestral abrasion. The development of certain elements of vertebrate limb-structure and concomitant dwindling of other elements may be adduced as more readily comprehensible effects of inherited use and disuse. But here we have not the same evidence of the determinate nature of the variations, and the theory of selection from among favorable indeterminate variations is not to the same extent, on the showing of the American school themselves, excluded. It seems, then, that where the evidence for determinate variations is strong, the theory of use-inheritance is difficult of acceptance, and where use-inheritance is more readily comprehensible there is less evidence that the variations are determinate" (pp. 14, 15).

For my own part, I wish to disclaim the idea of belonging to any "school" whatever. Those American observers who have especially devoted themselves to the morphology of extinct forms have independently reached certain conclusions, in which they agree; as to other results, they are by no means so concordant. It seems to me that the evidence points very strongly in certain directions, but new evidence may at any time altogether destroy the force of the old. So far as I can see, the theory of determinate variations and of "use-inheritance" is not antagonistic, but supplementary to natural selection, the

latter theory attempting no explanation of the *causes* of variation. Nor is it for a moment pretended that use and disuse are the sole or even the chief factors in variation. On the contrary, we know that many other and even more important factors enter into the process.

Turning now to Professor Morgan's criticisms of the palæontological evidence, we may say that the objection drawn from the imperfection of the geological record and from the small number of individuals contained in the museums, can be allowed little weight. So far as several of the mammalian phyla are concerned, the number of missing links must be very small, the wonderful series of American fresh-water Tertiaries being in this respect quite unrivalled in the known world. Of the better known species, the collections already contain hundreds and sometimes thousands of individuals available for study. If results obtained from such material point in one direction, it is surely most illogical to assume that specimens yet to be discovered will probably lead to opposite conclusions. The probabilities are all the other way. Professor Morgan seems also to suppose that individuals "in the early stages of life" are uncommon as fossils; but this is very far from being the case; they are abundantly represented in the collections and show no more tendency to indeterminate variation than do the adults. But even were the young stages unknown, before their absence could be allowed weight as an objection, it would be necessary to show that such very slight changes were of "elimination value."

I am unable to see why the evidence afforded by foot-structure is any less cogent in support of determinate variations than that derived from the teeth, except in so far that not nearly so many completely preserved feet are found. But where they do occur in numbers, the result is the same. The carpus and tarsus of the equine series from *Hyracotherium* to *Equus* form as striking an example of this as could be desired. The non-mechanical variations do not occur. The difficulty of comprehending how teeth can be modified by use, must be freely admitted. But it should be remembered that a completely formed tooth is not by any means a dead, inorganic mass. Its health depends upon use, and I have seen fossils which clearly demonstrate the ill-effects of disuse of teeth in the individual.

Further, the principle already quoted from Arbuthnot Lane with regard to the skeleton, will doubtless apply to the teeth; "that a force which produces no obvious change in the skeleton of the antecedents, but only a tendency to change, can, acting as a developmental factor, cause the apparently spontaneous development of that change in the offspring." The admission, quoted by Professor Morgan, that "the new points do not always occur where there has been previous abrasion," is due to the fact that freshly formed and unworn teeth were examined in that regard, overlooking later stages of wear. In all cases known to me, the new points appear in places where, at some stage, there is special abrasion. Of course, it would be folly to pretend that the mechanics of dental evolution have been completely worked out or that no difficulties exist. On the contrary, only a beginning has been made, but as a *working hypothesis*, the assumption that the effects of use and disuse can be inherited, and that mechanical factors do have a part in the result, has already rendered such good service, that we feel justified in retaining it.

That the effects of use and disuse are not the only factors in producing variations in tooth-structure, we have clear evidence. Thus Nathusius has shown that in the swine defective nourishment may have a remarkable effect in modifying the character of the teeth. "Die Zähne des Versuchsthiers haben einen ausserordentlich dünnen Schmelzüberzug, so dünn, dass derselbe auf den Kauflächen von mol. 1 bereits vollständig, von mol. 2 beinah ganz abgenutzt ist, während bei dem gut genährten in Vergleich gezogenen Thier bei mol. 1 nur eine schwache Abnutzung stattgefunden hat und bei mol. 2 sogar nur die Haupthügel des vorderen Jochs oben so weit ihre Spitzen verloren haben, dass man in dem massiven Schmelzring einen kleinen Knochenkern erkennt.

"Dieser dünne Schmelzüberzug ist sehr wenig in Falten gelegt, es ist dies besonders auffallend an dem noch in der Höhle befindlichen mol. 3 dessen Haupthöcker beinahe ganz glatt sind. Alle Nebenhöcker und Warzen sind schwach entwickelt, an mol. 1 sogar kaum eine Spur davon vorhanden.

"So hat denn dieser Versuch in frappanter Art ergeben, in welchem Grade nicht nur die Stärke des Schmelzüberzuges, sondern auch das Zerfallen der Zahnkronen in zahlreiche und

crenellirte Nebenhöcker und Warzen abhängig ist von der Ernährung des Thieres" (Schweineschädel, pp. 102, 103).

I do not wish to be understood as in any way deprecating the extremely candid, fair, and open-minded criticism to which Professor Morgan has subjected the evidence drawn from the study of American fossils; but I cannot consent to be bound by the admissions of members of the "American school." While I freely grant that the evidence presented in the foregoing pages in favor of mechanical factors in evolution is not convincing or conclusive, I think it may fairly claim to afford something more than "a presumption in favor" of such factors.

PRINCETON, October 12, 1891.

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## EXPLANATION OF THE PLATES.

(Where not otherwise indicated, all the figures are of natural size.)

## PLATE XXII.

FIG. 1. *Mesohippus Bairdi*. Skull, from the side.  $\times \frac{3}{4}$ . This skull is drawn from a specimen in the Princeton Museum, with details added from specimens in the Academy of Natural Sciences, Philadelphia. *C.* canines; *Ty.* tympanic bulla; *par.* paroccipital process; *Ms.* mastoid portion of the periotic.

FIG. 2. *Mesohippus Bairdi*. Skull, base view of a somewhat larger specimen.  $\times \frac{3}{4}$ . *i.f.* incisive foramen; *c.* canine alveolus; *m. 1.* first molar; *ac.* alisphenoid canal; *Ty.* tympanic bulla; *par.* paroccipital process; *c.f.* condylar foramen.

FIG. 3. *Mesohippus Bairdi*. Atlas, dorsal view. Cope collection. *v.c.* vertebrarterial canal; *a.n.* atlanteal notch.

FIG. 4. *Equus caballus*. Atlas, ventral view.  $\times \frac{1}{3}$ . After de Blainville.

FIG. 5. *Mesohippus Bairdi*. Axis, from the side.

FIG. 6. " " Axis, postzygapophyses seen from above.

FIG. 7. " " The same, another specimen.

FIG. 8. " " Axis, seen from the front.

FIG. 9. " " The same, another specimen.

FIG. 10. " " Fifth cervical vertebra, from the side.

FIG. 11. " " Sixth cervical vertebra, from the front.

FIG. 12. " " The same, from the side.

FIG. 13. " " Second dorsal vertebra, from the side.

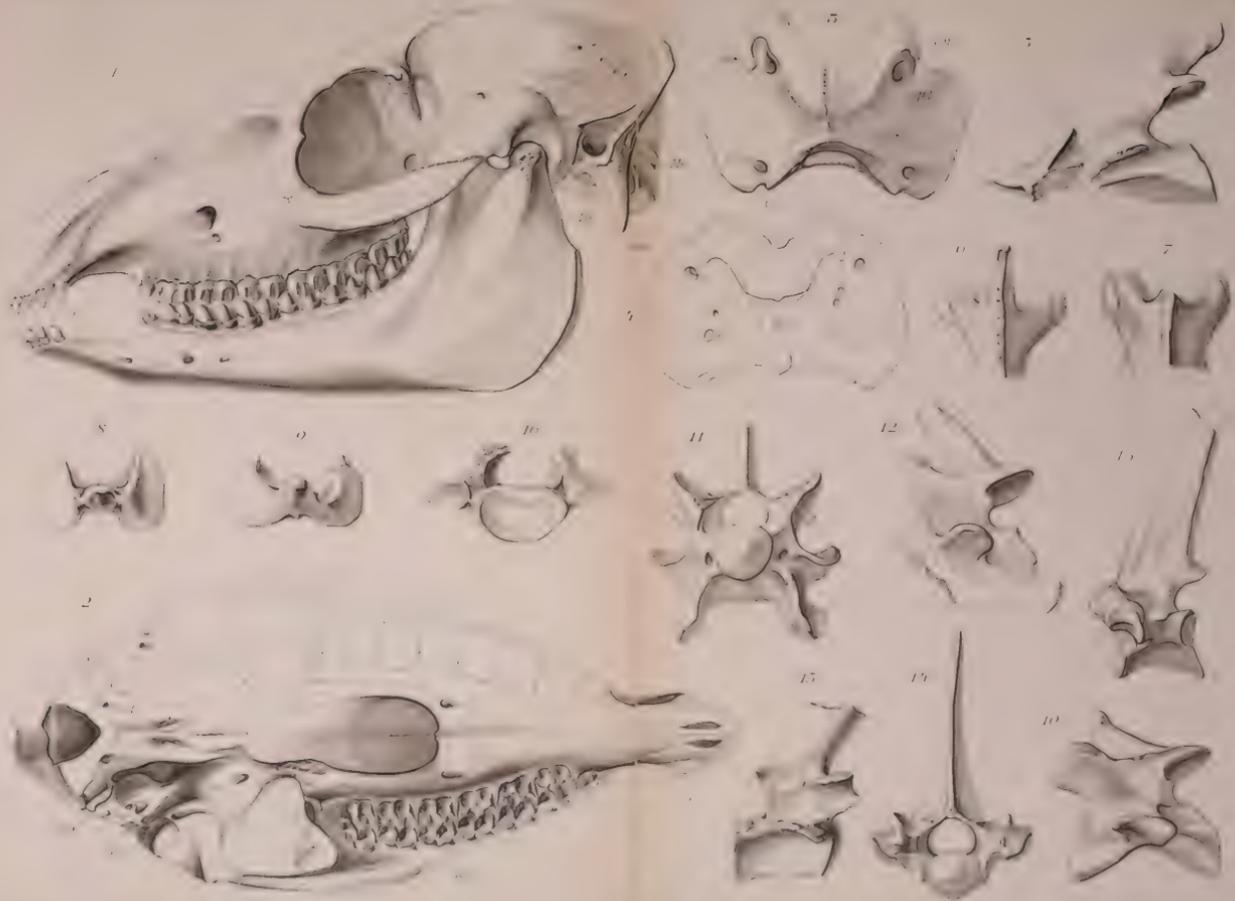
FIG. 14. " " The same, from the front.

FIG. 15. " " Last dorsal vertebra, from the side. Cope collection.

FIG. 16. " " Last lumbar vertebra, from behind.











## PLATE XXIII.

FIG. 17. *Mesohippus Bairdi*. Skull, longitudinal section. *o. c.* occipital condyle; *B. S.* basi-sphenoid (crushed out of place); *Cb. F.* cerebellar fossa; *C. F.* cerebral fossa; *F. S.* frontal sinus.

FIG. 18. *Equus caballus*. Skull, longitudinal section.  $\times \frac{1}{4}$ . After de Blainville.

FIG. 19. *Mesohippus Bairdi*. Left humerus, from the front.  $\times \frac{2}{3}$ . *e. t.* external tuberosity; *i. t.* internal tuberosity; *bc. g.* bicipital groove; *d. r.* deltoid ridge.

FIG. 20. The same, from the outer side.  $\times \frac{2}{3}$ .

FIG. 21. The same, proximal end.

FIG. 22. The same, distal end.

FIG. 23. *Mesohippus Bairdi*. Left ulna and radius, from the outer side. *R.* radius; *U.* ulna.

FIG. 24. *Mesohippus Bairdi*. Radius, proximal end, from the front.

FIG. 25. " " Radius, distal end. *s'*, scaphoidal facet; *l'*, lunar facet.

FIG. 26. *Mesohippus Bairdi*. Right manus, from the front. *S.* scaphoid; *L.* lunar; *C.* cuneiform; *Tm.* trapezium; *M.* magnum; *U.* unciform.

FIG. 27. *Mesohippus Bairdi*. The same, from the outer side.

FIG. 28. " " The same, proximal view.

FIG. 29. *Equus caballus*. Carpus, from the front.  $\times \frac{1}{4}$ . After de Blainville.

FIG. 30. *Mesohippus Bairdi*. Metacarpals II., III., and IV., proximal ends.

FIG. 31. *Mesohippus Bairdi*. Right innominate bone, from the side.  $\times \frac{2}{3}$ . *t. i.* tuberosity of the ischium. (Cope collection.)

FIG. 32. *Mesohippus Bairdi*. Left tibia, from the front. *T.* tibia; *F.* fibula.  $\times \frac{2}{3}$ .

FIG. 33. *Mesohippus Bairdi*. The same, distal end.

FIG. 34. " " Left tarsus, from the front. *cf.* fibular facet of calcaneum; *Cb.* cuboid; *N.* navicular; *C.<sup>3</sup>* ecto-cuneiform; *C. 1 + 2*, coalesced meso- and ento-cuneiforms.

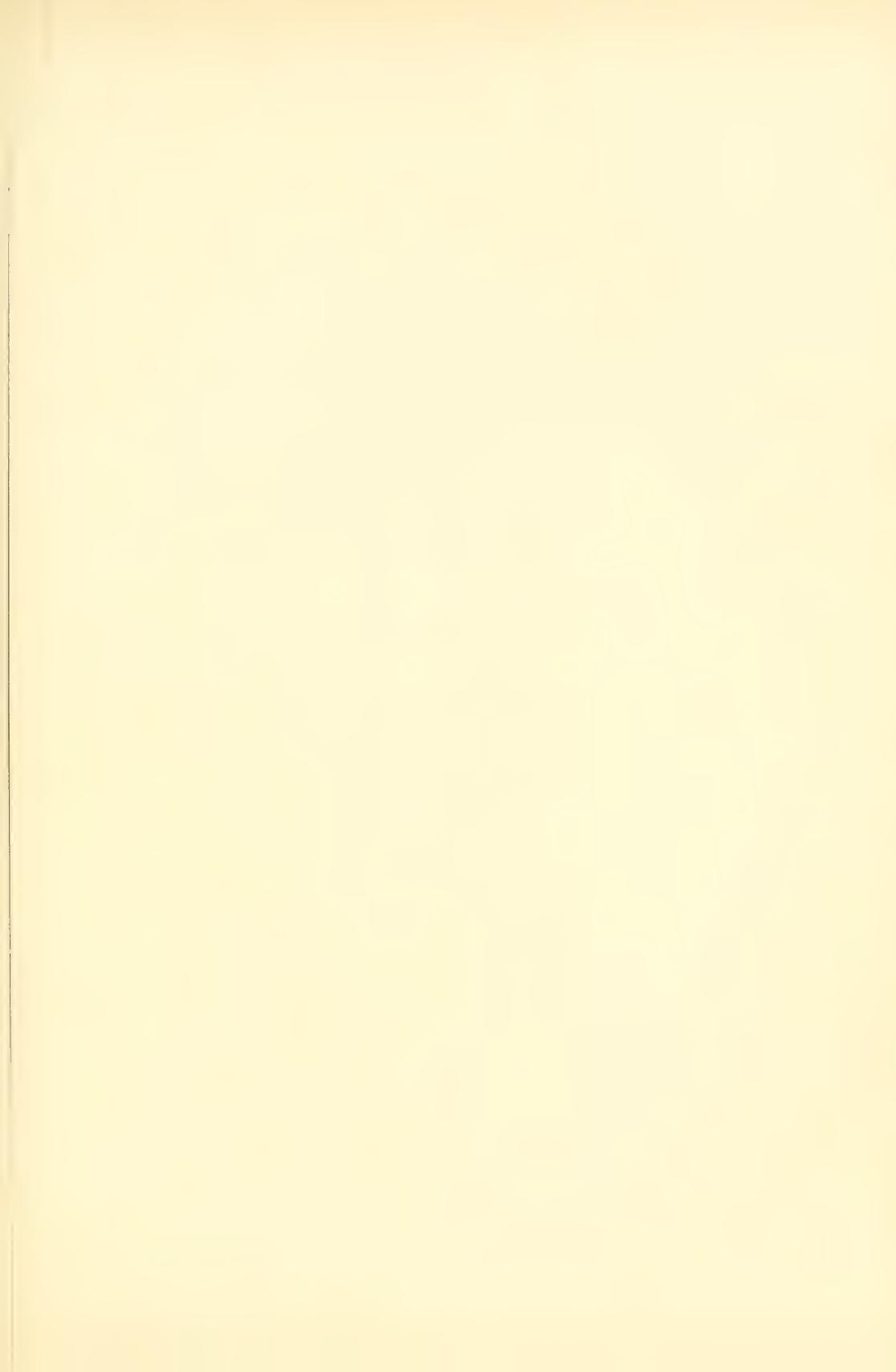
FIG. 35. *Equus caballus*. Right tarsus, from the front.  $\times \frac{1}{4}$ . After de Blainville.

FIG. 36. *Mesohippus Bairdi*. Left tarsus, distal end.

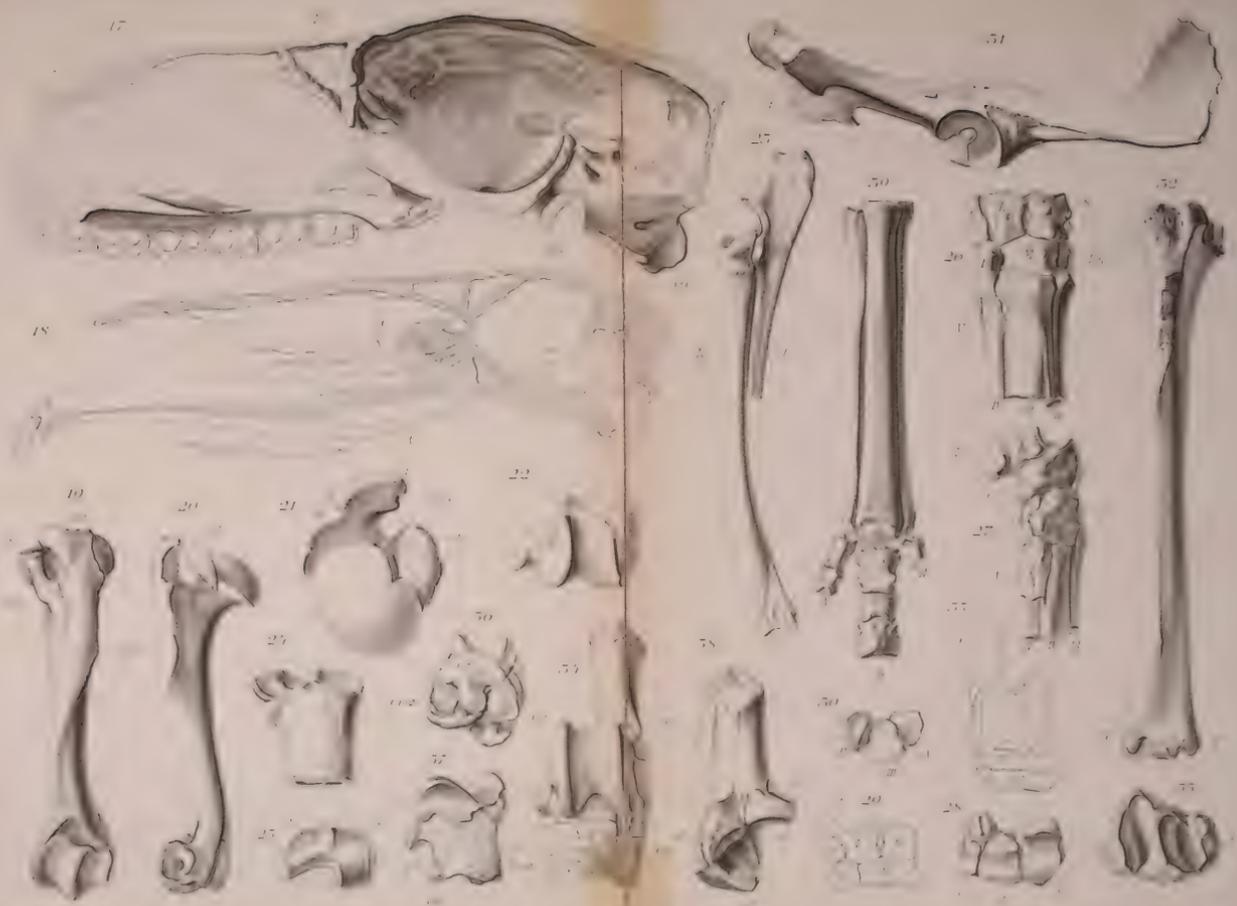
FIG. 37. " " Left astragalus, plantar side. *c'*, *c''*, *c'''*, facets for the calcaneum; *cb.* for the cuboid.

FIG. 38. *Mesohippus Bairdi*. Left calcaneum, from the medial side. *a'*, *a''*, *a'''*, facets for the astragalus; *cf.* for the fibula.

FIG. 39. *Mesohippus Bairdi*. Right metatarsus.  $\times \frac{2}{3}$ .









## THE GROWTH AND METAMORPHOSIS OF TORNARIA.

T. H. MORGAN.

BALANOGLOSSUS, and its larval form Tornaria, seems to occupy a more or less central point in the family tree of the Triploblastica. The adult worm is related to all appearances, on the one side, to the vertebrates; on the other, through such a form as Cephalodiscus, possibly to Rhabdopleura, Polyzoa, and Phronis. The larval Tornaria has characteristics which are supposed to indicate a relationship to the Echinoderms, or even, it has been suggested, to the Trochophore of Annelids. Few animals present so many possibilities to the morphologist.

The growth and metamorphosis of Tornaria have not been thoroughly studied by the modern methods of technique; and the following is an attempt to partially fill up this gap in our knowledge of the group.

The material was collected at Wood's Holl, Mass., while enjoying the opportunities of The Marine Laboratory. I desire to express my obligations to the director, Professor C. O. Whitman, and to the trustees, for the privilege of studying at the station.

During August (1890), Tornaria were at times very abundant. When the surface of the water was calm they were caught in the tow-net at flood tide, during both the day and night. Great difficulty was experienced in keeping the Tornaria for any length of time during the period of metamorphosis. Many developed abnormally; and the oldest one was kept only seventy hours after it had been put into the aquaria. The Tornaria belonged, undoubtedly, to the same species described by Alexander Agassiz in his important paper on Balanoglossus and Tornaria (1873). He referred this Tornaria to *Balanoglossus Kowalevski*, which is the common form of the New England coast. Bateson, in 1884, working on the young of *B. Kowalevski*, found in the Chesapeake Bay, showed clearly that it had a direct develop-

ment, without interpolation of the Tornaria. Recognizing the identity of the northern species of *B. Kowalevski* to the southern species of the Chesapeake, it became evident that the one had a free-swimming, Tornaria stage, and the other a direct development, or else a mistake had been made in assigning the northern Tornaria to *B. Kowalevski*. The latter, I believe, is the explanation, and for these reasons. The Tornaria came suddenly and in great numbers, *and were of all ages*. The numbers gradually diminished, then disappeared. At the time of occurrence there was a decided change in the nature of the tow-stuff, notably in the presence of many small hydro-medusæ of several species, of the larvæ of Polygordius, of young Ctenophors, and small crustacea in abundance. Many or all of these must have been brought in by currents from outside; and these, like the Tornaria, remained for a time, and then disappeared. Finally,—and this in itself seems conclusive,—the size of the mature eggs of *B. Kowalevski* of Wood's Holl correspond exactly in size to the egg of the southern species as given by Bateson. These are large and contain much yolk, while the youngest Tornaria which I caught in the tow-net were only about two-thirds as large as the eggs of *B. Kowalevski*. These facts, I believe, give us sufficient reason to reject the supposed relationship of the New England Tornaria to *B. Kowalevski*; so that, as yet, we do not know the locality from which the Tornaria came, unless, indeed, it prove to be identical with the Tornaria found by Bourne on the English coast, and which he says is identical with *Tornaria Krohnii* of the Mediterranean.

The greater part of the following work was done as holder of the Adam T. Bruce Fellowship, 1890-91, in the Morphological Laboratory of Professor W. K. Brooks.

#### STRUCTURE OF TORNARIA.

The youngest Tornaria collected are shown in Pl. XXIV., Figs. 1, 2, 3, and measured about  $\frac{1}{4}$  mm. in length. The larva is very transparent; and the large, thin-walled digestive tract is seen within the animal. This is already divided into its three compartments, as seen in the figures. The anterior of these is the œsophagus, and is a flat tube connecting the mouth with the next division, or so-called stomach. This is large, and fills up

much of the interior of the larva. The walls are thin, however, without any trace of yolk in them. The stomach is separated from the posterior (endodermic) portion of the digestive tract—"the intestine"—by a diaphragm-like partition. The partition is pierced in the centre by a small opening, not seen in the figure, richly supplied with long cilia, so that the stomach and intestine are placed in communication. Posteriorly the intestine opens by an anus. Near the mid-dorsal line above the intestine lies a small vesicle, shown in Fig. 2, with flattened epithelial wall communicating with the exterior by a small pore somewhat in the left of the middle line. This is the anterior (unpaired) enterocœl, *e*, and is shown on a larger scale in Fig. 4. In the latter figure the flask-shaped enterocœl is seen lying upon the stomach (the cell walls and nuclei of the latter are seen), and the flattened cells forming the walls of the enterocœl are seen to become more columnar on the walls of the tube which opens to the surface by the water pore. There is no connection whatever in an embryo of this age between the cavity of the anterior enterocœl and that of the digestive tract. In Fig. 1 there is seen to be a thin band of a muscular nature running upwards from the enterocœl to the apical plate at *mb*. Goethe has figured a very young embryo of Tornaria, and the figure has been widely copied. He shows a large pouch running out from the œsophagus, and calls this the earliest stage in development of the water system. The pouch has columnar cells forming its walls, and lying above it is a mass of flattened cells which he does not name. The latter are, however, I believe, the true enterocœl, and the evagination merely an artifact due to a fold in the œsophageal walls. The indistinctness of the lower wall connecting the enterocœl with the digestive tract indicates this, and the relation of the small mass of cells lying above the artifact, to the muscle band points to its own identity with the water system.

The path of the ciliated bands may be gathered from the figures. In general, we may say there are two bands present in such an embryo. The more anterior band, *lb*, I shall speak of as the longitudinal or circumoral band. The posterior band may be spoken of as the circular, *cb*. The longitudinal band may, I think, at this stage, be spoken of as a single band having a more or less sinuous course over the ventral (towards the oral

side) and lateral region of the embryo. At one point, however, in the region of the apical plate the two sides, right and left, come into contact with one another, or, more exactly, they fuse with the apical plate. This is shown in Fig. 2, and on an enlarged scale in Fig. 4. The union, as the figures show, is so close that I could not actually determine by observation that the band on entering the apical plate emerged again on the same side (right or left) of the embryo, to be continued forward in the preoral region. However, when speaking of the later stages of the embryo, I shall give my reasons for believing it better to assume this the true course of the bands. The circular band runs around the posterior end of the embryo and is seen in the lower end of the figure, *cb*. In Fig. 4 there is seen, right and left of the middle of the apical plate, the two eyes of the *Tornaria*. The structure of these is better seen in older stages and will be described later. Serial sections of this embryo show that there is no trace as yet of the posterior enterocoels, nor of the gill pouches.

Fig. 5 is a drawing of an older stage. The course of the ciliated bands is almost the same as in the last figures. The anterior longitudinal band has a more sinuous course, foreshadowing the arrangement found in the later stages. The circular band, *cb*, as before, runs around the posterior part of the embryo. The water tube is seen in side view opening to the exterior, and if the embryo be rolled over so that the dorsal surface is turned upwards, there may be found in the region of the external opening of the water pore, but beneath the surface, a small solid mass of cells. It lies above and to the right side of the opening of the enterocoel, but entirely separated from the latter organ, and its position is indicated approximately by *v* in Fig. 5. Two sections through this region are shown in Pl. XXV., Figs. 13 and 14. In Fig. 13 two large cells in close contact with the thin ectoderm are seen. At each end they send out processes which adhere closely to the inner surface of the ectoderm. The ectoderm itself, in this region, is extremely thin; and at the place where the section is cut the surface is folded a little, so that not only the cut end is exposed, but a part of the inner surface as well, and it is on the latter that the two cells are lying. The other section (Fig. 14) shows the remaining cells of this thickening; these are not in such close

contact with the ectoderm, being continuous, however, with the two cells of the preceding section at their inner part. This mass of cells forms the beginning of an important organ, which I shall speak of as the proboscis vesicle, instead of the older name, "heart." It is not possible to say with absolute certainty from what layer these cells arise. They come neither from the digestive tract, nor from the anterior enterocœl, but, it is possible that they may come either from the ectoderm, or from mesenchyme cells. Spengel described them as having an ectodermic origin. On the contrary, all the evidence I can get gives strong probability that they really come from one (or more?) mesenchyme cells which were applied to the inner surface of the ectoderm. They are never, so far as I have seen, even in their earliest stages, intimately fused with the ectoderm, but lie applied to its inner surface, and if in reality they came from a thickening of ectoderm at this place it could be easily recognized. Again, as they lie on the inner surface of the ectoderm, they strongly resemble the scattered mesenchyme cells found in similar positions. The fate of these cells is important, and we may now follow them through some of the later stages. By increasing in number, they form a large and solid mass of cells which pushes into the space between the ectoderm and enterocœl, but retains for a while its contact at one point with the ectoderm. An optical section, a side view of the enterocœl, Fig. 15, shows this solid germ of the proboscis vesicle. Later, the connection with the ectoderm is lost, as the cell mass pushes nearer to the enterocœl, and at the same time becomes rounded, and the cells arrange themselves in columnar order around a small central cavity, as shown in Fig. 16. This is also an optical section, but actual sections were also cut to verify each of these stages. The anterior enterocœl has also enlarged greatly during this period, and the vesicle moves nearer and nearer to this enterocœl, until it comes to lie in the corner where the duct of the enterocœl joins the central cavity, also lying on the right side of this duct, as in Fig. 17. Where the vesicle touches the wall of the enterocœl, the latter pushes somewhat inwards, and a slight proliferation of cells takes place. The vesicle lying against the walls of the enterocœl does not apply itself entirely to it, but there remains a space between the two, which remains a part of, and opens

below into, the general blastocœl space. Lastly, the stage of development is reached, shown in Fig. 18. The larva has reached the stage figured in Fig. 6. The upper part of the wall of the anterior enterocœl has thickened greatly; not over the whole extent, however, but more in the shape of a ring. The transparent structure is seen from the right side. At the lowest level of the figure, or on the side away from the observer, the duct of the enterocœl is seen opening into a horn-like prolongation of the enterocœl. Above this is seen the large proboscis vesicle, which is applied closely to the walls of the enterocœl. At the point of contact, the wall of the enterocœl projects to some extent into its own cavity, and at this point the lining cells proliferate into the lumen. At the level nearest to the observer lies the right horn of the enterocœl. Fig. 19 is a longitudinal section through Fig. 18 in the plane of the paper and on the middle line (but turned in the opposite direction). Above is the cavity of the enterocœl with its large cavity and its walls thickened at two opposite points where the section cuts through the thickened ring of cells. The uppermost part of the enterocœl does not as yet have its walls thickened to any extent. Just below the enterocœl is a cavity opening into the general blastocœl space. It is roofed over by the floor of the enterocœl, and below is bounded by the wall of the proboscis vesicle (*v*). This is the cavity of the "heart," or proboscis blood-vessel, which is filled with non-corpusculated fluid, and is seen to be merely a part of the general blastocœl cavity partially surrounded by the walls of the enterocœl and proboscis vesicle. The upper walls of the latter, forming the lower and posterior boundary of the "heart" cavity, are thickened, the cells seeming to be somewhat muscular.

The series of figures represented by 20, 21, 22 are from sections cut at right angles to Fig. 17, and shown by the letters *a*, *b*, *c*. Fig. 20 (*a*) passes across the enterocœl, showing the ring cut in two places. At the lower part of the figure appears the cavity of the vesicle (*v*) with its walls applied closely to the walls of the enterocœl. Between the two lies a small cavity filled with blood (*a*), which is the heart cavity, or proboscis blood-vessel. Only part of the next section is shown in Fig. 21 (*b*), which represents parts of the enterocœl, the heart, and the vesicle. The walls of the latter are nearer together, and the

cavity of the heart is correspondingly enlarged. Fig. 22 (*c*) shows the opening of the heart into the general blastocœl space. The blood which fills the heart is bounded by the gelatinous-like substance filling the cavity of the blastocœl.

In older stages the proboscis vesicle applies itself very closely to the enterocœl, and extends farther upwards, *i.e.* in the direction of the thickened ring. A series of cross-sections of an older stage are shown in the Figs. 23, 24, 25, 26, and their plane with reference to the enterocœl is shown by *d, e, f, g*, of Fig. 18. Fig. 23 (*d*) shows the opening of the heart (*h*) out into the blastocœl cavity. The lower wall is applied closely to the stomach wall (*w*). A narrow partition (*v*) runs across the enterocœl, and separates the right and left horns. Fig. 24 (*e*) is at a higher level, and cuts through the heart (*h*) where it projects into the cavity of the enterocœl. It is bounded by the walls of the enterocœl on two sides, and posteriorly by the wall of the vesicle (*v*). Fig. 25 shows the heart (*h*) hanging in its cavity of the enterocœl. The walls of the enterocœl are thickened over the blood-vessel, and are very irregular in outline. Posteriorly (above) is seen the small lumen of the vesicle (*v*). Fig. 26 (*g*) is from a section through the ring of tissue, and shows to what extent the walls have thickened in this period.

Returning to the larva shown in Fig. 5, we find four new enterocœls are in process of formation, making five in all. I shall speak of these as the second and third pairs of body cavities, or simply as the paired body cavities, as distinguished from the anterior unpaired enterocœl. The third pair appear slightly before the second although their appearance is almost simultaneous. The second pair arise at two opposite points on the side walls of the posterior part of the stomach at the point marked *bc*<sup>2</sup> in Fig. 5. At these points there is a proliferation of cells (*bc*<sup>2</sup>), as shown by the series of Figs. 27, 28, 29, Pl. XXV. So far as I can judge from the sections obtained, it appears that we have here a process of proliferation of the walls of the stomach, so that the wall at this point, by division of its cells, becomes two-layered. There is no evidence of evagination or pouching, although it could not positively be denied that some of the cells may pull out from the wall and come to lie on its outside. The outer cells are more granular, and stain more deeply with hæmatoxylin than the cells of the wall. In other cases I have seen a few

isolated cells on the outer wall of each side of the stomach quite near to each other, and subsequently I suppose they unite to form the body cavity. Fig. 30 is from one of the youngest stages found, and shows only two cells ( $bc^2$ ) outside of the wall. The cells which have thus collected on the outer wall soon arrange themselves around a central point or line. This seems to be accomplished by the peripheral cells pushing inwards under the more central cells, *i.e.* between the central cells and the walls of the digestive tract, and ultimately arranging themselves somewhat as shown in Fig. 31 ( $bc^2$ ). At this time, all essential connection with the wall of the digestive tract is lost, and the increase in size of the body cavities is entirely at the expense of these few granular cells which have thus early been separated from the walls of the digestive tract. The later stages of this pair of body cavities will be spoken of farther on.

The origin of the third paired cavities is simpler and more clearly made out than the preceding. The earliest stage I have seen is shown in Fig. 32 ( $bc^3$ ). There arises on each side at the level of the diaphragm-like partition separating the stomach from the intestines, and underneath the preceding body cavity, a *solid* evagination of the intestine. Each is from the beginning composed of two walls. Very early these evaginations pinch off from the intestine, and form, as in the second pair of body cavities, a solid mass of cells arranged around a central point. Also, as in the preceding case, the third pair of permanent body cavities is formed entirely at the expense of these few cells. In origin the third body cavities are undoubtedly to be regarded as gut pouches or enterocoels, but it must be remembered that at first these are *solid*, and only secondarily acquire a lumen. This may have some connection with the fact that the animal is feeding during the time when the pouches are formed, and thus food matter is prevented from entering the pouch as it might were it hollow. The second pair of body cavities does not so obviously arise as a pouch from the endoderm, but may be considered an abbreviated condition, and might be referred back to the same general process.

Returning to the surface views, we have in Fig. 6, Pl. XXIV., a figure of a *Tornaria* at its most fully developed stage; that is, at a time just prior to its transformation into *Balanoglossus*. The figure is turned in an opposite direction from Fig. 5, but

the comparison between the various parts may be readily seen. The most prominent difference between the two consists largely in the more complicated foldings of the longitudinal ciliated bands. This is especially marked in what I shall speak of as the anterior lateral fold (*ac*) and the posterior lateral fold (*bc*), shown in Fig. 6. These are now much more marked than in Fig. 5, extending farther posteriorly. Along the course of the ciliated bands are to be seen large yellow-brown pigment spots. The circular band, which is now very conspicuous, has also large pigment spots along the lower edge posterior to the cilia. At *A* is seen, in side view, the thickening of the apical plate. Beneath the surface is seen the large digestive tract. The mouth (*m*) leads into an œsophagus, which is broad from side to side (see Fig. 8). Along the upper walls of the œsophagus, in that part nearest to the stomach, are seen on each side (only one side in the figure) three large gill pouches. The œsophagus opens into the large stomach, the latter is followed by a large intestine from which it is separated by a fold in the gut walls, and the intestine opens at *n* to the exterior. Lying upon the upper posterior part of the stomach is the large anterior enterocœl with its water pore near the mid-dorsal line. It is at a stage of development shown in Pl. XXV., Fig. 18. A conspicuous muscle band runs from the upper end of the enterocœl to the under surface of the apical plate. At *bc*<sup>2</sup> and *bc*<sup>3</sup> are seen the two large paired enterocœls which nearly encircle the digestive tract. The posterior lies about the level of the septum between stomach and intestine; and the more anterior paired enterocœl is just in front of this, and separated by a narrow depression from the posterior.

A series of sections through the larva will show the relation of the various internal organs. Three of these are given in Pl. XXVI., Figs. 33, 34, 35. The first of these (Fig. 33) passes below the mouth, cutting the œsophagus and water system. On each side the longitudinal ciliated band is cut seven times. The ectoderm is thickened at the ciliated bands, and its nuclei stain more deeply. The area enclosed *within* the anterior band — the circumoral area — is very thin in section, as seen at *x*, *y*, and *z*, but with the exception that just below the mouth the ectoderm is thicker (*m'*) than elsewhere in the circumoral area, and ciliated. In the mid-dorsal line the ectoderm is quite

thick, and also thickened between  $x$  and  $y$  and  $x$  and  $z$ . The thickened ectoderm of the band is richly ciliated, and the region just below the mouth has a band of long cilia. We may say in general that the area within the circumoral (longitudinal) band has very thin walls, while the extra-oral ectoderm is relatively thicker. Reference to Fig. 6 will make clear these areas of Fig. 33. The œsophagus ( $\alpha$ ) is quadrilateral in outline; and the cells, which are somewhat crowded, have long cilia which almost fill up the lumen. On its outer walls are numerous mesenchyme cells. The anterior enterocœl is cut transversely above the upper end of the proboscis vesicle, and below the thickened ring.

Fig. 34 is from a section about the middle of the embryo, as shown by line 34, Fig. 6, Pl. XXIV. The large stomach is seen to fill up almost the entire interior of the section. In the dorsal and ventral line (above and below in the figure) the ectoderm is thick, and belongs to the extra-oral area. Four ciliated bands bound the edges of this ectoderm. The ectoblast along the sides is extremely thin, and belongs to the circumoral area. In the mid-dorsal line the ectoblast has a well-developed nerve-fibre layer on its inner surface, and this is the area from which in later stages the nerve cord is formed. Lastly, Fig. 35 passes between the longitudinal and circular bands, as shown in line 35, Fig. 6, Pl. I. The section passes through the posterior part of the stomach, near to its connection with the "intestine." The posterior pairs of body cavities are seen at the sides, almost encircling the digestive tract. Each contains a narrow lumen, and the walls are formed of a single layer of columnar cells. The ectoderm in this section (which is extra-oral) is exceedingly thick. At one point, owing to a slight obliquity of the section, a portion of the circumoral area is cut.

In Fig. 36 is shown a part of a section of *Tornaria* at right angles to the last series, passing through the body from side to side, and is drawn to a much larger scale than the last. The ectoderm is better shown than in the preceding figures. In the upper right-hand portion of the figure the ectoderm is exceedingly thin, formed of flattened ectoderm cells. At  $l$  is cut the lower limb of the circumoral band, and then comes the thickened extra-oral ectoderm, lying between the longitudinal and circular bands, and corresponds to that shown in Fig. 35. It

contains several gland cells which stain deeply, as shown in the figure. At *cb* the section passes through the circular band. It is seen to be composed of three rows of cells, each richly ciliated and with large nuclei. The protoplasm of the cell is often striated at right angles to the surface, as though continuous with the cilia. Immediately below the circular band is a pigment spot. It is seen to be formed of a finely granular pigment area surrounding a clear central spot, — a window, as it were, through which the pigment may be seen. All of the pigment spots, both on the longitudinal and circular bands, have this same structure. In Fig. 42, Pl. XXVII., another of these pigment spots is shown, drawn to a larger scale. It is taken from the lower limb of the longitudinal band, and has exactly the same structure as in the preceding case. Whether the pigment is in the same cell that has the clear portion in its outer end, or whether in other cells, I could not determine from sections. Judging from the extent of pigmentation, it seems probable, at any rate, that it must be contained in more than a single cell. Returning to Fig. 36, we see that the ectoderm over the posterior (oral) pole of the embryo is quite thick, though not so much so as in the extra-oral area. In the centre of this plate lies the anus, where the ectoderm runs in, and becomes immediately continuous with the endoderm of the intestines. (The anus is not seen in the figure.) The central part of the section is largely filled by the digestive tract. The diaphragm-like partition separating the stomach (*S*) from the intestine (*I*) is conspicuous. It is seen to be formed by a fold in the walls of the mid-gut, and therefore two-layered. There is formed in the centre of the diaphragm a small opening, around which the large cells are richly ciliated with exceedingly long cilia. During life this bunch of cilia is seen in constant action, often with a rotary motion, churning up the contents of the stomach. The cells lining the stomach division are tall and columnar, and are not ciliated (except at one place, to be spoken of later). The cells of the intestine are not so tall, and often show, as in the figure, a plasmodium-like outline. The second and third body cavities are seen at the sides of the digestive tract. Each is a sac with walls composed of a single layer of cells surrounding a small central cavity. The somatic wall is formed from higher cells than the splanchnic.

The œsophagus of a larva of this stage has been shown in cross-section in Fig. 33. Its connection with the stomach is now shown in longitudinal section in Fig. 37. A distinct groove marks the point of union, and the section shows a gelatinous-like secretion filling the groove at *gr.* The cilia on the dorsal wall (*d*) of the œsophagus do not continue into the stomach, while those over the ventral side continue, after a slight interruption at the groove, as a narrow band down the anterior wall of the stomach; the cilia become smaller as the band runs down the wall, and cease about the middle of the stomach. The cells forming the stomach wall in this region are higher than elsewhere, as shown in cross-section by Fig. 38. This band of cilia is also found in other species of *Tornaria*, and seems to be a distinctive feature of the larva. The gill pouches arise as evaginations from the upper part of the œsophagus. Three pairs appear in this larva almost simultaneously, but the first is larger than the second, and the second than the third. A fourth pouch arises just prior to the transformation of the larva, and at this time the first one or two develop the tongue bars. Fig. 8, Pl. XXIV., shows a view of the dorsal surface of the œsophagus of the larva shown in Fig. 6. The left side is an optical section, and the right a surface view. The œsophagus is exceedingly broad, and the pouches arise from the upper outer corners.

The apical plate of the larva, is shown in surface view by Fig. 7, Pl. XXIV. To obtain this, the upper part of the larva was dissected away, mounted in glycerine, and stained in methyl green, which brings out distinctly the course of the ciliated bands. Each of these four bands is clearly seen to end sharply in the region of the apical plate, with the points turned in from right to left, and left to right, the anterior two pointed towards each other, and the more posterior likewise toward each other. The earlier stages of these bands (as shown in Fig. 4) showed no such breaking in their course, but were simply continuous with the thickened ectoderm of the apical plate. I have assumed in their earlier stages that the ciliated bands are continuous over the apical plate, across the sides, so that there is a single circumoral band. However, in the older stages, as seen in Fig. 7, this is not the case, but there is a *tendency* to a separation of the circumoral band into two separate bands, the one above and anterior to the mouth, and the other if the bands

were united across the apical plate would then be spoken of as postoral.

Now if in the younger stages the bands actually crossed from right to left, I think we would expect them to be actually united in the older forms across the apical plate from right to left; but since each ends abruptly in these older stages, it seems to me to indicate a secondary change. Consequently I think it more *probable* that the longitudinal bands go through exactly the same changes that we find in the typical Echinoderm larva; viz. at first a simple continuous band, and secondarily a fusion of the two with the apical plate, resulting later in a new arrangement of the bands. In the Tornaria, however, the fusion of the bands must occur very early, or at the very beginning, for in the youngest larva figured they are already found. Later there is seen a tendency to unite from right to left in the Tornaria, and this is actually accomplished in the Echinoderm larva.

The two eyes are semi-circular bodies right and left of the median plane, surrounded by a semi-circular zone of pigment, as seen in Fig. 7, and on an enlarged scale in Fig. 43, Pl. XXVII., which is also a surface view. The details of the eye are best seen in Fig. 44, which is from a section parallel to the upper surface of the apical plate. The clear crescentic portion is seen to be formed by a series of rod-like bodies, each being continuous on its outer end with a pointed bristle-like portion. The bristles seem to be cuticularized, and each ends in a sharp point, the points being drawn together at a central point. The clear rod-like portions of the cells cannot be traced after they enter the pigment zone, but undoubtedly the nuclear ends of the cells lie here. Fig. 44' is the next section beneath 44. In this the clear inner portions of some of the cells are still seen, and near them in the pigment zone a few large nuclei, which I am inclined to believe belong to the inner ends of the eye elements. Whether the pigment is in or between the retinal elements I could not determine, but judging from the quantity, I think much, if not all, belongs to the inner ends of the elements. There is seen in Fig. 44', on the concave side of the eye, a collection of small nuclei, but these do not seem to belong to the eye itself. It seems probable, then, that each element of the eye consists of a nucleated and pigmented inner end, followed by a transparent rod-like portion, and ending in a bristle-like point.

The apical plate itself is seen in cross-section, in Fig. 45. The ectoderm is here exceedingly thick, and has beneath it a broad zone of nerve-fibre layer. To the lower end of the plate the muscle band is attached, and runs thence to the anterior enterocœl. The apical plate must form the larval nervous system to a very large extent, if we may judge by the thickness of the nerve-fibre layer. The plate differs, however, very essentially, I think, from the apical plate of the Trochophore, inasmuch as there are no nerve-fibre bands running from it. This can be determined by staining the apical plate and examining the inner surface. The ectoderm and nerve-fibre layer are simply continuous with the general extra-oral area.

Scattered mesenchyme cells are found in the blastocœl space between the digestive tract and ectoderm of *Tornaria*. The blastocœl space itself is filled by a watery somewhat gelatinous substance, and scattered in it here and there may be found a few mesenchyme cells as shown in Figs. 33, 34, 35, 40. Sometimes one or two may be seen in such sections applied to the ectoderm, both over the circum- and extra-oral areas, but these are not numerous, and do not seem to form a continuous plexus. Portions of the ectoderm cut away, stained, and mounted with the inner surface upwards, will generally show a few of these amœboid-like cells. Also now and then a mesenchyme cell can be seen on the wall of the stomach or intestine. But the most interesting fact is that these cells are relatively very numerous over the œsophageal wall as shown in Fig. 33. Over the wall they form almost a continuous layer of branching cells. The interesting bearing of this will be seen in a later comparison between *Tornaria* and the Echinoderm larvæ.

#### METAMORPHOSIS OF *TORNARIA*.

Agassiz has given most excellent figures of the larva during its period of metamorphosis. The larva becomes more opaque, and changes its shape, becoming more elongated antero-posteriorly. The whole of the anterior region of the digestive tract becomes pulled inwards, so that the gill-pouches lie at a more posterior level of the embryo—behind the lower limb of the longitudinal ciliated band. The anterior enterocœl does not take part in this movement, and consequently comes to lie

anterior to the œsophagus. *The larva decreases greatly in size during the period of metamorphosis.* The longitudinal ciliated band becomes more indistinct, and the anterior region of the Tornaria elongates to form the proboscis. The circular ciliated band moves back farther and farther by the lengthening of the body in the region between the lower limb of the longitudinal and the circular band. The ciliated bands of the forming proboscis become very faint, and there is a tendency for the whole surface of the proboscis to become rounded by obliterating the furrows in the circumoral area. The larva moves about over the bottom by means of the circular band of cilia, which do not vibrate now so rapidly as in the younger stages.

The most important change which takes place during this period is the formation of the dorsal nerve chord, which is intimately connected with the formation of the collar. During the period of metamorphosis there appears a narrow groove running around the embryo parallel to the lower limb of the longitudinal band, and between it and the circular band, nearer to the former. Fig. 39, Pl. XXVI., shows this groove at *g*, and the level of the lower limb of the longitudinal band is shown by *l*. Between these the ectoderm is thickened and filled with deep-stained gland cells. This is the beginning of the collar. In the mid-dorsal line the grooves from the sides do not meet, but each turns forward and becomes continuous with the lower limb of the longitudinal band. This is shown in surface view by Fig. 46, Pl. XXVII., which shows part of the mid-dorsal surface. At *l* and *l'* are seen the parts of the longitudinal ciliated bands of one side, which become continuous before reaching the mid-dorsal line. Also on its opposite side the same band is seen. At *g* is seen the groove on each side which marks the posterior limit of the collar. Before reaching the middle line, each groove turns forward and becomes continuous with the longitudinal ciliated band of that side. There is thus left in the dorsal mid-line a plate of ectoderm, which is found to lie at a lower level than the surface of the collar. It is still, however, continuous with the general ectoderm of the surface. After this the two dorsal ends of the collar begin to roll over towards one another, as shown in Fig. 47, and at the same time the plate of ectoderm sinks beneath them and out of sight. The collar groove becomes

more distinct, and the longitudinal ciliated band disappears. The lower limb of the latter marks the anterior end of the collar. Serial sections show clearly the changes which have taken place in the dorsal region during this period.

The first change is shown by the transverse section shown in Fig. 48. This is from a larva a little older than that shown by Fig. 6, Pl. XXVII., but not so old as that shown by Fig. 46, Pl. XXVII. In the mid-dorsal line the ectoderm is seen to have developed more of the nerve-fibre layer than elsewhere, and a plate of this ectoderm is sinking a little below the general level of the ectoderm. Figs. 49 and 50 are from older larvæ at about the stage shown in Fig. 46. Fig. 49 passes through the anterior part of the neural plate, which is very broad, and at its two ends the collar is seen rolling over the plate. Fig. 50 is about the middle of same plate, the intermediate sections not being figured, and here the plate is seen to be not nearly so wide as in the preceding figure, but to have sunken farther beneath the surface. In both 49 and 50 the plate is broader than the average. The series of figures 51-55 inclusive show a later stage in the development of the chord when the collar has met and fused above the middle line. Fig. 51 is the most anterior section, and in this region there is always a small lumen in this part of the chord. The fusion of the collar above the chord is complete. Fig. 52 is from the middle of the chord, and here the lumen is entirely obliterated, leaving a solid chord fused above with the ectoderm. Fig. 53 is a section just back of the collar, where the nerve chord is seen to be in process of formation by the same changes that took place in the collar region. Figs. 54 and 55 give the more posterior sections through the chord, which is here seen to be merely a thickened plate of ectoderm, not yet beneath the surface.

The account of the formation of the nerve chord given by Bateson for *B. Kowalevski* differs in some points from the above description. According to his account the middle part of the chord simply delaminates from the ectoderm, but at the two ends it arises by invagination. In the *Tornaria* development we have seen the invagination takes place through the whole length of the chord, in *exactly the same way that the nerve chord of Amphioxus is formed.*

A longitudinal section of the whole larva just after the meta-

morphosis is shown in Fig. 40, Pl. XXVI. In hardening, the anterior end of the proboscis has been drawn in somewhat, and therefore is seen to be flattened in the figure. The ectoderm has greatly thickened over the whole surface, which is probably the cause of the opaqueness of the embryo at this period. The longitudinal band has almost disappeared, and the circular band (*cb*) is by no means so distinct. The method of disappearance of the longitudinal band and the thickening of the ectoderm is shown by Figs. 56 and 57, Pl. XXVII. These are from transverse sections in the anterior region of the larva, in which *d* represents the mid-dorsal line, *x* the posterior later area bounded by the longitudinal band, *y* indicates the middle lateral furrow. Fig. 56 represents the conditions found in Tornaria, and Fig. 57 a larva during the period of metamorphosis. The thickening of the circumoral area at *x* and *y* takes place by an increase in number of the few cells forming the ectoderm in that region, so that the ectoderm is gradually built up into the same structure as that over the extra-oral area. At the same time the distinction between ciliated bands and ectoderm is lost, and the whole proboscis becomes ciliated.

The walls of the digestive tract of Fig. 40 have thickened, but still retain the same divisions seen in the Tornaria. At the anterior end of the œsophagus in the middle line, an evagination of modified cells has taken place at *nc*. This lies very near to the external opening, but is without doubt formed from endoderm. The œsophageal region of this embryo had not yet been pulled back as Agassiz has described; later the part *nc* will lie nearer to the enterocœl. This evagination is the first appearance of the notochord (Bateson). The distinction between stomach and intestine is still seen, although in older stages, after the intestine has pulled back, the diaphragm-like partition disappears. Parts of the second and third body cavities are seen cut across in its section. The gill pouches are not shown in this figure, since they lie to the right and left of the middle line, but in Fig. 41 is seen a part of a transverse section through one. This figure shows in detail the structure of the second gill pouch of the series. The pouch *gp* is applied to the ectoderm wall, and, moreover, the pouch itself is divided by a fold in its wall into two parts. This fold forms the tongue bar which is so conspicuous a feature of the adult gills.

The larva soon assumes the shape of the adult *Balanoglossus*. The oldest larva I obtained was kept seventy hours after it was caught in the tow net. In Fig. 9, Pl. XXIV., is shown the larva from dorsal view, and as drawn from a preserved specimen. Agassiz has given a figure of the living larva at about this stage. The larva is divided into three regions, — the proboscis, the collar, and the body proper. The circular band of cilia is still retained and has moved far back towards the anal end of the larva, owing to the increase in length of the collar and the region just behind it.

The internal organs as shown by sections exhibit in many points the transition between the *Tornaria* and the adult. The series of Figs. 58–66, Pl. XXVIII., are from transverse sections of this larva, and illustrate the most important changes which have taken place. Their planes with reference to Fig. 9, Pl. XXIV., are shown by the lines 58–66.

We may first examine the structures shown in Fig. 58, which is a transverse section through the anterior collar region. The ectoderm is very thick and ciliated and is filled with gland cells staining deeply. The inner layer of the ectoderm is formed of a nerve-fibre layer, but in the ectoderm in the dorsal line — above the nerve chord — it is not present. The nervous system (*N*) is completely separated from the ectoderm and is partially arched over by the body cavities. The chord is separated into two parts by a narrow crescentic lumen. The cells above this are arranged in a single row and have no nerve-fibre layer. The cells below the central cavity are very numerous and have a well-developed nerve-fibre layer in the lower part of the chord. The digestive tract — œsophagus in this section — shows a tendency to division into two parts by lateral constrictions in its walls, forming a larger lower part and a smaller upper, *the latter is directly continuous into the notochord farther forward*. In the corners of the folds are two thickened chitin-like rods. The space between the walls of the digestive tract and the ectoderm is filled up by the body cavities of the collar (*bc*<sup>2</sup>) (first paired cavities). Each sac has a splanchnic and somic wall, which are applied to the digestive tract and body walls respectively. (In this section the body cavities have to some extent shrunk away from the ectoderm and digestive tract.) The large central space of the sacs is filled with a branching menchymatous-like tissue. Between the nerve chord and the digestive tract

is another pair of body cavities ( $bc^3$ ) enclosing a large space between them ( $dv$ ). These ( $bc^3$ ) are the anterior extensions of the last pair of body cavities and bound an anterior extension of the dorsal blood-vessel ( $dv$ ), which runs into the proboscis and joins subsequently the proboscis blood-vessel (heart).

A section more anterior to the last, passing through the base of the proboscis and the anterior edge of the collar, is shown by Fig. 59. The section cuts the collar below and at the sides, but just anterior to the collar above. The collar ectoderm is here thick as in the last section. In the upper part it turns back at the sides to become continuous with the ectoderm of the proboscis. Over the proximal end of the proboscis (just anterior to the mouth), particularly on the upper side, near  $w\phi$ , the ectoderm is greatly thickened, having a broad zone of the nerve-fibre layer. It is this part which is directly continuous with the lower part of the nervous system of the last figure. The external opening of the anterior enterocœl (the water pore) pierces this thickened ectoderm on the dorsal surface and a little to the left of the middle line at  $w\phi$ . Beneath the ectoderm, in the upper part of the proboscis and above the digestive tract, is a mass of somewhat spongy tissue. There are several distinct structures here. At ( $dv$ ) is the anterior end of the dorsal blood-vessel. The section passes through the point at which it fuses with the proboscis blood-vessel, and the anastomosing cells across the lumen seem to break the large vessel up into smaller ones. The rest of this area is filled by portions of the body cavities. The digestive tract is divided into two portions, an upper and a lower. The separation is exactly the same as in the preceding case. In the folds are seen the chitin-like rods. The upper division passes through the plane in which the dorsal division of the digestive tract becomes continuous with the notochord ( $nc$ ), and the cells already have assumed the peculiarities of the notochordal tissue. Parts of the anterior ends of the collar body cavities fill the space between the digestive tract and the ectoderm.

A section just anterior to the last is shown in Fig. 60, passing also through the base of the proboscis. Over the greater part of the section the ectoderm is greatly thickened, but on the mid-ventral line it is thin and passes here into the mouth. The centre of the section contains several important organs. In the

mid-ventral part is seen the notochord (*nc*). It contains a narrow central cavity which is continuous with the cavity of the digestive tract. The walls are formed by large vacuolated cells with the protoplasm especially collected near the lumen. Beneath the notochord is a single chitin-like rod which is formed by the union of the two rods found in the folds of the digestive tract. Above the notochord, in the middle line at *h*, lies the proboscis blood-vessel (heart). This is bounded above by the proboscis vesicle (*v*), and at the sides by the right and left horns of the anterior enterocœl (*e*), thus preserving the same relations found in younger stages. The cells lining the walls of the enterocœl begin to show muscular differentiations in their outer ends. The proboscis vesicle is lined by a single layer of cells. A section farther forward through the proboscis is shown by Fig. 61. The ectoderm is still comparatively thick, with quite a wide zone of the nerve-fibre layer. The notochord (*nc*) is still present and similar to that in the last section. The chitin rod does not extend so far forward. The two horns of the enterocœl have united into the single large anterocœl. The walls of the latter are proliferating, so that the cells encroach upon the central cavity. At *v* is seen the ending of the proboscis vesicle. The walls of the heart (*h*) hang from this point into the central cavity, so that the heart is seen to run across from the lower to the upper wall of the enterocœl, as shown in the earlier stages. Fig. 63 shows part of a section between Figs. 60 and 61, and shows the point at which the cavity of the heart passes across.

A section through the middle of the proboscis is shown in Fig. 62. The ectoderm is not so thick nor does it contain so broad a zone of the nerve-fibre layer. The centre is filled by the anterior enterocœl, whose walls are beginning to form the musculature, the proboscis and the cells by proliferating to fill up the central cavity.

We may next examine the sections posterior to the collar. Fig. 64 is from a section passing through the first pair of gill pouches. The ectoderm is thick and ciliated, but does not show the gland cells found in the collar region. Beneath the ectoderm in the mid-dorsal line lies the solid nerve chord. The digestive tract has on each side of the middle line two enormous pouches which are richly ciliated where they join the gut. They have not yet come into contact with the ectoderm, but

have almost obliterated the lumen of the body cavity above them. In the mid-ventral line the walls of the body cavities of the two sides come into contact, and at the point of union is left a large space — the cavity of the ventral blood-vessel (*vv*). Around the nerve chord there are four dorsal extensions of this (last) pair of body cavities. The upper pair are simple extensions of the body cavities from the sides. The small pair below the nerve chord at *bc*<sup>3</sup> come also from the same pair of body cavities, but arise back of the nerve chord, and extend forward into the proboscis region. It is this pair of extensions that go to form the dorsal blood-vessel that is to be seen just beneath the nerve chord and bounded by the walls of the two cavities.

Fig. 65 passes through the second pair of gill pouches, which have broken through to form a pair of gill slits. At the external openings the ectoderm becomes continuous with the endoderm. The inner openings of the gill slit into the digestive tract are on each side richly ciliated. The small isolated block in the upper part of the section contains the pair of extensions from the body cavities (*bc*<sup>3</sup>), which enclose between them the dorsal blood-vessel, and it is this pair that we saw in the last section beneath the nervous system. The ectoderm in the mid-dorsal line is thicker than elsewhere and contains a deeper zone of nerve fibres. It is this ectoderm that is continuous with the nerve chord of the last figure. In the lower part of the section the body cavities (*bc*<sup>3</sup>) completely fill up the region between the digestive tract and ectoderm. The cells of their walls, especially in the ventral region, show a differentiation into muscle fibre. The nucleus lies in the inner part, and the outer shows a deeply staining portion which I think undoubtedly represents the contractile portion of the cell. It is thus seen that the second pair of gill openings has been formed before the first pair. Whether this is the rule I have no means of knowing, as I did not have enough material to settle the point. Nor did I have embryos old enough to show the origin of the collar pores which form in the region of the first pair of gill pouches.

A section through the posterior portion of the larva is shown in Fig. 66. The ectoderm is not so thick as in the anterior regions, and has almost no zone (except in the mid-dorsal line) of nerve fibres. The digestive tract is swung by the mesen-

teries, and is wide from side to side, but narrow from above downwards. The body cavities form between them in the mid-dorsal and mid-ventral line large blood-vessels. In the upper part of the body cavities a few cells connect the somatic to the splanchnic walls. The posterior body cavity, which is seen in Figs. 63, 64, 65, is noticeably free at this stage from these anastomosing cells, while the collar body cavities, as seen in Figs. 58 and 59, contain a great number of branching cells.

Sections between those of Figs. 64 and 65 show that in this region the digestive tract has its walls folding in a very complicated manner. The folding may be due, as Agassiz suggested, to the pulling in of the anterior region of the digestive tract during metamorphosis. The sections posterior to Fig. 65 are much like this one, as the body cavities extend to the very end of the embryo. The digestive tract opens at the posterior end by a large anal opening.

#### THE NASSAU TORNARIA.

A few specimens of a very large and interesting *Tornaria*, caught in deep water (but at the surface) off Nassau, Bahamas, have been given to me by Dr. H. V. Wilson. They were procured during May, I believe, and are approximately all in the same stage of development. It is not my purpose to enter into a minute description of this larva, but rather to call attention to some of its more obvious peculiarities. These larvæ measured 4 mm. in length. The external appearance seems very different at first sight from the *Tornaria* previously described. This is caused to a large extent by the peculiarities of the longitudinal ciliated band. A careful study of the course of this ciliated band shows, however, that in its essential features it reduces back to the same plan, and the details in which it differs would seem to have been acquired to fit it for a more perfect pelagic life. Weldon found the same larva at Nassau in October, when many were in process of transformation into *Balanoglossus*. Those I have were caught, as I said, in May, and were all of the same age and younger than those described by Weldon. Those which were kept in the laboratory in dishes were, Professor Brooks tells me, soon transformed into young *Balanoglossus*. The arrangement of the longitudinal ciliated bands in this larva

are so unique that I have added three figures, 10, 11, 12, to Pl. XXIV. to show the course of the bands. A view of the apical plate of the larva is shown in Fig. 10. The figure is placed in a corresponding position to Fig. 7 for comparison with the apical plate of the New England Tornaria. The longitudinal ciliated band of the Nassau larva is drawn out into tentacle-like process hanging freely, like a fringe, from the surface of the larva. The ciliated band runs up along one side of a tentacle round its free end and down the opposite side; it then crosses over to follow the same course on the next tentacle of the series. Besides the four bands corresponding to those of Fig. 7, the apical plate of the Nassau larva is further complicated by the presence of other bands. These arise by the edges of the anterior lateral and posterior lateral folds being drawn upwards nearer to the apical plate. Thus if the parts *b* and *b*<sup>1</sup> of Fig. 6 were drawn upwards towards the apical plate, they would form the bands shown by *b* and *b*<sup>1</sup> of Fig. 10. These bands in the Nassau larva are also drawn out into a series of tentacles. In this way the apical plate of the larva has secondarily acquired a most marked *radial symmetry*, as seen in the figure. The centre of the apical plate itself contains a small more opaque spot which contains the eyes. In the centre of this is a smaller, lighter area. Running across the plate from right to left is a deep groove. This groove is bounded at its sides by four narrow ciliated bands which are not drawn out into tentacles, and which at the ends of the groove become each continuous with four ciliated bands, and these latter, at first not tentacular, soon become so. Moreover, the four ciliated bands bounding the edge of the grooves do not quite meet across the middle line, but end in four points before reaching the eye spots. The arrangement is thus seen to be identical with the apical plate of the New England form. The extra-oral area in the middle line has over its surface curious clear spots, as seen in the figure, each bounded by a halo of pigment. Sections show these clear areas to be large cells much like those found in the pigment bands of the New England Tornaria. In the field posterior to the eyes there is seen a faint furrow in the outer posterior line. The circumoral area between the ciliated bands is very clear and pushes in below the general surface of the larva. In the living animal the tentacular areas are much nearer together than

shown in the figure, where they were separated somewhat, so that the course of the bands might be more clearly seen. The radial symmetry is also somewhat distorted.

Fig. 11 shows a part of a side view of the larva, spread out flat on a slide, so that the circumoral area or furrow is seen between the bands. Only by this means can the bands be traced with certainty. The figure may be oriented by referring it to Fig. 6. The one is of the right side, and the other the left. The letters *o* and *p* between the figures indicate the same bands. The band *o* comes from *above* the mouth, runs along the side until it reaches the point above *q*, and then turns upwards towards the apical plate, and then the tentacular arrangement commences. The band *p* comes from below the mouth and runs a parallel course to *o*, and forms what I have spoken of as the lower limb of the longitudinal band. At the point *q* this band makes a slight upward course, then turns downwards, and then upwards once more to *o*. The reference letters *op* and *ac*, in Figs. 11 and 10, show the relationships of the bands. The anterior lateral fold is shown by *ac* in Figs. 10, 11, and 6.

Below the lower limb of the longitudinal band, and not far from it, is shown in Fig. 11 (*cb*), a portion of the circular band with large flame-like cilia (or fused cilia?).

Fig. 12 shows the anterior view of the larva in the region around the mouth. The whole of the digestive tract is seen beneath the surface, passing as a cylindrical tube from mouth to anus. The ciliated band *p* (as in the last figure) is seen to run upwards on one side of the middle line, until just *below* the mouth it crosses over and runs in a parallel course along the opposite side of the middle line. The band *o* turns forward also on each side of the middle line, but more to the left than the band *p*, and *at a higher level*, and also crosses the middle line to pursue a similar course on the other side. The mouth lies between these two bands, the *o*-band being pre-oral, the *p*-band post-oral. The *p*-band crosses the middle line at an inner level to the *o*-band. The anterior lateral areas of the two sides are shown at *ac*, all the tentacles on the left being thrown over to one side.

From the mouth the œsophagus runs upwards and forwards, as seen in the figure, for a short distance, to join the upper end of the cylindrical stomach. The latter is very long and runs

backwards in the middle of the Tornaria to the level of the circular band, where it is separated from the intestine by the diaphragm-like partition. The intestine runs for a short distance, and ends at the anus.

Sections show that the anterior enterocoel is well developed, and corresponds to the stage shown in Fig. 6. There is no trace as yet of the second and third body cavities, but the whole blastocoel cavity between digestive tract and ectoderm is filled with a gelatinous substance. Weldon figures the body cavities in older stages, claiming them to be exactly similar to those of the New England Tornaria. I infer that these body cavities have not yet developed from the endoderm in the larvæ I studied. A description of the other points in the anatomy and histology of the Nassau larva would be largely a repetition of the preceding pages. The collection of mesenchyme cells on the outer wall of the œsophagus is very marked. They seem to form an anastomosing network over its whole surface.

#### HISTORICAL AND CRITICAL.

The free-swimming larva was first described and figured by Johann Müller, in the year 1848, and was believed to be the larva of an Echinoderm. He gave to it its present name because "das Thierchen . . . dreht sich immer, fort im Kreise und durch die Thatigkeit seinem Wimpern. Daher es den Namen *Tornaria* fuhren mag."

Müller saw and described all of the principal organs of the larva, including digestive tract, anterior enterocoel and its madreporic-like opening, the posterior body cavities, ciliated bands, apical plate and its muscle band. It seems to me probable that his somewhat diagrammatic figures of the apical plate may not be quite exact. The longitudinal ciliated band is described as crossing over from right to left at the apical plate in very young forms, thus separating off, as in *Bipennaria*, an anterior isolated "plastron."

In the preceding sections I have given my reasons for believing that at first the longitudinal band is a continuous circumoral band, and secondarily breaks, with a *tendency* to form two bands. Müller's extensive knowledge of Echinoderm larvæ helped him greatly to understand the structure of Tor-

narria, but at the same time may have led him to overlook some of the differences in the two.

Krohn, in 1853, described as a Holothurian larva a Tornaria, at the time of metamorphosis. In 1866, Alexander Agassiz described the New England Tornaria—the same considered in the preceding pages. He thought Tornaria was the larva of some Echinoderm, probably of a very primitive starfish, as it retains permanently the embryonic features of Brachiolaria. At the same time he pointed out that Tornaria differs in some essential points from all Echinoderm larvæ; viz. in the circular band of cilia, and peculiarities of the water system. He did not state, as Metschnikoff later said he did, that he had seen the anterior enterocœl arise from the digestive tract, but says explicitly that “the mode of formation of the water system, *though I have not traced it*, is probably similar to that of the Brachiolaria as a diverticulum of the digestive tract.”

Fritz Müller<sup>1</sup> referred the larva to the Echinoderms, and discovered the proboscis vesicle, which he believed to be the earliest representative of the heart. E. Metschnikoff described in 1866 a small worm-like larva, which he caught in the tow net at Naples. He points out that it is the young of Balanoglossus, but did not recognize its connection with Tornaria. The anterior enterocœl he misinterpreted as possibly the nervous system, and affirms that gill slits are absent. Nevertheless, in the single figure accompanying the paper he distinctly figures a pair of gill pouches, but wrongly believed them to represent liver sacs. The peculiarities of Balanoglossus he thought were so great that one had best consider the animal the representative of a small group most nearly related to the Annelids, and pointed out that Keferstein's homology of the proboscis to the Nemertian proboscis is false. Metschnikoff thought that the proboscis of Balanoglossus is homologous to the cephalic lobes of Annelids. The larva which he caught is to be compared to an Annelid larva of the Mesotrochal type. Kowalevsky's paper on the anatomy of the adult appeared in 1866. This gave the first exact account of the adult structures, overlooking, however, the dorsal nerve chord. Delle Chaije had discovered Balanoglossus in 1826, and Keferstein had given a description of it in

<sup>1</sup> I have not seen this paper, and quote on the authority of Metschnikoff and Spengel.

1863, but our present knowledge of the anatomy began with Kowalevsky.

Again, in 1869, Metschnikoff published a paper on *Tornaria*, and here for the first time was the relationship between the *Tornaria* of Müller and the *Balanoglossus* of Delle Chaije pointed out. This paper is one of the most important contributions to the subject. He confirms Müller's statement that the longitudinal ciliated band develops before the circular band. The paired gut pouches are more clearly recognized than by Müller. The formation of the mesenteries and body musculature is recognized; also the formation of dorsal and ventral longitudinal vessels. The pulsating heart is described as having a sort of pericardium. The larva was kept for about a month, and its transformation into the worm-like *Balanoglossus* seen. A pair of gill pouches was described, and later the ciliated gill slits; and their resemblance to the gill slits of *Appendicularia* recognized. The resemblance of the *Tornaria* to the Echinoderm larva is insisted upon, and therefore the relationship of *Balanoglossus* to a Holothurian-like Echinoderm is rendered very probable, and the author regards the muscular proboscis as a large ambulacral foot. Metschnikoff traced the formation of the musculature of the proboscis from the anterior enterocœl, and points out that in the young *Balanoglossus*, at least, it does not open in the anterior portion of the proboscis as described by Keferstein, Kowalevski, and Agassiz.

Alexander Agassiz published in 1873 a paper giving an excellent account of the metamorphosis of the New England *Tornaria*. He recognized the relationship between *Tornaria* and *Balanoglossus* that Metschnikoff had pointed out, and therefore abandoned his former belief of the Echinoderm nature of the adult of *Tornaria*. He verified many of Metschnikoff's and Müller's descriptions, and added that in the New England *Tornaria* four pairs of gill pouches arise almost simultaneously along the œsophagus. He also saw the division of each gill slit into two by the formation of the tongue bar, and described the formation of the gill skeleton. Agassiz also saw the *Tornaria* undergo its transformation into the small *Balanoglossus*-like worm, and the change was described as taking place suddenly, accompanied by an opaqueness of the body wall, and the pulling in of the œsophageal part further into the body.

Spengel published a short paper on *Tornaria* in 1877, but I have not been able to see this. Reference is made to it below by Metschnikoff.

The substance of it was, I believe, incorporated in Spengel's latter paper in 1884. Alexander Goette published a brief notice of a young stage of *Tornaria* in his paper on *Comatula* in 1876. The figure is of a very young stage of *Tornaria*, and has been copied into the text-books. The important structure that it shows is the origin of the anterior enterocœl as an evagination of the digestive tract. Without questioning that this may be the real origin of the enterocœl, I do not believe, however, that the figure shows this as pretended, but that the so-called evagination is only an artefact, and that the true enterocœl is shown just above this already formed, and in close connection with the muscle band from the apical plate. Balfour, in 1879, expressed the opinion in his text-book that *Tornaria* is intermediate in structure between the larva of the Echinoderm and the Trochosphere type common in the Mollusca and Chætopoda. The eye spots, the muscle bands from the apical plate, and the circular band of cilia, and the terminal anus are Trochosphere characters. Metschnikoff published in 1881 another paper on the systematic position of *Balanoglossus*, which is one of the most suggestive speculations about the group. Assuming the relationship of *Tornaria* to the Echinoderm larva, this necessitates that *Balanoglossus* shall be referred to the Echinoderm type; and inasmuch as the fundamental form of the Echinoderm is bilateral, this is not difficult. The water pore is the madreporic pore; the proboscis corresponds to a single ambulacral tentacle, and the blood-vessels find their homologues in the Holothurian, as do also the peritoneal body cavities. The gills of *Balanoglossus* are probably not new structures, but represent the retarded and rudimentary portions of the water system, and "it is interesting that according to the observations of Spengel, the most anterior gill pouches communicate with the peritoneal cavity of the collar, so that the gill openings function as the outlet of the water vascular system." Also according to Spengel's observations, the nervous system presents great similarities to the same organ in Echinoderms. Balfour's comparison between *Tornaria* and the Trochosphere will not hold, because the contractile muscle band to the apical plate is not double, as in the

Trochosphere; the terminal anus is found in typical Echinoderm larvæ; the œsophagus is endodermal, the ectoderm and its thickened bands are as in the Echinoderm larva, the origin of the muscle cells from enterocoels is common to Tornaria and Echinoderm larva, and also the wandering mesenchyme cells of the œsophagus. Metschnikoff therefore includes in a group Ambulacraria, the two sub-types Radiata (Echinoderm) and Bilateralia (Enteropneusta), and the following section is most significant. "Es erscheint mir wahrscheinlicher das Balanoglossus eine modificirte Thierform repräsentirt, bei welcher die Ausbildung des radiären Bauplanes, resp. der mannigfalligen Differenzirungen des Wassergefäß systems, so wie der Cutis ausgebleiben ist; obwohl es natürlich auch denkbar wäre dass Balanoglossus eine primitivere Form als die Echinodermen uns darstelle. Meine meinung stütze ich hauptsächlich auf die unpaare Bildung der Tornaria, weil die paarigen Blindschläuche der Bipinnarien und Plutei primitiver erscheinen."

Fewkes records *Tornaria* from Newport, R.I., in 1888. He found much younger individuals than did Agassiz, but belonging to the same species. Two figures are given of these. The youngest form is slightly younger than the earliest stage I have figured, and has not yet formed the circular ciliated band. He speaks of the anterior longitudinal band as divided into two separate bands, but seemingly without having carefully studied the structure of the apical plate. He describes on each side of the youngest larva two branching structures which he believes to be Nephridia like those in *Polygordius*. This is undoubtedly a mistake, and probably may be accounted for by the presence of wandering mesenchyme cells in the blastocœl.

Bateson published in 1884 the first of his series of papers dealing with the embryology of *B. Kowalevski*. The first three parts dealt with the different stages of development, and a fourth was devoted to a discussion of the ancestry of the Chordata. The embryo of *B. Kowalevski* has a direct development that is without a *Tornaria* stage. The blastula invaginates at one pole (without formation of mesenchyme) to form a typical gastrula, the blastopore ultimately closes at the point where the anus subsequently opens. The archenteron gives off five pouches, — a single large anterior pouch, the anterior enterocœl which subsequently communicates with the exterior through a

dorsal pore, a pair of collar pouches with exceedingly small openings into the archenteron, and a posterior pair of folds with larger openings into the archenteron. These evaginations subsequently pinch off and form the body cavities. The nervous system forms in the mid-dorsal collar region by delamination of ectoderm, and at its two ends it increases by invaginations. The details of the later stages need not be given here. The upper anterior fold of the digestive tract is continued forward under the proboscis gland with the base of the proboscis, and Bateson speaks of this as the notochord, and believes it to be homologous with the same organ in the Vertebrates. A single pair of gill slits first appears, and others form behind it seriatim. The tongue bar develops in them. The collar pores are formed by hollow invaginations of ectoderm opening into the body cavity of the collar, and are to be compared to the brown funnels of *Amphioxus*. The so-called heart (proboscis vesicle) is formed from an accumulation of mesenchymatous tissue. Bateson's statement that the cavity of the sac of the proboscis gland opens anteriorly into the enterocœl, is an error, I believe. Its origin from a closed vesicle in *Tornaria* points to this, and I have examined carefully the adult of *B. Kowalevski* and found no opening. Bateson does not decide whether *Tornaria* or the larva of *B. Kowalevski* represents the more primitive form of development. He minimizes the supposed relationship of *Tornaria* to the Echinoderm larva, and appears not to believe in the relationship to the Echinoderms. On the other hand, he draws attention for the first time to the relationship of *Balanoglossus* to the Vertebrates. The following similarities of organs in the two forms point to this relationship: 1, the notochord; 2, the gills, branchial skeleton, and blood supply; 3, the central nervous system; 4, the origin of the mesoblast; 5, the peculiar fate and remarkable assymetry of the anterior pouch; 6, the atria (or folds of the collar); 7, the excretory funnels. There followed a speculative portion on the ancestry of the Chordata.

Spengel published in 1884, after Bateson's first contribution, an abstract of his work on the anatomy and embryology of *Balanoglossus*. He showed that in *B. Kupfferi* there is a right and left water pore (I may state here that in a single individual of *B. Kowalevski* I found a pair—right and left—of water

pores, presumably a case of atavism). Spengel shows clearly that the proboscis vesicle (so-called heart) does not contain blood and is completely closed on all sides. The connection between the anterior blood sinus (of the proboscis) and the blood-vessels of the trunk is shown. The collar pores arise as evaginations from the first gill slits and connect secondarily with the cavity of the collar. The nervous system of the adult is described, and it is stated that it arises as an ectodermal invagination in the collar region of the embryo. The reproductive gonads open by a series of small pores to the exterior.

M. A. F. Marion described two new species of *Balanoglossus* in 1886, but did not enter into any discussion as to the position of the animals. Also R. Koehler published a paper in 1886 on the anatomy of another new species, and later (July, 1886) he published a short paper on the ancestry of *Balanoglossus*. He rejects any affinity with the Echinoderms and follows Bateson in the belief of a Chordate relationship, but believes a more precise opinion may be given as to the systematic position of *Balanoglossus* than Bateson expressed. *Balanoglossus* is degenerate, and its larval form has adapted itself *secondarily* to the same conditions as the larva of the Echinoderms; hence its *outward* similarity. The ancestry of the Chordata goes back to the Worms (probably to the Chaetopoda). *Balanoglossus* branched off from the main stem before the earliest Chordate arose. Later another degenerate branch arose represented by the degenerate series Cyclostomes, Amphioxus, and Tunicates. Haldeman described also in this year a species of *Tornaria* found at Beaufort, N.C. (U.S.A.) It differs from the New England *Tornaria*, and is in many respects like that described by Metschnikoff.

Weldon, in 1887, published a preliminary note on two new species of *Tornaria* from the Bahamas. The Nassau larva is the same that is described in the preceding section, where a longer reference is made to the discovery.

In 1888, Schimkewitsch published a short paper on a new species of *Balanoglossus*. He suggests that the pulsating vesicle of *Tornaria* may prove homologous to the pulsating vesicle of the Molluscan larva. The cavities of the paired enterocoels are homologous with the cavities of the muscle plate of the vertebrate embryo. The generative organs have

no connection with the ectoderm, as affirmed by Bateson, but arise from the peritoneum as a series of sacs attached by a hollow stalk. One may regard *Balanoglossus* as a modified Trochophore, having a single anterior body segment and a head ganglion under the apical plate. The Trochophora has acquired certain modifications; viz. dorsal nerve tube, gill slits, etc., which ally it to the Chordata. Bourne records (1889) *Tornaria* from the coast of England, believing it to be *Tornaria Kröhnii* of the Mediterranean. The figure of the larva (13, measuring 1 mm. in length) that he gives, seems to be identical with the New England form figured by Agassiz and myself (Fig. 6, Pl. I.). The question immediately arises as to whether this larva, if identical, has so wide a distribution, and gives possibly a hint as to the parent form, and locality, of the New England larva. The time of year recorded is also worthy of note, — both are recorded about August 9. (The English form also September 21.) The youngest larva figured is at the same stage described by Fewkes (see *ante*). Bourne did not observe the formation of the anterior (left) enterocœl, and remarks rather carelessly that this body cavity is formed probably from the amœboid cells found scattered in the segmentation cavity. Unfortunately, no evidence at all is given in support of this statement. He says “the ‘heart’ (proboscis of Bateson) of Agassiz, Mit-schnikoff, and Spengel makes its appearance . . . at this stage as a vesicle lying just above and to one side of the proboscis pore, . . . and an examination of the figures 7 and 8 shows that it is formed as an invagination of the ectoderm just above and to one side of the proboscis pore,” as described by Spengel. I have given my reasons for dissenting from this view of Spengel, and I think have discovered earlier stages in the development of the proboscis gland than seen by Bourne. It is interesting, however, to note that Bourne believes the anterior right enterocœl to come from mesenchyme, and I believe the proboscis gland to have this mode of origin. If these statements were both true, then the identity of the anterior enterocœl and the proboscis gland would be proven, and, moreover, an interesting relationship established between the enterocœls and mesenchyme. I cannot, however, accept Bourne’s statement of the origin of the anterior left enterocœl without some evidence. On the other hand, I believe Goette’s statement that

it arises from the *oesophagus* to be based on an obvious misinterpretation, and hence conclude that as yet we do not know how this organ arises in Tornaria, and that all that remains is to fall back upon the work of Bateson, where it is clearly demonstrated that in the larva of *B. Kowalevski* the left enterocœl arises as an evagination from the digestive tract. Bourne is further in error, I believe, in his description of the formation of the *first* paired body cavities ("collar cavities"). These he describes as arising from two buds at opposite points on the upper edge of the "*intestine*" in connection with the *second* paired body cavities, and later the upper ends of these proliferations, pinching off, forms the first pair or collar cavities, and the remaining cells form the second paired body cavities. An examination of a larger number of embryos would have shown, I believe, that in reality the collar cavities arise independently from the posterior (last) paired cavities, by proliferation of the wall of the stomach, and that the account given by Bateson for *B. Kowalevski* will apply in general to the Tornaria as well.

Again in 1890 Schimkewitsch published an abstract of two Russian memoirs on the homology of various organs of the Enteropneusta, Echinodermata, and Chordata. He accepts the *Pentactula* (Semon) as the type for Echinoderm development. The anterior anterocœl of Tornaria and Echinoderm is homologous to the anterior left body cavity of *Amphioxus*, which also communicates with the exterior. The proboscis vesicle of *Balanoglossus* is a part of the cœlom, and may represent the myocœl of the proboscis segment. The blood-vessels are much alike in *Amphioxus* and *Synapta* (as well as in Annelids and Nemertines). The gill clefts remain alone characteristic of the Chordata. The gonads of Annelids, Nemertines, Enteropneustra, *Amphioxus*, and Echinoderms are formed on the same type, and the genital openings of *Balanoglossus* and Nemertines are probably homologous with the ectodermal part of the segmental organ. The nerve tube of *Balanoglossus* corresponds to that of the Chordata.

In their *Lehrbuch d. Entwicklungsgeschichte*, etc., Korschelt and Heider state in their general summary of the groups that a comparison of the Tornaria with the Echinoderm larva is difficult to carry out, inasmuch as there is no homologue for the circular band of Tornaria. The latter has an apical plate and

eye spots which are absent in the Echinoderm larva, and the resemblance between the two larvæ is only superficial. The presence of apical plate and its muscle band points rather to a relationship of the Tornaria to the Trochophora. There are several similarities between Balanoglossus and Chordata, but the comparisons made are not always on a sound basis.

There are a few other recent papers of a general interest in this connection which may be briefly mentioned here. Caldwell in 1882 pointed out a relationship between the Brachiopods and Phoronis, and thought that the Polyzoa might be a related but now a degenerate branch. Further, he thought it possible that Sipunculus and Phascolosoma might be related to the same types, but on the other hand there is the same probability that they may be farther stages in degeneration of segmented forms like Echiurus. Lankester, in the article "Polyzoa" (*Encyclopædia Britannica*, 1885), gives a most suggestive classification of the same forms. Under the name Padoxonia he includes Sipunculoides, Brachiopods, and Polyzoa,—the last including, 1st, Pterobranchia (Rhabdopleura, Cephalodiscus); 2d, Vermiformia (Phoronis); 3d, Eupolyzoa (true Polyzoa). The interrelation of Rhabdopleures, Cephalodiscus, and Phoronis and the true Polyzoa is discussed, and Lankester also points out the resemblance of Polyzoa to the Brachiopods. Harmer, in 1887, in an appendix to McIntosh's paper on *Cephalodiscus Dodecalophus* calls attention to the relationship of this animal to Balanoglossus. He believes, therefore, that Cephalodiscus (and possibly also Rhabdopleura) must be removed from the Polyzoa and placed amongst the Hemi-Chordata. The egg embryology has not been studied, but Harmer studied the development of the buds and finds, as in Balanoglossus, there is present in the youngest stages five body cavities,—a single anterior pouch opening to the exterior by a pair of water pores,—in the collar region a pair of cavities right and left,—and lastly a posterior pair of sacs forming the musculature of the digestive tract. There is a thickened portion of the ectoderm forming the nervous system in the dorsal part of the collar. The reproductive organs are represented by a pair of gonads, lying in the posterior body cavity and opening by a pair of small pores to the exterior. There is also a pair of gill slits opening from the œsophagus to the outside, beneath the opercular folds of the collar. The

resemblance to *Balanoglossus* in all the essential points is most striking, and points almost certainly to a near relationship between the two forms. The author points out the possible relationship of *Cephalodiscus* (and *Balanoglossus*) to *Phoronis*, and is inclined to believe that *Rhabdopleura* shows more affinities to *Cephalodiscus* than to the *Polyzoa*.

Finally, in 1890, Lang discussed the relationship of *Balanoglossus* to *Cephalodiscus*. All of the differences between the two forms may be explained by the sedentary condition of *Cephalodiscus*. The organization of *Cephalodiscus* shows characteristics corresponding to the young stages of *Balanoglossus*. But it cannot be affirmed with Harmer that *Cephalodiscus* is a more primitive form than *Balanoglossus*, for it is just as easily maintained that the peculiarities of *Cephalodiscus* would arise if *Balanoglossus* assumed a fixed condition. There are many difficulties, Lang thinks, in assuming a philogenetic connection between *Cephalodiscus* and *Polyzoa* (and *Phoronis*).

#### THEORETICAL.

Two conclusions we may draw, I believe, which are something more than possibilities. First, that the similarities of *Tornaria* to the Echinoderm larva, say *Auricularia*, are not to be explained away by calling them superficial resemblances, but we must conclude that they have profound morphological significance. Secondly, that the relationship of *Balanoglossus* to the Chordata is a genetic connection. The reasons for these beliefs may be stated briefly, first for the relationship to the Echinoderm, and secondly to the Vertebrates; afterwards the less important, because more speculative, problems may be discussed. Those zoölogists who have worked both on *Tornaria* and Echinoderm larvæ have, as we have seen, in nearly every case recognized the resemblances between the two forms. This furnishes a fair argument, I think, as to the general resemblance; but if we descend into details, we find even more striking similarities. First in importance is the identity in the two groups of the anterior antero-coel and its dorsal water pore. We have every reason to believe this organ to be in *Tornaria* a diverticulum from the digestive tract (Bateson has shown this to be the case in the larva formed by a direct development). The anterior

enterocœl opens in both forms by a water pore on the dorsal surface a little to the left of the middle line. We have good reason to believe that the ancestor of *Tornaria* had two of these dorsal openings — right and left. This is indicated in the adult of *B. Kupfferi*, and I have found it in a single specimen of *B. Kowalevski* when its presence was presumably atavistic. Moreover, *Cephalodiscus*, which is undoubtedly related to *Balanoglossus*, has a pair of these dorsal water pores. It is also of the greatest importance that when these two openings are present they both communicate with the single unpaired enterocœl. In the *Auricularia* there has been discovered in some cases at least a pair of these dorsal pores, opening on the dorsal surface right and left and communicating with the single anterior enterocœl, as pointed out by Ludwig and more recently by Brooks and Field. Subsequently the right pore disappears, and the left remains, resulting in the condition found in *Tornaria*. The formation of muscles from the cells of the inner wall of this enterocœl is common to the two groups. Finally, an intimate connection between a part of this enterocœl and the so-called heart or anterior blood-vessel is found in both *Balanoglossus* and *Echinoderm*. The presence in both *Tornaria* and *Auricularia* (as shown by Field) of a mesenchymatous vesicle closely connected with the anterior enterocœl, and in the one case certainly, and in the other presumably, also connected with the formation of the heart, is most significant. The presence of wandering mesenchyme in the blastocœl is common to the two; but more important is the accumulation of many of these cells around the endodermal œsophagus. This can hardly be explained by mere chance. The œsophagus itself is almost entirely endodermal in *Tornaria*, as is indicated by the shortness of the stomodæal invagination in the larva studied by Bateson, and in *Tornaria* by the formation of gill pouches and “notochord” from its walls. The œsophagus of *Auricularia* is also almost entirely endodermal in its origin. The division of the digestive tract into three compartments is the same in each, although this is hardly of great importance. The course of the longitudinal ciliated band is very similar in the two; indeed, the one might almost be substituted for the other; and if I have been fortunate in my comparison of a breaking at the apical plate and of a secondary tendency of a new fusion from right to left, we see an exactly

similar process to that found in Auricularia. The histology of the ciliated band is exactly the same in the two larvæ, and the continuity between the cilia of the longitudinal band in the region *in front* of the mouth with the ciliated upper dorsal surface of the œsophagus may in some degree represent a similar fusion found in Auricularia and recently described by Semon. Lastly, the sudden and very great diminution in size of the larvæ at the time of metamorphosis is unique; and as we have an exactly similar phenomenon in the metamorphosis of the Holothurian larva into the young Holothurian (Pentactula), we may, I think, add this to the other resemblances.

The differences between the larvæ have been pointed out in the preceding section. The apical plate and eyes seem to be absent in the Auricularia, although there may be a rudiment (?) of the first of these in the Echinoderm larva. The muscle band from the apical plate in Tornaria has no homologue in Auricularia. The presence of two posterior pairs of enterocœls in Tornaria is not readily to be explained, and is, it seems to me, the one great difficulty in our comparison. The anterior enterocœl in the Holothurian, for instance, gives rise not only to the same structure as the anterior enterocœl of Tornaria, but also to the posterior body cavities of the Holothurian as well. The problem of enterocœl formation and its apparently close connection with metamerism is still one of the unsolved problems of morphology, and until we have a clearer knowledge of the meaning of the phenomenon, all detailed comparisons in which the subject is involved must remain open. The large posterior circular band of Tornaria seems to have no homologue in Auricularia, and is apparently a structure *sui generis*.

But what seems to me to be the most essential point in the comparison of Tornaria and Auricularia is one that is not generally emphasized; viz. that it is the young Tornaria that resembles most closely the Echinoderm larva, and not the older Tornaria. If we compare the young Tornaria before the development of the circular band with the other larva, the resemblance amounts almost to an identity, so that the larvæ are almost indistinguishable. *This identity cannot be explained by an adaptation to similar conditions of life in the two forms*, for the reason that the most essential and vital points of comparison relate to the internal organs. The anterior body cavity with its left dorsal

water pore, the development of the proboscis vesicle, and the meshwork of mesenchymatous cells over the œsophagus in the two forms will defy explanation as external adaptation.

Moreover, the points of difference between the larvæ come into the later life of the *Tornaria*, and it must not be overlooked that the posterior ciliated band must not only have had a later origin in the larval history, but has as well an essentially different structure from the longitudinal band.

Concerning the relationship between *Balanoglossus* and the Vertebrates, I have little new to add to what Bateson has already given, nor does the subject come so much within the scope of the present paper. The resemblances which Bateson pointed out have been quoted on a previous page and need not appear again. I have called attention to the close similarity in the method by which the neural plate is formed in the *Tornaria* and in *Amphioxus*. In passing, I may say it seems to me that the evidence given by both of these forms and by the ontogeny of the Vertebrates points out that ancestrally the dorsal nerve chord probably arose as a single median unpaired structure, as has been suggested by others, and that its later bilaterality may be entirely a secondary phenomenon, so that all attempts to reduce it back to the paired chords of Annelids or Nemertians may be futile.

I have studied with some care the structure of the gills of *Balanoglossus* and their supporting chitinous bars, and have satisfied myself as to the identity of the structures in *Balanoglossus* and *Amphioxus*. The tongue bars growing down from the dorsal side in both forms divide each gill slit into two parts. Moreover, the relationship of the chitinous rods in the primary and secondary (tongue) bars is identical in the two forms. To find such an astonishing agreement in these details, which are in all extremely complicated, can only point, I believe, to a relationship between *Balanoglossus* and *Amphioxus*.

One word, before leaving the subject, as to the "notochord." Whether we are justified in regarding the forward extension of the dorsal wall of the gut in *Balanoglossus* and *Cephalodiscus* as the homologue of the *chorda dorsalis* of the Vertebrates is open, perhaps, to doubt. Nevertheless it seems probable that they must be looked upon as part of the same process; viz. a specialization of the dorsal wall of the gut into other than diges-

tive functions, and it is certainly significant that the cavity of the notochord of *Balanoglossus* is continuous with the strongly marked dorsal groove above the œsophagus. It has been objected to Bateson's comparison that the dorsal aorta of the Vertebrates is beneath the notochord, and the dorsal blood-vessel in *Balanoglossus* is above it, and that in the latter the blood flow is forward, while in the former it runs backwards. The objection is trivial, inasmuch as it assumes the necessity of the identity of the two blood-vessels. Indeed, it seems to me that this very difference of the vessels in the two groups is of great assistance in a comparison between them. As the notochord arose in Vertebrates from *before backwards* by the union of the two sides of the digestive wall, the lateral blood-vessels of the folds, at first double, would tend to unite into a single trunk, and we find in the ontogeny of Vertebrates this process of union of the blood-vessels to form the dorsal aorta is actually brought about. Bateson's reasons, then, for including *Balanoglossus* with the Vertebrates in the large group Chordata seem to me to be valid. However, it does not follow that the whole length of the *Balanoglossus* of to-day represents the length of the ancestral form from which the Chordata arose. I should rather regard the greater part of the length of *Balanoglossus* as a secondary acquirement; as an adaptation to its peculiar habitat in a tube in the sand. The Nermertines and many Annelids furnish us analogies.<sup>1</sup>

If we grant this much concerning the relationships of *Balanoglossus* on the one hand to the Echinoderms, and on the other to the Vertebrates, we have gone perhaps as far as the facts permit. To follow out detailed comparisons between groups that must have separated so long ago, and to give each an exact place in a newly constructed phylogenetic tree is likely — and we have obvious examples — to be disastrous.

<sup>1</sup> No one knows how long the ancestral Vertebrate may have been. We may have been unconsciously prejudiced by too close comparisons with Annelids. For instance, it does not seem to be plausible that the anal end of the Vertebrate was ever at the distal end of the "tail"; that is, to have opened out from the last tail metamere, as in Annelids. On the contrary, it seems more plausible that the vertebrate tail may represent a dorso-posterior outgrowth of the body beyond the anus. If the trunk was already metameric it is conceivable that the tail may have secondarily become so; or, the metamerisation of the trunk and tail may have been acquired at the same time and each due to the same laws.

The relationship of *Tornaria* to the Trochophore (or even to the Veliger) is much more difficult to safely determine than the relationship to *Auricularia*. Balfour expressed himself—and the view has been taken by others—as inclined to believe in a relationship to the Trochophore. Metschnikoff has shown the very great difficulties in the way of such a comparison. He pointed out the absence of the anterior enterocoel in the Trochophore, the differences in the position of the ciliated bands, the presence of *two* muscle bands from the apical plate of the Trochophore, and the ectodermal origin of the œsophagus of the latter. To these we may now add that the apical plate of these two forms is only superficially similar. The nerve-fibre layer in *Tornaria* does not form nerve bundles and branching ganglion cells as in the Trochophore. The eyes are not at all similar, but exceedingly different, most probably essentially so. There is no structure in *Tornaria* similar to the head kidneys of Trochophora. The ciliated bands have essentially different histological structures. In the Trochophore they are formed by large columnar cells, while in *Tornaria* the longitudinal band is formed of exceedingly small and closely crowded cells. Thus while we cannot positively deny that these larvæ have had a common form in the past, yet the evidence we have at present goes against any such supposed relationship.

So much for the more important larval forms. We may now for a moment examine into the affinities between the adult *Balanoglossus* and other groups. The Nemertinean is a form to which many zoölogists have turned to find similarities to *Balanoglossus*. Both are long animals living in the sand, having each a delicate and richly ciliated ectoderm; the mouth with a proboscis at one end, the terminal anus at the other. Both have closed blood-vessels and serially arranged gonads. I admit a sort of natural suggestiveness in these comparisons, but the points of similitude formerly emphasized have been largely shown to be false homologies, and I have been unable to find any important resemblances which are common to the two groups. The proboscis of the Nemertine is entirely different from the so-called organ of *Balanoglossus*, and the nervous system, gill slits, notochord, enterocoels of the latter have no homologues to all appearances in the Nemertine, and there seem to be no grounds for comparison between the larval forms.

With the adult Echinoderm it is different, as there are many points, besides the similarities of the larvæ, common to the two groups. If we assume with Semon that the *Pentactula* comes nearest to the ancestral type of the adult Echinoderm, we have found a form with which it is not difficult to compare the adult *Balanoglossus*. Briefly these resemblances may be pointed out. In each there is a diffuse nervous system formed by the ectoderm with a nerve-fibre layer beneath. Certain parts of the ectoderm have been specialized to a slight degree, in each forming more central nerve paths. The body cavities present close similarities both in their origin and fate; the musculature being formed from its walls and the peritoneal epithelium giving rise to the generative products, the gonads, opening by very short simple tubes to the exterior. More important is the close connection between the locomotor water system of each, which comes from the anterior enterocœl, and while I do not think that we can directly compare the proboscis of *Balanoglossus* with an ambulacral foot of Echinoderm, as Metschnikoff has done, still the fundamental arrangement of the two systems of organs is the same. Moreover, the madreporic plate and the dorsal water pore of *Balanoglossus* are practically identical; also the blood system and its close connection with the anterior enterocœl in the two forms is very similar.

In *Balanoglossus* we have discovered an animal outside the group Chordata, showing very primitive structures and relationships and having already a mouth opening on the ventral or abneural (natural) side of the body. Now if the evidence brought forward to show its resemblance to the Chordata be valid, there is no necessity to believe, nor any reason for assuming, that the present chordate mouth is a new structure and that an old mouth of some kind or other has been lost during the past. And if *Balanoglossus* be related through its larva with the Echinoderms, as I have attempted to show in the preceding page, we see how old a phylum that of the Vertebrates must be, and hence the futility of attempting to derive them from any such highly specialized animals as the Annelids of to-day.

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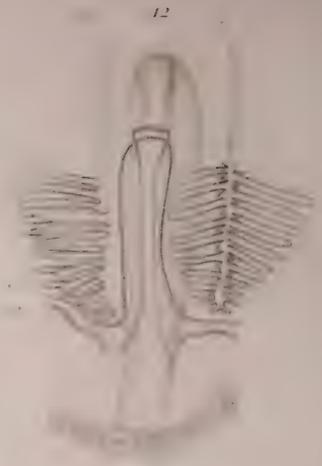
- A.* Apical plate.
- ac.* Anterior lateral fold.
- b, b'*. Upper turn of longitudinal band.
- bc<sup>2</sup>*. Second (paired) body cavities.
- bc<sup>3</sup>*. Third (paired) body cavities.
- cb'*. Circular ciliated band.
- d. v.* Dorsal blood-vessel.
- e.* Anterior enterocoel.
- g.* Posterior collar groove.
- g. p.* Second gill pouch.
- gr.* Groove at union of cesophagus and stomach.
- h.* Heart or proboscis blood-vessel.
- I.* Intestine.
- l.* Lower limb of longitudinal band.
- l'*. Part of longitudinal band joining *l*.
- l. b.* Longitudinal band.
- m.* Mouth.
- m'*. Ciliated circumoral region below mouth.
- m. b.* Muscle band from apical plate to enterocoel.
- n.* Anus.
- nc.* Notochord.
- o.* Cesophagus.
- o.* Pre-oral part of longitudinal ciliated band.
- p.* Post-oral part of longitudinal ciliated band.
- pc.* Posterior lateral fold.
- q.* Upper wave of lower limb of longitudinal band.
- S.* Stomach.
- v.* Proboscis vesicle = "heart."
- v. v.* Ventral blood-vessel.
- w.* Digestive tract wall.
- w. p.* External opening of ant. enterocoel = water pore.
- x.* Posterior lateral area.
- y.* Middle lateral area.
- z.* Anterior lateral area.

## DESCRIPTION OF PLATE XXIV.

- FIG. 1. Youngest larva caught, seen from side view.  
FIG. 2. Same, seen from behind.  
FIG. 3. Same, seen from front.  
FIG. 4. Enlarged view of apical plate and enterocel of same larva.  
FIG. 5. Older larva than last. Proboscis vesicle, *v*, and paired body cavities appear. Right side shown in figure.  
FIG. 6. Fully formed Tornaria. Left side shown in figure.  
FIG. 7. Apical plate, with eyes and ciliated band of last. Seen from above.  
FIG. 8. Oesophagus and three pairs of gill pouches of larva in Fig. 6. Seen from above.  
FIG. 9. Young Balanoglossus. Seventy hours older than Fig. 6. Alcoholic specimen.  
FIG. 10. Apical plate of Nassau larvæ. Seen from above.  
FIG. 11. Side view of part of Nassau larva, showing longitudinal band, *o* and *p*, and circular band, *cb*, also the anterior lateral and middle lateral areas.  
FIG. 12. Part of Nassau larva, seen from in front, with digestive tract seen through body walls; also longitudinal and circular bands.











## DESCRIPTION OF PLATE XXV.

FIG. 13. Section through wall of young larva (Fig. 5), showing beginning of proboscis vesicle, *v*.

FIG. 14. Next section in same series.

FIG. 15. Optical section of anterior enterocoel and proboscis vesicle, *v*. Older than last.

FIG. 16. Optical section. Same, but older.

FIG. 17. " " of still older organs.

FIG. 18. " " of enterocoel, vesicle, and heart, *h*, of larva of Fig. 6.

FIG. 19. Longitudinal section through 18 in plane of paper.

FIG. 20. Section through Fig. 17 at line *a*.

FIG. 21. " " " " *b*.

FIG. 22. " " " " *c*.

FIG. 23. " " 18 " *d*.

FIG. 24. " " " " *e*.

FIG. 25. " " " " *f*.

FIG. 26. " " " " *g*.

FIG. 27. Section through side wall of stomach to show origin of the first paired body cavities, second pair of enterocoels, collar body cavities, *bc*<sup>2</sup>.

FIG. 28. Section to one side of last.

FIG. 29. Section to other side of last.

FIG. 30. Section through side wall of stomach of still younger stage than Fig. 27.

FIG. 31. Section through older stage than Fig. 27. All connection with digestive cells lost.

FIG. 32. Section through last paired body cavities. *bc*<sup>3</sup>, showing their origin.





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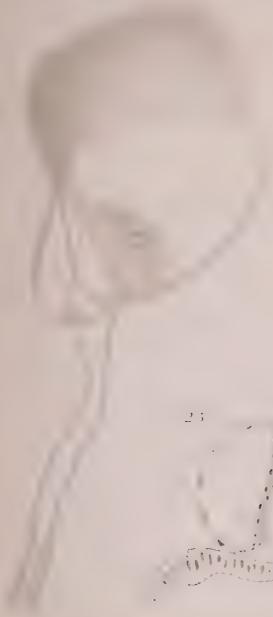
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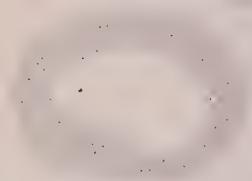
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## DESCRIPTION OF PLATE XXVI.

FIG. 33. Section through Fig. 6, posterior to mouth, and cutting cesophagus and enterocoel. See line 33, Fig. 6.

FIG. 34. Section of same series in middle of larva. See line 34, Fig. 6.

FIG. 35. Section in same series through last pair of body cavities. See line 35, Fig. 6.

FIG. 36. Section at right angles to last, and cutting larva from right to left. Only part of the section figured.

FIG. 37. Section of larva, same age, showing connection of cesophagus with stomach.

FIG. 38. Section through anterior wall of stomach in mid-ventral line.

FIG. 39. Longitudinal section of wall of embryo.

FIG. 40. Longitudinal section in antero-posterior plane through a larva immediately after metamorphosis.

FIG. 41. Section through second gill pouch of larva of same age as Fig. 40.





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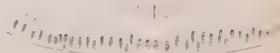
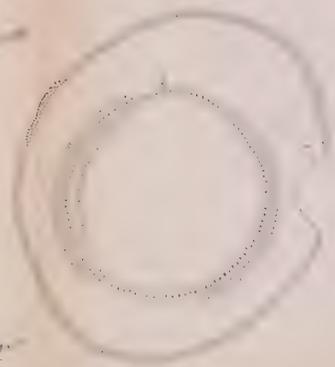
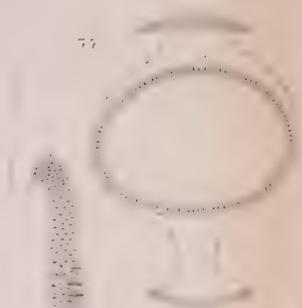
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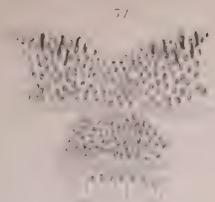


## DESCRIPTION OF PLATE XXVII.

- FIG. 42. Section of longitudinal ciliated band to show structure of pigment spot.  
FIG. 43. Surface view of eyes of *Tornaria*, Fig. 6.  
FIG. 44. Section of same, and in a parallel plane.  
FIG. 44'. Section of same, posterior to Fig. 44.  
FIG. 45. Antero-posterior section of apical plate of Fig. 6.  
FIG. 46. Surface view of mid-dorsal surface of larva at time of metamorphosis, and older than Fig. 6.  
FIG. 47. Same of older larva.  
FIG. 48. Cross-section through mid-dorsal line in collar region of embryo between Figs. 6 and 46.  
FIG. 49. Cross-section through mid-dorsal line in anterior collar region of Fig. 46.  
FIG. 50. Same through middle of collar region.  
FIGS. 51-55. Series of cross-sections through dorsal nerve cord of young *Balanoglossus*. Fig. 51, in anterior region of collar. Figs. 53-55, behind collar.  
FIG. 56. Section through anterior end of *Tornaria*, showing posterior-lateral and mid-lateral areas,  $x$  and  $y$ .  
FIG. 57. Section through same region of larva during metamorphosis.











## DESCRIPTION OF PLATE XXVIII.

FIG. 58. Cross-section through young *Balanoglossus*. See Fig. 9, line 58, through anterior collar region.

FIG. 59. Same through base of proboscis above. See line 59, Fig. 9.

FIG. 60. Same through base of proboscis. See line 60, Fig. 9.

FIG. 61. Same through proboscis. See line 61, Fig. 9.

FIG. 62. Same through anterior proboscis. See line 62, Fig. 9.

FIG. 63. Portion of section through base of proboscis between 60 and 61.

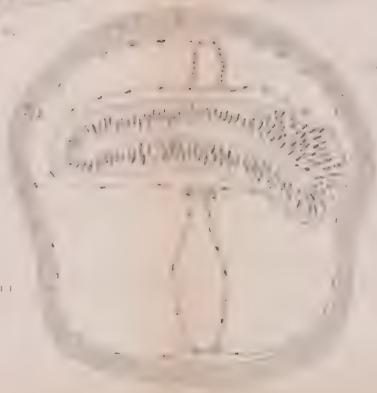
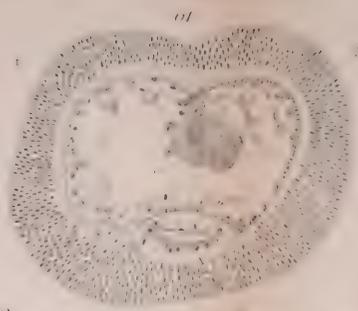
FIG. 64. Same as 58, through first pair of gill pouches. See line 64, Fig. 9.

FIG. 65. Same as 58, through second pair of gill slits. See line 65, Fig. 9.

FIG. 66. Same as 58, through posterior end of larva. See line 66, Fig. 9.









## A HUMAN EMBRYO TWENTY-SIX DAYS OLD.

F. MALL.

SEVERAL years ago Dr. C. O. Miller of the Johns Hopkins University gave me a very young human embryo which was so well preserved and so perfect in all respects that it justified a very careful study. He very kindly has procured for me the following history.

"The woman, twenty-nine years old, had been married nine years, and had always menstruated regularly every twenty-eight days, the period each time lasting three days. She had given birth to four healthy children, the last having been born January 1, 1888. Her last menstrual period began on October 6, 1888, and ended on the 9th. Her next menstrual period should have begun on November 3, but on account of its falling out, she concluded that she was pregnant, and, on November 20, began taking large doses of ergot, which she had repeatedly taken to produce abortion in earlier pregnancies, but with no result. Several days later she applied to a professional abortionist who used instruments, after which she had a continuous metrorrhagia, and called for me to attend her. On November 27, just fifty-two days after the beginning of the last menstrual period, the unbroken ovum came away. It was kept in a cool place for three hours, and then without opening placed in eighty per cent alcohol."

When the specimen came into my hands it was found covered with villi two or three millimetres in length, without which it measured 22 mm. in diameter. Upon opening it I found that the embryo had been hardened without any irregular shrinkage. A year later it was shown by staining a portion of the membranes that the cells were preserved excellently; and the embryo was then stained with alum carmine, imbedded in paraffin, and cut into sections at right angles to the branchial arches  $15\ \mu$  thick.

## AGE.

The nape-breech length measured 7 mm. and the vertex-breech 6 mm. The study of mammalian embryos, as well as a series of human embryos, tells us that this embryo cannot be over a month old. From the results of post-mortem examinations of women shortly before the beginning of menstruation, Bischoff, Williams, Dalton, Leopold, and others place ovulation two or three days before the beginning of menstruation.<sup>1</sup> Especially on account of the study of several cases in which the earliest possible cohabitation took place a week or two after the last menstrual period, embryologists and gynecologists reckon the duration of pregnancy from the beginning of the first period which has fallen out.

So in order to estimate more accurately the age of this embryo, we must subtract twenty-eight from the time which has elapsed since the beginning of the last period (fifty-two days), and add two for the time between ovulation and menstruation. The shape and size of this embryo correspond with that described by others as the fourth week, and twenty-six days is in all probability its age.

## EXTERNAL FORM.

The embryo is flexed upon itself, forming almost a circle (Pl. XXIX., Fig. 1). The head shows the outline of the brain within, and also a marked elevation over the region of the Gasserian ganglion. The nasal pit is a large shallow depression, being well exposed on both sides. The lense is small, and is surrounded by a groove which is continued between the superior maxillary process and nasal pit.

Three branchial arches are visible on the right side, and four on the left. The ventral end of the first is bulbous, while from its dorsal end the superior maxillary process arises. The second is also bulbous on its ventral end, the major portion of the trunk hanging over the third arch. This is the embryonic operculum which will finally close the sinus præcervicalis. The third arch lies more towards the median line, that is, it is within the sinus præcervicalis. The fourth arch is visible only

<sup>1</sup> His, *Anat. mensch. Embryonen*, II, Leipzig, 1882.

on the left side; it lies deep in the sinus præcervicalis, and is almost covered by the third arch.

The clefts are irregular in shape, as shown in the figure; and the first, second, and third show marked depressions at their dorsal ends, which indicate the blending of the ectoderm with the seventh, ninth, and tenth nerves.

On the dorsal side of the branchial region, alike on both sides of the head, there is a marked depression which lies immediately over the otic vesicle. The vesicle, however, is fully separated from the ectoderm.

The protovertebræ are more marked on the right than the left side; twenty-seven on the right, and twenty-four on the left. On the right only the last seven cervical, all the dorsal and lumbar, and five sacral are visible; while on the left two occipital, all the cervical and dorsal, and but two lumbar are seen. The sections, however, show that the muscle plates are the same on both sides.

The extremities are well marked, the anterior being somewhat larger than the posterior. The anterior on the right side is flat, and bent directly towards the median line; while on the left it hangs away from the mouth. The posterior on the right is bent towards the head, and on the left side it is simply an oval mound.

Upon the body proper there are three marked elevations: two for the heart, and one for the liver. In general, these elevations are the same on both sides.

The umbilical cord is large, and lies on the left side of the body, as described by Waldeyer<sup>1</sup> and by Janošik.<sup>2</sup> In most embryos described it lies on the right side. The cord is short, and midway between the embryo and its attachment to the chorion it shows a decided enlargement. The umbilical vesicle is large, measuring 7 mm. in length and 5 in diameter.

#### METHOD OF STUDY.

The embryo was stained with alum carmine, and cut into serial sections 15  $\mu$  thick. Although thinner sections undoubtedly would have been better to study the histology, for my purpose I

<sup>1</sup> *Studien des physiol. Inst. zu Breslau*, Heft 3, 1865.

<sup>2</sup> *Arch. f. mik. Anat.*, Bd. 30.

desired sections in no way distorted. On account of greater ease in studying the sections, I cut the embryo at right angles to the nape-breech length, at the same time striking the branchial arches nearly at right angles. In all there were 351 perfect sections, none lost, and only two or three slightly distorted. The sections were enlarged  $66\frac{2}{3}$  diameters, which at the same time increased their thickness to 1 mm. Every second section was now drawn on wax plates 2 mm. thick, and the external outline of the section cut out. Before working the interior of the enlarged sections, they were carefully piled, in order to obtain the form of the exterior of the embryo. Next, I made a plaster mould of the pile of plates, in order to keep them in position. The plates were constantly kept within the half-mould, in order to keep the model from becoming distorted. This latter procedure proved of great value, as the plates were cut into pieces in order to model the various organs. All the wax representing the tissue between the organs and the exterior of the body on the left side was removed, exposing the organs as shown in the figure on Plate XXX. Then the organs were freed from the opposite side, and the pieces of wax blended so as to isolate each organ by itself.

The body cavity was modelled as a corrosion preparation, by drawing its outline on a second set of plates, and removing all the wax representing the body cavity, then piling the plates again, and finally casting the whole with Wood's metal. The metal was next smoothed and imbedded in plaster of paris, from which it was removed by boiling. The plaster mould was now cast with solder, and the wax broken off. By this method a metal cast of the whole cœlom was obtained.<sup>1</sup>

The shrinkage while imbedding in paraffin was slightly over ten per cent, so our model, which represents the section of the embryo enlarged  $66\frac{2}{3}$  times, is but sixty times larger than the specimen while in alcohol. All the measurements I give have been reduced to correspond with those of the alcoholic specimen.

<sup>1</sup> Plates made of pure wax with a sheet of thin paper on either side, can be obtained from Grüber of Leipsic. Plates of this sort can best be cut by means of a jig-saw. I cast most of my plates by pouring the melted wax in a tank containing hot water. The tank was of such a size that 500 grammes of wax made a plate two millimetres thick. In most cases it is desirable to work with wax softened by adding about five per cent of Burgundy pitch and about ten per cent of resin.

## CENTRAL NERVOUS SYSTEM.

When the neural tube is straightened it measures from end to end 17 mm. with a diameter of 1.5 mm. for the fore-brain, and 0.5 mm. at the point between the posterior extremities. Its general shape is shown, Plate XXX., which corresponds quite well with His's *Br.*<sub>3</sub>.<sup>1</sup> On the exterior it is plainly shown that the cerebrum and optic vesicle are attached to the fore-brain.

The cerebral hemispheres are represented on both sides by oval projections from the fore-brain, extending somewhat over the surrounding tissue on the mid-brain side, and under the eye. Viewed from the median side the pit represents a stage midway between His's *Br.*<sub>3</sub> and *K. O.*<sup>2</sup> On the median line between the two hemispheres there is a fold of medullary tube-wall which extends more than a third across the cerebrum, and has a tendency to cut it in half. It measures 0.4 mm. in perpendicular, and projects 0.16 mm. into the fore-brain vesicle. Compared with His's figures, this is undoubtedly the epithelial covering of the choroid plexus.

Towards the mouth from the cerebrum there is the opening into the optic vesicle. It is triangular in shape, with the base on the oral side, and the apex pointing towards the inter-brain. The opening within the stem of the optic vesicle is round, and ends as a circle about the secondary ocular vesicle. Viewed from the outside, the secondary ocular vesicle is a round pit, in which lies the lense. There is no slit on the oral side of the stem (Plate XXX., Fig. 1).

The inter-brain shows a marked constriction in its middle, both on the outside and also within its lumen. This undoubtedly was caused by a shrinkage when the specimen was hardened.

As the mid-brain and hind-brain are approached, the walls gradually become thicker and thicker, until the after-brain is reached, when the ventral side alone increases, while the dorsal walls become very thin. From the origin of the facial nerve to the origin of the pneumogastric, the walls of the dorsal half of the neural tube are very thin. From now on, the thickness of the walls of the tube, with the exception of the extreme dorsal

<sup>1</sup> *Abhandl. d. K. S. Ges. d. Wiss.*, Bd. XIV., 1888.

<sup>2</sup> *Abhandl. d. K. S. Ges. d. Wiss.*, Bd. XV., Figs. 2 and 5.

and ventral sides,<sup>1</sup> is much the same in transverse section, the thickness gradually diminishing as the tail is approached.

#### CRANIAL NERVES.

The olfactory pit is sharply defined and is composed of five or six layers of cells. Throughout its extent cell divisions are present, most numerous, however, at its concave oral side. In this region there are marked pyramidal cells with their base towards the outside of the body and their apices pointing towards the brain. These cells undoubtedly mark the beginning of the olfactory nerve as pointed out by His. In *Amblystoma* and *Necturus* these cells are much more pronounced and can be traced in the various stages from the olfactory pit to the brain.

There is as yet no indication of a permanent optic nerve. The primary optic vesicle still communicates with the fore-brain while the distal or rod-and-cone layer of the secondary vesicle shows peculiar changes. The layer is about twice as thick as the proximal or pigment layer, and in both these are nuclear figures. The location of these cells, which are dividing, is on the margin which corresponds with the layer about the central canal in the spinal cord. The pigment layer is about five cells thick, while the rod-and-cone layer is about eight.

The rod-and-cone layer is composed of two distinct zones, — a distal or hyaline and a proximal or cellular. The hyaline zone lies next to the lense and seems to be composed of cilia, all being directed towards a centre lying within the lense. The granular zone is composed in great part of round cells between which are many bipolar and unipolar cells. The unipolar cells are more numerous than the bipolar and project, with their pole, towards the position which is later to be rods and cones. The bipolar send one pole in the same direction and the other into the hyaline layer.

At a point in the stem of the optic vesicle nearest the mouth there enters a vessel which is undoubtedly the *arteria centralis retinae*. As this perforates the hyaline layer, the "cilia" become shorter, but are in no way directed towards this artery,

<sup>1</sup> His, *Deckplatte, Bodenplatte.*

*i.e.* the future direction of the optic nerve. No doubt this layer is identical with the peripheral veil as described by His.<sup>1</sup>

It is extremely difficult to locate the origin of the third nerve. At the floor of the mid-brain there is a suspicious spot composed of several dozen cells which are somewhat separated from the remaining cells and lie partly within the terminal veil (Pl. XXX., Fig. 1, III.). No nerve fibres extend from the brain into the surrounding tissue.

The trochlear nerve is well marked as a small group of cells in the ventral wall of the isthmus between the mid-brain and hind-brain. The cells lie just under the terminal veil, and each sends a single short pole towards the dorsal part of the brain. They extend but half-way around the tube.

The Gasserian ganglion with its three branches marks the trifacial. Upon its ophthalmic branch a small group of cells indicates the ciliary ganglion. From the Gasserian ganglion numerous fibres enter the hind-brain as its sensory root. The motor root arises more ventral from a large group of cells and passes as a large bundle of fibres into the inferior maxillary branch of the nerve.

The sixth nerve is represented as a small group of cells, dorsal, but somewhat aboral from the first branchial cleft. None of the cells send prolongations from the brain to form a distinct nerve, but all of the unipolar motor cells are pointed in one direction.

It is extremely difficult to isolate the facial nerve from the auditory nerve ganglion. Following it from the second branchial arch it passes through the heart of the acoustico-facial ganglion, and after entering the neural tube passes towards the ventral side of the same, making an arch around the ganglion of the sixth to take its origin near the median line.

The acoustic ganglion extends from the facial to the auditory vesicle, to which it is adherent, and then with the facial nerve sends twigs into the after-brain. The auditory vesicle is olive-shaped, is placed at right angles to the after-brain, and from its dorsal end there is a marked prolongation, the beginning of the aquæductus vestibuli. The walls are of quite even thickness throughout, and the lumen is of the same general shape as the vesicle.

<sup>1</sup> His u. Braune's *Archiv*, 1889 (*Randschleier*).

Between the auditory vesicle and the after-brain lies the upper ganglion of the glosso-pharyngeal which receives fibres from a group of cells lying in the floor of the after-brain, and sends a bundle of fibres more dorsally into the same. On the ventral side there is a bundle of nerves which communicates with a second ganglion, the ganglion petrosum. The ganglion petrosum is in direct continuity with a slight invagination of ectoderm at the dorsal part of the second branchial groove, sends a branch into the third arch, and communicates with the ganglion jugulare of the vagus.

The vagus is composed of two enormous ganglia, as shown in Pl. XXX. The two ganglia are united by a band of cells, and from the ganglion nodosum a branch passes to the aboral and lateral side of the fourth branchial arch. At the central end of the nerve numerous branches pass into the after-brain. The ganglion jugulare receives at once twigs from the accessory nerve, which soon arrange themselves into a bundle to become fully separated before the ganglion nodosum is reached.

The accessory nerve arises as a row of bundles between the vagus and first cervical, and emerges from the after-brain midway between its dorsal and ventral walls. As the twigs approach the first cervical nerve, the origin becomes more ventral, and are continuous with the ventral root of this nerve. Although the rudimentary ganglion, first described by Froriep as the ganglion of the accessory, has been verified by His for the human embryo, I cannot find any trace of it in this specimen. I have had no difficulty in finding it in dog and cat embryos, and therefore must conclude that it is wanting in this embryo. This is what we should expect to find from time to time, especially in an organ which is in process of degeneration.

The hypoglossal nerve arises as a group of fibres parallel to but more ventral than the accessory. The bundles are arranged to correspond with the myotomes of the head, and on the aboral side arise in common with the accessory and the first cervical nerve.

#### THE SPINAL NERVES.

The spinal nerves are all distinctly marked by a large dorsal ganglion which sends small bundles of fibres into the cord, and a ventral root which arises from the motor cells in the anterior

horn of the same. The ganglia are largest in the cervical region, and gradually diminish in size as the tail is approached. The eight cervical nerves are united by anastomoses, which are destined to form the cervical and brachial plexuses respectively. The distal ends of the upper eight dorsal nerves are divided into two branches. Beyond these the remaining dorsal, lumbar, and sacral nerves end as a single branch. In all, twenty-nine spinal nerves can be identified; *i.e.* eight cervical, twelve dorsal, five lumbar, and four sacral. Beyond this there is a group of myotomes, which towards the tip of the tail run into one another. In this region the dorsal ganglia are not fully separated from the spinal cord; in fact, the whole seems yet to be blended with the ectoderm.

#### SYMPATHETIC NERVES.

Ónodi<sup>1</sup> has shown quite conclusively that the sympathetic nerves arise from the spinal. In our embryo, although there are as yet no sympathetic ganglia, there are marked branches from the first six dorsal nerves extending directly towards the chorda. These branches, without their ganglia, are spoken of by His for a human embryo 7 mm. long, in his last communication.<sup>2</sup> It will be seen from the reconstruction that all the sympathetic nerves arise from the oral branches of the spinal nerves. Three are in front of the cœliac axis, and three behind. From the study of other mammalian embryos I find that at about this stage the sympathetic nerves become encircled about the cœliac axis; and as this vessel moves aboralwards, the successive branches are entangled, and in this way form the splanchnic nerve. In the adult the cœliac axis is back of the twelfth dorsal vertebra, and the solar plexus encircles it. This plexus communicates by means of the great splanchnic nerve with the fifth to the tenth dorsal nerves. Under favorable conditions it may be traced to the third, second, or even the first dorsal.<sup>3</sup> Now in the various stages of development, the cœliac axis is successively opposite the various dorsal vertebræ; and as it moves backwards it carries with it these sympathetic twigs from the spinal nerves, which all unite to form the splanchnic.

<sup>1</sup> Ónodi, *Arch. f. mik. Anat.*, Bd. XXVI., 1886.

<sup>2</sup> His u. Braune's *Archiv*, Supplement-Band, 1890.

<sup>3</sup> Beck, *Phil. Trans.*, 1846.

## SKELETON.

The bulk of the framework in this specimen is composed of multipolar cells. Although these play a very minor part in adult higher animals, they are no doubt in embryos almost the sole element which holds the tissues together. Besides these there is the chorda dorsalis, which begins in the entoderm at the base of the third branchial arch, and extends to the tip of the tail. As the chorda passes between the two vertebral arteries, it is surrounded by various compact groups of cells which mark the bodies of the future vertebræ. On the oral side of the first cervical nerve the group marks the occipital bone; it is the most conspicuous mass, extends from one side of the body to the other, and sends two processes oralwards and lateral to the two vertebral arteries. Next in distinctness is the first cervical vertebra, while the following cervicals gradually diminish; the first three dorsal are faintly outlined.

## THE MUSCLE PLATES.

The occipital cartilage is bound to the first cervical by means of a muscle plate on either side. On the oral side of the occipital there are three muscle plates lying over the three bundles of nerve roots of the hypoglossal nerve. The plate nearest the occipital is bound to the cartilage on one end, while the remaining two have no cartilage between them. The plates gradually become larger and larger as the dorsal region is approached, and beyond this become smaller and smaller, until the tip of the tail is reached. In all, there are thirty-eight in number.

Especially well marked in the dorsal region are hollow outgrowths from the plates into the body wall. The rest of the plate is solid, but from the aboral and ventral corner these epithelioid prolongations extend beyond the beginning of the body cavity. On the median side of each plate there is a hyaline border which marks the beginning of muscle fibres. Between this border and the nerve stem lies a group of cells quite marked at the point the nerve ends, and gradually diminishing in number as the dorsal ganglion is approached. Many of these cells, as they enter the hyaline border of the myotome, become unipolar with the pole pointing towards the nerve root.

## HEART.

The heart, shown in profile in the figures, is 1.6 mm. wide, 1.5 high, and 1 deep. The ventricles are contracted and empty while the auricle is distended with blood. The right auricle is larger than the left, and into it empties the sinus reuniens, which is guarded by a well-marked valve. The left auricle is smaller, and partly separated by a septum, which extends towards, and half-way to, the auriculo-ventricular opening. Between this septum and the auriculo-ventricular opening is a free communication between the two auricles,—the embryonic foramen ovale. The ventricle is also partly divided into two compartments which communicate with each other, and also with the auricle above. A partial septum divides the auriculo-ventricular opening into two channels, making the left auricle and ventricle, and right auricle and ventricle communicating freely with each other. There is no free direct communication between an auricle and an opposite ventricle. The whole aorta arises from the right ventricle. The arrangement is such that the flow of blood may be from the right auricle to the right ventricle, and bulbus aortæ, or right auricle, foramen ovale, left auricle, left ventricle, right ventricle, and then bulbus aortæ. At its origin the bulbus is, upon transverse section, hour-glass shaped, and nearly separated into two tubes.

The walls of the auricles are much thinner than those of the ventricles. In the ventricle there are many bridges extending across the lumen, making the walls sponge-like in appearance. Between the auricle and ventricle there is a marked constriction in the walls which extends about one-tenth the distance to the auricular-ventricular opening.

## ARTERIES.

After the bulbus aortæ leaves the ventricle it is fully surrounded by the cavity of the pericardium until it breaks up into the aortic arches. In this region the walls are quite thick, being composed in great part of round cells. As the bulbus passes into the aortic arches, these cells are continued into the indifferent mesodermal cells of the body.

There are three completed aortic arches lying within the

third, fourth, and the tissue aboralwards from the fourth branchial arches. They are the third, fourth, and fifth aortic arches. Their general direction and shape is shown on Plate XXX. The two sets of arches unite to form the two aortæ, which again unite, between the sixth and seventh cervical nerves, to form a single aorta. In His's embryo B the division is about at the same point;<sup>1</sup> while in embryo A it is at the fourth dorsal.<sup>2</sup> As the aorta passes backward, it gradually becomes larger and larger, so that its diameter in the lumbar region is several times that in the cervical.<sup>3</sup> Here it very abruptly breaks up into two large branches which pass into the cord as the umbilical arteries.

Although there are many blood corpuscles scattered throughout the tissue of the embryo, I can make out definitely only a few arteries. The artery arising from the third aortic arch, and passing along the dorsal side of the branchial cavity up to the eye, is undoubtedly the internal carotid. Slightly beyond the eye it breaks up into numerous small branches, the most prominent passing towards the mid-brain, and undoubtedly represents the posterior cerebral. In His's diagram<sup>4</sup> this same twig passes between the inter- and mid-brains, and this throws it in front of the third nerve. In the neighborhood of the eye no branches could be found which arise from the carotid, but a large branch passes through the retina. This indicates that the ophthalmic is present, but cannot be followed in the sections.

From the fifth aortic arch, on either side, there is a branch which passes to the lung, and breaks up into a network of capillaries about the pulmonary buds. This is the pulmonary artery.

On the dorsal side of the aorta there are, on either side, twenty-one segmental arteries, the first being in front of the first cervical nerve, and the last behind the twelfth dorsal. The second segmental communicates on either side with a large branch — the vertebral. This branch extends as far forward as

<sup>1</sup> *Atlas*, Pl. I., Figs. 1 and 3.

<sup>2</sup> Replace Figs. 70 and 72, Pl. V., *Atlas*, into Fig. 4, Pl. I.

<sup>3</sup> See, also, His's embryo R, *Atlas*, Pl. XII.; embryo B, Pls. II., III.; and embryo A, Pl. V.

<sup>4</sup> *An. mensch. Em.*, III., Fig. 122, S. 188.

the otic vesicle, and gives off two distinct twigs, one extending in front of the vagus nerve, and the other just in front of the first cervical; they probably represent the anterior and posterior cerebellar arteries.

The origin of the vertebral is much more anterior than in the adult. His,<sup>1</sup> and recently, Hochstetter,<sup>2</sup> have shown that the vertebral is in many respects a segmental artery, and the condition of things in this embryo confirms this view. The second cervical segmental artery ends in a **T**, as shown in the plate. Undoubtedly the cross-piece of the **T** is to transfer the origin of the vertebral back to the second; and so on. Following the segmental branches backward, I find that between the fifth and sixth cervical nerves, a branch passes from the segmental into the anterior extremity. Although this twig arises (as far as the relation of the subclavian artery to the brachial plexus is concerned) one segment too far forward, I think it must represent the future subclavian.<sup>3</sup> From this point on down to the first lumbar, the segmental arteries gradually diminish in size. Below the first lumbar nerve no segmental branches arise from the aorta.

Between the lateral and ventral sides of the aorta there are fourteen pairs of segmental branches, which pass to the Wolffian body. Each pair arises on the ventral side just opposite the origin of the branches which pass towards the spinal cord. The anterior branches, which are quite small, arise between the seventh and eighth cervical nerves, and pass directly to the anterior end of the Wolffian body. Back of this pair the branches are of about equal size, the last being in front of the first lumbar nerve.

On the ventral median line of the aorta there are two distinct branches, — cœliac axis and the omphalo-mesenteric. At the fourth lumbar several small branches are given off from the ventral side of the aorta, and break up into a capillary network which extends throughout the mesentery.

Although the branch to the stomach and liver has already all its relations to these organs, as the cœliac axis in the adult, its origin is far too far forward. Other embryos, however, demon-

<sup>1</sup> *An. mensch. Em.*, III., S. 193.

<sup>2</sup> *Morph. Jahrbuch*, 1890.

<sup>3</sup> Hochstetter pictures the segmental artery below the seventh nerve as giving rise to the vertebral and subclavian arteries.

strate that the origin of this vessel is constantly shifting as the following table shows:—

	Length in Millimeters.	Origin of Cœliac Axis.
His's embryo M . . . .	2.6	Opposite 1st dorsal nerve. <sup>1</sup>
Dog embryo . . . . .	10	“ 2d “
His's embryo B <sub>2</sub> . . . .	7	“ 2d “
Dog embryo . . . . .	10	“ 4th “
Human embryo . . . . .	7	“ 4th “
His's embryo A <sub>3</sub> . . . . .	7.5	“ 6th “
Cat embryo . . . . .	12	“ 10th “
Dog embryo . . . . .	13.5	“ 10th “
Adult, human . . . . .		Behind 12th “
“ cat . . . . .		“ 12th “
“ dog . . . . .		“ 12th “

<sup>1</sup> Omphalo-mesenteric vein. *Atlas*. Replace Fig. 15, Pl. VI., into M<sub>4</sub>, Pl. VII.

<sup>2</sup> *Atlas*. Replace Fig. 35, Pl. II., into Fig. 1, Pl. I.

<sup>3</sup> *Atlas*. Replace Figs. 79 and 86, Pl. V., into Fig. 4, Pl. I.

It is only left for us to conclude that the stomach, liver, and pancreas receive their artery while they lie dorsal to the heart, and as their organs move backward the origin of the cœliac axis is gradually shifted in the same direction.

In these cases the omphalo-mesenteric artery is also shifted with the cœliac axis. In our embryo this vessel has a double origin, which indicates that this movement may be brought about by an anastomosis forming and then occlusion of the old origin. There is no twig from the omphalo-mesenteric to the mesentery.

The twigs which arise from the lumbar aorta at once break up into a capillary network which extends to and encircles the intestine, finally communicating with a vein which empties into the omphalo-mesenteric vein.

#### VEINS.

The veins which I have followed out are the jugular, cardinal, subclavian, omphalo-mesenteric, and umbilical. Their general course is shown in the reconstruction. It will be noticed that

the cardinal extends along the whole length of the Wolffian body, receiving the blood from this organ. The omphalo-mesenteric receives a vein from the mesentery, — the inferior mesenteric. The jugular and cardinal unite to form the ductus Cuvieri, which on the right side passes directly into the sinus reuniens, while on the left it flows across the dorsal side of the heart before it empties into the same.

On either side there are several large veins which arise in the anterior extremity, soon unite to form a single branch and empty into the ductus Cuvieri. On the left side these veins form a sinus around the united branch from the fourth and fifth cervical nerves, and then communicate with the cardinal vein as well as with the ductus Cuvieri.

It is the left omphalo-mesenteric vein which remains in the specimen. The vein passes around the dorsal side of the alimentary canal, and about in the middle of the liver unites with the umbilical vein. The united veins now become greatly narrowed and then again enlarge to form the sinus reuniens. From the distal side of the constriction the veins pass to the substance of the liver, while on the proximal side these efferent branches enter, forming a portal system.

#### CÆLOM.

A cast of the cœlomic cavity is shown in Fig. 2, Pl. XXIX. The picture was taken from the inverted model viewed from the dorsal and left sides. The slit along the dorsal side marks the mesentery while the grooves on either side of this indicate the position of the Wolffian bodies. The bulbous end of this model represents the pericardial cavity.

The pericardial cavity surrounds the whole heart, as shown in the sagittal section in Fig. 2, Pl. XXX. The cavity is perforated only where the large veins enter, and where the artery leaves the heart. The cavity completely surrounds the bulbus aortæ to its origin in the ventricle, the ventral side of this cavity being directly continuous with the ventral pericardial cavity. On the dorsal side the cavity is broken through for the transmission of the veins to the heart. Between the bulbus and the entrance of these veins the cavity extends across this median line as three distinct openings. On the dorsal side of the heart

on either side of the lungs the pericardial cavity communicates with the pleuro-peritoneal cavity by means of two openings, each of which has a long diameter of 0.5 mm. and a short diameter of 0.1 mm. The cavity now encircles the lungs, leaving, however, a dorsal and a ventral mesentery. More aboralwards a slit passes about the liver, and one about the stomach, as shown in Fig. 1. On the left side these two slits are quite smooth, and

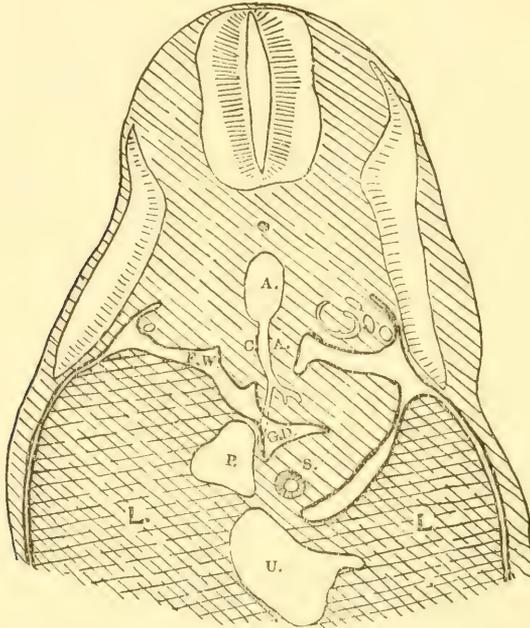


FIG. 1.—Section through the foramen of Winslow of a human embryo 7 millimetres long. Enlarged 50 times. *A.*, aorta; *C. A.*, coeliac axis; *S.*, stomach; *C. D.*, gastric diverticulum; *F. W.*, foramen of Winslow; *P.*, portal vein; *U.*, umbilical vein; *L.*, liver.

again run together on the aboral side of the liver. On the right, however, instead of a slit we have a pocket, or diverticulum, the cast of which is given in Fig. 2. The asymmetry of the two sides corresponds with the shifting of the stomach, and later the diverticulum forms the lesser peritoneal cavity.<sup>1</sup> Farther back the cavities on either side become symmetrical again, and then communicate with each other on the ventral side of the alimentary canal, as shown in Fig. 2, Pl. XXX.

<sup>1</sup> Development of the Lesser Peritoneal Cavity, etc., *Journal of Morph.*, V., No. 1.

The cavity next encircles the omphalo-mesentric vessels of the cord extending to the outside of the body. Behind the cord there is again a large communication from one side to the other. On the ventral side of the intestines, from the junction of the

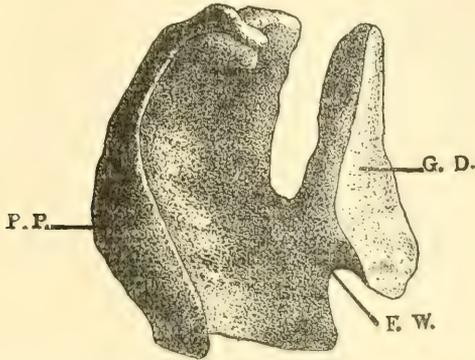


FIG. 2.—Corrosion preparation of gastric diverticulum of a human embryo 7 millimetres long. Enlarged 44 times. *P. P.*, pleuro-peritoneal cavity; *F. W.*, foramen of Winslow; *G. D.*, gastric diverticulum.

cord with the mesentery, a large papilliform projection hangs into this cavity (*P*). Still farther back the cavity encircles the Wolffian bodies, and finally ends by projecting deep into the tissues of the pelvis.

#### ALIMENTARY CANAL.

A lateral view of the cast of the branchial region is shown on Pl. XXX. The entoderm is directly continuous with the ectoderm, and the cast is carried to the full exterior of the body. On the dorsal median line the pocket which forms the hypophysis, extending between the mid-brain and after-brain, is shown. The first branchial pocket is bulbous and projects laterally, and then passes as a marked groove on the ventral side of the branchial cavity obliquely away from the mouth and towards the median line. It is destined to form the Eustachian tube.<sup>1</sup> The second pocket is equally as well marked but is hook-shaped, with the point reaching half-way to the median line. The third pocket points with its free extremity toward the second, and is yet in free communication with the branchial cavity. It is destined to become the thymus. The fourth pocket is irregular in

<sup>1</sup> Studies from the Biol. Lab., Johns Hopkins University, Baltimore, 1888.

shape, as shown in the figure. It is in general parallel with the alimentary canal and rests wholly between the fourth and fifth aortic arches.

The thyroid gland is as a small nodule lying in the median line on the ventral side of the second branchial arch.

Throughout their whole extent the branchial pockets at no point communicate with the exterior of the body. In no section is there a rupture of the membrane of His.

Immediately behind the branchial region the embryonic pharynx gives off the larynx, which farther back divides into the two bronchi. The intestinal tube now becomes dilated to form the stomach, below which arise the sprouts to form the pancreas and liver. The pancreas is composed of a small group of cells which lie in the mesogastrium, contains a lumen and communicates directly with the duodenum.

On the ventral side, however, this sprout is irregular, one branch boring into the liver, and the other ending as a sphere in the septum transversum. The liver is composed of two lobes, the right being about 1 mm. in diameter and half a millimetre thick. Its lateral border is symmetrical, and on its median side it is convex. It communicates along the septum transversum to the left lobe, which is very regular in shape.

Behind the liver the intestine makes an irregular curve towards the umbilical cord and to the left, and finally ends in the cloaca.

The cloaca is pyramidal in shape, with the apex pointing towards the tip of the tail. The highest point of the apex is blended with the ectoderm, and no doubt is about to break through. The intestine enters on the oral side of the base (speaking of the cloaca as a pyramid), and the allantois arises somewhat more aboralwards. The allantois is a small tube which is markedly dilated as it enters the cord, and then again becomes more constricted. On either side of the allantois and on the dorsal side of the intestine the Wolffian duct enters. Shortly before the duct enters the cloaca it gives off a blind tube, the beginning of the kidney.

The Wolffian body is a very large, somewhat lobulated body extending on either side of the intestine from the cloaca to the sixth dorsal nerve. Its general outline is given in Fig. 2, Pl. XXX. Upon transverse section, its free surface is small and

forms a complete semicircle in the cervical region, larger but more flat in the dorsal, and again somewhat smaller but semicircular in the lumbar region. The Wolffian duct extends throughout the body, extending just below the free surface and lying on the dorsal side in the lumbar region and on the ventral side in the cervical region. The glomeruli extend from the sixth cervical nerve to the fifth lumbar, and there are about two or three glomeruli to a segment. In the cervical region the tubule connecting the glomerulus with the Wolffian duct is slightly bent, in the dorsal region greatly convoluted, and in the lumbar region it is straight.

CLARK UNIVERSITY, WORCESTER, MASS.,  
May 14, 1891.

## DESCRIPTION OF PLATE XXIX.

FIG. 1. External view of the embryo before it was sectioned. Enlarged 20 times.

FIG. 2. Corrosion preparation of the pericardial and pleuro-peritoneal cavities. Enlarged 44 times. *P.* pericardial space; *A.* opening for aorta; *V.* opening for vein; *L.* space over liver; *M.* slit for mesentery; *W. B.* space for Wolffian body.





Fig. 1

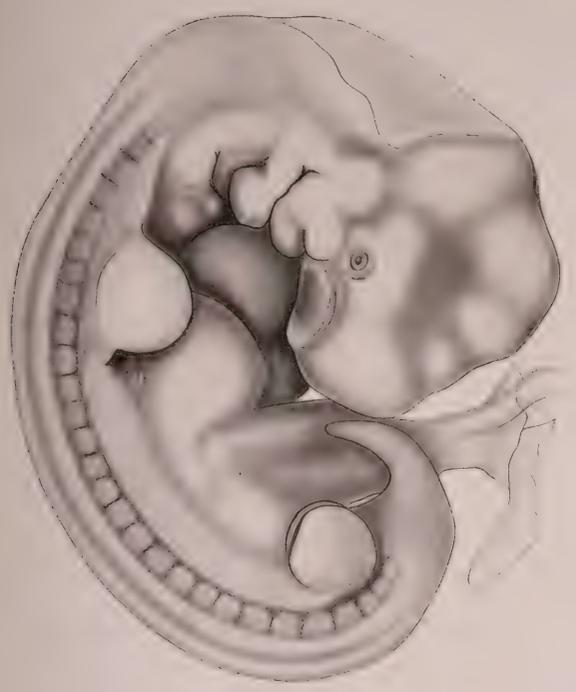


Fig. 2







## DESCRIPTION OF PLATE XXX.

FIG. 1. Reconstruction viewed from the left side. Enlarged 25 times. III., IV., V., etc. cranial nerves; *A. V.* auditory vesicle; 1, 2, 3, and 4, branchial pockets; *T.* thyroid gland; *B.* bronchus; *L.* liver; *K.* kidney; yellow, nerves; red, arteries; blue, veins. The dotted lines mark the extremities.

FIG. 2. The same as Fig. 1. Deeper view. *H.* hypophysis; *M.* mouth, mesentery; 1, 2, 3, 4, branchial pockets; *B.* bronchus; *P.* pancreas; *L.* liver; *W. B.* Wolffian body; *W. D.* Wolffian duct; *K.* kidney; *C.* cloaca; *O.* openings by which the pleuro-peritoneal cavities communicate; *P.* papilliform projection into the lower opening.





Fig. 1.

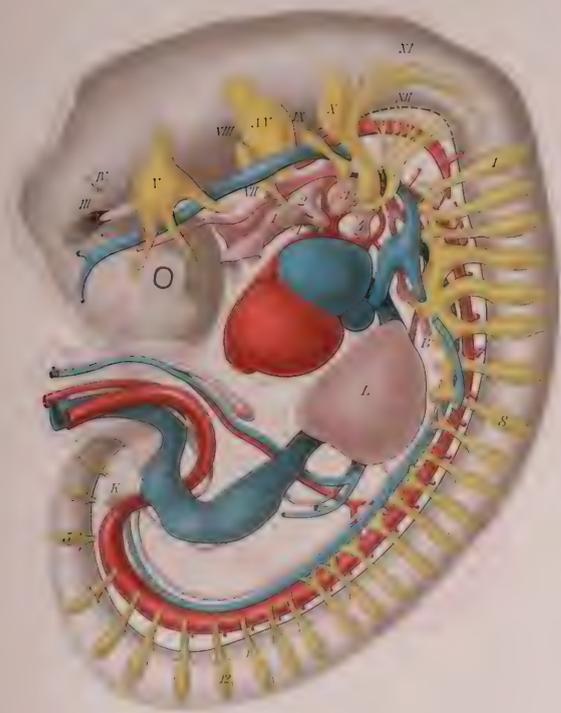
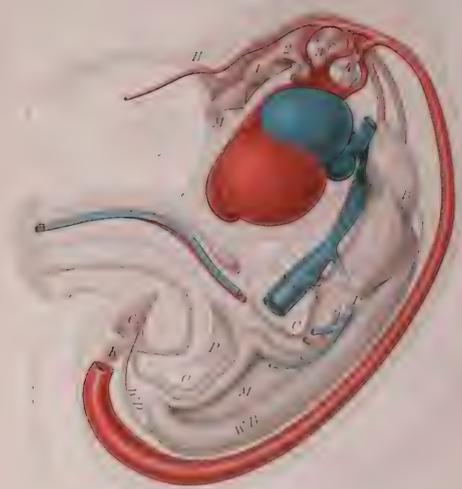


Fig. 2.





ON THE PRECOCIOUS SEGREGATION OF THE  
SEX-CELLS IN *MICROMETRUS AGGREGATUS*,  
GIBBONS.<sup>1</sup>

CARL H. EIGENMANN.

WHILE preparing the sections for the ontogeny of *Micrometrus aggregatus*, one of the viviparous Holconotidæ, I frequently observed large, indifferent cells in the mesoblast. I at first supposed them to be cells in a pathological condition. When, however, all the eggs from one ovary were observed to contain such cells I re-examined every embryo, and soon found that the cells are not pathological, but are a normal structure present in all embryos of a certain age. Further study showed them to be sex-cells of the future germinal epithelium. Since our knowledge of the early stages of the sex-cells of vertebrates does not extend back beyond the condition described by Balfour for Elasmobranchs, and since I have been able to trace them back to probably the fifth segmentation, I have thought best to give their history from their appearance, or rather, from the time when they become distinguishable from the surrounding cells till they are lodged in the mesentery of the hind gut, where Balfour has described them for Elasmobranchs.

Our knowledge of the sex-cells in general has been summed up by Weismann as follows: "In certain insects the development of the egg into the embryo, that is, the segmentation of the egg, begins with the separation of a few small cells from the main body of the egg. These are the reproductive cells, and at a later period they are taken into the interior of the animal and form its reproductive organs. Again, in certain smaller fresh-water crustacea (Daphnidæ) the future reproductive cells become distinct

<sup>1</sup> It gives me great pleasure to acknowledge my indebtedness to Dr. Silas M. Mouser, of San Francisco, California, who extended to me the use of his perfectly equipped bacteriological laboratory, without which courtesy my work would have been materially retarded.

at a very early period, although not quite at the beginning of segmentation, *i.e.* when the egg has divided into not more than thirty segments. Here also the cells which are separated early form the reproductive organs of the animal. The separation of the reproductive cells from those of the body takes place at a still later period, viz. at the close of segmentation, in *Sagitta*, a pelagic free-swimming form. In vertebrata they do not become distinct from the cells of the body until the embryo is completely formed." It will be seen that in some vertebrates (*Micrometrus*) a similar segregation of "germ plasm" takes place quite early. In brief, the sex-cells of *Micrometrus* first become normally conspicuous in the mesoblast of the head, where the germ layers are fused before any protovertebræ are formed. They can be seen in earlier stages, but they do not stand out so prominently from the other cells. In exceptional cases, as will be seen later, the sex-cells can be traced back to probably the fifth segmentation.

The cells can best be demonstrated by hardening twenty-four hours in the strong mixture of osmic, chromic, acetic acid, followed by Delafield's or Grenacher's hæmatoxylin.

In order to elucidate the figures accompanying this paper, as well as some parts of the text, it is necessary for me to give a brief account of the early stages of the fish, since it differs so essentially in general development and in every detail from that usually obtaining in teleosts.

The whole early development is an abbreviated one. To this fact, and to the small yolk, are to be attributed most of the peculiarities of its early stages. During the ninth segmentation the outermost layer of cells begins to spread over the yolk. During segmentation a mass of protoplasm fills a pit in the entodermic pole of the egg. Near the end of the tenth segmentation the horny layer forms a thin layer over the whole of the yolk exclusive of this entodermic mass of protoplasm; the deeper layers now begin to spread over the yolk. During the thirteenth segmentation the blastopore closes. At this time the embryo is composed of two layers, a one-cell deep primitive entoderm of small cells covering the yolk (in the embryonic axis this layer is several cells deep) and a two to three cell deep ectoderm. The growth is now so rapid that at the time Kupffer's vesicle appears the larva is free from its zona radiata. The periblast

consists of a few (less than twenty) large nuclei lying in the cortical layer of the yolk. The remaining development is emphasized chiefly by the formation of the very large intestine, the early communication of the intestine with the exterior by means of the first gill-slit, which is open almost as soon as the larva is hatched, and the enormous Kupffer's vesicle which sometimes reaches a length equal to one-half that of the yolk. The early connection of Kupffer's vesicle with the forming intestine and the presence (occasional?) of a neurenteric canal connecting Kupffer's vesicle with the neural canal leaves no doubt of the homology of this structure with the post-anal vesicle of Elasmobranchs.

The sex-cells can first be distinguished from the surrounding cells about the time the blastopore closes. The earliest ones distinguishable, exclusive of abnormal cases, are from an ovary in the eggs of which the blastopore is not yet closed, or just closed (Fig. 1), and in which the mesoderm is not yet split off from the entoderm. Only two cells which can with certainty be said to be sex-cells are seen in one of these eggs (Fig. 1). They differ from the surrounding cells in having well-defined, rounded outlines, and in the distribution of the chromatin in the nucleus. The chromatin of the surrounding cells is collected in one, or, if the cells are undergoing division, in two or three masses. The chromatin of the sex-cells is uniformly distributed in small granules. The protoplasm of the smaller egg stains somewhat deeper than that of the surrounding cells. The larger egg has a large, light court surrounding the nucleus; the peripheral substance is stained, but slightly different from that of surrounding cells. The protoplasm of both eggs contains yolk granules similar to those found in the blastodisc. These eggs measure as follow: nucleus  $5\ \mu$ ; diameter of smaller egg,  $13\ \mu$ ; diameter of larger egg,  $15\ \mu \times 18\ \mu$ ; its court,  $13\ \mu$ .

In another egg of this ovary, in which the blastopore is closed, a sex-cell similar to the smaller one described lies just at the margin of the future mesodermic cells.

In a third egg there are two large cells lying on the yolk. Not all eggs of this stage show the sex-cells equally well. In some eggs in which the blastopore is closing none can, with certainty, be made out.

In another ovary, in an egg in which the blastopore is not yet closed, large cells are seen in the entoderm and also in the ectoderm (Fig. 2). In fact, if the large cells were not so numerous in the ectoderm, the conclusion would naturally suggest itself that the sex-cells really arise in the ectoderm and migrate to the entoderm before mesoderm is formed at all. There are, however, too many large cells in the stage shortly preceding the closing of the blastopore in the outer portion of the blastoderm. The fact is, the inner cells of the blastoderm segment more rapidly toward the close of segmentation than the outer cells, and many of the outer cells become distended through intracellular digestion of the surrounding ovarian fluid. The outer cells, therefore, and, when the two-layered condition is reached, the cells of the ectoderm, are larger than those of the entoderm. It is still possible, however, that the sex-cells arise in the ectoderm. If, however, they are segregated as early as the fifth segmentation, that is, before there is any differentiation into ectoderm and entoderm, as is probable, it seems to be of no great importance whether at the time of the separation of the blastoderm into ecto- and entoderm the cells lie in its outer or inner portion.

The eggs of the last-mentioned ovary were killed in the strong solution of osmic, chromic, acetic acid, and stained with Grenacher's alcoholic borax carmine. This method of staining does not differentiate the sex-cells. They can only be distinguished by their size. They measure  $18 \mu$ .

In the eggs of another ovary, in which the cells have become heaped up in the head region, the chorda and neural thickenings are formed for some distance back, and the mesoblast is separated from the entoderm by a well-marked line; the sex-cells stand out from the surrounding cells with great prominence (Figs. 3 and 4). This is not due to any marked change in the sex-cells themselves, but rather to the fact that the surrounding cells have undergone further division and are crowded so that the boundaries are not defined, while those of the rounded sex-cells are well marked.

The largest and most conspicuous cell of this stage lies in the mesoblast just beside the chorda. It measures  $18 \times 23 \mu$ , and has a nucleus measuring about  $6 \mu$ . On comparing this size with segmenting eggs, it is found that it agrees in size with some of

the cells of an egg undergoing the ninth segmentation and in all probability it is a cell remaining unchanged from that stage. It contains yolk particles. Most of the sex-cells are collected in a limited region at this stage in the thickened portion of the embryo, where the three germ layers fuse. This would lend force to the supposition that they are derived from two cells at most — one dextral and one sinistral. There are a few scattered cells in other parts of the embryo which cannot be so derived unless they early migrate from their original position.

There are, on an average, thirteen sex-cells in an egg of this stage. The largest number noticed is seventeen, the smallest nine. These, in an egg containing fifteen, which was cut into thirty sections, the first of which is tangential to the thickened part of the embryo, are distributed as follows: Section 5 has two cells, section 6 (Fig. 4) has seven, section 7 has three (Fig. 4 *a*), section 13 has two, and section 14 has one lying in the mesoderm on the side of the egg opposite the neural thickening. Twelve of the fifteen sex-cells lie in the thickened portion of the embryo where the germ layers are fused. The one lying in the ventral part of the mesoderm is stained slightly darker than the others. The staining varies, however, in the collected ones, as, indeed, does the staining of individual cells of the blastoderm.

In an egg with fifteen sex-cells there are nine in the thickened portion, five in close proximity to it, and a ventral one.

In another there are fourteen inside the thickened region, two outside, and one ventrally placed. In the other eggs I cannot find any ventral cell.

The position and character of the sex-cells in the stage with two well-formed, and one or two outlined protovertebræ is gathered from three eggs killed with Flemming's strong solution of osmic, chromic, and acetic acid, and stained with Delafield's hæmatoxylin. This method at times differentiates the sex-cells from the surrounding ones very clearly.<sup>1</sup> The sex-cells in some larvæ are stained dark brownish gray, while the remaining cells are stained bright blue—especially the nucleolus and the proto-

<sup>1</sup> A large number of larvæ were treated in this way, and though they were carried through the whole process from killing to sectioning together, the results were so disastrously different that this method cannot be depended upon to always give satisfactory results.

plasm immediately surrounding it. In an embryo cut in a sagittal direction there are two cells having the character of the sex-cells in the front part of the head (Fig. 5), probably closely connected with the rudiments of the ear (?). One lies in the mesoblast some distance behind (Fig. 5, *s.c.* ?), and a group of them lies just in front of the first protovertebra (Fig. 6), and two lie at the posterior extremity of the embryo; but about the character of those two cells I am not positive.

The cells in this embryo measure 13–18  $\mu$ ; the nucleus, 4–6  $\mu$ . They are distributed in detail as follows: sections 14–18 being on the left of the median line of the body, sections 24–30 to the right of it; section 15 has one in the mesoblast of the head, three cells in front of the first protovertebra; section 16 has four in the same region, just in front of the first protovertebra; section 17 has one in the same region, and one larger, with more regular outlines further forward; section 18 has one in the region of the ear, and two in the posterior end of the embryo; section 24 has one in the region of the ear, and two in the mesoblast of the head just before the first protovertebra; section 25 (Fig. 6) has five in the mesoblast of the head; section 30 has a dark cell on the edge of the mesoblast well forward, the nature of which is open to doubt. The great majority of the sex-cells in this embryo have collected in the mesoblast of the head just in front of the first protovertebra; only two out of all these cells are as yet posterior to the head, and the character of these two cells is doubtful.

In another embryo of this stage (cut transversely), in which there are seven in the left and eight in the right side of the body, the cells are all found in the cephalic region, or at least very near it.

In still another, cut in a plane slightly inclined to the horizontal, approximately the same conditions are found.

In several places, as in Fig. 6, the cells are grouped together.

In a larva just hatched, the longest diameter of which, measuring in a straight line, is 0.45 mm., there are ten sex-cells. In this embryo about nine protovertebræ have been formed. Most of the sex-cells are large, the largest having a diameter of 23  $\mu$ , with a nucleus of 8  $\mu$ . The smallest cell measures but 11  $\mu$  in diameter. The distribution of these cells has become markedly changed from the conditions obtaining in

the two-protovertebræ stage. But two of the cells, in the embryos examined, are now found in the cephalic region, one on either side a short distance posterior to the origin of the chorda. These cells may correspond to those two seen in the ear region in the stage having but two protovertebræ. A small cell which *may* belong to this series lies in the tissue of the future heart. The remainder are distributed as follows: one below the seventh sinistral protovertebra; three in the left side of the tail, *i.e.* in the region in which protovertebræ have not yet appeared; and three in the right side of the tail.

The cells in this stage stain deeper and much more uniformly than the surrounding cells with Grenacher's hæmatoxylin. They greatly resemble the very early conditions of these cells, and the number would seem to indicate that there has been no segmentation since the two-protovertebræ stage. In other larvæ of the same stage there are ten, eight, five, and nine cells, respectively.

In larvæ about 0.62 mm. long, the general distribution of the preceding stage is maintained. The cells in the gill region, however, are seen to vary both in number and position. In five embryos examined they are, in detail:—

No. 1. None in gill region; one doubtful cell in the heart.

No. 2. One on the right side of the first gill-slit region; another (or two?) on the left.

No. 3. Three in the region of the right gill; none on the other side.

No. 4. One on each side in the gill region, that of the left side inconspicuous (or absent?).

No. 5. Two dextral, somewhat further forward than usual, the inner one apparently penetrating the brain.

There is also apparently one or two cells near the middle of the body, as in the preceding stage. These are in the five embryos as follows:—

No. 1. One in the sixth protovertebra, near its dorsal wall (not distinct).

No. 2. One dextral, about 0.36 mm. from the posterior end.

No. 3. One sinistral, 0.25 mm. from the posterior end; another 20  $\mu$  further forward on the right.

No. 4. One in the fourth protovertebra of the right side, and another below the end of the fifth.

No. 5. One dextral and one sinistral cell about 0.30 mm. from the posterior end.

The remaining cells are all in the posterior part of the larva, and vary in number from two to eight on the right, and from four to nine on the left side of the body.

In a larva 1.1 mm. long, the anterior cells are as in Fig. 7. One is in the mesoblast over the posterior part of the heart; the other lies apparently between the hypoblast and brain. The cells are somewhat different from those usually observed, but a comparison with the sex-cells of another larva from the same ovary, treated in the same way (Fig. 8), leaves no doubt of their character. Further than this I have not been able to follow these anterior cells, and am not able to conjecture what becomes of them.

Those of the middle of the body or of earlier stages probably migrate caudad, though they may atrophy. In larvæ 1.2 mm. long, the sex-cells are arranged on either side in the mesoblast above the anus. The two sides are not symmetrical; there is usually a group of several cells, the remainder being scattered. In one larva all the cells but one are on the left; in another the majority are on the right side. The number of cells, about ten, remains unchanged (Fig. 8).

In larvæ 2.5 mm. long the sex-cells have attained the position figured by Balfour (Pl. X., Fig. 8) for Elasmobranchs. That is, they are found in the mesentery and the mesoblast adjoining it from above the anus forward. In one larva they are distributed as follows, counting sections about  $16\ \mu$  thick from the anus forward:—

- Section 1. Four median (Fig. 9).
- Section 2. One median.
- Section 3. One on left, two on right (Fig. 10).
- Section 4. One on right.
- Section 5. Two on right.
- Section 7. One median.
- Section 11. One on right.
- Section 13. One on left.
- Section 26. One median?
- Section 29. One on right?

There are fourteen, probably sixteen cells in this larva, and the number of cells cannot have been increased much since their

earliest condition, even if we assume that two or more have been lodged in the gill region, and two in the anterior part of the body. The majority of the cells in this larva are confined to a region only 0.20 mm. long; and if we consider the doubtful cells in sections 26 and 29, the total length over which these cells are distributed is about 0.50 mm. from the anus forward. The sex-cells in this stage measure 9-13  $\mu$ . Balfour's admirable account of these "primitive ova" (Elasmobranch Fishes, pp. 130-136) might almost be used bodily to describe the same structures in *Micrometrus* and *Abeona*,—2.5 mm. long. He observed that the younger ones contain many yolk spherules, and suggests that the cells themselves may have migrated to their position from a peripheral portion of the blastoderm, since "they are the only mesoblast cells filled at this period with yolk spherules." He was at a loss as to how they arose, and thought he could detect cells intermediate in size between them and the neighboring cells. As has been seen, the yolk particles simply remain unchanged from the original condition when the sex-cells are segregated.

In connection with the origin of the primitive cells, an egg containing about 1700 cells, in which no sign of gastrulation (*i.e.*, separation of blastoderm into two layers) can yet be noticed, deserves attention. The blastoderm covers the entire yolk, exclusive of the entodermic mass of protoplasm. Many of the features of this egg are abnormal, but these very characters may be instructive. There are in this egg six very large cells in the blastoderm. The relation to the surrounding cells and their relative size may be gathered from Fig. 11, *s.c.*? A nucleus is not present in these cells, but the highly granular protoplasm is radially arranged. The granules are more dense near the centre of the cell, so that the peripheral part is less deeply stained with fuchsine, and, in fact, the whole mass of the cell appears less compact than that of neighboring cells, and gives one the impression that these cells are disintegrating. The radial arrangement of protoplasmic granules, would, however, point to cell division. A spindle and dividing nucleus cannot be seen.

Three of these cells lie in close proximity. Two others are placed near each other, and the sixth lies in their neighborhood.

The other features are two multinuclear cells lying in the

yolk. In contrast with the former, the substance of these cells is denser; that is, stains deeper than that of the normal cells. The contours are also much more regular and rounded than of the blastoderm cells (Fig. 11). They resemble in all respects but their multinuclear condition the primitive sex-cells in older eggs. They contrast very strikingly with the smaller, more refringent, periblast nuclei, so we cannot possibly be dealing with that structure — unless, indeed, this should be an atavistic condition; but the distinct contour and similarity between the nuclei of these and the blastoderm cells speak very decidedly against such a conclusion. The larger one contains three nuclei, and measures  $23 \times 20 \mu$ ; the smaller,  $18 \times 20 \mu$ . I have found several similar cells in another egg of this stage, from another ovary.

Only one cell of all those examined in later stages approaches these. It is a large uni-nucleated cell lying in the yolk just below the edge of the entoderm in a larva with about ten proto-vertebræ. It is stained very dark, and contains yolk granules. Its position so near the oviferous mesoderm may permit the supposition that it has dropped from its normal position. It measures  $18 \times 22 \mu$ , with a nucleus of  $6 \mu$ .

Another segmenting egg, the cells of which have become separated by reagents, is probably still more instructive. It contains one very large cell  $47 \mu$  in diameter, with a central denser mass about  $22 \mu$  in diameter. I am inclined to think that this is a sex-cell which has come to a state of rest still earlier than usual. Two or four of such cells would give rise to all the sex-cells observed in the subsequent stages. If this cell really is a sex-cell, then the substance of the germinal epithelium is segregated as early as the fifth or sixth segmentation. This seems to me to be highly probable.

Several figures (Fig. 6) would seem to indicate that one of the larger cells of an early stage divides and gives rise to the groups of smaller cells in a later stage. This can scarcely be the case, since the number of cells in the earlier and later stages are about equal, unless a number of the earlier cells atrophy or are resorbed. The loss of four cells, two in the gill region, and two in the region of the fifth body somite, is probable, but even with the addition of these, the number of cells in the last stage examined does not exceed the average

number in early stages when the cells are quite large. The reduction in size can, therefore, be explained only by supposing that the individual cells are reduced in size during development. It would be interesting to consider here the causes that lead these sex-cells to again grow and divide. Since, however, this process does not begin in the stages under consideration, this matter must be left till later stages are examined. Another question seems more pertinent. In how far do the sex-cells, in the ontogeny of *Micrometrus*, repeat the phylogenetic history of these elements in vertebrates? I am not aware that the sex elements have been traced nearly as far back in any other vertebrate, and to explain the origin of the sex-cells in vertebrates in general from a type the development of which differs so much from related species is perhaps rash. Still it is not evident how causes which have brought about the changes in the early history of *Micrometrus* should affect the sex-cells. In *Branchiostoma* the germinal region is much more extensive than in the Craniata. It is true that the ovaries and testes extend well forward in many fishes during the breeding season, but in embryos of several species I have examined, the "anlage" of the sexual organs is confined to a much more restricted region in the posterior part of the body cavity, and its anterior extension is a later, secondary feature. *Micrometrus* would indicate that the present position of the sexual glands in Craniata is not the primitive one, but that the anterior glands in *Branchiostoma* probably represent the earlier condition. From this position the germinal region has been extended backward, the anterior part undergoing atrophy still later.

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I have not been able to examine the special literature bearing on this subject, since the observations were completed in California, at a distance from modern scientific libraries. For this reason I shall be pardoned, if, perchance, I have not given due credit to the works of predecessors.

INDIANA UNIVERSITY, BLOOMINGTON, INDIANA,  
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## ABBREVIATIONS.

<i>a.</i>	anus.	<i>n. r.</i>	neural ridge.
<i>al.</i>	alimentary tract.	<i>op.</i>	optic stalk.
<i>au.</i>	auditory vesicle.	<i>pc.</i>	pericardium.
<i>ch.</i>	chorda.	<i>pr. ec.</i>	primitive ectoderm.
<i>bl.</i>	blastoderm.	<i>pr. ent.</i>	primitive entoderm.
<i>ec.</i>	ectoderm.	<i>s. d.</i>	segmental duct.
<i>ent.</i>	entoderm.	<i>s. c.</i>	sex-cells.
<i>ht.</i>	heart.	<i>seg. c.</i>	segmentation cavity.
<i>hy.</i>	hypoblast.	<i>so. mes.</i>	somatic mesoblast.
<i>mes.</i>	mesoderm.	<i>sp.</i>	splanchnic mesoblast.
<i>m. yk.</i>	margin of yolk.	<i>yk.</i>	yolk.
<i>n. c.</i>	neural canal.		

## EXPLANATION OF PLATE XXXI.

All the figures are made with an Abbe camera and Zeiss D and 4.  $\times 355$ .

FIG. 1. Part of a section nearly tangential to the yolk of an egg shortly before the closing of the blastopore. Osmic chromic acetic. Grenacher's hæmatoxylin.

FIG. 2. Part of a section of an egg shortly before the closing of the blastopore. Osmic chromic acetic. Grenacher's alcoholic borax carmine.

FIG. 3. Cross-section of the anterior part of the embryonic axis before any protovertebræ are outlined. There are two sex-cells in front of this section, five just behind it, and two farther back. Osmic chromic acetic. Grenacher's hæmatoxylin.

FIG. 4. Section parallel to the tangential over the head of a similar embryo, and from the same ovary as Fig. 3.

FIG. 4 *a.* Outline of the next section.

FIG. 5. Section of the head parallel to the sagittal of a larva, with two well-formed protovertebræ, showing sex-cell in auditory thickening (?). Osmic chromic acetic. Delafeld's hæmatoxylin.

FIG. 6. Another section of the same embryo, showing the group of sex-cells just in front of the first protovertebra.

FIG. 7. Section through the head of a larva 1.1 mm. long, showing position of sex-cells. The section is oblique, the auditory vesicle of one side showing and the optic stalk of the other. The middle of the figure is median to the larva, as is seen by the neural canal, *n. c.* Grenacher's alcoholic borax carmine.

FIG. 8. Cross-section through the anterior part of the anus of another larva from the same ovary, showing the group of sex-cells in the as yet united somatic and splanchnic mesoderm.

FIG. 9. Cross-section through the corresponding region of a larva 2.5 mm. long. Osmic chromic acetic. Grenacher's hæmatoxylin.

FIG. 10. Another section of the same larva further formed.

FIG. 11. Part of the blastoderm of an egg containing about seventeen hundred cells, large sex-cells, and multinucleated cells.











## SOME POINTS IN THE DEVELOPMENT OF THE TOAD-FISH (*BATRACHUS TAU*).

CORNELIA M. CLAPP.

THE following observations were made during the summer of 1891, while studying, under the direction of Dr. C. O. Whitman, at the Marine Biological Laboratory, Wood's Holl, Mass.

### THE BLASTOPORE.

In examining the younger embryos of *Batrachus tau*, my attention was attracted to the appearance of the blastoderm, as seen in Fig. I. *c*. The egg was placed in weak osmic acid, for a few moments, when the outline could be clearly seen through the egg membrane.

Earlier stages were obtained, and treated in the same manner.

Fig. I. *a*, represents the blastoderm at the time of the first appearance of the axial thickening.

Fig. I. *b*, shows the embryonic ring when the embryo is well defined, and a little after the time when the notch first makes its appearance.

The point of special interest to be noticed, in these early stages, is the form of the blastopore, and its closure at some distance behind the embryo.

In Fig. I. *c*, the two sides of the embryonic ring are seen to approach each other, as they grow over the yolk, forming an acute angle behind the embryo, and giving rise to a very conspicuous notch.

In Fig. I. *d*, this notch is seen at a little distance behind the embryo; a shadowy connection may be traced between the germ ring and the embryo.

In later stages, this notch is seen to retreat farther behind the embryo, as the thickened margins of the blastoderm unite, and it disappears shortly before the completion of the closure of the blastopore.

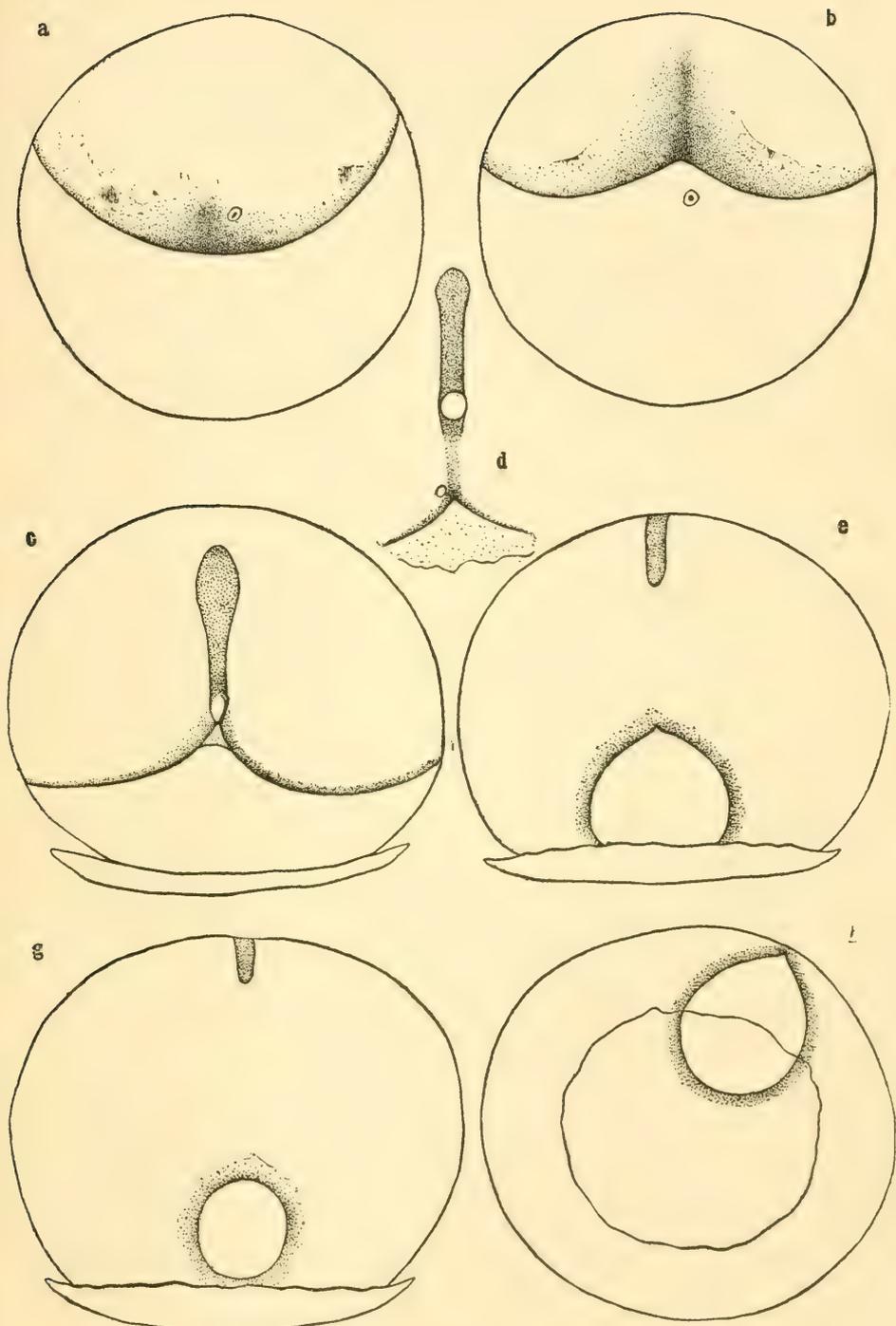


FIG. I.

In "A Preliminary Notice of the Development of the Toad-fish,"<sup>1</sup> Dr. Ryder gives a figure of the embryo in about the same stage of development as seen in Fig. I. *c*. The peculiarity in the growth of the blastoderm over the yolk seems to have been overlooked, for the embryo is represented, as in the ordinary teleost, developing at the margin of the blastoderm.

There is a striking resemblance between the appearance of the blastoderm in Fig. I. *c*, and Balfour's diagram of the Elasmobranch type of development,<sup>2</sup> and also great similarity between Fig. I. *e* and *g*, and Figs. 1 and 2, Pl. VIII., of Balfour's "Elasmobranch Fishes."

The egg of *Batrachus* is enormous, as compared with that of the pelagic fish egg, being about 5 mm. in diameter, and also larger than the egg of most amphibians, owing to the accumulation of food yolk. In this respect there is an approximation to the condition seen in the Elasmobranch egg, and to this must be attributed the peculiarities of the blastopore.

In comparing Fig. I. *e* and *g*, with Balfour's figures of *Pristiurus*, before mentioned, the following points may be noticed:—

In the case of *Pristiurus*, at the time when about two-thirds of the yolk has been enveloped by the blastoderm, we find the embryo folded off from the yolk, and connected with it by a narrow umbilical cord, the embryo being still at the edge of the blastoderm, and the tail extending beyond it.

At a later stage, but before the closure of the blastopore, the circulation of the yolk sack is well established, and a venous trunk occupies the position of the linear streak which marks the line of coalescence behind the embryo. Fig. I. *e* and *g*, shows the same form and position of the blastopore in *Batrachus* as seen in *Pristiurus*; but, on examination, it is found that the caudal portion of the embryo is not free from the yolk, at the time of the closure of the blastopore, neither are there any blood-vessels in the yolk sack.

In *Batrachus* we find a teleost exhibiting one of the interesting features of the Elasmobranch type of development, the closure of the blastopore being evidently delayed, in consequence of the great amount of food yolk, and giving rise to the yolk blastopore, which Balfour describes as "the anterior and ventral portion of the primitive blastopore."

<sup>1</sup> *Bull. of U. S. F. C.*, 1886.

<sup>2</sup> *Comp. Em.*, II. p. 126.

A notched blastopore, at a *distance* behind the embryo, has hitherto been unknown among teleosts.

In rare cases a notch has been observed at the posterior end of the embryo, in transitory stages of pelagic fish eggs. In such cases the caudal lobe is divided as in Elasmobranch embryos. Two instances have been reported by Agassiz and Whitman, and one by Kingsley and Conn. Although due to the same processes of growth, this notch cannot be the same as that seen in the egg of the Elasmobranch or Batrachus.

It should be mentioned that the germ ring is remarkably narrow as compared with that of other teleosts, especially pelagic forms. This is due, probably, to the extension of the germ ring over a larger yolk sphere.

In Fig. I. *c*, the position of Kupffer's vesicle is unusual. When first seen, it lies at the extreme posterior end of the embryo, at the notch of the blastopore. In a later stage, Fig. I. *d*, this vesicle is seen to lie a little in front of the hind end of the embryo. It seems probable that the embryo has lengthened somewhat backward.

It is interesting in this connection to refer to some rare appearances in the blastoderm of the chick. A marginal notch in the blastoderm has been observed by Pander, Balfour, His, Rauber, and others, while the extension of the primitive groove through the area opaca to this notch has been seen by Dr. Whitman and Dr. Böhm.<sup>1</sup>

In comparing the Elasmobranch and Avian embryos, Dr. Whitman<sup>2</sup> says: "In the exceptional form of blastoderm which I have described, the streak connecting the primitive groove with the marginal notch may be considered analogous to the linear streak of the Elasmobranch, while the marginal notch corresponds to the anterior angle of the yolk blastopore."

These exceptional forms seem to point to the same fundamental principle of embryonic formation in Elasmobranchs and Aves.

<sup>1</sup> *Archiv für Anat. und Phys.*, 1884, p. 14. Dr. T. H. Morgan has informed me that he also has observed the notch and the extension backwards of the primitive groove to it in the chick.

<sup>2</sup> *Quart. Jour. Mic. Sci.*, Vol. XXIII. New series, 1883.

RELATION OF THE AXIS OF THE EMBRYO TO THE FIRST  
CLEAVAGE PLANES.

The question of the coincidence of the first or second plane of cleavage with the axis of the embryo is one that has attracted considerable interest of late. As the egg of *Batrachus* offers unusually favorable conditions for deciding this question, I have undertaken some experiments expressly for this purpose.

It is well known that the eggs of *Batrachus* are adhesive. They may be found attached to the under side of boards or stones, or to the inside of tin cans, in the shallow water of the bays or inlets along the coast. A cavity is often excavated beneath a large stone by the parent fish, and the eggs deposited on the roof of this cavity.

The adhesive disk, as represented in Fig. I. *f*, is about 3 mm. in diameter. It is a transparent thickening on one pole of the egg membrane, at the time of oviposition, and by means of it the egg is glued firmly to the rock.

The blastoderm develops at the free pole of the egg, as seen in Fig. I. *a* and *b*, so that the first stages of cleavage can easily be seen with a lens through the egg membrane.

On the 22d of June eggs were artificially fertilized.

Having chloroformed the fish, the abdomen of the female was opened, and the ovaries cut so as to allow the mature eggs to fall and fasten themselves to the bottom of shallow glass dishes. The testes of the male were removed, and after being cut into fragments, were placed in the dishes with the eggs. Soon after this the eggs were supplied with fresh sea-water and left to develop. The adhesion of the yolk to the egg membrane, as it rested on the disk area, prevented rotation.

The first line of cleavage appeared seven hours after fertilization, and on the seventh day the axis of the embryo could be distinctly seen as a light streak in the blastoderm.

The method of determining the relation of the first cleavage planes to the axis of the embryo was as follows:—

The exact position of each egg was represented by circles on paper, and the paper and the dish containing the eggs were oriented by fastening a label on each in the same relative position. When the first line of cleavage appeared, the direction was indicated in the circle representing that egg, by the diam-

eter, and when the axis of the embryo was visible, that was indicated by an arrow drawn across the same circle.

The result of this experiment is seen by an examination of the circles given in Fig. II. Of the twenty-three developing embryos, *three* show coincidence of the axis of the embryo with the first cleavage plane (Fig. II. 1, 2, 3). There is no case of

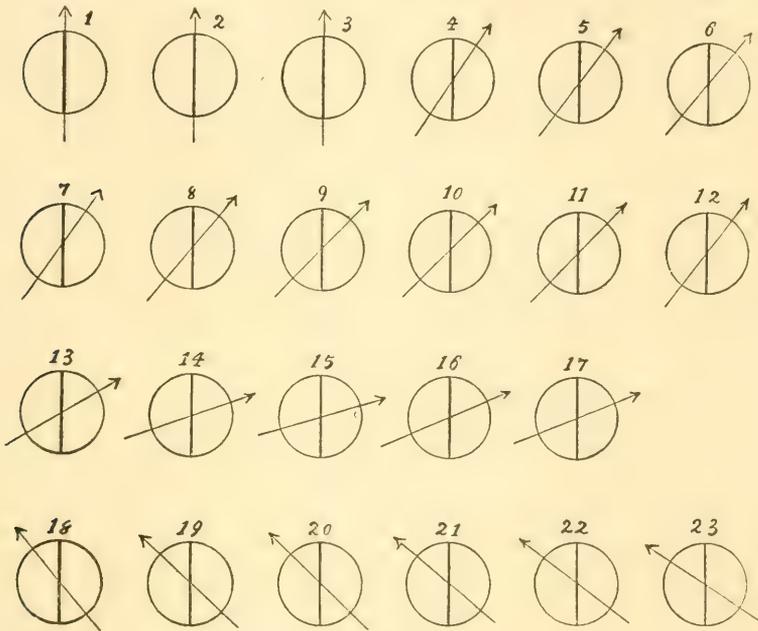


FIG. II.

exact coincidence with the second cleavage plane. Fourteen of the embryos have the head directed towards the right of the first line of cleavage, the axis of the body being at an angle with the first cleavage plane of from  $30^{\circ}$  to  $70^{\circ}$ . In the remaining six the head was to the left of the first cleavage plane, the angle varying as before.

#### STAGES OF CLEAVAGE.

Dr. Brooks<sup>1</sup> has described a segmenting fish egg, which he says is probably that of *Batrachus tau*. He does not figure the two- or four-cell stages, but the arrangement of the cells

<sup>1</sup> *Studies from Biological Laboratory*, Vol. II.

in the eight-cell stage differs considerably from what I have observed.

Fig. III. 4-6 have been introduced mainly for the purpose of showing peculiarities of the eight-cell stage not shown by the figures given by Dr. Brooks. The two- and four-cell stages are much the same as in other fish eggs. In passing to the eight-cell stage, the four cells elongate at right angles to the first plane of cleavage, and the two planes of the third cleavage divide these cells unequally, the four central cells being small, while the end cells are much larger (Fig. III. 4-6).

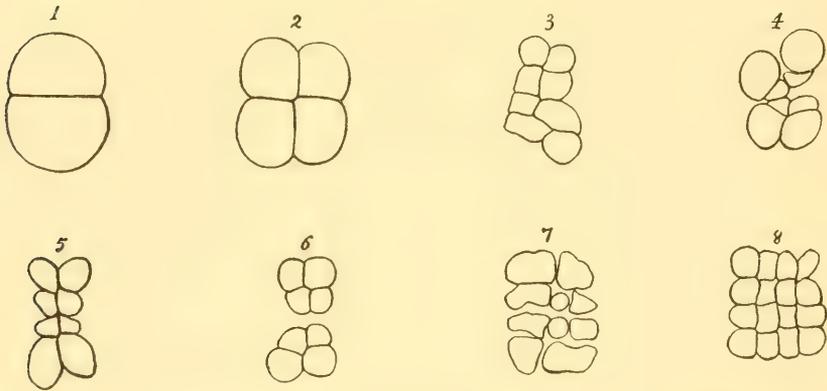


FIG. III.

The bilateral symmetry is perfect with reference to either the first or second line of cleavage, and it is so well marked in these cases that it suggests the coincidence of the axis of the embryo with the first cleavage plane.

Fig. III. 3 is somewhat asymmetrical, while Fig. III. 8 shows a remarkably symmetrical sixteen-cell stage. Fig. III. 7 shows that stage in process of cleavage.

#### POSITION OF ADHERENT EMBRYOS.

In the paper referred to above, Dr. Ryder describes the young adherent embryos as having their heads *invariably* directed towards the opening of their retreat, and adds: "It would seem that the direction from which the light comes has a great deal to do in determining the direction of the axis of the body of the future embryo."

A different explanation of this fact is given by Dr. Ryder in a recent paper.<sup>1</sup> He says: "The future axis of the whole brood of embryos was *predetermined* in the body of the parent."

It was observed during the past summer that the embryos *within the egg membrane* do not have their heads all turned the same way, but in every possible direction, and it is only after the young toad-fish are hatched that the heads of the whole brood are turned in the same direction.

During the larval period the yolk sack is attached to the inside of the egg membrane, and the possibility is suggested that the turning toward the light is effected at the time of hatching, when, according to Dr. Ryder, the attachment of the yolk sack may take place.

<sup>1</sup> *Proc. of Am. Phil. Soc.*, Vol. XXVIII., p. 141.



DEVELOPMENT OF THE EPIPHYSIS IN  
*COREGONUS ALBUS*.<sup>1</sup>

CHARLES HILL.

THROUGH the papers of Leydig ('90), Selenka ('90), and Hoffmann ('85), the evidence is accumulating that we have at least two outgrowths from the roof of the embryonic brain in the region where we have heretofore found only the single epiphysial outgrowth. The evidence is further strengthened by the discovery of the secondary parietal vesicle described in adult forms by Wiedersheim ('80), Ahlborn ('83), Beard ('89), and Ritter ('91). In view of the prevailing uncertainty as to the homology of these two outgrowths, and as to their relation to the roof of the brain and to one another, it has seemed to me advisable to communicate some observations on the subject that have been made incidentally while working on the primitive segmentation of the brain of *Coregonus albus* (Günth).

In *Coregonus*<sup>2</sup> there are two epiphysial outgrowths from the roof of the primary fore-brain. These may be best seen in a sixty-day embryo (7 mm. in length). In Fig. I. there is shown the anterior part of a living embryo at this stage, as seen from

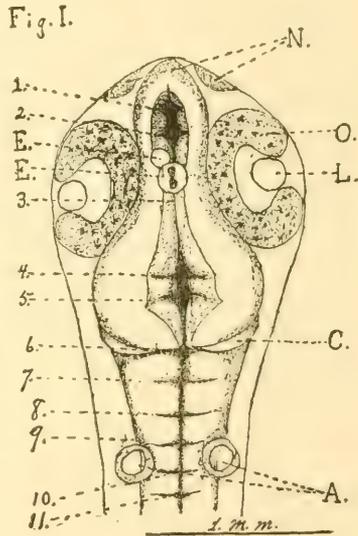


FIG. I.—Anterior portion of embryo, 7 mm. long, of *Coregonus albus*.

<sup>1</sup> Work from the Zoölogical Laboratory of the University of Michigan, under the direction of Professor Jacob Reighard.

<sup>2</sup> I desire to acknowledge my indebtedness to the Michigan State Board of Fish Commissioners for a liberal supply of material.

the dorsal surface and somewhat from in front. In the medulla there is represented only the floor, which shows a series of five parallel, transverse grooves,—(7), (8), (9), (10), (11). These grooves are broader and deeper towards the middle line, and become gradually narrower and shallower towards each side. They separate five transverse ridges, that are higher at the middle line and lower or less prominent towards each side. A longitudinal groove, the ventral part of the neural canal, passes along the median line of the floor of the medulla, and separates each transverse groove and ridge into two equal lateral parts. The auditory vesicles (*A*) lie on each side of the medulla, a little in front of the groove marked 10. Each one of these grooves marks the median line of a neuromere, as defined by Orr in *Lacertilia*, while lines drawn midway between these grooves, and parallel to them, indicate the limits between the individual neuromeres of Orr. Thus each of the ridges here described is equivalent to the posterior half of one of the neuromeres of Orr together with the anterior half of the next neuromere posterior to it. I adopt the nomenclature of Orr and describe these neuromeres merely for the purpose of fixing definitely this stage of development, and, for the present, do not wish to be understood as having accepted his interpretation of them.

The cerebellum (*C*) extends laterally farther than the medulla, and in the figure, owing to the point of view, appears to be partly covered by that part of the brain anterior to it. In its floor there is but one groove (6), which resembles those of the medulla. Only a part of this groove appears in the figure.

That part of the brain in front of the cerebellum tapers anteriorly; so that, in a dorsal view, it has the outline of a pear. The sides of this anterior pear-shaped portion are concave; and in these concavities, close against the brain, are the two optic vesicles. Nothing was seen, at this stage, to justify a division of this part of the brain into primary fore-brain and mid-brain. Four transverse grooves,—(1), (2), (4), (5), an anterior pair and a posterior pair—mark its base. The distance between these two pairs is considerable; and while in this figure no groove is shown in the wall between these two pairs, in other embryos a fifth very small groove was seen in the position indicated by (3).

On the roof of the brain — in the median line, and in a plane passing through the middle of the optic vesicles — is seen the posterior epiphysial outgrowth *E*. It is a small spherical body, having its lateral walls thickened so that the cavity within is laterally compressed. This cavity is narrowest at the middle, on account of the greatest thickness of the lateral wall of the vesicle falling at the middle of its antero-posterior axis; consequently, in a dorsal view, the cavity has the form of a dumb-bell. Just in front of this vesicle, and a little to the left of it, is a second similar outgrowth *E'*. This anterior evagination is

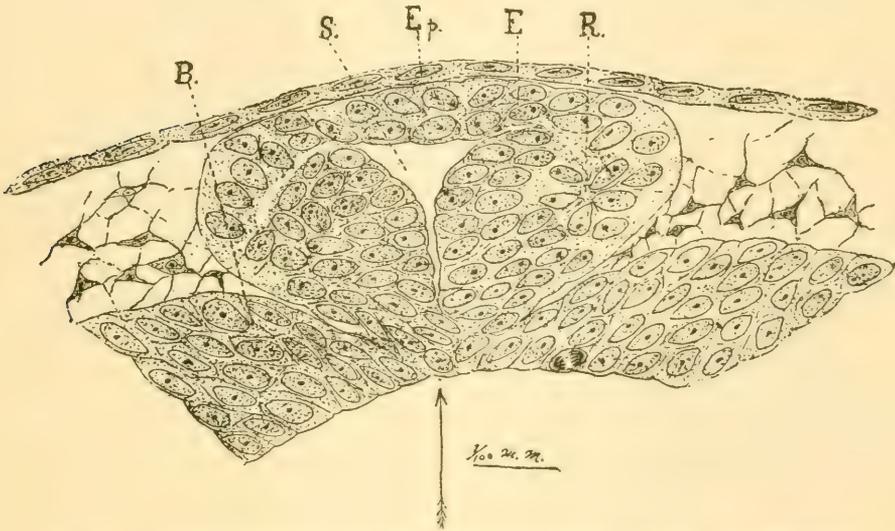


FIG. II. — Transverse section through the posterior epiphysial vesicle of *Coregonus albus*.

smaller than the posterior one, and appears to be solid. It lies close against the wall of the posterior vesicle, and is partly hidden by it.

Fig. II. shows the dorsal face of a transverse section through the middle of the posterior epiphysial vesicle. The arrow in the figure indicates the position of the median plane of the brain. The epiblast (*Ep*) lies close against the distal end of the vesicle, and is made up of a single layer of flattened epithelial cells. No mesenchyme is present between this epiblast and the dorsal surface of the posterior epiphysial vesicle. The vesicle (*E*) has the outline of a top, and is connected with the brain roof (*B*) by the apex of the top, which thus forms a very

short, thick, conical stalk. The vesicle is flattened dorso-ventrally, and has a triangular cavity (*S*). One angle of this cavity points towards the brain cavity below, into which it may be traced in the other sections, while the other two angles terminate in the lateral thickened walls of the vesicle. Some of the cells (*R*) near the middle of the thickened right lateral wall are arranged radially, while the dorsal right angle of the triangular lumen seems to form an arch which communicates with the central area, surrounded by these radiating cells. In the left half of this epiphysial vesicle there is evidence of a similar structure. The roof of the brain is thinner directly beneath

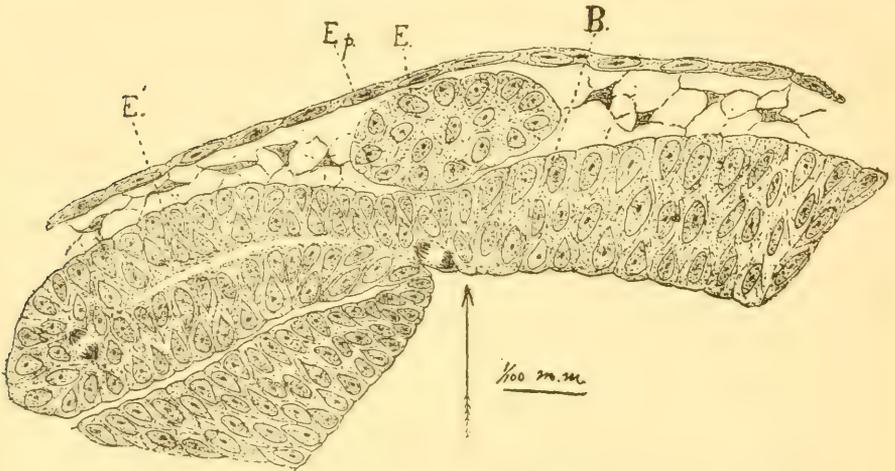


FIG. III. — Transverse section through the anterior epiphysial vesicle of *Coregonus albus*.

the posterior vesicle, and on all sides of this point it becomes gradually thicker. There is thus formed a cup-shaped depression on the dorsal surface of the brain, and in this depression the conical stalk of the vesicle lies.

Fig. III. is from the same series of sections as Fig. II. Three sections intervene between it and the section shown in Fig. II. The section passes through the middle of the anterior epiphysial vesicle (*E'*) and through the anterior part of the posterior vesicle (*E*). The sections are 10  $\mu$ . thick, and the arrow, as before, shows the position of the median plane of the brain.

The anterior vesicle (*E'*) is transversely elongated; its dorsal

surface convex ; its ventral slightly concave, and closely applied to the roof of the brain. It is separated from the epiblast (*Ep*) by intervening mesenchyme. Along its middle there is a narrow cavity that communicates with the cavity of the brain, slightly to the left of the median plane. The portion (*E*) of the posterior vesicle is entirely free from the brain wall (*B*), and median in position. It is a solid mass of cells from the anterior wall of the posterior vesicle.

The stage just described shows the epiphysial vesicles ten days after their first appearance. The posterior vesicle appeared about two days before the anterior one, and could be seen in the living embryo as a small circle in the roof of the brain, in the median line. When the anterior vesicle appeared, its diameter was three-fourths the diameter of the posterior one, while it had the same position as shown in Fig. I. I was unable to study the anterior outgrowth in the living embryo for a longer period than twenty-five days, as at the end of that time it was so covered by the growth of the posterior vesicle and the surrounding brain wall that in a surface view of the brain it was entirely hidden.

Sections of stages earlier than that represented in Fig. I. show that these epiphysial vesicles arise as separate outgrowths from the roof of the brain. In each vesicle there is a cavity which opens separately into the cavity of the brain. In stages ten days earlier than that shown in Fig. I. there is, in longitudinal sections, an average of four sections that intervene between these openings, while in the transverse sections there is an average of five sections. Thus the opening of the anterior vesicle is a little more in front of the opening of the posterior vesicle than to the left of it. In stages ten days older than shown in Fig. I. these openings were obliterated, so that I was unable to establish their relation to one another.

From the study of sections it appears that the anterior vesicle shows an increase in size for about twenty days, and after that a decrease, while the posterior vesicle shows from the beginning a gradual increase. The following table is made from transverse sections, and gives the dimensions of the two vesicles in three different planes, each taken at right angles to the others :—

LENGTH.	AGE.	ANTERIOR VESICLE.			POSTERIOR VESICLE.		
		Dorso-ventral.	Transverse.	Longitudinal.	Dorso-ventral.	Transverse.	Longitudinal.
9. mm.	75 days	.037 mm.	.133 mm.	.07 mm.	.102 mm.	.135 mm.	.09 mm.
10.5 "	107 "	.027 "	.112 "	.07 "	.120 "	.147 "	.10 "
12. "	144 "	.015 "	.073 "	.05 "	.121 "	.152 "	.12 "

The first column under the anterior vesicle gives the length of the dorso-ventral diameter of the anterior vesicle. The second column gives the distance between the extreme left border of the anterior vesicle and the median plane of the brain. The measurements in the third column of the anterior vesicle are calculated from the number of transverse sections in which the vesicle appears.

The first column under the posterior vesicle gives the length of a vertical line drawn from the dorsal border of the posterior vesicle to the ventral border of the dorsal brain wall. The second column gives the length of the transverse diameter of the posterior vesicle. The third column is obtained in the same way as that for the anterior vesicle.

Besides this decrease in size of the anterior vesicle, its cells in older stages are more closely packed than in earlier stages, and show no karyokinetic figures. In early stages karyokinesis is frequently seen. I did not succeed in rearing embryos beyond 144 days, but, from the facts stated above, it seems very probable that this vesicle ultimately disappears.

In embryos seventy-five days old, the posterior epiphysial vesicle begins to grow anteriorly, so that the anterior vesicle is soon pushed to the left of the posterior one, and lies packed between it and the left brain wall. At the same time the fibres of the posterior commissure make their appearance just posterior to the union of the posterior vesicle with the brain roof. A little later there is a folding down of the brain roof anterior to these vesicles. This folding forms the posterior wall of the cerebrum, so that the epiphysial vesicles are clearly seen to be connected with the roof of the thalamencephalon.

Leydig ('90), in his recent paper, describes in *Lacertilia* two epiphysial outgrowths. He says the two lie in the median plane, the one just in front of the other; and that in the embry-

onic stage the anterior one is the larger, and partly covers the smaller posterior one. The anterior outgrowth soon separates from the brain, and develops into the eye-like parietal organ, while the posterior one remains connected with the brain roof, and forms the pineal gland (*Zirbelknopf*). My work on *Coregonus* does not cover adult forms, but, as far as studied, it is evident that while the early stages of these two epiphysial outgrowths of *Coregonus* agree in many details with the corresponding early stages of the two outgrowths in *Lacertilia*, as described by Leydig, yet the ultimate fate of these two outgrowths in the two forms is widely different. In *Coregonus* the anterior outgrowth, which is the smaller, gradually disappears, while in *Lacertilia*, according to Leydig, it develops into the adult parietal organ.

Selenka ('90), in *Lacerta* and *Anguis*, also describes two epiphysial outgrowths. The posterior outgrowth, he says, arises as a median thickening of the roof of the thalamencephalon. This he calls the epiphysis, and from its distal end he derives the parietal eye. Shortly after this there is another outgrowth, which he calls paraphysis, which comes from the roof of the prosencephalon. The paraphysis then grows backward and the epiphysis grows forward in such a way that the pineal eye comes to lie on the paraphysis as on a pillow. I could find no such outgrowth from the prosencephalon in *Coregonus*. The two outgrowths were both posterior to the depression, which, according to Rabl-Rückhard ('82), marks the anterior border of the thalamencephalon.

What relation these two epiphysial outgrowths bear to the primary and secondary parietal vesicles, described in adult *Petromyzon* by Ahlborn ('83) and in *Lacertilia* by Ritter ('91), remains yet to be worked out. It is probable that these organs will be shown to be homologous.

ZOOLOGICAL LABORATORY, UNIVERSITY OF MICHIGAN,  
September 9, 1891.

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## NOTES ON THE DEVELOPMENT OF SOME SPONGES.<sup>1</sup>

HENRY V. WILSON.

THE following notes deal with the gemmule development of *Esperella fibrexilis* (n. sp.) and *Tedania Brucei* (n. sp.), to which are added a few observations on the egg development of *Tedanione fetida* (n.g.) and *Hircinia acuta*. *Esperella fibrex.* is a small silicious sponge abundant near Wood's Holl, Mass. The others are Bahama forms found at Green Turtle Cay, the two silicious sponges, *Tedania* and *Tedanione* being closely related.

During the summer, *Esperella* and *Tedania* contain great numbers of good-sized embryos in all stages of development, and if the sponges are kept in aquaria for a few hours, some of the embryos will pass out through the oscula. The embryos thus set free are solid oval bodies covered with cilia, and are quite like the egg larvæ of many silicious sponges. They swim about for a day or so and then attach themselves to the wall of the dish, flatten out and undergo a metamorphosis. When the embryos inside the mother are examined, they are found not to be egg embryos, but true gemmules, *i.e.* internal buds.

I will first describe the development of *Esperella*. The mesoderm of *Esperella* contains cells which differ greatly in size and general appearance, though they shade one into the other. Some of the cells are much larger than the rest and have plump bodies which stain well. Such cells congregate together and form irregular groups in which the cells are rather closely packed. The group of cells rounds itself off, the outer cells becoming flattened and forming a follicle. The gemmule, as thus formed, is at first quite small, often showing not more than five cells in section, though a considerably larger gemmule may be directly formed from a group of cells (Fig. 1). The cells of the gemmule, once the follicle is formed, are very closely packed.

<sup>1</sup> Published by permission of Hon. Marshall McDonald, U. S. Commissioner of Fish and Fisheries.

The increase in size of the gemmule takes place by means of cell growth and division, and by the fusion of neighboring small gemmules. The latter process throws into shade the seemingly important question, Does a gemmule ever start as a single cell? In regard to the actual occurrence of such an origin for gemmules I may say, that after looking over a great number of preparations, my conclusion is, that perhaps a little group of mesoderm (gemmule) cells is so derived in very rare instances, but the case occurs so seldom as not to be worth consideration.

The gemmule continues to increase in size, without any striking change in its structure, until it is nearly as large as the

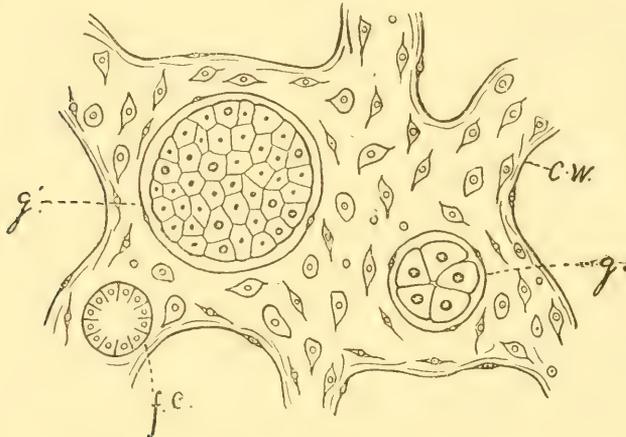


FIG. 1. Portion of *Esperella* mesoderm, showing two gemmules, *g* and *g'*, each surrounded by follicle of flattened cells. *g* is a very young gemmule; *g'*, considerably older; *c. w.* = canal wall; *f. c.* = flagellated chamber.

swimming larva. In this condition it may be spoken of as the ripe gemmule. The ripe gemmule is spheroidal and is made up of cells so closely packed and so filled with fine yolk granules that the cell boundaries are indistinct. The nuclei of the cells are very small. During the growth of the gemmule the surrounding tissue becomes largely incorporated in the follicle; and whereas the gemmule in its early stages lay in the mesoderm of the sponge, in its ripe condition it lies in one of the larger canals, suspended by strands of tissue which now bind the follicle to the canal wall. The ripe gemmule next undergoes a process which presents a superficial analogy to segmentation. The

solid gemmule splits up into irregular masses of cells. These continue to split up into smaller and smaller masses, the gemmule meanwhile increasing in size, owing to the absorption of fluid, so that the several masses of cells are distinctly separated from one another (Fig. 2). The splitting up continues until the solid gemmule has been plainly resolved into its constituent cells. The outer cells of the gemmule, very early in this process of "segmentation," arrange themselves so as to form a continuous layer of flat cells round the periphery. This layer, for convenience' sake, may be spoken of as the ectoderm. Inside the ectoderm at the close of "segmentation" is found a mass of amœboid cells connected together by their processes and sep-

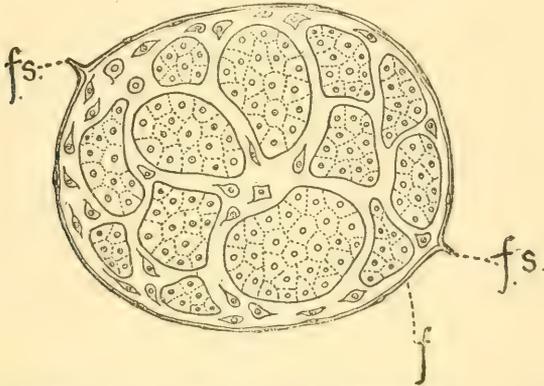


FIG. 2. Gemmule of *Esperella*, undergoing "segmentation." *f.* = follicle; *fs.* = strands of tissue, by which follicle is connected with canal wall.

arated by fluid. The flat ectoderm cells next become long slender columnar cells, having pigment in their outer ends and bearing cilia. The metamorphosis of the ectoderm cells does not, however, take place over one pole. Over this pole the ectoderm cells remain flat and without cilia. Further, the inner mass of cells at this pole become steadily denser, until this region of the embryo is occupied by a mass of irregularly polygonal cells closely appressed. In the mass of polygonal cells a bundle of long spicules lying in the direction of the main axis of the embryo is developed. In the remainder of the inner contents of the embryo, the cells are less closely packed and are of various shapes. The unciliated pole is made the more

conspicuous because of the pigment (orange) which covers the rest of the embryo. In this condition, the embryo breaks through its follicular wall, and passes out of the parent through one of the oscula (Fig. 3).

The first step in the metamorphosis of the larva consists in the flattening of its ectoderm. The flattening begins before the sponge attaches itself, and *gradually travels from the non-ciliated or spicular pole backwards*. While there is still a considerable remnant of the columnar ectoderm, the larva attaches

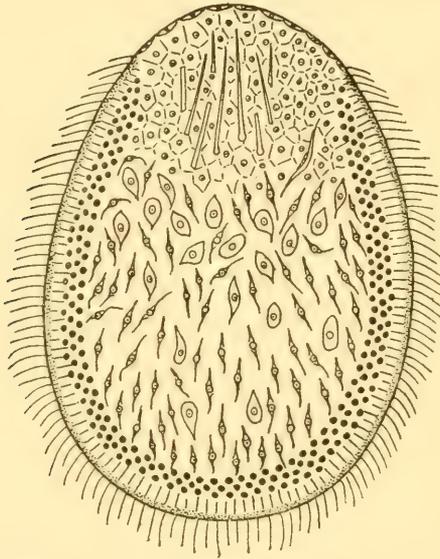


FIG. 3. Longitudinal section through the swimming larva of *Esperetta*. The nuclei of the columnar ectoderm cells form a conspicuous zone. In the outer ends of these cells is orange pigment. The inner mass of cells (parenchyme), in the region of non-ciliated pole, differs from the parenchyme in the rest of the body.

itself by the spicular pole, but obliquely, so that it lies somewhat on its side. The rest of the ectoderm then becomes flattened, and the larva is transformed into a thin, flat mass, circular in outline. The bundle of spicules, formerly at the non-ciliated pole, become distributed all over the body of the little sponge. The attached larva, at first circular in outline, speedily grows irregular in shape, and becomes surrounded by a thin ectodermal membrane. The subdermal cavities and canals appear as lacunæ in the substance of the larva, the sur-

rounding cells becoming flattened to form the epithelioid wall. The various canals and cavities, originally independent, open one into the other, and to the exterior, by simple perforation of the intermediate tissue. The oscula and pores are at first indistinguishable, and are scattered over the surface of the sponge, with no attempt at arrangement. Even in the adult I can see no morphological distinction between the pores and oscula. The difference in size is the only difference, and that loses its significance because of the occurrence of apertures, which hold several intermediate positions in this respect between pores and oscula.

The flagellated chambers arise as independent structures, which subsequently acquire connection with the canal system.

There are in the larva, when it first attaches, a large number of mesoderm cells, distinguishable from the rest by their size and bulky shape. Such cells I may call formative cells. They diminish greatly in number, and grow smaller in size during the metamorphosis. The formative cells contain as a rule several nuclei, and are destined for the most part to split up into much smaller cells. The particular way in which the flagellated chambers are formed in any larva depends on the behavior of the formative cells. (All the cells of the larva, I may add, are connected together by fine processes.) In some larvæ the formative cells arrange themselves round a central cavity (intercellular space) so as to form a hollow sphere. Numbers of such spheres, consisting of comparatively large cells, are found in some larvæ. Division of the cells then ensues, and the hollow sphere gradually assumes the nature of a flagellated chamber. In some larvæ, on the other hand, all the formative cells may break up into fine cells before the marking out of any flagellated chambers. The mesenchyme of such larvæ consists of a solid mass of fine cells, with here and there a formative cell. The flagellated chambers of such a larva must be formed directly from a group of fine cells, probably by some rearrangement of the cells round a central cavity. In other larvæ, both processes go on at the same time. Some of the formative cells arrange themselves in hollow spheres and form chambers directly; others break up into solid masses of small cells, which subsequently acquire a cavity. That a single formative cell itself ever forms a chamber, I do not believe.

In whichever way the flagellated chamber is formed, it at first has no connection with the canals. It, like any particular canal, is, in its origin, a lacuna, its cavity being an intercellular space.

In deciding phylogenetic questions, perhaps not much weight should be attached to a development like this; but whatever weight it has, is in favor of Metschnikoff's theory of the solid ancestry of sponges. The solid swimming larva itself, and the details of the metamorphosis (the origin of the flagellated chambers, excurrent and incurrent canals, and subdermal spaces, as independent lacunæ in a matrix of amœboid cells) are all understood on this theory. Conversely, if we hold to the view which regards the calcareous sponges (*Ascons*) as the primitive type, the development of *Esperella* may, of course, be regarded as an extreme case of coenogeny.

The development of *Esperella*, it seems to me, has perhaps a bearing on problems out of the range of pure morphology. Without discussing the matter in detail, I may point out the striking resemblance between this asexual development and the egg development of many silicious sponges. As in the egg embryo, there are formed in the gemmule embryo two germ layers. In the two embryos the layers are alike in many details of structure. The egg larvæ, again, are characterized by the absence over one pole of the columnar ectoderm (*Isodyctia* and *Desmacidon*, Barrois (1); *Reniera*, Marshall (2); *Chalinula*, Keller (3); *Esperia*, Schmidt (4), etc.). The account according to which the endoderm protrudes at this pole, is probably not correct, but it is likely that the ectoderm is only greatly flattened over this region. It is this characteristic more than any other, which I should pick out as a point of exact resemblance between the sexual and asexual larvæ. Barrois has described the egg development of two forms, in one of which (*Isodyctia*) the non-ciliated pole of the planula is never covered with columnar cells. This is paralleled by the *Esperella* larva. In another form (*Desmacidon*), the larva has at first a complete covering of columnar ectoderm (and cilia), which then disappears over one pole (and much later over the whole surface). This case is more or less similar to the gemmule development of *Tedania*; in this form, the embryo has at one time a complete covering of columnar cells (unciliated however), which

*flatten out* over one pole, while over the rest of the body they acquire cilia. In the metamorphosis, also, the gemmule development resembles the egg development, in that the ectoderm of the larva is flattened to form the ectoderm of the adult. As regards the formation of the chambers, canals, etc., the egg larvæ differ too much among themselves to permit any such comparison as I am carrying out.

Such a resemblance between the sexual and asexual larvæ as I have indicated, can, I think, only be explained on the supposition of some essential likeness between the mesoderm cells, which make up the gemmule, and ova. If for convenience' sake we adopt the point of view of Weismann, and regard the egg cell as characterized by the possession of a "germ plasm," the gemmule cells too (unless the resemblances between the gemmule and egg embryo are accidental) have some claim to the possession of this plasm. By making a little further use of Weismann's theory, the nature of the gemmule cell (*i.e.* a mesoderm cell, which, together with others, forms a gemmule), may perhaps be stated with some precision. Of the two polar bodies found in non-parthenogenetic eggs, Weismann believes that the first carries off ovogenetic plasm, the second carries off one-half the germ plasm. In the case of the sponge gemmule, a mesoderm cell does not itself become differentiated into an ovum, but the necessary amount of nutriment for the embryo is got by the association of numerous such cells. Hence there is in the gemmule cell no special histogenetic (ovogenetic) plasm, and consequently no first polar body. There is, of course, no fertilization, therefore no second polar body. The gemmule cell, according to this view, must be regarded as a true germ cell, in which all the germ plasm remains undifferentiated, *viz.* in which none of it is transformed into ovogenetic plasm. Further, the gemmule cell pursues the parthenogenetic course of development — it keeps all its germ plasm.

Gemmules apparently develop anywhere in the sponge mesenchyme. It must, therefore, be assumed that *any* mesenchyme cell may become a gemmule cell, and consequently that it contains germ plasm. The same conclusion is reached by the study of the egg development, for it seems that any mesenchyme cell may develop into an egg.

The gemmule development in *Tedania* pursues much the same

course as in *Esperella*. The early stages in the formation of the gemmule, owing to the extremely small size of the cells, cannot be followed with the same accuracy as in *Esperella*, but the process can be seen to be essentially the same. The "segmentation," or gradual dissolution of the gemmule into its constituent cells, takes place in the same way. The swimming larva is, except in a few details, like the larva of *Esperella*, and the metamorphosis takes place on the same lines.

In the egg development of *Tedanione*, there is a total segmentation, resulting in the formation of a solid morula. The larva, when set free, is a solid oval body, completely covered with a layer of columnar ciliated cells. The metamorphosis was not observed. The segmentation of *Hircinia* is likewise a total segmentation, resulting in the formation of a solid morula. The development of the ovarian egg in these two forms is essentially alike. The follicle during the growth of the egg is surrounded by a large number of comparatively densely packed mesenchyme cells, the duty of which is presumably to bring nourishment to the growing egg (compare Fiedler's account for *Spongilla*). The nucleus of the very young egg contains a single large nucleolus more or less centrally placed. While the egg is comparatively small, before it has reached more than one-half its ultimate size, two small spherical masses of densely staining chromatin are found adhering to opposite sides of the inner face of the nuclear wall. As a rule, in eggs which have reached the full size, only one or neither of these chromatin balls is present.

Occasionally, however, an egg is found of the full size and still with both of the chromatin balls. One of the masses is probably lost (thrown out?) at about the time when the increase in size is completed. The remaining mass is thrown out of the nucleus, and may sometimes be observed lying in the egg yolk near the nucleus. The nucleus of the ripe egg thus left without chromatin mass, is a poorly defined body in which neither nuclear membrane nor chromatin is visible. The maturation of the egg in these two sponges is seen to be very like that of *Spongilla*, as described by Fiedler.<sup>5</sup> Fiedler regards the two chromatin balls as polar bodies; but as an objection to this view it must be urged that they are formed (though not discharged) long before the egg has reached its full size.

My observation that layers similar to germ layers are developed in the asexual embryos of certain sponges recalls the account given by Dezsö,<sup>6</sup> of the formation of buds in *Tethya*. Dezsö claims that these buds develop from single cells, and that in them germ layers are formed. The construction he puts upon certain cells seems, however, an arbitrary one, and I find it difficult to carry out a detailed comparison between his observations and my own. Oscar Schmidt, as Dezsö calls to mind, described in 1878, germinal layers in the buds of *Loxosoma*, and emphasized the biological significance of the phenomenon.

In his paper "Zur Orientirung über die Entwicklung der Schwämme (*Zeit. f. W. Z.*, 1875), Oscar Schmidt makes the statement that in the silicious (and horny) sponges there is no true segmentation, the ovum very early losing its cellular character. To many others besides Barrois (1) this must have seemed a remarkable statement, and it would be interesting to know if the observations which led Professor Schmidt to this view were not made on a gemmule development resembling that which I have described.

UNIVERSITY OF NORTH CAROLINA,  
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