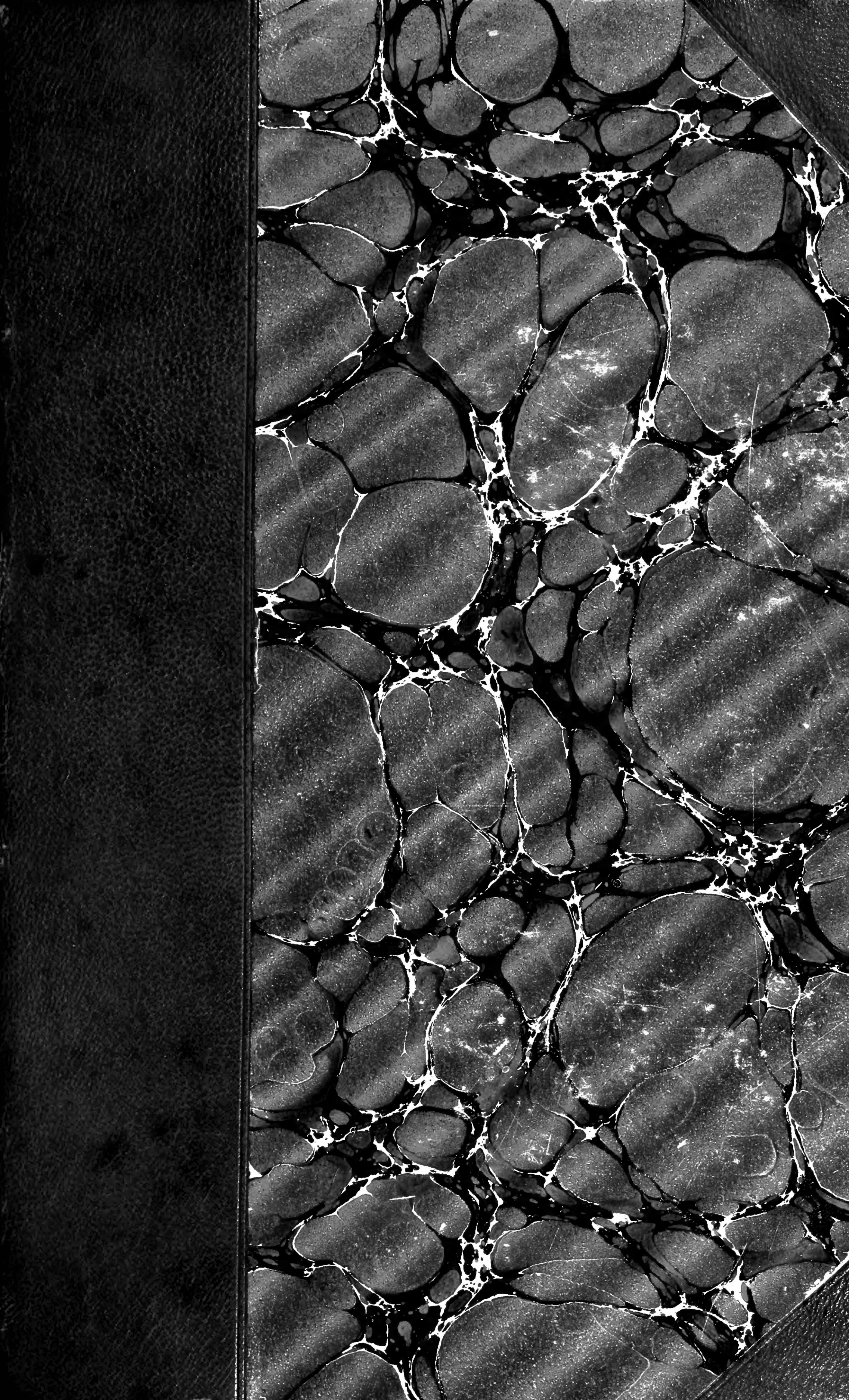

JOURNAL

OF

MORPHOLOGY.

EDITED BY

C. O. WHITMAN,

With the Coöperation of

EDWARD PHELPS ALLIS, JR.,
MILWAUKEE.

VOL. II.

BOSTON:
GINN & COMPANY.
1889.

CONTENTS OF VOL. II.

No. 1. — July, 1888.

No. 2. — November, 1888.

No. 3.—April, 1889.

Volume II. *July, 1888.* *Number 1.*

JOURNAL

OF

MORPHOLOGY.

OBSERVATIONS ON THE STRUCTURE OF THE GUSTATORY ORGANS OF THE BAT (*Vespertilio subulatus*).

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AMHERST, MASS.

THE present paper contains a description of the anatomy of the taste organs of a single species of Chiroptera. It is highly probable that further study of these organs in other species of this interesting group of animals will reveal important variations, respecting both position and structural characters, from the results embraced in this short memoir.

It will be of interest first to notice briefly the form and general appearance of the tongue of this mammal.

GENERAL DESCRIPTION OF THE TONGUE.

The organ measures 13.5 mm. in length, its greatest transverse diameter is 5 mm., and at its thickest part it measures 4 mm. Anteriorly, it is free from the floor of the mouth for 6 mm., or nearly half its length. The upper posterior surface is slightly convex, and has a nearly uniform breadth. In the anterior half of the organ the lateral margins gradually converge, blending at the tip in a slightly rounded or pointed extremity. The upper surface of this portion of the tongue is marked by several subparallel, transverse rugæ or folds, with corresponding depressions between them. These folds decrease in size as they approach the anterior extremity of the organ, and cease altogether at 1.5 mm. from its apex. The dorsal surface is unmarked by any median groove or raphé, except at the extreme posterior region. Here there is a wide and rather deep mesial groove, 2 mm. in length, beginning in front of the epiglottis and terminating midway between the two circumvallate papillæ.

In one of my specimens, near the line of union of the posterior and middle third of the tongue, is a rounded eminence, showing a tendency to a raised posterior part, as seen in the tongue of the Rodentia. This feature, however, is wanting in other tongues of *Vespertilio* which I examined.

The upper surface, including the lateral margins, is covered with closely-set tactile and mechanical papillæ, the points of which are directed backwards and inwards.

The fungiform papillæ are only fairly numerous, and are distributed with some degree of uniformity over the dorsal surface and upon the sides of the tongue. Posteriorly they terminate in front of the gustatory area, and they cease anteriorly a short distance from the tip. Those scattered over the anterior third of the dorsum are usually larger than those occurring elsewhere.

On each lateral half of the tongue, 2 mm. from the base, is situated a circumvallate papilla. The two papillæ are placed quite near the median line, the distance between them being only 0.6 mm. They are oval in form, of nearly equal size, and are placed obliquely to the long axis of the tongue, their anterior extremity being directed outwards.

A papilla of similar type to those just mentioned, but less developed and apparently in a transitional stage, is present at the posterior limit of each lateral border. Further investigation will be necessary to determine whether these papillæ are constant or not. In the specimens which I have examined I have always found them, although exhibiting striking variations in form, general appearance, and structure, from normal circumvallate papillæ. No papilla foliata was found.

The under surface of the tongue is perfectly smooth. Anteriorly there is a median ridge, with sloping sides, extending from the frænum to the tip.

GUSTATORY STRUCTURES.

The Circumvallate Papillæ. — These papillæ show no indications of lobation. Their upper surfaces are rounded, and they measure 0.30 mm. in their transverse diameter, and are 0.22 mm.

in height. Where they join the tongue, the transverse diameter is only 0.12 mm. Each papilla is encircled by a rather shallow and very wide trench. In some sections this extreme width of the trench (as shown in Fig. 1) is confined to its upper part, the lower portion curving beneath the papilla and becoming quite narrow. The ridge surrounding the trench, and forming its outer wall, has elongated tactile papillæ projecting from its surface (Fig. 1). The general surface adjoining this gustatory area is covered with large and small papillæ, quite symmetrical in arrangement, but presenting a great variety of forms. Serous glands are fairly numerous in the gustatory area, but none were found within the papillary body itself. The ducts of the serous glands open into the trench at its base and sides. The papilla at its upper part bears many secondary papillæ, the depressions between which are filled by the epithelium. The nerves are chiefly non-medullated and ramify throughout the papilla, but I was unable to trace their terminal branches with any distinctness. The large ganglion described by Poulton[1] in the circumvallate papilla of *Perameles*, and observed by me[2] in the circumvallate papilla of *Fiber*, I failed to detect any indications of here.

The two lateral circumvallate papillæ are asymmetrical, the right one being much less developed than the left. The latter, as seen in vertical section, is elliptical in shape, and joins the tongue by a narrow pedicel. The trench which surrounds this papilla is very wide at its upper part, and narrow and of uniform breadth at its lower. Serous glands are sparingly scattered through this region, and are entirely wanting within the papillary body.

The taste-bulbs are not very numerous in the circumvallate papilla of *Vespertilio.* They are disposed at the sides in a girdle of seven or eight tiers, the uppermost tier being nearly on a level with the top of the trench. From horizontal sections, made at different levels, I estimated the average number of bulbs in a tier at fifty. If we allow for eight tiers, we shall have four hundred bulbs for each papilla. I did not succeed in finding bulbs in the epithelium investing the upper surface of the papilla, nor was I able to detect them in the outer wall of

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[1] Quart. Journ. Micr. Sci., Vol. XXIII., 1883, p. 73.

[2] Journ. of Anat. and Physiol., Vol. XXII., 1888, p. 136.

the trench. The bulbs vary somewhat in shape, and in point of size they are the smallest I have yet observed, the nearest approach to them in this respect being those of the circumvallate papilla of the mouse. They vary in length from 0.025 to 0.030 mm., and their breadth is about 0.015 mm. Usually in a bulb of this area, the diameter of the peripheral end of the bulb exceeds that of the central. The latter is also curved slightly downwards. This form of bulb I have not observed before, although it is seen in those figured by Lovén in the circumvallate papilla of the calf. I did not succeed in finding a bulb with the peripheral processes of its gustatory cells projecting beyond the pore. One bulb (in vertical section) shows a fissure, 0.015 mm. long and 0.0015 mm. wide, caused by a separation of the edges of two adjoining peripheral cells.

I was unable to isolate the central or gustatory cells of the bulbs sufficiently well for study, but the peripheral cells do not differ materially from those already described in the taste organs of other mammals. They are elongated, slightly flattened, nucleated cells, with their two extremities tapering gradually to a point.

The number of bulbs in the left lateral circumvallate papilla could not be estimated from my sections with any degree of accuracy. The most noteworthy thing about them in this region is their very unusual arrangement (Fig. 3). They occur only on one side of the papilla; but here they form a continuous chain, seventeen tiers deep, extending from the base of the papilla nearly to its summit. Bulbs are likewise present in the lower half of the outer wall of the trench. Here I counted eight tiers. The bulbs of this region measure 0.024 mm. in length and 0.015 mm. in breadth, being thus a little smaller than those of the normal circumvallate papilla.

The Fungiform Papillæ. — These papillæ are distributed quite regularly over the dorsum and sides of the tongue, from the gustatory area nearly to the tip. Interspersed among those of the posterior part of the dorsum are a few which appear to be undergoing transition to the circumvallate type of papilla (Fig. 6).

In several instances taste-bulbs were present in the epithelium at the upper part of these papillæ. They are usually placed vertically, directly in the long axis of the papilla. By far the most interesting specimens (which are shown in Fig. 6) were found in a papilla from the posterior region of the tongue. In this papilla there are two well-formed bulbs, and placed between them is a third, which is either of a low order or undeveloped.[1] The largest bulb of the three measures 0.036 mm. in length and 0.016 mm. in breadth, and its apex appears to reach the free surface of the epithelium, its base penetrating the mucosa. Some of the isolated bulbs met with elsewhere in these papillæ, particularly those of the anterior dorsal surface, are even larger than those shown in Fig. 6. Neither serous nor mucous glands were observed near the fungiform papillæ.

The entire upper surface of the tongue is covered with papillæ of mechanical and tactile (?) function. They are quite closely set, except at the basal region, are largest at the posterior part of the dorsum, and gradually decrease in size as they approach the anterior extremity. These papillæ, when near the tip, enlarge slightly again. One from the posterior third of the tongue measured 0.11 mm. in height and 0.04 mm. in breadth. Behind the circumvallate papillæ, and also about the tip, are numerous rather coarse, retroverted, conical papillæ. Each papilla is seated upon a single papillary upgrowth of the mucous membrane, and is invested by epithelium of a uniform thickness. The outer layers of epithelium covering the upper surface and sides are usually partly, and occasionally wholly, cornified. These papillæ vary much in shape and general appearance. Many of them are cone-shaped, while others resemble, in external structure, minute fungiform papillæ. The upper surface is now and then flat or slightly convex, but usually the papilla terminates in a retroverted, horny spinule.

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[1] Figure 7 represents a vertical section through a fungiform papilla, from the anterior dorsal surface of the tongue of a pig, containing eight taste-bulbs.

EXPLANATION OF PLATE I.

LIST OF REFERENCE LETTERS.

c. e. Columnar epithelium. *g. p.* Gustatory pore. *gl. d.* Duct of serous gland. *m. m.* Mucous membrane. *p.* Elongated papilla. *p. e.* Pavement epithelium. *p. p.* Papillary processes of mucous membrane. *r.* Ridge. *s. e.* Stratified epithelium. *s. p.* Secondary papillæ. *t.* Trench. *t. b.* Taste-bulb. *t. b'.* Taste-bulb of outer wall of trench. *t. b.''* Taste-bulb undeveloped or of low type.

FIG. 1. — Vertical section through one of the circumvallate papillæ. (× 100 diam.)

FIG. 2. — Vertical section through the base of the same papilla, showing overhanging side with four lowermost tiers of taste-bulbs. (× 480 diam.)

FIG. 3. — Vertical section through the left lateral circumvallate papilla. (× 125 diam.)

FIG. 4. — Horizontal section through the lower part of one of the circumvallate papillæ, representing the taste-bulbs arranged in a zone. *gl. d.* Ducts of the serous glands which open into the trench at this level. (× 160 diam.)

FIG. 5. — Vertical section through a fungiform papilla of the mid-dorsal surface of the tongue, showing a single taste-bulb at its upper part. (× 400 diam.)

FIG. 6. — Vertical section through a fungiform papilla of the posterior dorsal surface of the tongue, which is probably undergoing transition to the circumvallate type. (× 480 diam.)

FIG. 7. — Vertical section through a fungiform papilla of the anterior lateral dorsal surface of the tongue of a pig. (× 200 diam.)

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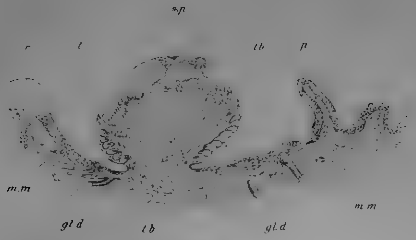

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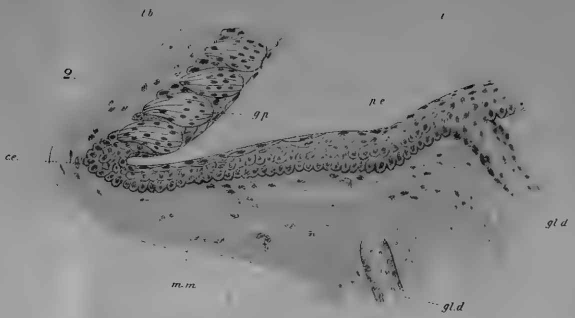

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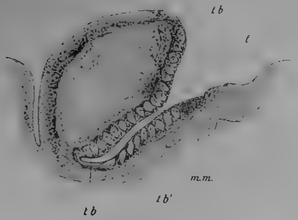

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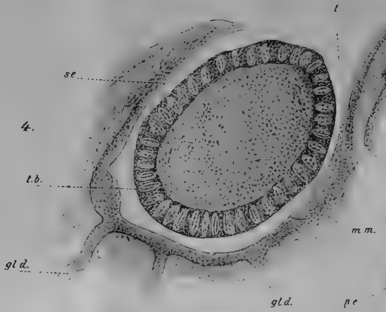

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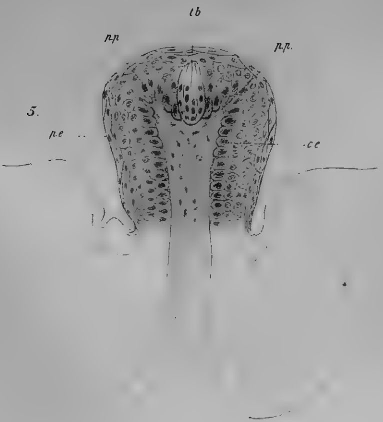

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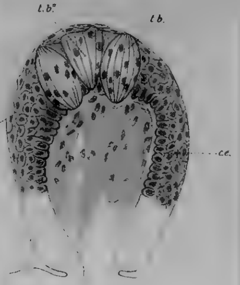

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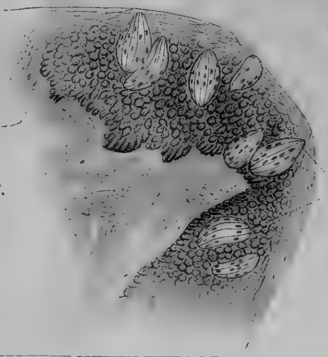

T. Hall, del.

ON THE TRITUBERCULAR MOLAR IN HUMAN DENTITION.

E. D. COPE.

DESCRIPTIONS of the molar teeth of man, given by anatomists, differ in important respects. Thus, F. Cuvier ("Dents des Mammifers") states that, while the crown of the first superior true molar consists of four tubercles, those of the second and third superior true molars consist of but three tubercles. In the American edition of "Sharpey and Quain's Anatomy" it is stated that the crowns of the superior true molars of man consist of four tubercles; and the same statement is made in Allen's late work on human anatomy.

My observations having shown me that both of these descriptions apply correctly to certain types of dentition, I determined to examine for myself, to ascertain, if possible, the extent and value of the variations thus indicated. My interest in the subject had been especially stimulated by the researches among the extinct mammalia, and the results which I had derived from them. These are, in brief, as follows: first, the quadritubercular type of molar crown, illustrated by the first superior true molar of man, belongs to the primitive form from which all the crest-crowned (lophodont) molars of the hoofed placental mammals have been derived; and second, this quadritubercular type of molar has itself been derived from a still earlier, tritubercular crown, by the addition of a cusp at the posterior internal part of it. This tritubercular molar in the upper series has given origin directly to the superior sectorial teeth of the creodonta and carnivora. In the inferior series, I have shown that in known placental mammalia at least, the primitive molar crown is quinquetubercular, or tritubercular with a posterior heel; that this form gave origin to the inferior sectorial tooth of carnivora by modification, and to the quadritubercular type — corresponding to the superior quadritubercular crown — by a loss of the anterior inner cusp and connecting crest. And from the quinque- and quadritubercular types of molar crown, the various specialized types of the ungulates have been derived.

Considerable significance, therefore, attaches to the question as to whether the superior true molars of *Homo sapiens* are quadritubercular or tritubercular. The inferior molars are also either quadritubercular or quinquetubercular; but less significance attaches to this modification than to that of the superior true molars. This is owing to two facts; viz., the fifth tubercle is not the anterior inner which completes the anterior triangle of the primitive inferior molar, but is a median posterior, such as is not uncommon in mammalia of Puerco and Eocene age; and second, because this tubercle is of quite small size, and is therefore more liable to variation from insignificant causes.

In the nearest allies of man, the anthropoid apes, the superior true molars are quadritubercular, the posterior internal tubercle of the last or third molar being usually smaller than in the other molars in the chimpanzee. The inferior molars are quinquetubercular, in the human sense, the gorilla not infrequently adding a sixth lobe on the external posterior margin of the crown. The molars of both series are quadritubercular, with an occasional posterior fifth in the inferior molars in the Cercopithecidæ and Cebidæ, excepting the genus Pithecia of the latter, where the superior molars are tritubercular. The superior molars of the Hapalidæ are tritubercular. In the Lemuridæ the second and third, and frequently the first, superior true molars are tritubercular. In the Tarsiidæ the superior true molars are tritubercular throughout. The superior molars of the extinct lemuroids differ, like those of the recent forms. Thus, in Adapis and its allies they are quadritubercular, but in Necrolemur they are tritubercular. In Chriacus (whose reference to the Lemuroidea is uncertain) they are tritubercular, as is the case, also, with Indrodon. In Anaptomophus they are of the true tritubercular type. This is the genus of Lemuroidea, which in its dental character most nearly approaches the anthropoid apes and man. I have elsewhere[1] pointed out that the formula is I. $\frac{2}{2}$; C. $\frac{1}{1}$; Pm. $\frac{2}{2}$; M. $\frac{3}{3}$. The canines are small, and there is no diastema in either jaw.

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[1] *Report U. S. Geol. Survey, Terrs.*, F. V. Hayden, Vol. III., 1885, p. 245, Pl. xxv. fig. 10, and Pl. xxiv*e*. fig. 1.

It may be readily seen, in consideration of these facts, that the appearance of tritubercular superior molars in the genus Homo constitutes a reversion to the lemurs, and not to the anthropoid apes or to the monkeys proper. And among lemurs the reversion is most probably to that type which presents the closest resemblance to Homo in other parts of the dentition. The genus which answers most nearly to this requirement among those at present known, is Anaptomorphus.

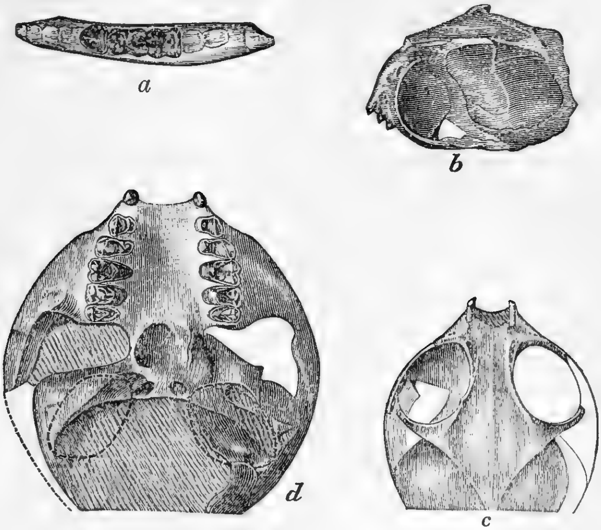

Figure 1.—Two species of Anaptomorphus. Fig. *a*, *A. æmulus*, lower jaw from above × 2. Figs. *b*, *c*, *d*, *A. homunculus*; *b*, *c*, natural size; *d*, $\frac{3}{2}$ natural size. Both from Eocenes of the Rocky Mountains.

In studying the dentition of man, I have examined the crania contained in the following six collections: those of the Academy of Natural Sciences of Philadelphia; of the Army Medical Museum of Washington; of the College of Physicians of Philadelphia; of the University of Pennsylvania; of the Boston Society of Natural History; and of my own museum. The first of these is especially valuable on account of the negro, Egyptian, and Hindu crania it contains. My acknowledgments are due to the Board of Curators, of which Professor Leidy is chairman, for the opportunity of studying it. I am also indebted to the Boston Society of Natural History, and its learned curator, Professor

Hyatt, for the opportunity of examining Hindu and Chinese crania in their museum. The collection of the Army Medical Museum at Washington is especially important on account of the Kanakas, Esquimaux, Peruvians, and North American Indians which it possesses. I am under great obligations to its distinguished director, Dr. J. S. Billings, for the facilities which he placed at my disposal. The museum of the Philadelphia College of Physicians contains the collection made by the late Professor Hyrtl of Vienna, of crania of Eastern and Mediterranean Europeans. In this department it is unrivalled, and I am greatly indebted to the council of the college, and its curator, Dr. Guy Hinsdale, for the opportunity of examining it. Some French skulls in the University of Pennsylvania were of value in the investigation. My own collection, though small, contains a number of Maoris, Australians, Tahitians,[1] and North American Indians, which have proved to be of importance. Of English and Europeo-American crania, I have been able to examine but few of what might be termed the thoroughly amalgamated race. Of the latter there are probably many crania in the war collection of the Army Medical Museum, but how free the race of each may be from foreign intermixture, of course it is impossible to know. In selecting such as are supposed to be "stock Americans," those of persons with English names have been preferred, although many now true Americans are of German ancestry. In order to increase the list of this class of examinations, I have imposed on the forbearance of my friends by frequent inspections of their dentitions in *ore aperto*.

I suspect that the characters thus obtained will prove of importance in a zoölogical and ethnological sense. They have been already found to be of great fixity, and hence significance, in the lower mammalia. The only reason why they should be less so in man is, that the modification in reverting to the tritubercular molar is a process of degeneracy, and may be hence supposed to be less regular in its action than was the opposite process of building up, or addition of the posterior internal cusp. Some justification for a light estimate of its value may

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[1] For the Maori and Australian skulls, I am indebted to Mr. Speechey Gotch of Melbourne; and for the Tahitians to Dr. Chassaniol, Chef de la departement de Santé de Taiti, of Paris. My best acknowledgments to these gentlemen are hereby expressed.

be found in the following tables. But it must be remembered that it is not always possible to determine exactly the race of the person represented by a skull, even when care in its identification has been exercised. Emigration and war have constantly rendered races impure, and transplantation on a large scale has in some parts of the earth produced hybrid races. The results of a study of human crania are sure to be more or less vitiated by these circumstances. We obtain averages rather than exact definitions. Nevertheless, the extremes of the series of variations are likely to be found to be characteristic of established forms of man, and will thus justify my belief in the value of the characters presented. To ascertain the relation of these variations to the races is the object of the present inquiry.

The cause of the tritubercular reversion belongs to the class of agencies active in evolution of organic types, of whose real nature we know little. It cannot be said to be due to a contraction of the maxillary arcade, for the Esquimaux and some other peoples which display the tritubercular dentition are not deficient in this respect. Nor do tritubercular molars require less space than the quadritubercular, for the external width of the crown is the same in both cases. They generally require less material however than a quadritubercular crown, since a triangle is smaller than a square drawn on the same base line; however, in some men of the lower races who present the tritubercular molars, their outline is nearly square. The hypothesis advanced to account for the reduction of the number and quality of human teeth observed in the higher races, as well as for the replacement of the prognathous jaw by the orthognathous, is that such changes are due to a transference of material and of growth energy from these parts to the superior part of the skull and its contents. The relative superiority of the dimensions of these parts in the higher races is thus accounted for.

In the following tables the tubercular formulæ are represented by numbers. Only the last three, or the true molars, in each jaw are considered. Tubercles of reduced size are represented by fractions. Thus $\frac{4-4-4}{5-5-5}$ indicates that each superior molar is quadritubercular, and each inferior molar quinquetubercular. This represents the extreme of the series represented by the lowest races. The formula $\frac{4-3-3}{4-4-4}$ indicates that the true molars have four, three, and three, tubercles respectively, and that the inferior true molars have four each. This represents the extreme common among the higher races. In the table which follows, the numbers attached to crania in the respective collections are appended, and initials indicating the collection follow. Thus A. M. M. refers to the Army Medical Museum, Washington; C. P., the College of Physicians of Philadelphia; U. P., the University of Pennsylvania; B. S., the Boston Society of Natural History; E. D. C., my private collection; no initials follow the numbers of the Academy of Natural Sciences of Philadelphia.

$$\frac{4-4-4}{5-5-5}$$

Malay[1] of Madura, *1339; Malay, 425; Negroes, 63 and 258, C. P.; S. Sea Islander, 86, A. M. M.

$$\frac{4-4-4}{5-4-4}$$

Malays, 47 and 433 (latter of Sumbawa); Negroid Egyptians, 43, 798, 852*, 869.

$$\frac{4-4-4}{4-4-4}$$

Malay, 1338 (of Amboyna).

$$\frac{4-4-4}{?}$$

Tahitian, E. D. C.; Kanakas, 143 and 1308, C. P.; Malay, 425 (Java); Negro, 963; Hindu, 1070, B. S.

$$\frac{4-4-3\frac{1}{2}}{5-5-5}$$

Marquesas Ids., 1531, C. P.; Greek of the Morea, 55, C. P.

$$\frac{4-4-3\frac{1}{2}}{5-5-4}$$

Peruvian, 932 (Arica).

$$\frac{4-4-3\frac{1}{2}}{5-4-4}$$

Malay, 430 (Amboyna); Italian, 114, C. P. (Elba); Peruvian, 2300, A. M. M.

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[1] Just what is meant by the "Malays" of the Philadelphia Academy collection I do not know.

$$\frac{4-4-3\frac{1}{2}}{5-4-5}$$

Negro, 4122, C. P.; Kaffir, 1358; Pessahs, 1095–*7; Gipsy, 31, C. P.; Montenegrin, 29, C. P.; Tablunka, 106, C. P.; Germans, 1063–4 (Tübingen); Feejees, 292–3, A. M. M.

$$\frac{4-4-3\frac{1}{2}}{?}$$

Australian, E. D. C.; Tahitian, E. D. C.; Negroes, 901, 903, 914, 920, 921, 927, 964; American Negro, 980, A. M. M.; Chatham Id., 1557, A. M. M.; Peruvians, 68, 452; 2 N. Amer. Indians, E. D. C.; Ponka India, 487, A. M. M.; Comanche, 6563, A. M. M.; Sicilian, 110, C. P.; Esquimaux, 1859, A. M. M.; French, 1579, A. M. M.; Anglo-Americans (Wilderness Battle-Field, Va.), 6305–6–7, A. M. M.; Kanakas, 286, 434, and 584, A. M. M.; Hottentot, B. S.

$$\frac{4-4-3}{5-5-5}$$

Madagascar, two (Hovas); Samoan Id.; N. Amer. Indians, 1345 (Lipan), and Hudson's Bay Ind.; Mexican, 714 (Ancient); Peruvians, 72, 1373, 1465; Italian, 118, C. P.; Lombard, 117, C. P.; Czech, 131, C. P.; German, 239, C. P.

$$\frac{4-4-3}{5-5-4}$$

N. Amer. Indians, 530 and 1804 (Pawnees), A. M. M.

$$\frac{4-4-3}{5-4-5}$$

Italians, 2 (Giurgevo and Piedmont), C. P.; Gipsy, 18, C. P.; Ural, 33, C. P.; Bulgar, 94, C. P.; Slav, 84, C. P.

$$\frac{4-4-3}{5-4-4}$$

N. Amer. Indian (Spokane), E. D. C.; Italians, 46 and 47 (Terracina and Ragusa), C. P.; Albanian, 123, C. P.; Viennese, ♀ 59, C. P.

$$\frac{4-4-3}{4-4-4}$$

Negroid Egyptian, 885; Swede, 1549.

$$\frac{4-4-3}{?}$$

2 Tahitians, E. D. C.; Kanakas, 291, 451, 455, 570, 588, 844, 1057, A. M. M.; Chatham Id., 5721, A. M. M.; Esquimaux, 1232, A. M. M.; N. Amer. Indian, 380 (Chippewa), A. M. M.; ? Anglo-Americans, 5721,

3257, 6785, A. M. M.; Jew, 3, C. P.; Rouman, 96, C. P.; Chinese, 873, B. S.; Hindu, 137, B. S.

$$\frac{4-4-?}{?}$$

Kanakas, 79, 280, 283, 421, 423, 427, 431, 457, 463, 599, 709, 862, A. M. M.; Chinese, 958, 5130, 5139, A. M. M.; Peruvian, 1765 (Ancon), A. M. M.; Peruvian, 2302, A. M. M.; S. Sea Islander, 344, A. M. M.; Indian of Yucatan, 629, A. M. M.; Mojave, 209, A. M. M.; Hindu, 123, B. S.

$$\frac{4-3\frac{1}{2}-4}{4-4\,?}$$

Circassian, 762.

$$\frac{4-3\frac{1}{2}-3\frac{1}{2}}{5-5-5}$$

Negro, 1343 (Archipelago); American Negro; S. German, 1289.

$$\frac{4-3\frac{1}{2}-3\frac{1}{2}}{5-4-5}$$

N. Amer. Indian, 1794 (Ute), A. M. M.; Hindu, *1344, Bengal; Gipsy, 98, C. P.; S. German, 1158; Italians, 2, 8, and 109 (Tessino and Roveredo), C. P.; Greek, 53 (Cephalonia), C. P.; Bosniak, 100, C. P.; Cossack of Don, 101, C. P.

$$\frac{4-3\frac{1}{2}-3\frac{1}{2}}{5-4-4}$$

Patagonian, 1232 (last infer. mol. $4\frac{1}{2}$); Negro lunatic, 55.

$$\frac{4-3\frac{1}{2}-3\frac{1}{2}}{?}$$

African Negroes, 580, 685, 902, 917; Kanaka, 861, A. M. M.; American Negro, 411, A. M. M.; Peruvian, 1326; 2 N. Amer. Indians, E. D. C.; Mound Builders, 1049–1123, A. M. M.; Piegan, 6486, A. M. M.; Cheyenne, 5560, A. M. M.; ? Anglo-Americans, 2, A. M. M.; Esquimaux, 1182, 1194, 1250; Hollander, ♀ 10, C. P.; Hindu, 124, B. S.

$$\frac{4-3\frac{1}{2}-3}{5-5-5}$$

Malay, 1340 (Macassar), 1341 (Java); Finn, 1539; Czech, 79, C. P.; Viennese, 61, C. P.; French, U. P.

$$\frac{4-3\frac{1}{2}-3}{5-4-5}$$

Algerine, 3900, C. P.; Uskoke of Banjaluka, 90, C. P.; Styrian, 85, C. P.; Hindu, 432; Latin, 115, C. P.; Albanian, 97, C. P.; German of Siebenbürgen, 76, C. P.

$$\frac{4 - 3\tfrac{1}{2} - 3}{5 - 4 - 4}$$

Hungarian, 14, C. P.; Russian, 35, C. P.; Australian, (1327); Negroes (Benguela), 421, (Mozambique), 423; Hottentot, 1351; Aztec; Circassian; Moravia, ♀ 135, C. P.; Croat, ♂ 134, C. P.; Galician, 139, C. P.; Serb, 96, C. P.; "Pizgau," 66, C. P.; Saltzburg, 65, C. P.

$$\frac{4 - 3\tfrac{1}{2} - 3}{4 - 4 - 4}$$

Swedes, 1487–50.

$$\frac{4 - 3\tfrac{1}{2} - 3}{? \quad ? \quad ?}$$

Negro (Dey), 1100; Peruvian; Kanaka, 576, A. M. M.; Dutch, 434; Malay, 39; Bengal, 20, A. N. S.; Hindu, 1330; Fellah, 999; Kabardine Caucasus, 38, C. P.; Ital. Piedmont, 45, C. P.; N. Amer. Indians (Flathead), E. D. C., (Cheyenne), 6525, A. M. M., (Ponka), 486, A. M. M., (Sioux), ♀ 2049, A. M. M.; Mound Builders, 169, A. M. M.; Esquimaux, 1183, 1189, 1245, A. M. M.; ? Anglo-Americans, 6847, 5922, A. M. M.; German, 1066; Chinese, 879, B. S.

$$\frac{4 - 3\tfrac{1}{2} - ?}{?}$$

Kanakas, 564, 569, 571, 591, A. M. M.; Peruvian, 2308, A. M. M.; Arucanian, 970, A. M. M.; Chuktchi, 277, A. M. M.; Esquimaux, 1779, A. M. M.

$$\frac{4 - 3 - 3\tfrac{1}{2}}{?}$$

Chukchi, 263, A. M. M.

$$\frac{4 - 3\tfrac{1}{4} - 3\tfrac{1}{4}}{?}$$

? German-American, 6445, A. M. M.

$$\frac{4 - 3 - 3}{5 - 5 - 5}$$

Dalmatian, 132, C. P. · Greek (Trieste), 56, C. P.; Indians (Santa Barbara, Cal.), 3.

$$\frac{4 - 3 - 3}{5 - 5 - 4}$$

Gipsy, 130, C. P.; Trieste, 120, C. P.; Apache, 1168, A. M. M.

$$\frac{4 - 3 - 3}{5 - 4\tfrac{1}{2} - 4\tfrac{1}{2}}$$

Modoc, E. D. C.

$$\frac{4-3-3}{5-4-4}$$

Druse, 122, C. P.; Idria, 89, C. P.; Carniola, 87, C. P.; S. Tyrol, 121, C. P.; Paris, 3916, U. P.; 4 Anglo-Americans, E. D. C.; French, 867 (Paris), U. P., 1620, A. M. M. Kurd, 28, C. P.; Thug Hindu, 128 (A. N. S.); Esquimaux, 676 (trace of $\overline{5}$ on $\overline{2}$ and $\overline{3}$); Italian (Calabria), 48, C. P.; Greeks (Candia), 54 and 51, C. P.; Slovak, 73, C. P.; Czech, 4, C. P.; Lithuania, ♀ 21, C. P.; Bukovina, ♀ 78, C. P.; Tyrol, ♀ 67, C. P.; Upp. Austria, 63, C. P.; Moravia, 5, C. P.; Hollander, ♂ 9, C. P.

$$\frac{4-3-3}{5-4-5}$$

"Krakuse" (Czech or Pole, large), 82, C. P.; "Kumanie" (? Hungary), 71, C. P.; Pole, 24, C. P.; Volhynian, 36, C. P.; Podolian, 37, C. P.; Hindu (Bengal), 1344; Tatra (large), 83, C. P.; Wallach, 95, C. P.; French, 105, U. P.

$$\frac{4-3-3}{4-4-4}$$

Tchuktchi; Zagrebin, 126, C. P.; Croat, 77, C. P.; Mixed German and Croat, 17, C. P.; French, 1082; do., 1801, A. M. M.; Anglo-American, 1108.

$$\frac{4-3-3}{?}$$

Peruvian, 1478; do., 2299, A. M. M.; Turkish grave, 127, C. P.; Crimean, 34, C. P.; Cossack, 133; Ruthenian, 103, C. P.; Armenian, 99, C. P.; Esquimaux, 675, 679, A. N. S.; Esquimaux, 1211, 1218, 1219, 1206, 1221, 1225, 1226, 1230, 1231, 1241, 1244, 1251, 1278, 1781, 1782, 2113, A. M. M.; Chuktchis, 256–7, A. M. M.; N. Amer. Indians, 5550 (Pawnee), 6561, 6565 (Comanches), 7023 (Cheyenne), 170, (Mound Builder), A. M. M.; Kanakas, 580, 841, A. M. M.; Indians of Yucatan, 626–628, A. M. M.; American Negroes, 981–983 (Richmond, Va.), 6615 (S. Carolina; m. 2 on one side is $3\frac{1}{2}$); 6 Anglo-Americans, E. D. C.; ? Anglo-Americans, 95, 6305–6–7–8, 6640, 739, 2699, 1768, 5116, 5145, 5708 ♀, 5940, 6550, A. M. M.; Hindu, 425, B. S.

$$\frac{4-3-3}{4-4-5}$$

Hungarian, 15, C. P.

Neolithic Man.

Through the kindness of Mr. Thomas Wilson, honorary Curator of the Department of Prehistoric Anthropology in the United States National Museum, I have had the opportunity of examining a number of dentitions of men of the Neolithic period of France. The best preserved of these includes both series in place in both jaws, the last two inferior molars of one side and the last inferior of one side being absent. This man was disinterred from a cemetery on the island of Thinic, on the coast of Brittany. Teeth of a considerable number of men, in a separate condition, were obtained by Mr. Wilson from the dolmen of Poulzongue, near the town of Gramat, in the department of Lot, Central France, and have also been examined by me.

The dental tubercular formula of the man of Thinic is $\frac{4}{4}\,\frac{4}{4}\,\frac{3}{5}$. The second superior molar is a perfect quadritubercular, while the third is an equally perfect tritubercular, of somewhat reduced size. This dentition is, then, exactly intermediate between extremes. It is further advanced than that of the lowest existing races, but has not reached the final modification of the most specialized. The dental characters of the men of Poulzongue vary between the type of the man of Thinic and the formula $\frac{4}{4}\,\frac{3}{4}\,\frac{3}{4}$. Several of them have the second superior molar plainly tritubercular, and perhaps as many have the fourth tubercle imperfectly developed. But no indication of a tritubercular first superior molar is observed, such as occurs in a few Esquimaux. The resemblance of perhaps half of the superior molars of Poulzongue to those of Esquimaux and the more specialized Indo-Europeans is distinct. Pointing in the direction of the latter, are the small size of the teeth and the frequent occurrence of caries.

The Accessory Anterior Internal Tubercle.

This tubercle is characteristic of the genus Lemur (Fig. 11) and some of its extinct allies. Such are the *Chriacus pelvidens* and *C. truncatus* Cope, the former figured in Tertiary Vertebrata (Report U. S. Geol. Survey Terrs. III.), Vol. XXIII., *d*, Fig. 7.

I have found it well developed in the Malay (Fig. 2, *aai*), No. 1339. It is present in three Tahitian crania in my collection, and I have observed it in another Micronesian cranium, and in some others. This character is decidedly lemurine, but whether to be properly termed a reversion or not may be questioned in view of the fact that it always occurs, so far as yet known, in dentitions most remote from that type in other respects. It might be rather regarded as a survival or as a character which has persisted from the "protanthropos" which was itself immediately derived from lemurine ancestors.

Anomalous dentitions.

I have observed the following examples of aberrant molars. In an Esquimaux (A. M. M.) the formula of the superior molars of one size is 3—4—0; in another (B. S.) it is 3—3—4. In a French skull (A. M. M.) we observe on one side 4—4—3; on the other side, 3½—3—3½. The posterior superior molar is, by reason of its late and retarded development, the most liable to exhibit abnormalities. In a Tahitian skull in my collection, it is tritubercular on one side and obtusely haplodont (conic) on the other.

General Conclusions.

For clearer understanding of these characters, they are arranged in the form of a table. Only the principal races are represented, and hybrids, when determinable, are omitted.[1] The characters of the superior molar teeth only are referred to. These are classified under four heads, viz.: first, tubercles 4—4—4; second, tubercles 4—4—3½ or 4—3½—3½; third, tubercles 4—3½—3; fourth, tubercles 4—3—3. As already remarked, the extreme types of the series give the most precise indications of race, while the intermediate conditions have a various range.

In the first table the most obvious results are, that only the three lowest races present four tubercles on all the superior molars, and that of those with tritubercular second and third molars, Europeans and their American descendants greatly predominate. Also that of uncivilized races, the Malays and

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[1] Mulattoes, Mestizoes, Half-breed Indians, Gipsies, etc., are omitted.

Negroes never, and Micronesians very rarely, present this type of dentition, while in the Esquimaux it considerably predominates, examples of tritubercular first molars even occurring.

	"Malays" (? Nigritos).	Australians and Micronesians.	Negroes and Egyptians.	Peruvians.	North American Indians.	Chinese and Japanese.	Hindus.	Esquimaux and Chuktchi.	Europeans and Europeo-Americans.	Totals.
4 — 4 — 4	6	4	7				1			18
(4 — 4 — ?)		13		2	1	3	1			20
4 — 4 — 3½ 4 — 3½ — 3½ 4 — 4 — 3	1	23	17	9	27[1]	1	5	6	39	128
4 — 3½ — 3	3	2	5	1	5	1	1	3	24	45
4 — 3 — 3		2		2	8		3	19	56	90
Total . .	10	44	29	14	41	5	11	28	119	301

I now give a table of the characters of the superior molars in the Europeans and Europeo-Americans examined. The number is not sufficient for final conclusions; nevertheless there are some indications of value. Some of the one hundred and nineteen dentitions examined are referred with doubt to their respective races. Thus the Europeo-Americans may have been in many instances immigrants, as many such left their bones on the battle-fields of the American civil war, where many of the crania were picked up. The supposed Germans are largely Austrians, so that some of them may be more or less Slavic or Magyar. Allowance for these would reduce the number of tritubercular molars.

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[1] Ten crania in the Museum of the Cincinnati Soc. Nat. History, mostly Mound-Builders, have the formula 4 — 4 — 3.

	Lapps and Finns.	Magyar.[1]	Slavs.	Western Asiatics.	Greeks and Italians.	Germans and Scandinavians.	French.	Europeo-Americans.	Totals.
$4-4-3\frac{1}{2}$			2		3	2	1	3	11
$4-3\frac{1}{2}-3\frac{1}{2}$			1	1	3	3		2	10
$4-4-3$			5		7	3		3	18
$4-3\frac{1}{2}-3$	1	1	6	2	3	8	1	2	24
$4-3-3$		2	11	4	7	6	6	20	56
Total . .	1	3	25	7	23	22	8	30	119

As results we have the following: the tritubercular dentition appears in 11 out of 25 Slavs; in 7 out of 23 Greeks and Italians; in 6 out of 22 Germans and Scandinavians; in 6 out of 8 French; and in 20 out of 30 Europeo-Americans. The only great race which presents a similar high percentage of tritubercular molars is the Esquimaux, where they occur in 21 out of 30 dentitions. The tendency is most marked in Slavs, French, and Europeo-Americans, and is least marked in Greeks and Italians and in Germans. The former subrace stands in the series between the intermediate type of the North American Indians and the other Europeans. In the Germans the number with tubercles $4-3\frac{1}{2}-3$ is large. If these be added to the number with $4-3-3$, we have 16 out of 22.

It is important to remember in this connection that the distinguished ethnologist and archæologist, W. Boyd Dawkins, affirms that the earliest inhabitants of Britain and some other parts of Europe were Esquimaux. He refers especially to the men of the caves, whose implements and arts he declares to be identical with those used by the Esquimaux of the present day.[2] As it is evident that the lemurine or tritubercular reversion commenced with the Esquimaux, it may be that in some instances at least its appearance in men of Anglo-Saxon and other European races is due to inheritance alone. But it is also reasonable to suppose that in this case as in other evolutions, the

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[1] Perhaps improperly included in this table.

[2] *Early Man in Britain*, 1880, p. 233.

cause which produced this modification of the Esquimaux dentition is still active, and its recent appearance in the most civilized races must be due to this unknown cause. The progressive character of the French dentition in this respect is in broad contrast with the primitive character of that of Italians and Greeks. The characters seen in the latter go far towards sustaining Professor Huxley's hypothesis, that the dark Mediterranean sub-races consist of a mixture of Egyptian with the Indo-European stock.

In conclusion it may be stated, that the tritubercular superior molars of man constitute a reversion to the dentition of the Lemuridæ of the Eocene period of the family of Anaptomorphidæ. And second, that this reversion is principally seen among the Esquimaux and the Slavic, French, and American branches of the European race. Observations on some of the races of the Indo-Europeans are yet so imperfect that some additions to the above list yet remain to be made, as for instance, probably, the English sub-race. The neolithic dentitions examined are intermediate between the two extremes, thus showing an advance over the lowest existing races.

The Origin of the Quadritubercular Molar.

This question has an interest beyond the history of human dentition. I will now inquire whether any mechanical cause can be assigned for the retention of the quadritubercular structure.

It may be recalled that I have shown that the development of a fourth tubercle on the posterior side of the internal tubercle of the tritubercular superior molar has been the origin of the dentition of the non-carnivorous types, which are principally Ungulata. The mechanical action of the inferior against the superior molars cannot have been very different in the early Ungulates from what it was in the early flesh-eaters, since the canine teeth, which partly direct this motion,[1] are equally developed in both. But the history of the canines in the development of the Ungulates is exactly the reverse of what it has been in the flesh-eaters. In the former the canine has grown successively smaller, and has been in most of the lines completely

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[1] See mechanical origin of the dentition of the carnivora, Proceedings American Association Advanced Science, 1887.

aborted. Whence, then, has come this different history? It has been probably partly due to the substances used as food. The softer and often tougher animal tissues permitted the shearing motion through their elasticity and extensibility carrying the friction beyond the opposing transverse edges of the crowns, vertically along their sides. The grains and vegetable substances, on the other hand, possess no such elastic qualities, and are cut or broken by the approach of the edges themselves. The pressure would be direct and brief, and not a continued shear. Just how this would result in the development of the fold on the posterior side of the crown of the superior molar is a question of nutrition not yet explained by actual observation; but it is generally observable, however, that in dentition, folds of the surface have resulted from ordinary use, not too severe. In the case of the shearing which developed the carnivorous dentition, the animal used force to cut the meat in the manner necessary to do it. This shearing force is so great as to wear the crown, rather than to encourage growth. The temporary force required by the act of crushing vegetable matters (excepting such as approach flesh in their characters) is more of the nature of impact, and is of very brief duration. The fourth tubercle has been the result, and I have described its various complex derivatives elsewhere.[1]

Can it be possible that a largely, or exclusively meat diet has been the mechanical cause of the development of the tritubercular molar in man? Its great predominance in the Esquimaux suggests this explanation. The lower and quadritubercular races are largely granivorous and frugivorous, but whether so predominantly so as to restrain the modification in question, I do not know. It is probable that the tritubercular molar expresses a change which is both phylogenetic and physiological.[2]

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[1] In 1874, in the Journal of the Philadelphia Academy of Natural Sciences, I homologized the various parts of the mammalian tooth-crown structures and traced their phylogeny. The same was done about the same time by Kowalevsky. Not being then familiar with the capacity of dense substances, as dentine and enamel, to yield their form to continued strains, I did not pursue the question of the origin of these forms through use in mastication, although I suspected such origin. This was done in 1878 by Prof. J. A. Ryder, in an able paper on "The Mechanical Genesis of Tooth-Forms," *Proceedings Acad. Phila.*, p. 45. With minor exceptions, I have adopted the views there set forth.

[2] After I had nearly completed this investigation, I received during October of this year (1886) the admirable monograph of Dr. Wortman on the dentition of the ver-

tebrata. He describes human dentition more thoroughly than previous authors, and refers to the tritubercular modification in the following language (p. 444): "The superior molars, like those in the lower jaw, are three in number, and have quadritubercular crowns normally, but many examples can be found in which the postero-internal cusp, the last one added in the quadritubercular molar, is little more than a cingulum, and is scarcely entitled to the appellation of a cusp." And in a footnote he observes, "It is probable that this condition, of which I have seen a number of examples in the higher races, is a degenerate one, and is an effort to return to the tritubercular stage."

Dr. Wortman has, at my suggestion, examined a large number of Esquimaux crania contained in the Army Medical Museum at Washington, which were not accessible at the time of my visit to it. He confirms the value of the tritubercular second superior true molar as a race character.

The conclusions described in this paper are mostly embraced in a preliminary one which appeared in the *American Naturalist* for November, 1886.

NOTE. — The discussion of the functional relation of the tritubercular to the quadritubercular molar dentition on a preceding page, has reference to the early mammalian types, and to the question of origin of the quadritubercular at that period. The relations of the parts of opposite jaws are different in the tritubercular races of men, since the interaction of the crowns in mastication is no longer alternate but opposite.

EXPLANATION OF PLATE II.

FIGURES NATURAL SIZE.

FIG. 1. Chimpanzee, *a* superior, *b* inferior molars. Mus. Academy Philadelphia.

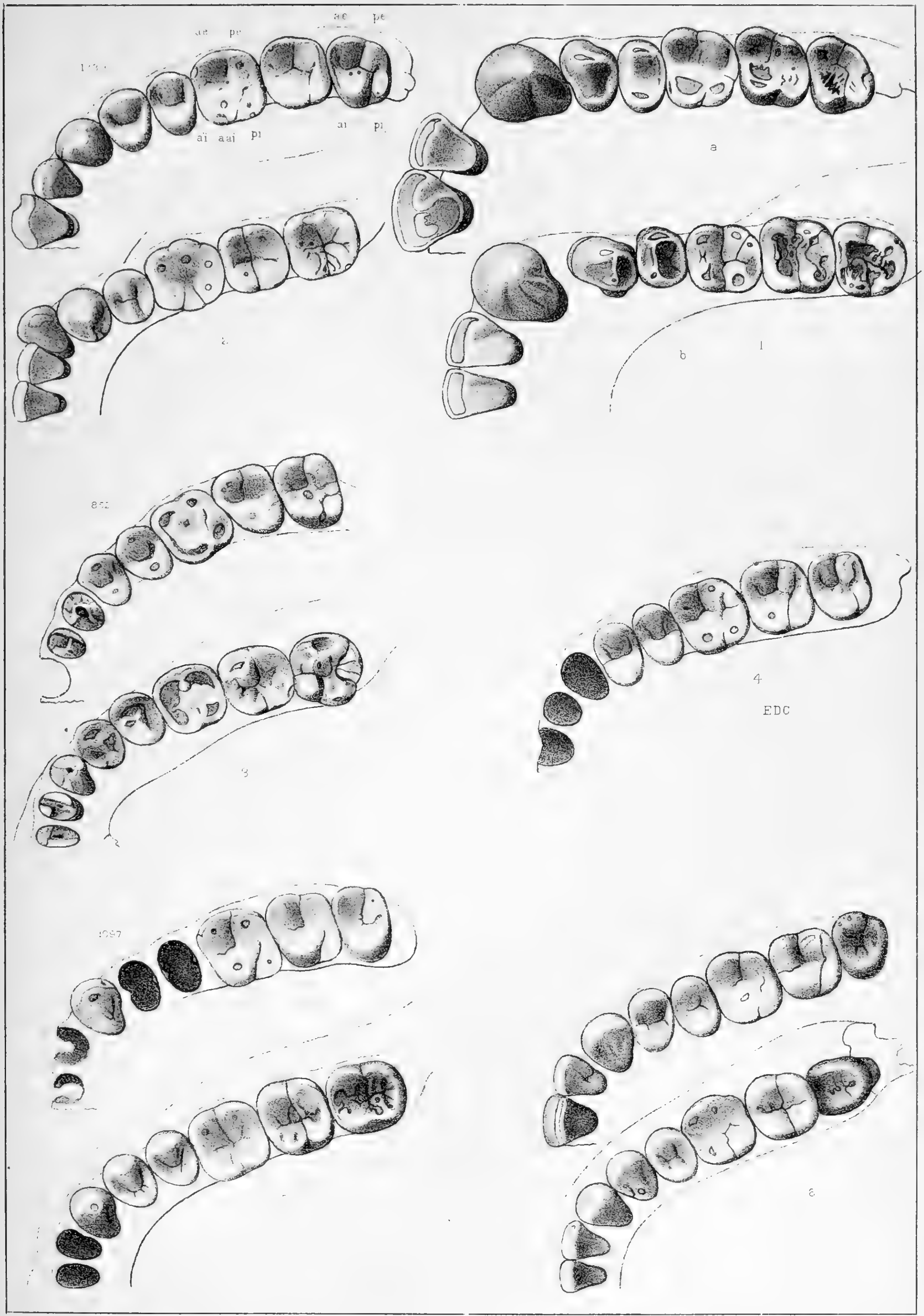
FIG. 2. Malay of Madura, No. 1339, Mus. Academy Philadelphia. Superior molars all quadritubercular, and m^1 with the lemurine (Fig. 13) accessory anterior internal tubercle (badly represented by artist).

FIG. 3. Negroid-Egyptian (Morton), No. 852, Mus. Academy Philadelphia.

FIG. 4. Tahitian, without lower jaw. From Dr. Chassaniol, the colonial physician of Tahiti. Mus. E. D. Cope.

FIG. 5. Pessah, No. 1097, Mus. Academy Philadelphia. Formula $\frac{4\ 4\ 3\frac{1}{2}}{5\ 4\ 5}$.

FIG. 6. Neolithic man from Isle Thinic, Brittany; from collection of Thos. Wilson, Esq.



T. SINCLAIR & SON LITH PHILA

1. SIMIA NIGRA. 2-6. HOMO SAPIENS

EXPLANATION OF PLATE III.

FIG. 7. Spokane from Rock Lake, Witman County, Washington Territory, of the Kamaka tribe; collected by C. H. Sternberg. Mus. E. D. Cope; $\frac{4\ 4\ 3}{5\ 4\ 4}$.

FIG. 8. Hindu of Bengal, No. 1344, Mus. Academy Philadelphia; $\frac{4\ 3\frac{1}{2}\ 3\frac{1}{2}}{5\ 4\ 5}$.

FIG. 9. Swede, No. 1487, Mus. Academy Philadelphia. From Professor Retzius; $\frac{4\ 3\frac{1}{2}\ 3}{4\ 4\ 0}$.

FIG. 10. Esquimaux of Greenland, No. 1221, A.M.M.

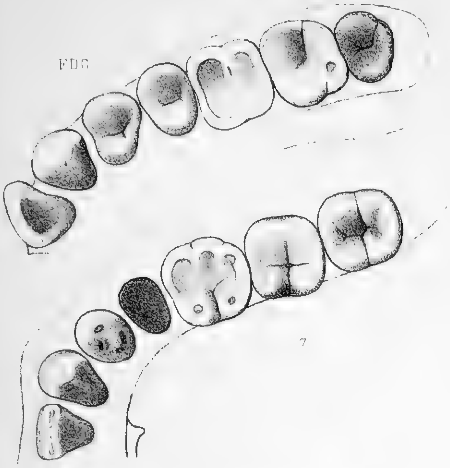
FIG. 11. Alaskan Esquimaux, No. 2669, A.M.M.

FIG. 12. Europeo-American, No. 1108, Mus. Academy Philadelphia; $\frac{4\ 3\ 3}{4\ 4\ 4}$.

FIG. 13. *Lemur collaris*, Madagascar. Mus. E. D. Cope. Superior molars tritubercular with accessory anterior internal tubercle.

LETTERING.

ae, anterior external tubercle; *pe*, posterior external; *ai*, anterior internal; *pi*, posterior internal; *aai*, accessory (lemurine) anterior internal tubercle.



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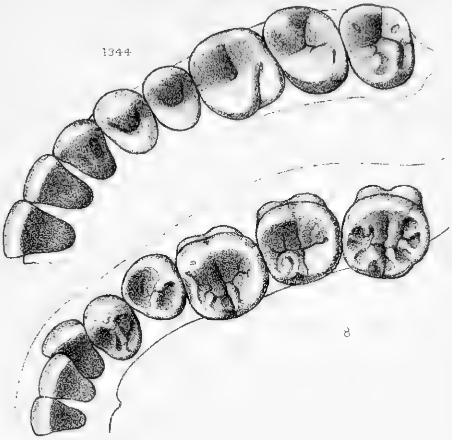

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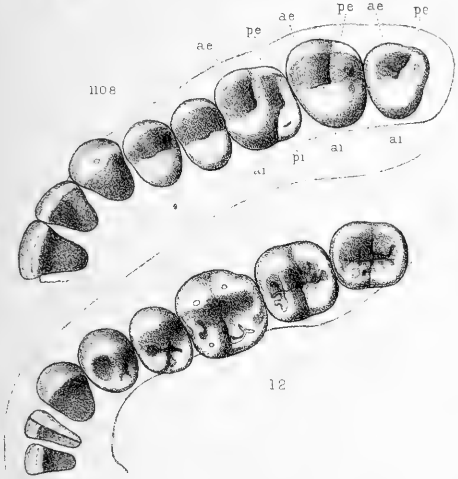

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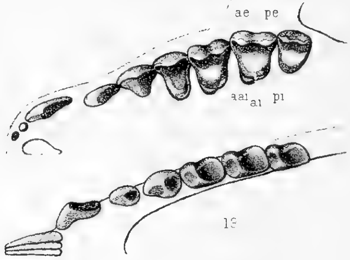

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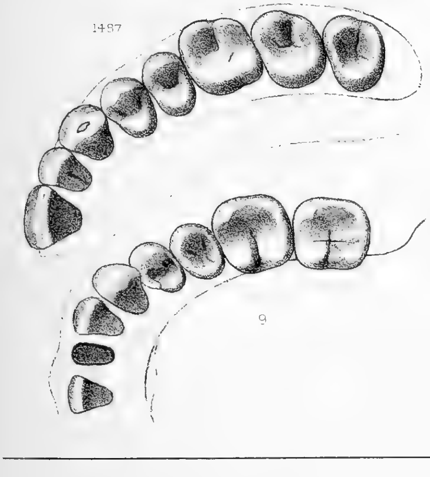

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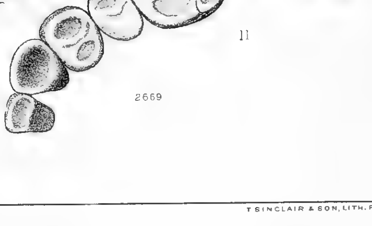

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7-12. HOMO SAPIENS. 13. LEMUR COLLARIS

THE SEAT OF FORMATIVE AND REGENERATIVE ENERGY.

C. O. WHITMAN.

THE question as to the role of the cytoplasm, presents itself under two forms:

1. Is the cytoplasm a passive body, moving only as it is acted upon by external forces, or in response to influences emanating from the nucleus?
2. Or does it behave rather like an organized body, endowed with subtle powers of its own, and capable of automatic as well as responsive action?

There is a strong tendency at the present time to refer all kinetic changes in the cytoplasm to the agency of the nucleus, and to ascribe to the former the passive role of a nutritive substance. The kinetic phenomena of the egg during maturation and impregnation have already been considered in their bearing on this important question.[1] A number of decisive proofs of pure nuclear action were pointed out, and at the same time an attempt was made to support the opinion that the cytoplasm is capable of automatic as well as responsive action. The present paper is chiefly devoted to the consideration of phenomena displayed in the cytoplasm, and to the discussion of the question, whether the regenerative and formative power of the cell resides in the nucleus or in the cytoplasm, or in both taken as a highly complex physiological unit.

The Doctrine of Isotropy. — Pflüger's interesting experiments[2] with the amphibian egg to determine the influence of gravitation upon the direction of cleavage-planes, led him to conclude that the entire egg is "*isotropic.*" In other words, to quote from the

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[1] Oökinesis. *Journ. Morph.*, I., 2, p. 227, December, 1887.

[2] Ueber den Einfluss der Schwerkraft auf die Theilung der Zellen. *Arch. f. d. ges. Physiologie*, XXXI., pp. 311–318, and XXXII., pp. 1–79. 1883.

author, "the fertilized egg possesses absolutely no essential relation to the later organization of the animal, no more than a snowflake stands in any essential relation to the size and form of the avalanche which under certain conditions develops from it. That the germ always gives rise to the same form, is due to the fact that it is always brought under the same *external* conditions." Immediately after the appearance of Pflüger's papers, it was pointed out by Agassiz and Whitman[3] that, "if gravitation were the sole guiding agency in cleavage, its effect ought to be *instantaneous*, and it should be possible to change the direction of a cleavage-plane already in progress." It was also shown that the *time* required to bring about a transposition of the third cleavage-plane, suggested *a corresponding internal transposition of the active protoplasmic matrix of the ovum, including of course the nuclei.* "If a body constituted like the ovum is restrained by artificial means from taking its normal position, a redistribution of material must immediately set in and continue until the equilibrium is restored. The active portion of the ovum, having a lower specific gravity than the passive nutritive elements, would eventually recover its normal position, and thus *the virtual axis of the ovum would inevitably right itself in spite of the inability of the ovum to rotate bodily.*" Later observations have fully verified these suggestions.

As now maintained by Born,[4] Hertwig,[5] Weismann,[6] Kölliker,[7] and others, the cytoplasm alone is isotropic, while the nucleus is the seat of the directive and form-giving power in development.

In this modified form, the doctrine of isotropy makes a much nearer approach to truth, but I believe that it is far from correct in its estimate of the functional importance of the cytoplasm.

The logical consequences of this view are clearly presented by Oscar Hertwig[5] (p. 306) in the following words: "*An die Kernsubstanz also sind die Kräfte gebunden, durch welche die*

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[3] On the Development of some Pelagic Fish Eggs. *Proc. Amer. Acad. Arts & Sciences*, XX., p. 40, 1884.

[4] Biolog. Untersuch. *Arch. f. mik. Anat.*, XXIV., 1885.

[5] Das Problem der Befruchtung und der Isotropie des Eies. *Jenaische Zeitschrift*, XVIII., 1885.

[6] Die Continuität des Keimplasma's als Grundlage einer Theorie der Vererbung. 1885.

[7] Die Bedeutung der Zellenkerne für die Vorgänge der Vererbung. *Zeitschr. f. wiss. Zool.*, XLII., 1885.

organisation des Thieres bestimmt wird. . . . Es erscheint gleichgültig, ob bei der ersten Theilung der eine Kern sich mit der sogenannten animalen, der andere mit der vegetativen Dottersubstanz umhüllt oder ob beide Kerne sich in vegetative und animale Dottersubstanz in dieser oder jener Weise theilen. . . . Der Dotter ist nicht so organisirt, dass aus einer bestimmten Portion desselben ein bestimmtes Organ hervorgehen müsste." It is conceded (p. 304) that the cytoplasm may have a low grade of organization; but it is an organization that changes from moment to moment (p. 309), not a "*feste Organisation*" bearing fixed relations to the future organism.

The opposing view finds the differentiating and formative principle either in preformed elements of the cytoplasm ("*physiological molecules*" Lankester, "*polarized molecules*" Pflüger, "*idioplasma*" Nägeli), or in a definite organization of the cytoplasm itself (Van Beneden and others). "Though the substance of a cell," says Lankester[8] (p. 14) "may appear homogeneous under the most powerful microscope, excepting for the fine granular matter suspended in it, it is quite possible, indeed certain, that it may contain *already formed and individualized*, various kinds of physiological molecules." And again, "The development of one kind of cell from another kind is dependent on internal movements of the physiological molecules of the protoplasm of such cells."

Van Beneden[9] has made a thorough study of the structure of the egg of *Ascaris megalocephala* with a view to ascertaining if "les plans de symétrie de l'embryon ne se trouvent pas déjà préformés dans l'œuf lui-même et si l'un des traits les plus caractéristiques de l'organisation de l'espèce, la symétrie qui la distingue, ne se trouve pas déjà indiquée dans l'œuf. L'œuf d'un animal à symétrie bilatérale aurait-il, comme l'animal dont il provient et qu'il doit devenir, une extrémité antérieure, une extrémité postérieure, une face ventrale, une face dorsale, une droite et une gauche? les matériaux qui doivent servir à édifier la moitié droite du corps siègent-ils dans la moitié droite de l'œuf et la substance

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[8] Notes on Embryology and Classification. London, 1877.

[9] Recherches sur la maturation de l'œuf et la Fécondation. *Arch. de Biologie*, IV., 2 & 3, 1883.

de la tête ne se trouve-t-elle pas concentrée en un point déterminé du corps ovulaire?"

Both views recognize the necessity of assuming that the course of ontogenetic development is in some way predetermined in the egg; but while one finds the *force motrice* in the nucleus, the other would locate it in the cytoplasm. The advocates of the former appeal to the so-called isotropy of the cytoplasm, to the conspicuous part played by nuclear bodies in fecundation and cleavage, to the incapacity for regeneration shown by enucleate fragments of infusoria, etc.; while the supporters of the latter insist on the constancy of premorphological relations (axial relations, relation of first cleavage-plane to the median plane of the future embryo), the remarkable structural features exhibited in some eggs, cleavage in planes not previously marked by karyokinetic division, etc. The truth appears to me to lie on both sides, the error consisting only in unduly exaggerating the relative importance of one or the other factor. Just now the weight of authority seems to be turning in favor of the first view, a result which must be attributed very largely to the influence of recent discoveries and theories respecting the nature of fecundation. The question is one of such fundamental importance, that it seems desirable to analyze closely the facts bearing on the subject. It is for this reason that I have dwelt more at length on the movements of the germinal vesicle and the pronuclei.

Especially important is the study of the structure of the egg, and the modifications which it undergoes during the period of maturation. One of the most important contributions in this direction is unquestionably Van Beneden's great work on Ascaris. No other biologist has yet gone so deeply and thoroughly into the subject, nor has any one discussed it with a keener appreciation of its theoretical importance. Such well-marked structural features as are claimed to exist in this egg are inconsistent with the idea that the cytoplasm is isotropic.

Polar Rings. — Among the more extraordinary examples of cytokinesis may be mentioned the polar rings in the egg of Clepsine, first described by Grube[10] (pp. 15–16), and recently more in detail by Robin[11] (pp. 97–105) and Whitman[12] (pp. 20–29, 39–41).

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[10] Untersuchungen ueber die Entwicklung der Clepsinen. Königsberg, 1844.

[11] Mémoire sur le Développement embryogénique des Hirudinées. Paris, 1875.

[12] The Embryology of Clepsine. *Quart. Jour. Mic. Sci.*, July, 1878.

Although it is by no means certain that the hyaline protoplasm of these rings is not in part derived from the germinal vesicle, it is quite clear that the phenomena are very different from the polar phenomena attending the division of the first cleavage-nucleus. These remarkable exhibitions of polarity in the cytoplasm appear early in the pronuclear stage, and continue not only during the centripetal march of the pronuclei but even after the first cleavage-nucleus has entered upon its kinetic phases of division. *Thus we have two distinct series of polar phenomena in progress at the same time, one displaying itself in the cytoplasm, the other in the nucleus.* We cannot suppose that the cytokinetic series is dependent upon the karyokinetic series for two reasons: first, because the former begins earlier than the latter; and second, because such cytokinetic displays are unknown in other eggs. The second ground would also hold against referring them to pronuclear influences. Allowing that it may yet be possible to demonstrate that these movements originate in response to pronuclear influence, it would still be very difficult to believe that they are sustained throughout by the continuous action of the same agency. It would be altogether more probable, as a little reflection will show, that the movements once started are capable of maintaining themselves, independently of the inciting cause.*

Cytokinetic Phenomena. — The cytoplasm exhibits a great variety of changes and conditions, variously described as 'polar concentration,' 'radiating bands,' 'waves of contraction,' 'zonal constrictions,' 'automatic cortical layer,' 'amœboid movements,' 'phases of segregation,' 'astral radiations,' 'rhythmic contractility,' 'migratory movements,' 'crown of folds' (Faltenkranz), 'autonomic movements' (rotation, circulation, pulsation), etc.

While some of these phenomena might, with considerable reason, be claimed as purely cytokinetic, most of them are so intimately associated with karyokinetic activity that they must be explained, either as the direct result of the latter, or as the effect of impulses generated by the interaction of nucleus and

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* The polar and parapolar circles described by Van Beneden (No. 9) in the egg of Ascaris, are not comparable with the polar rings of Clepsine. For the 'disque polaire' arises before, and disappears with, the penetration of the spermatozoon; the polar rings (Clepsine), on the contrary, appear after the penetration of the spermatozoon, and are not wholly dissipated until after the completion of the first cleavage.

cytoplasm. The hypothesis of reciprocal action is not incompatible with the opinion that the conditions of this action are furnished, in the first instance, if not continuously, by changes of a chemical or molecular nature, which arise quite independently, either in one factor alone, or in both. The source of the initiatory impulse would still be an open question. Our knowledge of the phenomena above designated is too incomplete to furnish a key to the solution of this problem. For the purpose we have in view, it will be sufficient, therefore, to refer to a few of the more important examples, in which each factor may be supposed to play a more or less important part, deferring the discussion of the main question until we come to consider phenomena of a more decisive nature.

Following the penetration of the spermatozoon into the ovum, various forms of contraction in the vitellus have been observed; and these are generally regarded as the effect of impulses generated by the spermatic element. The usual sequence of events certainly accords very well with this view, but there are one or two facts which should make us hesitate to accept it. In some aquatic animals, in which the sexual cells unite before ovipositing, the time of these contractions bears no constant relation to the time of union, but does bear such a relation to the time of contact of the egg with water, whether this contact be brought about artificially or in the natural course of events. Still another cogent reason for not ascribing these contractions to the *independent* action of the male pronucleus is found in the fact that similar, though more sluggish, movements may, in some well ascertained cases, be induced by placing *unfertilized* eggs in water. The most general of these movements is the flattening of the pole, and the gradual contraction of the whole vitelline sphere, resulting in the formation of a perivitelline space.

The Constriction Attending the Exit of the Polar Globules. — The flattening of the pole is attended, or followed, in some cases, with a very remarkable constriction, which, beginning in the equatorial zone, travels towards the animal pole, finishing up with a nipple-like protuberance, from which the first polar globule is expelled. The exit of the second polar globule is sometimes preceded by a similar but weaker constriction. This constriction has been observed (No. 12, p. 18) in the eggs of different species of Clepsine; and the same, or a closely analogous constriction, has been described by Kupffer and Benecke[13] (p. 19) in the egg of Petromyzon, and by Ransom[14] (pp. 463, 464, 477, 479) in the egg of the Stickleback and some other fresh-water teleosts.

This constriction has been confounded by the last mentioned authors with yolk-contraction, and brought into connection with the formation of the perivitelline space ('breathing-chamber' of Ransom, 'Eiraum' of Kupffer and Benecke). This space probably results from contraction of the vitellus as well as from expansion of the egg membrane, but the constriction is a special act of the vitellus to expel the polar globule. The elimination of polar globules is thus a process involving co-operant actions of both factors; and if the part performed by the polar amphiaster is karyokinetic, the associated act of the vitellus may be characterized as cytokinetic. I have before referred to the centrifugal movement of the germinal vesicle as an instance of repellant action, and I regard this constriction as a part of the same action. *It is thus a phenomenon of maturation, not of impregnation.*

Ransom, as well as Kupffer and Benecke, explains the phenomenon as a result of the penetration of the spermatozoon, and hence has failed to distinguish it from other phenomena of a similar, though not identical, nature. Bearing this fact in mind, we are enabled to find in their descriptions — especially that of Ransom — an exact parallel of the special constriction which always accompanies the formation of polar globules in Clepsine. Ransom's account is extremely interesting, and has attracted so little attention from later embryologists, that it seems worth while to introduce a portion of it here. After stating that slow contractions begin from the first moment of entry of the spermatozoa, causing first a flattening of the germinal pole, and afterwards slight changes of outline due to 'travelling waves' at other parts of the surface, he proceeds as follows: —

"Gradually more vivid contractions commence, at various times after fecundation, according to the temperature. In warm weather they have been noted in six minutes, in cooler weather

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[13] Der Vorgang der Befruchtung am Eie der Neunaugen. Königsberg, 1878.

[14] Observations on the Ovum of Osseous Fishes. *Proc. Roy. Soc. London*, VII., 1856.

in fifteen or twenty minutes after impregnation. They cause a flattening of one side of the yolk-ball, to see which it is often necessary to roll the egg over. *The flat surface gradually becomes a sulcus, giving a reniform outline to the yolk. It then extends all round, giving rise to a dumbbell shape. This sulcus, which may be termed equatorial, travels with considerable but variable rapidity towards the germinal pole, producing as it passes on, the flask form. The sulcus is lost by passing forwards to the germinal pole, not by relaxation. It is seen for a brief space affecting the thickness of the germinal disc only, to which it gives a nipple-like form, while the food-yolk is round. When effaced, the whole yolk-ball is globular and at rest, the germinal disc being no longer prominent. This series of forms recurs with more or less of regularity, and with some variations both of time and form, about fifteen or twenty times, each series being the result of a travelling wave*" (No. 14, pp. 463–464).

Had Ransom succeeded in connecting the formation of polar globules with the more regular and prominent 'wave,' which he has so vividly described, he would doubtless have seen the necessity of distinguishing this wave from the movements which follow it, precisely as Kupffer and Benecke distinguished in the egg of Petromyzon a 'zonal constriction' which invariably accompanies the appearance of the second polar globule. They did not succeed in tracing the origin of the first polar globule; but they have described a constriction (p. 15) around the germinal pole (Fig. 7, *l*), which appears immediately after the spermatozoa come into contact with the egg; and this, I would suggest, may have the same relation to the first polar globule that the 'zonal constriction' has to the second.

Polar Aggregation. — In the formation of the germinal disc of many pelagic fish ova, we meet with very remarkable cytoplasmic movements. In the fresh-laid egg, the germinal protoplasm forms a cortical layer of uniform thickness around the yolk. But this condition lasts only for a few seconds, during which the spermatozoon finds an entrance into the egg. This event is followed at once by a polar concentration of the peripheral layer of protoplasm, which results in the gradual formation of the germinal disc with its centrally placed pronuclei.

Is it in one or both of the pronuclear bodies that we are to look for the cause of the polar aggregation of protoplasm? Is the protoplasm a passive mass, moved at the expense of nuclear energy alone, or has it motor energy of its own? In the latter case, are the conditions necessary to action supplied by the nuclei or by the protoplasm, or by both? Although we are yet a long way from a solution of these questions, it may be possible to show that the protoplasm is an active rather than a passive factor in the movements we are considering. Any view which represents the germinal protoplasm as a passive body, moving only as it is impelled by nuclear forces, appears to me irreconcilable with the following facts: —

1. In most meroblastic vertebrate ova (including those of many teleostei), the germinal disc is already formed before fecundation takes place. The *male* pronucleus cannot therefore be a necessary factor in the formation of this disc.

2. In many pelagic fish ova, where the disc forms after fecundation, the polar amphiaster is formed before polar concentration begins. The cause of concentration cannot therefore, in this case, be referred to the centrifugal movement of the germinal vesicle, nor to any changes which this body undergoes prior to the formation of the polar amphiaster.

If this conclusion holds equally in the first class of eggs, we are fully warranted in affirming that the germinal disc forms independently, not only of the male pronucleus, but also of the germinal vesicle and its derivatives, since in these eggs the disc is formed before fecundation and before the polar amphiaster divides.

The validity of these conclusions may be disputed by those who hold with Weismann (No. 6, pp. 90–122) that the two pronuclei are identical in their molecular structure, and that both act alike upon the protoplasm, but in proportion to their mass. It might be argued that a definite *quantity* of karyoplasm ('Keimplasm') is requisite in order to concentrate the protoplasm in the form of a polar disc. If the mass of the germinal vesicle, or of its pronuclear elements, be large enough, it would form a germinal disc without the aid of the male pronucleus; if it fall short of the requisite mass-measure, it would have to be reinforced by the male pronucleus before it could accomplish the work. It will be time to accept this view when it has been shown that there *are* such quantitative relations as the theory postulates. Such an explanation of the disc-formation would take no account of the polarity of the egg, and would leave inexplicable the difference between telolecithal and controlecithal eggs. Besides, this view assumes that the pronuclei are homodynamous, a point which cannot be conceded, since male pronuclei do not behave towards one another as they do towards female pronuclei.

A special feature in the polarity of the fish egg, noticed by Kupffer[15] and by Hoffman[16] (p. 88), is the formation of a temporary discoidal thickening ('Gegenhügel,' Kupffer) at the vegetal pole. Here, then, is a disc-formation at the point farthest removed from the nuclear bodies, and this fact appears to be fatal to the above theory. We are reminded of the rings in the egg of Clepsine, and their concentration into two polar discs. It appears not improbable that the two sets of phenomena are similar in nature, and determined by like forces. In the fish egg the disc-formation is not preceded by a ring-formation; and the nearest approach to the ring-rays are the 'radiating bands' or 'beaded streams' described by Ryder[17] (p. 17).

Raffaele (Mitth. d. Zool. Station z. Neapel, VIII., 1, 1888) has recently described a very singular phenomenon in the egg of *Labrax*. The egg has a single large oil globule at the pole opposite the germinal disc. This oil globule is enveloped with protoplasm, which, on the side facing the germ, thickens up until it takes the form of a long club-shaped body. This body elongates in an axial direction, and the distal portion, which is gradually constricted off, eventually assumes a globular form and rests on the inner face of the germ. Ryder has noticed protoplasmic bodies in the egg of Gadus ('segmenting corpuscles') which, as Raffaele suggests, may have a similar mode of origin. It occurs to me that this body of protoplasm may correspond to Kupffer's 'Gegenhügel,' and that it is diverted from its usual peripheral track by the presence of the oil globule.

The Artificial Division of Infusoria. — The artificial division of infusoria has been resorted to as a means of deciding, experimentally, the question of the relative importance of the nucleus. M. Nussbaum[18] was the first to establish

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[15] Die Entwickelung des Herings im Ei. *Jahresb. d. Comm. z. wiss. Untersuchung der deutschen Meere in Kiel*, IV.–VI., 1874–1876.

[16] Zur Ontogenie der Knochenfische. Amsterdam, 1881.

[17] The Embryography of Osseous Fishes. *Report of the Commissioner of Fish and Fisheries for* 1882.

[18] Die spontane und künstliche Theilung der Infusorien. *Arch. f. mik. Anat.*,

the general fact, that enucleate pieces of an infusorium are incapable of regenerating lost parts, while nucleate pieces soon regain the specific form. "*The nucleus is thus indispensable to the preservation of the formative energy of the cell.*" Gruber,[19] whose experiments were begun at about the same time as those of Nussbaum, has reached the same general result. But one of Gruber's experiments, which was at first supposed to show that regeneration is possible without the presence of a nucleus, brings out a fact of considerable importance. A *Stentor cœruleus* was selected, in which spontaneous fission had already begun, as indicated by the concentration of the rosary-formed nucleus into a simple oval form, and by the beginning of a new peristome at the middle of the body. A transverse section was made just in front of the new peristome, and so close upon the nucleus that it nearly all escaped from the cut surface of the posterior half of the Stentor. The anterior portion retained no part of the nucleus. The two parts were isolated, and on the following day each was found to have become a complete Stentor. As the plane of division was nearly the same as that which would have been followed if the process of spontaneous fission had not been interfered with, Gruber (No. 19, p. 13) finally concludes, contrary to his first interpretation, that this was not a case of regeneration, but of reproduction. The process of reproduction once initiated by nuclear action may go on, so he thinks, to completion without further assistance from the nucleus. He insists, however, that the first impulse to division is given by the nucleus, since in all cases where artificial division is executed *before* the process of spontaneous fission begins, enucleate parts are incapable of regeneration. While finding no reason to doubt the accuracy of Gruber's observations, I must contend that they do not warrant the conclusion so forcibly stated in the following words: "Auf rein empirischen Wege werden wir hier vor die unumstössliche Thatsache gestellt, dass *der Kern der wichtigste, dass er der arterhaltende Bestandtheil der Zelle ist*" (No. 19, p. 16). Allowing that regeneration is impossible in the absence of a nucleus, that is no proof that the nucleus is the sole seat of regenerative power, nor is it a proof that the nucleus is

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XXVI., January, 1886, p. 485. Cf. also *Sitz-Ber. d. Niederrh. Ges. f. Natur- u. Heilkunde*, 1884, p. 262.

[19] Beiträge zur Kenntniss der Physiologie und Biologie der Protozoen. *Berichte d. Naturforsch. Ges. zu Freiburg*, I., H. 2, 1886. Also *Biolog. Centralbl.*, IV., p. 717, and V., p. 137.

a more important factor than the cytoplasm. There is not a single observation to prove what is so confidently asserted, that the nucleus gives the 'Anstoss' to division. This may be so and it may not. The observations prove, (1) that, in some of the higher Protozoa, *the whole process of reproduction by fission, with exception of the initiatory steps, may be accomplished independently of nuclear action; and* (2) *that the initiatory steps cannot take place if the nucleus and the cytoplasm are artificially separated.* The whole truth is well stated by Nussbaum (No. 18, p. 516): "*Kern und Protoplasma sind nur vereint lebensfähig:* beide sterben isolirt nach kurzerer oder längerer Zeit ab." It is clearly impossible therefore, by any such experiments as Gruber has carried out, to settle the question of the precise *locus* of the regenerative energy.

On general theoretical grounds, as well as by the fact that enucleate forms are found among the Protista, we are compelled to accept the generally received view, that the nucleus is secondary in origin. It may be true, as suggested by Gruber[20] (p. 151), that these so-called enucleate forms contain nuclear substance in solution, and that the first step in the phylogeny of the nucleus consisted in the formation of scattered granules, the coalescence of which would give rise to the single nucleus. But it is hardly necessary to add that we do not see how this (or any other) mode of explaining the origin of the nucleus as a *secondary* body can be brought into harmony with the idea that it embodies the whole regenerative energy of the cell.

Interesting and instructive as are these experiments in the artificial division of the higher Protozoa, they do not alone furnish a satisfactory basis for general conclusions. They require to be supplemented by similar experiments on the simpler forms of Protozoa, and by much more complete observations than have yet appeared on the normal processes of fission and coalescence exhibited in the Heliozoa. In proof of this we have only to refer to Gruber's own observations on *Actinophrys sol*[21] (pp. 63–67) and *Actinosphærium eichhornii*[22] (pp. 381–382). *Actinophrys*

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[20] Ueber Kern und Kerntheilung bei den Protozoen. *Zeitschr. f. wiss. Zool.,* XL., 1, p. 121.

[21] Untersuchunge nueber einige Protozoen. *Zeitschr. f. wiss. Zool.,* XXXVIII., p. 45, 1883. Also *Zool. Anzeiger,* No. 118, 1882, p. 423.

[22] Ueber Kerntheilungsvorgänge bei einigen Protozoen. *Zeitschr. f. wiss. Zool.* XXXVIII., p. 372, 1883.

is capable of breaking up into parts without the concurrence of any visible changes in the nucleus. The enucleate individuals — if such they are entitled to be called — may agree perfectly with the nucleate individual in outward form and behavior. They live and grow, and coalesce not only with one another, but with the nucleate form. Whether they are capable of generating a nucleus or not was not ascertained. The multinucleate *Actinosphærium* breaks up in a similar manner without the intervention of the karyokinetic process; but here the individual parts generally contain one or more of the original nuclei. Two or more individuals may coalesce, but the coalescence extends only to the cytoplasm, the number of nuclei being the sum of those contained in the separate individuals before fusion. These remarkable facts appear to bear out Gruber's conclusion: "That the nucleus has no importance for those functions of the cell which do not stand in direct relation to reproduction; such as locomotion (pseudopod-formation), inception of food, excretion (pulsation of contractile vacuoles), and growth. Even on the external form it may be without influence" (No. 21, p. 66). Gruber (No. 19, p. 12) still maintains the accuracy of this view in every particular except that relating to the influence of the nucleus on the form of the cytoplasm. He now holds, in common with Weismann, Hertwig, Kölliker, Strasburger, and many other German biologists, that the form-creating and form-conserving principle is confined to the nucleus. How, when, or where the nucleus manifests its form-moulding power remains a mystery; but that it gives the first impulse to the regenerative act must be inferred — so the argument runs — from the fact that the violent separation of nucleus and cytoplasm destroys the regenerative power in all cases, except where the process of reproduction is begun before separation is executed. This is the focal point of the question with which we set out.

Aside from experiments in the artificial separation of nucleus and protoplasm, the principal arguments in support of this view are drawn from the phenomena of fecundation and cleavage, and are involved with certain theories of heredity which cannot be dealt with here. The observations of Gruber on *Actinophrys* and *Actinosphærium*, if the phenomena are not of a pathological nature, — and such an interpretation seems to be precluded, — should certainly make us hesitate to ascribe all the form-regulating power of the cell to the nucleus. This reserve is rendered imperative by other facts yet to be mentioned, for one of which we are again indebted to Gruber[23] (p. 221). In summing up the results of his "Studies on Amœbæ," he states, "that two very closely related species of Amœba may have quite unlike-formed nuclei; while species differing widely in external form may have quite similar nuclei." Plainly this is the contrary of what might be expected if the formative power lay exclusively in the nucleus.

No Form-Correlation between Nucleus and Cytoplasm.—It may be put down as an indisputable fact that no *form-correlation* exists between nucleus and cytoplasm. Except during the process of division, the nucleus seldom departs from its typical spherical form. It divides and subdivides, ever repeating the same steps and ever returning to the same round or oval form. So far as can be seen, its influence upon the cytoplasm is equal in all directions; and hence it would seem that its formative power, if it have any, could only contribute to the maintenance of the spherical form of the cytoplasm. How different with the cell! It preserves the spherical form as rarely as the nucleus departs from it. Variation in form marks the beginning and the end of every important chapter in its history. While the nucleus repeats over and over again its little cycle of form-changes with mechanical regularity, the cell marches straight on from form to form, never returning, and never repeating, differentiating, developing, and adapting itself at every step to its environment and to the work it is destined to perform. From the egg onward through all the stages of histogenesis and form-evolution, we search in vain for a single intimation anywhere that either the form of the organism or the forms of the individual cells are moulded by direct nuclear influence. At the beginning of any ontogenetic series, when we get the most rapid and vivid displays of nuclear energy, we see that the environment of each cell is much more potent in determining its form than the nucleus. True, certain conditions of the environment may be said to be largely the result of nuclear activity; and to this extent the nucleus may be said to determine, indirectly, the form of the cell. But this is very different from saying that the nucleus has a direct controlling

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[23] "Studien über Amoeben." *Zeitschr. f. wiss. Zool.*, XLI., p. 186, 1884.

power over the specific form of the cell, as claimed by Gruber, Weismann, and others. When the end of the ontogenetic series is reached, we find the reproductive power of the nucleus greatly diminished, and its influence over the form of the cell proportionally reduced. Indeed, in the majority of cases the form of the cell now appears to be maintained entirely independently of the nucleus, and whatever modification of form the latter exhibits appears to be the result of mechanical pressure. The form of the nucleus is now determined by that of the cell rather than the reverse.

If we study the more varied form-changes of the nucleus which occur in the life-cycle of one of the higher Protozoa, we are struck with the fact that the external form of the infusorium is, to all appearance, completely independent of what transpires in the nucleus. A single nucleus may divide a hundred times or more without the slightest effect on the form of the infusorium. The products of these many divisions may undergo various changes of form, and ultimately coalesce to form a single nucleus, and yet no change of form in the cytoplasm. The multinucleated form may break up into parts, some without, others with one or more nuclei, and the enucleate, uninucleate, and plurinucleate individuals all agree in presenting the same specific form. The nucleus may pass from the oval form to that of a long rosary; then, after a period of vegetative life on the part of the cytoplasm, return to the original oval form, and undergo the regular changes of division, the whole cycle of transformations coming to a conclusion without producing any discernible effect on the cytoplasm beyond that of simple fission. Each part carries with it the power to resume at once the form which characterized the original whole. The nucleus gives no evidence at any time of holding the formative power; but we have seen from Gruber's experiment on Stentor, above referred to, that the cytoplasm does exercise this power, and that *it does so even in the absence of a nucleus.*

Gruber does not attempt to deny this; but he thinks it necessary to assume that the power exhibited by the cytoplasm in the case mentioned, was communicated to it in the form of molecular motion, the original impulse being given by the nucleus. As we have seen, there is nothing in his experiments which makes such a conclusion necessary, and the burden of proof properly falls to him who makes the assumption.

One needs only reverse the case to see the illogical nature of the position. Let us suppose that it has been ascertained by numerous experiments that the nucleus of an infusorium is incapable of karyokinetic division when separated from the cytoplasm, except in those cases where the division is already in progress at the time of separation. Would there be anything either in the general rule or in these exceptional cases, from which to conclude that the performances of the nucleus are first set in motion by some impulse from the cytoplasm? Would the incapacity of the nucleus to divide when placed in abnormal conditions demonstrate its inability to divide autonomically under normal conditions? If artificial isolation were found insufficient to arrest a series of complex movements already begun in the nucleus, would the death of the nucleus, shortly after the completion of these movements, furnish any ground for denying that they were automatic? These questions appear to present the matter in a just light, and to carry with them their own answers. The point would hardly seem to deserve the attention given it, were it not for the great importance of the question under consideration, and the fact that we are dealing with the opinion of a high authority, — an opinion for which experimental evidence of a crucial nature is claimed, and an opinion fully indorsed by so eminent a thinker as Weismann.

Schneider's Experiment. — Schneider's[24] (p. 509) experiment with Thalassicolla, although not affording any decisive evidence as to the precise location of the formative power, is yet of some interest in this connection. The extracapsular or cortical protoplasm was removed, leaving the central capsule free. At the end of twelve hours the whole surface of the capsule showed delicate pseudopodial extensions, and soon after appeared a distinct extra-capsular layer ("matrix" of the pseudopodial rays), which gradually grew to normal thickness. The experiment was repeated three times in succession on the same individual, and each time with the same result. The extra-capsular envelope gave no evidence of sharing the regenerative power, but died shortly after isolation. This envelope, according to Brandt[25]

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[24] Zur Kenntniss des Baues der Radiolarien. *Mül. Arch.* 1867, p. 509.

[25] Koloniebildende Radiolarien (Sphaerozoëen). *Fauna und Florad es Golfes von Neapel.* XIII. *Monographie,* 1885.

(p. 84) takes no share whatever in the production of spores; and thus it appears that the central capsule is the seat of the reproductive as well as the regenerative energy. During "vegetative life" the various functions (digestion, locomotion, sensation, etc.) all appear to be performed by the extra-capsular cytoplasm; but the whole functional activity, as supposed by Brandt, is under the *regulative* influence of the central capsule. In the Sphærozoa colonies the division of labor is carried still farther; for while the pseudopodial rays have their special functions, certain definite areas of the matrix ("Klumpen von Assimilationsplasma") provide for the digestion of the starch granules which are produced by symbiotic algæ; and different layers or zones are distinguishable even in the central capsule. That there should be such a complete separation of functions between the central core and the cortical layer of the same body of cytoplasm is no less instructive than it is remarkable. It is a capital illustration of the possibilities of organization and the physiological division of labor without any corresponding division into distinct morphological units.

Recent studies tend to show that the only important substance conveyed into the egg by the spermatozoon is that which takes the form of the male pronucleus. The unavoidable conclusion would appear to be that the pronuclei are the sole bearers of hereditary tendencies. This is unquestionably a point of cardinal importance, and it furnishes the strongest argument that has yet been advanced in favor of regarding the nucleus as the seat of the formative power. This side of the question could not be fairly dealt with within the limits of the present paper, as it would lead to a consideration of the whole problem of heredity. It is my purpose, however, to return to this subject at no very distant date.

The Idea of a Formative Power. — Let us now consider whether any rational basis can be found for the idea of a formative power as a resultant from, and an expression of, physiological unity. I am fully conscious that the subject is one of profound mystery, the solution of which appears to lie as far beyond our grasp to-day as at any time in the past. We draw nearer to the problem, but the effect is rather to enhance than to reduce its apparent magnitude. Every step in advance only brings us to a keener sense of the subtle and incomprehensible nature of the force or forces contemplated. We see the effects only imperfectly, and are baffled in every attempt to understand the mode of action. For the present we must be content to search for the *direction* in which answers lie; and herein is found the chief value of theories.

The more important speculations on this subject have taken the form of theories of heredity. In most of these theories, at least those of recent date, we find a fundamental idea which must be accepted as true; namely, that the sexual cells reflect in some way in their chemico-physiological constitution all the typical structural features of the parent-organism. How all the hereditary tendencies can be contained in a single cell, and with such completeness that the developing organism repeats step for step the chief form-phases of a genealogical history stretching through countless myriads of generations, back from the present into the very dawn of life, and ultimately unfolds every detail of structure and feature of the parent-organism, is a mystery that transcends our understanding. The preformationists of last century took refuge in the celebrated inclusion (Einschachtelung, emboitement) theory, which made the real mystery unapproachable by hiding it behind an endless series of miracles. The triumph of the epigenesists brought with it the reclamation of the problem, but left us with the indefinable *vis essentialis* of Wolff, the *nisus formativus* of Blumenbach. In more recent times we have seen various metaphysical hypotheses of extra-organic agents or forces supplanted by physiological hypotheses which seek the cause of the phenomena in intra-organic forces. But the reaction which followed the fierce struggles with vitalism has left its impression on most of the theories now in vogue. Biological problems have been brought more and more under the influence of mechanical conceptions, which regard all phenomena from an objective standpoint. Science has vindicated this method, and as a *method* it is unassailable. It is no less indispensable to research in the organic than in the inorganic world; but the biologist is reminded at every turn that the method is not exhaustive, and from the nature of the case it never can be. The biologist does not hesitate to follow the shibboleth of "molecular motion" to its final goal, but he must beware of being blinded by any artifice of method to distinctions which lie beyond it. He accepts the authority of the chemist and the physicist for the fact that the primary elements of the organism are identical with those found in inorganic matter, and with them repudiates the notion that life is "*a force having no connection with primary energy or motion.*" But no one disputes the fact that the living organism represents *special combinations* of matter and force, and displays phenomena which find no parallel in non-living matter. Hence it does not appear at all irrational to conclude that vital phenomena are the manifestations of special forces, resultants of course, and yet *quite unlike the elementary forces from which they are derived.*

If from the same elements by different chemical combinations, we get new substances, differing widely *inter se* in their chemico-physical constitution, and totally unlike their primary constituents, then why not new forces in the same way? The chemist and the physicist agree in referring the differences of substances to a dynamical cause, and their mechanical conceptions do not prevent, but compel them to ascribe a specific energy to each different atom and molecule. In spite of the tendency of physical thought to regard "all matter as one and all energy as one," chemistry and physics are built up on the assumption that chemical elements are unlike, and that in different modes of combination is given the basis for that infinite variety of substances with which we meet. If the primary energy is in each case called by the same name, "polarity," it is nevertheless understood that these polarities are as unlike as the elements which manifest them. It is just here that we see the foundation for those *qualitative* distinctions which, in the mind of the biologist, must ever overshadow in importance the physicist's factors of quantity and motion.

All physical explanations, no less than biological, lead ultimately to the conception of intrinsic forces. The chemist's unit, like the physicist's, is the embodiment of energy. From a comparatively few atom-energies an endless number of molecule-energies are built up; these aggregate in units of a higher order, some statical, others dynamical; and so on through what Nägeli calls *micellæ* and *micellar aggregates,* until we arrive at the living cell. In this ascending series each new aggregate represents a unit, the individuality of the parts being merged in that of the whole. The grounds for distinguishing various organic, physiological, and biological units, are thus of the same general nature as those which compel us to discriminate between physical and chemical units. Of course these higher units combine both atomic and molecular structure; but they have superadded to, and including this, a structure as a whole, which is entirely ignored in the expression "molecular aggregates." As they result from the union, not of simple or complex molecules, but of complex molecular groups, their structure may be said to be at least as widely separated from the molecule as this is from the atom. The power which such a unit represents as a whole is not the same as the powers represented by its constituent elements when uncombined, nor is it the sum of these several powers. Derived from them, and yet wholly unlike them, as water is something totally unlike its chemical elements or any simple mechanical addition of these elements.

It is precisely this point which is so persistently ignored in all so-called physico-chemical theories of heredity. And yet all analysis and all observation leads to the conclusion, that molecular structure is not directly responsible for vital phenomena. In claiming that "physiological units" have something higher than molecular structure and power, I am not treading on ultra-scientific ground, but following the course already sanctioned by chemistry and physics, and the only one which can ever reconcile physico-chemical and biological conceptions.

Admit — what no one denies — that a molecule is totally unlike its constituent elements, that its energy is unlike that of its atoms, taken individually or collectively; and further, that simple molecules, without losing their structural integrity, may unite to form complex molecules, and we have only to carry the same process a few steps farther to reach those units whose integral structure is no longer adequately described as molecular. If analysis fails to discover a physiological bond which is capable of binding molecular aggregates into units of the vital order, its failure must be attributed to imperfection of methods, for observation bears constant and unvarying testimony to its existence. If analysis and observation combine to show that whatever force an organism expends is the correlate and equivalent of force taken into it, and if chemical and physical processes underlie all vital phenomena, it does not by any means follow that there is any identity between vital activity and physico-chemical forces. The power which *causes* chemical elements to combine is not identical with the power which *results* from their combination ; nor is the power which breaks down a chemical compound identical with the powers of its separate elements.

The views here enunciated are not contradicted by the long-established fact, that the laws which regulate the formation of chemical compounds are the same for both organic and inorganic bodies. The position taken does not affirm that organic compounds differ from inorganic either in material constituents, or in the forces which hold these constituents together. What we do affirm is this : We cannot stop with the most complex molecules revealed or revealable by chemical or physical research ; we must pass from *organic* to *living*, *organized* matter, not by the supervention of new laws, but by ultra-chemico-physical, or chemico-organic combinations, which are absolutely beyond the highest possibilities of chemical analysis. Inability to define these higher modes of combination is no reason for doubting the testimony of all our senses to their existence. And why should we expect chemical research to bring any positive confirmation of their reality, when all chemical analysis presupposes conditions which are the absolute negation of vital conditions ? Does self-stultification ever become more complete than in the assumption that vital forces and conditions are discoverable precisely there where they confessedly do not exist ? Or is it rational to conclude that, because vital conditions have arisen from non-vital, the exclusive study of the latter will reveal the former ? So long as the chemist's methods debar him from the study of physiological modes of aggregation will he be impotent to divine the links which connect molecular motion with sensibility, and just so long will "physiological chemistry" remain a delusive misnomer.

A complex aggregate of atoms, so bound together by mutual affinities as to represent a physical unit, possessing, as a whole, properties and powers derived from but unlike those of its constituent elements, and existing by virtue of, and only during the maintenance of, the chemical connexus of these elements, is a conception which may be carried straight forward up to the cell. The living cell may be regarded as a system of very complex chemico-organic units, bound together by subtle chemico-physiological bonds, and displaying in their collective capacity functions and powers which are entirely foreign to them as individual and isolated elements, and which are therefore indissolubly identified with the physiological connexus or consensus.

Vague and unsatisfactory as such a view may appear, and as the best possible view must be from the limitations of our knowledge, it may yet contribute something towards a clearer conception of what we have called the formative power of the cell. It will be sufficiently clear now that we have not in mind a phantom-form which, like a mould, impresses its shape upon plastic material; but a power which represents the resultant of the consentient reactions of indwelling forces. Such a power declares itself in every living organism and in every developing germ.

The action of the formative power has often been likened to the architectural power displayed in crystallization; and if the essential distinctions are kept in view, such a comparison is justified by one or two very instructive analogies. If the physicist is not compelled to recognize a special crystallizing force, he is at least unable to deny that a crystalline aggregate reacts upon the parts in such a manner as to determine the *direction* of that marvellous "constructive power" with which the molecules are endowed. When we see a crystal reproduce its lost apex; or, as in the oft-cited experiment of Lavalle, an angle of an octohedral crystal spontaneously replaced by a surface, as the result of an artificially produced surface at the corresponding angle, we have no alternative but to infer a *physical correlation of parts*, under the influence of which the *direction* of forces is determined. So in the development of a germ, in the repair of injured parts, and in the regeneration of lost parts, the fact is irresistibly forced upon us, that *the organism as a whole controls the formative processes going on in each part.* The formative power then belongs only to the organism as a physiological whole; and it does not represent a sum or aggregate of atomic, molecular, or other forces, but results from special combinations of ultra-molecular units, and disappears as such the moment the physiological connexus is destroyed.

This idea may appear, at first sight, to stand in contradiction with the fact that parts of an organism, resulting from spontaneous or artificial division, possess the same formative power as did the undivided organism. But it must be remembered that most organisms do not admit of such division, and that in those that do admit of it, everything depends on how the division is made. The extra-capsular portion of a Radiolarian does not reproduce the central capsule, nor does the non-nucleated fragment of an infusorian regain its lost parts. Even here, then, it is not permissible to disregard the physiological correlation of parts, since both nuclear and cytoplasmic elements are indispensable to the preservation of the formative power. We still have to regard such organisms as physiological wholes, although the physiological connexus may be representable in aliquot parts.

The principle holds true of every organism, irrespective of whether the mass is divided into cells or not. The fact that physiological unity is not broken by cell-boundaries is confirmed in so many ways that it must be accepted as one of the fundamental truths of biology.

A CONTRIBUTION TO THE INTERNAL STRUCTURE OF THE AMPHIBIAN BRAIN.

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INTRODUCTION.

This contribution to the structure of the Amphibian brain is the result of observations which began in 1879 and have extended at wide intervals over several years. The most systematic of these studies, beginning in Munich in 1886, were directed to the nerve-fibre courses, and interrupted by the discovery of the *corpus callosum*, which naturally led off to the comparative study of the encephalic commissures in the vertebrata. They form the chief portion of the present paper, and have long been withheld from publication in the hope that an opportunity would arise to make them more thorough. As this seems now more distant than ever, it appeared to me best to publish them in their present shape, with the intention of attaching to each new point the degree of certainty to which the evidence entitles it. Only by carefully distinguishing between fully and partially established facts can a contribution of this unfinished character acquire any permanent value. The most carefully observed region is the medulla oblongata of *Cryptobranchus*, with reference especially to the cranial nerve tracts and nuclei. The structure of the cerebellum in the *Urodela* has been well worked out, also the region of the optic lobes, thalami, and posterior portion of the hemispheres in the *Urodela* and *Anura*. Much remains to be done in respect to the *peripheral distribution of the component parts of the several cranial nerves.* Only after this has been thoroughly worked out can we certainly determine the homologies of the cranial nerves and their segmental relations in the Amphibia. The present results go far enough to show that the determination of definite nuclei corresponding to definite peripheral sensory and motor areas is well within the range of possibility. In fact, the provisional character which I have given to some of the conclusions here reached is chiefly due to the close connection between several of the cranial nerves at, or close to, their exit, which makes it necessary to follow each component bundle in continuous sections peripherad to a point where their further distribution can be traced macroscopically. This I believe is possible with several of the nerves, but has not as yet been successfully accomplished.

The genera studied include *Amphiuma*, *Cryptobranchus*, *Necturus*, *Siredon*, *Proteus*, *Rana*, and *Siren*.

The following are some of the most important results arrived at : —

1. The determination of the chief motor and sensory nuclei of the 5th to 10th pairs, which enables me in some degree to homologize the intra-axial elements of the Vagus and Trigeminal systems, and demonstrate the independence of the Auditory system and system of the motor nerves of the eyeball.

2. The discovery of a new sensory tract and nucleus, the fasciculus communis, common to the 10th, 9th, and 7th (or 8th) pairs.

3. The determination of the relations of the posterior longitudinal fasciculus (uncrossed Müllerian fibres), to the 8th, 6th, 4th, and 3d nerve tracts, and of the nucleus of the latter nerve with the fibres of the posterior commissure.

4. The passage of a portion of the descending trigeminal tract through the cerebellum and the direct connections of this bundle with the large mesencephalic nucleus.

5. In the encephalon, the determination of the direct motor tract to the prosencephalon, and of direct sensory tracts to the mesen- and diencephalon.

The principal characteristics of the Amphibian brain, as compared with that of the Sauropsida and of the Fishes, excluding the Dipnoi, are the following: The olfactory lobes are not sharply defined from the cerebral hemispheres. The corpora striata are not prominently developed. The cerebellum is always small, and is either in a primitive or degenerate condition in the *Urodela*. The pineal eye pierces the skull, but does not develop further.[1] Finally, an important distinction is that the

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[1] According to Spencer it is more rudimentary in the *Urodela* than *Anura* and in the latter forms a vesicle which subsequently degenerates.

gray matter of the brain immediately surrounds the ventricles, the central gray, and with the exception of the layers of cells in the optic lobes of the *Anura*, there is nothing developed in the nature of the cortical gray matter. The *Urodela* are further distinguished from the *Anura* by the small size of the optic lobes, which are barely marked off from the thalami, by the frequently extensive development of the superior commissure, and by the primitive condition of the ventriculus communis or unpaired cavity of the prosencephalon.

I. THE DIVISIONS AND CAVITIES OF THE ADULT BRAIN.

The division of the brain into five large segments is invariably well marked. The olfactory lobes do not appear as fully distinct segments, but form the anterior portion of the prosencephalon, sometimes separated from the hemispheres by a prominent lateral swelling or median indentation. The line of separation is much more clearly indicated in horizontal sections. The olfactory nerves arise either from the edge or base of the lobes. The lobes are broad and truncate anteriorly in the *Urodela*,[1] but taper in *Proteus* as in the Frog. The diencephalon and mesencephalon are subequal in size in the genera with small functional eyes, such as *Siredon*, *Necturus*, and *Siren*, these two segments presenting the appearance of an elongate cylinder slightly compressed opposite the posterior commissure. In the blind *Proteus* the mesencephalon is smaller than the

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[1] The classification adopted is from Baur's valuable memoir, "Beiträge zur Morphogenie des Carpus und Tarsus der Vertebraten, I Theil, Batrachia," Jena, 1888. The recent Amphibia are arranged in three orders: —

PROTEIDA.		URODELA.		ANURA.
Fam. *Proteidæ.*	*Proteus.*	Fam. *Cryptobranchidæ,*	Cryptobranchus.	
	Necturus.	*Sirenidæ,*	Siren.	
			Pseudobranchus.	
		Amphiumidæ,	Amphiuma.	
		Amblystomatinæ,	Amblystoma (Axolotl), etc.	
		Also the *Cæciliidæ,*	*Plethodontidæ.*	
		Desmognathidæ,	*Salamandridæ.*	
		Pleurodelidæ.		

Baur considers the *Cryptobranchidæ* the most central family of the *Urodela*, from which the *Sirenidæ*, *Amphiumidæ*, and *Amblystomidæ* may have sprung, p. 55. I find that the brain structure fully supports this conclusion.

diencephalon. In the *Salamandridæ* the mesencephalon is larger than the diencephalon, and it is of much greater proportionate size in the *Anura*, owing to the large optic nerve nuclei. The size of the roof of the mesencephalon is in direct proportion to the functional perfection of the eyes. The cerebellum is invariably small in the *Urodela* and *Proteida*, but attains a segmental size and importance in the *Anura*. The metencephalon, or Medulla oblongata, forms the fifth, and invariably the largest segment.

The proportions of these segments are very similar to those observed in the *Dipnoi* (see Fulliquet, '86), but differ widely from those in the lower fishes. The great relative size of the prosencephalon in the Amphibia is, however, deceptive, since the walls are comparatively thin and the ventricles much larger than in the two mid-segments.

Surface characters of the brain, Plate IV. In carefully prepared specimens many of the more important structures of the superficial encephalic walls may be seen upon the surface.

In the hemispheres of *Siren*, Fig. 5, are observed nerve tracts from the postero-lateral regions. Between the hemispheres posteriorly lies the large supraplexus which covers the roof of the ventriculus communis, Fig. 8, and in most of the *Urodela* extends far forwards. The inner surfaces of the hemispheres are in close contact with each other in the *Urodela* and *Proteida*, but I have observed no actual union of the olfactory lobes such as is found in the *Anura*. The lamina terminalis, *t*, Fig. 3, extends well forwards, and is sharply defined in the ventral aspect.

The characters of the roof of the Diencephalon are very well marked. Just behind the supraplexus are two oval or round swellings, which represent the ganglia habenarum with distinct median contours, but closely applied to each other in forms in which the supracommissura is well developed, such as *Menopoma*, *Amphiuma* (Osborn, '83 and '84, Fig. 4), and *Axolotl*, Fig. 1. Arching between them and spreading beyond, into the thalami, is a grayish band which probably represents the supracommissura. This commissure underlies the pineal process, and is not seen upon the surface in *Necturus*, Figs. 2 and 8, but is apparently present in *Proteus*. Immediately behind this the whitish plates connected with the ganglia diverge, leaving a slit-like, oval or triangular space, in the centre of which lies the proximal portion of the pineal stalk or processus pinealis, *pn.* Close behind this a white or grayish streak represents the postcommissura. Upon the floor of this segment is an oval space, bounded by a whitish area which represents the recessus opticus, or proximal portion of the primitive optic stalk, which recess in *Necturus* and *Proteus* extends directly into the centre of rudimentary optic nerve. There is a striking similarity, which may be merely superficial, between this area and that surrounding the processus pinealis. The most prominent features of the floor are the infundibular lobes, probably homologous with the lobi inferiores of the Teleosts, which terminate in the large hypophysis. These lobes extend anteriorly into the flattened floor of the 3d ventricle, and laterally into the sides of the thalami. Above them, the cerebral peduncles diverge around the infundibulum into the lower portions of the thalami.

The roof of the Mesencephalon is distinguished by a longitudinal grayish line, probably caused by the thinning of the wall; on either side of this is a whitish tract the meaning of which is unknown. Posteriorly the roof thins out into the valvula, a triangular area from which arises the 4th nerve. This nerve is apparently atrophied in *Proteus.* The slender band representing the cerebellum extends across behind this, continuous at the sides with the lateral fold of the medulla.

The figures do not represent the actual condition of the Metencephalon, since the metaplexus has been removed. The metacoele, or 4th ventricle, is shallow and widely open in the *Urodela,* and varies considerably in shape. In *Proteus* the lateral edges are approximated opposite the 10th nerve. On either side of the longitudinal sulcus, in the centre of the floor, are observed two long white tracts shining through and giving off lateral branches opposite the exit of the VII., VIII. nerves. This tract is the posterior longitudinal fasciculus, and can be very clearly seen in well-preserved specimens. On the ventral surface is seen the anterior sulcus continuous with the fissure of the cord. It diverges at two points in the medulla of *Proteus,* the meaning of which is not known. I have not observed in the floor of the 4th ventricle of the *Urodela* any trace of the foldings seen in the medulla of *Rana*

(Osborn, '86, Fig. 2, text), which I have suggested may be remnants of the embryonic neuromeres. The origin of the cranial nerves is described elsewhere.

The Ventricles of the Brain. A comparison of the encephalic ventricles of these genera, in longitudinal section, brings out some interesting facts, Figs. 7, 8, 9. *Cryptobranchus* approaches the piscine type, and *Rana* the Sauropidan type: they are at opposite ends of a series. The roof of the *Cryptobranchus* brain is nearly straight in the mid-region; in *Rana* it is much folded, so that the cerebellum and postcommissura are brought together; these folds and the lateral outgrowth of the optic lobes produce the diverticulum of the mesocœle, the optocoele (Wilder), and the tori-semiculares in the walls. The position of the trigeminal nucleus affords a means of comparing the optic lobes of the *Urodela* and *Anura* (see below). A still more important difference is in the fore-brain. In *Rana* the cerebral commissures lie in the lamina terminalis proper; there is no extended ventriculus communis. In the lower *Urodela* (the *Salamandridæ* have not been examined), the commissures traverse a fold of the floor, and there is a large ventriculus communis in front of this, *a*, Fig. 7. *Necturus* shows a remarkable development of the ventricular plexuses, which extend well into the lateral ventricles and backwards nearly to the cerebellum. The elevation of the floor which contains the corpus callosum and anterior commissure is very similar in position to the commissural band between the corpora striata in the Teleosts. (See Appendix, Note 7.)

SEGMENTATION OF THE BRAIN.

Under this head we may consider the larger encephalic segments and pass by the neuromeres, which, as recently demonstrated by Orr ('87, p. 335), have a special significance with relation to the origin of the cranial nerves, exclusive of the first and second pairs. The neuromeres and central nuclei, when fully investigated, will undoubtedly enable us to establish a closer comparison between the brain and spinal cord segments than can ever be drawn from the peripheral distribution of the cranial nerves.

As above pointed out, the chief points of contrast between the brains of the *Anura* and *Urodela* are the large optic lobes and cerebellum of the former. The cerebellum is generally found to have a direct relation to the size and activity of the limbs; it is extremely small in the limbless forms, intermediate in the Salamanders, and so on, increasing to the *Anura*. Are we to consider the Urodele cerebellum as in a degenerate or in a primitive condition? The limbs of *Cryptobranchus* (*Menopoma*) are well developed and fully functional; they are, moreover, in the most primitive condition known among the Amphibia (Baur, '88, p. 55). If the relation above mentioned holds good here, we may infer that the cerebellum is also in a primitive condition in the central *Urodela* phylum. It may be considered in a degenerate condition in some of the limbless types.

This correlation has a direct bearing not only upon the question of the number of the larger encephalic segments in the Amphibia, but upon the origin of this segment. By many authors the cerebellum is considered a distinct segment equivalent, for example, to the mid-brain. By others it is considered as a portion of the roof of the hind-brain. The hypothesis I offer is that the cerebellum is primitively intersegmental, and secondarily acquires a functional importance equivalent to that of the other segments, (Osborn, '87, p. 940).

The cerebellum of *Cryptobranchus* (see also p.) is chiefly composed of *decussating tracts*, passing on the one side into the lateral regions of the medulla, on the other into the mesencephalon. It may even be questioned whether we have here the essential elements of the cerebellum, the structure is so extremely simple. It has been stated that the posterior commissure, which invariably marks the dorsal boundary between the dien- and mesencephalon, is not a commissure in the strict sense of the word, but consists of fibres from the two tegmental tracts[1] decussating to the opposite side of the brain. Similarly, the superior commissure, described independently by Bellonci ('81) and myself ('84, p. 268), consists of fibres passing across the roof of the third ventricle from the diencephalon to the opposite prosencephalic segment (see *scs* in all the fig-

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[1] With special relations to the tegmental tracts (Pawlowsky) and the nucleus of the third nerve (Darkschewitz).

ures). There is thus a striking similarity in the fibre courses of these three dorsally decussating tracts. In *Cryptobranchus*, in which we have the most primitive type of brain thus far observed among the Amphibia (Plate IV., Fig. 7), these three tracts are nearly subequal, the superior commissure containing the largest proportion of fibres.

This anatomical evidence for the serial homology of these commissures is supported by the facts of their embryological development. I have followed these stages in the frog, in which the superior commissure is extremely reduced; it would probably be much more clearly shown in *Cryptobranchus* embryos. These commissures develop nearly, if not quite, simultaneously with the anterior commissure, at the period immediately following the constriction of the neural tube into four vesicles. In the dorsal median line this constriction is clearer between the two posterior segments than between the first and second (compare *cbl* and *pcm* in Cut 1 with *scm*).[1] But in horizontal sections these three constrictions are equally great, Cut 2. It is noteworthy that the floor of the neural tube, which evidently has no relation to these dorsal commissures, is also the only region in which from the first there is no constriction between these vesicles, the constrictions occurring, first, at the point of the cranial flexure; second, opposite the anterior commissure, *acm*.

The inference to be drawn from these facts depends largely upon the question whether there is really a serial homology between these commissures in their primitive condition. If not, there remains considerable ground for the supposition that the intersegmental folds are lines of retarded growth in the sides and roof of the neural tube to be traversed at an early period by the commissures.

In the last number of this Journal, Orr ('87, p. 347) has contributed valuable observations on the lizard's brain, which certainly support, and possibly extend, this hypothesis to embrace also the anterior commissure. He finds, what I had not observed, that the fibres of these commissures are possibly continuations of the primitive lateral longitudinal fibres, although not positively observed to enter them, concluding as follows: "The superficial position of these three commissures, anterior, superior, and posterior, their similar connections with the lateral

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[1] See Appendix. Note 1.

bands, and their relation to the constrictions of the brain, suggest at this period a striking homology between them." (See Plate XVI., Fig. 62, F.) This does not include the cerebellum, the tracts of which he has not followed. It is true that the fibres beneath the fore-brain branch from the lateral longitudinal band in much the same manner as do those passing to the region of the other commissures; but I cannot at present adopt his view that they represent the anterior commissure, because the development of this commissure, as I have found it in the Amphibia and Mammalia, indicates that it is strictly commissural, and not the decussation of a longitudinal tract, as must be inferred if its fibres pass directly into such a tract. Immediately beneath the anterior commissure in the Amphibian forebrain, I have observed fibres decussating from longitudinal bundles to the opposite hemisphere (op. cit., Fig. 11, Plate XIV.), which probably represent those attributed to the anterior commissures by Orr (op. cit., p. 346).

Upon these grounds, pro and con, the hypothesis may be restated as originally: that the early constriction of the brain roof which gives rise to the four vesicles is for the accommodation of three nerve-fibre tracts decussating dorsally, viz., the superior and posterior commissures and the cerebellum, which in their primitive condition have a serial homology.

If in some of the lower vertebrates, *e.g.*, the *Urodela*, the cerebellum is intersegmental, and in other vertebrates, lower and higher, it becomes equivalent to the other segments, it merely accords with what we may conjecture as to the probable evolution of the encephalic segments, that they were not primary features of the vertebrate brain, but were defined secondarily, with the concentration of certain groups of functional centres at certain points. The neuromeres are probably remnants of the true primitive segmentation.

II. THE CRANIAL NERVES.

EXIT FROM THE BRAIN.

I. The olfactory nerves arise from the lateral or infero-lateral portion of the olfactory lobes and are distributed in the usual manner in the olfactory sac, as shown in the figures of *Proteus*. They vary little in size throughout the Amphibia.

II. The optic nerves are, as a rule, very much reduced in the *Urodela*, and are in a degenerate condition in the *Proteida*. Both in the *Proteus* and *Necturus* the primitive epiblastic stalk of the optic vesicles is persisent. In *Proteus* and in some examples of *Necturus* the lumen of the stalk is persistent in the adult condition.[1] This lumen opens into the ⊥-like expansion of the bottom of the 3d ventricle, which is almost invariably found just in front of the chiasma, and demonstrates that this recessus opticus is the proximal portion of the primitive optic stalk.

III., IV., VI. These nerves require no special comment. Their development is naturally parallel with that of the 2d pair. I have made a doubtful observation of the presence of the 3d pair in *Proteus*, but have seen no trace of the 4th and 6th, although it is quite possible that their rudiments will be found in sections. The 3d and 4th pairs pass off independently. The 6th pair, according to Fischer ('64, p. 125), unites with the Trigeminus. I have not been able to determine whether this passes into or through the Gasserian ganglion or unites with the 5th beyond it. The more difficult problems arise with regard to the homologies of the Trigeminal, Facial, and Acoustic nerves, which can only be settled by obtaining serial sections through the nerves, brain, and skull *in situ*. This arises from the fact that the Trigeminus is always reinforced by a branch of the Facial, and that the latter and Acoustic are given off so close together that it is difficult to determine into what bundle the minor roots of each pass. A clear idea of the exit of these nerves, as found in *Cryptobranchus*, is given in Fig. 6, which is reconstructed from the sections, while the relation of the nerves to the encephalic tracts is given in Fig. 21; see also Figs. 15 to 18.

V., VII. The main division of the Trigeminus is given off as a single root from the antero-lateral region of the medulla, V. 1, 2, and it is reinforced by two smaller roots, V. 3.[2] The Facial

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[1] This fact when observed was communicated to Professor Kupffer, who made use of it in a paper upon the relation of the growth of the optic nerve to the stalk. The epithelial stalk in long sections extends outwards from the recessus opticus as far as the nerve can be followed, and is *peripheral*, the fibres lying at the side.

[2] Fischer described four branches from the Gasserian ganglion, instead of the usual three, in *Siredon* (op. cit., p. 128): 1. To the skin of the nose region; this he be-

arises from two closely applied roots, V.–VII. *u* and *l*, which may be described as the upper and lower roots. The upper root apparently passes directly forwards as the reinforcing branch of the Trigeminus. I may anticipate by saying that this is probably to be regarded as a detached sensory root of the 5th, and not as properly a part of the 7th. But it is, thus far, somewhat uncertain whether some of the fibres of the lower root do not also join the 5th. The lower root passes directly outwards, and either wholly or for the most part unites with the 8th. For a short distance these roots form a single trunk, and it is at this point that the chief uncertainty arises as to their distribution. A short distance outwards the 8th turns back into the auditory capsule, and the 7th extends and divides into two branches, *R. mentalis* and *R. alveolaris*, then into four (Fischer, op. cit., p. 135).[1]

VIII. The 8th springs from four roots. The most anterior root, VIII. 1, is small, and is given off immediately below and behind the lower root of the 7th. Behind this is the large root of the 8th, VIII. 2, and this is reinforced by another small root, arising somewhat internal and posterior to it, VIII. 3 and 4, by two small branches. This root may possibly join the lower division of the 7th, this uncertainty being expressed in Fig. 21 by its double designation, VII.–VIII.

IX., X. The Glossopharyngeus arises by three roots, IX. 1, 2, 3, which unite to form a single branch, passing back into the ganglion of the Vagus. Behind these, two more roots, X. *a* and *b*, unite to form a single branch, also passing back to the ganglion. Somewhat internal to these two roots, and extending at about equal intervals backwards, arise five small roots, which unite to form the third main branch of the Vagus system, X. 1–5. Some distance behind these is given off the 12th pair, on either side of the anterior fissure, much nearer the median line than any of the preceding nerves.

The above description of the exit of the 5th to 10th pairs applies especially to *Cryptobranchus*, but so far as the main branches are concerned holds good of the other genera as well.

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lieved is formed from the fibres coming from the 7th. 2. Ramus nasalis. 3. Ramus maxil. superior. And 4. Ramus max. inferior. I have observed but three main branches from the ganglion. See Appendix, Note 2.

[1] See Appendix, Note 2.

Proteus presents the widest departure from the common type, inasmuch as the Trigeminus and upper root of the Facial are given off very close together, and, so far as observed, but two branches spring from the Gasserian ganglion. The 9th and 10th pairs arise some distance behind and are followed by the 12th, which springs from two small roots and has the same position as the succeeding nerve, as an anterior spinal nerve root (Fig. 3).

THE MEDULLA OBLONGATA OF CRYPTOBRANCHUS.

General Structure. I have not made a close examination of the entire section of the medulla at different levels, having devoted most attention to the lateral regions, which are especially connected with the tracts and nuclei of the cranial nerves. As we would naturally anticipate, in an animal of such low organization as *Cryptobranchus*, the transition from the spinal cord to the medulla is a gradual one, but it by no means follows that we can readily homologize the medulla and spinal cord sections.

As we ascend from the level of the 10th pair (Fig. 10), at which the general arrangement of the gray and white matter of the cord is fully preserved, we find the tracts and nuclei of the posterior nerves, and the deep ascending tracts, which are at the extreme lateral limits of the medulla, are gradually thrust downwards by the nuclei and tracts of the more anterior nerves. Thus the nuclei of one pair of nerves are overlapped from above, and then replaced by the nuclei of the pair in front of them, and so on. This superposition of the posterior by the anterior nuclei is exclusively in the lateral portions of the medulla, and none of the nerves between the 12th and 6th pairs arise from the region corresponding to the anterior horn of the gray matter of the cord.

The *central* region of the medulla is in general composed of five main areas. 1. At the floor of the ventricle on each side is a mass of sensory cells.[1] 2. Below these, scattered along the whole medulla, are multipolar ganglion cells, which are especially large and numerous opposite the exit of the Acusticus. 3. On either side of the sulcus are the large fibres of the posterior longitudinal fasciculus, and below these are the Müllerian fibres. 4. Below this, in the median line, are decussating fibres and the

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[1] Nucleus centralis, Stieda.

decussating processes of the ganglion cells.[1] 5. The remaining area, which makes up the main central region of the medulla, is composed of the sensory and motor tracts.

The area of large ganglion cells, as shown in Figs. 10, 11, and 12, is continuous with the cells of the anterior horn. It is also clear that the main motor and sensory tracts which occupy the anterior and lateral columns, at the level of Fig. 10, are thrust down, with the ascending Trigeminal tract, to form the area 5. With the exception of the posterior longitudinal fasciculus, none of the nuclei or tracts of the cranial nerves below the 6th pair occupy the *central* region of the medulla. It follows that the lateral region of the medulla is exclusively composed of the cranial nerve tracts and nuclei and the central region is composed of the main sensory and motor tracts of the cord and special sensory and motor centres. These regions are pretty sharply defined from each other. The lateral region above the level of the Vagus is bounded by the ascending Trigeminus tracts.

The Tracts and Nuclei, Plate V. A general description of the fibre tracts and nuclei is necessary to introduce the special study of the origin of each nerve. In the section opposite the 12th nerve, we find the columns of the cord and horns of gray matter well defined. Between the posterior and lateral columns, at the extreme periphery of the cord, is a small bundle, the trigeminus ascendens, 5*t*.[1] On the posterior horn is another small round bundle, not hitherto to my knowledge described, which from its common relations to a number of the cranial nerves we may call the fasciculus communis. Opposite this, upon the lower side of the posterior horn, is another round bundle, which from its relation to the Vagus is believed to represent the fasciculus solitarius of Lenhossek, *fs.* Above this section, Fig. 11, opposite the exit of X. 4 and 5, is seen a small nucleus contributing to the fibres of the fasciculus communis, *fcn.*; then the nucleus and ascending bundle of the 9th, then the ascending trigeminal tract; below this is the exit of a portion of the fasciculus communis, and the nucleus and a root of X. 4. In the centre of the medulla is the posterior longitudinal fasciculus, which is now a more compact and well-defined tract than in

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[1] Connected with the crossing Müllerian fibres, (Ahlborn).

the lower levels, and increases in distinctness as we ascend. The nucleus and bundle of the Glossopharyngeus increases in size, and the large ascending bundle of the Trigeminus is thrust downwards, Figs. 11 and 12; at the level of the exit of the 9th pair, the sensory nucleus and upper and lower roots of the 7th come into view, as well as a third nucleus of the 9th, *9n*, which takes the place of the internal nucleus of the 10th. The fasciculus solitarius has entered the 10th, also a large bundle of the fasciculus communis, *fc'*, and a fresh bundle of this fasciculus is now forming, *fc''*. It is noteworthy that although the two bundles of the Facial and the Trigeminal root are well formed, there is apparently no trace of the Auditory. Above this level, however, the auditory tract, *8t*, forms rapidly between the ascending 5th and the lower 7th tracts. It has apparently two nuclei, Fig. 14, and encloses the fasciculus communis. The Auditory is given off by the union of four tracts, and above this the 7th arises by its two roots. The upper and lower nuclei of the 7th are then replaced by the large sensory nucleus of the 5th, which rapidly reinforces the already large ascending tract. A glance at the series of figures will show how the sensory nuclei of the 9th, 7th, and 5th pairs replace each other in regular succession, while the 8th, so far as observed at present, belongs to a separate system. A schematic arrangement of these nuclei is shown in Fig. 21, the level at which each transection is taken being indicated at the side.

Glossopharyngeus and Vagus. These nerves are closely related to each other; the glossopharyngeus arises dorsally, contributing mixed fibres, and the vagus ventrally, also contributing mixed fibres. The definite homology of these roots with the 9th and 10th pairs of the higher vertebrates is uncertain.

The posterior roots of the *Vagus*, X. *ab*, 1–5, of this system, arise from at least three sources. 1. The fasciculus solitarius. 2. The fasciculus communis. 3. A special nucleus in the floor of the 4th ventricle. The two ascending fasciculi are both found in the region of the posterior horn. (1) The fasciculus solitarius[1] appears to arise from the

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[1] This bundle in the human medulla contributes also to the 9th pair, and extends to the level of the 8th Cervical (Krause). Hoffmann-Rauber, Lehr. d. Anat., 1886, p. 397.

lateral columns of the cord; at least, no special group of nerve cells has been observed contributing to it. The fasciculus communis, however, is closely applied to a nucleus of small sensory cells, *fcn.*, from which it appears to be reinforced. The fasciculus solitarius enters the two posterior roots. (3) The three middle roots arise from the nucleus in the floor of the ventricle, 10 *n*, which is apparently composed of *motor* cells. (2) The two anterior roots, *a*, *b*, arise from the fasciculus communis, which is thereby reduced to a small bundle.

The *Glossopharyngeus* arises from four sources. 1. The fasciculus communis. 2. A large sensory nucleus. 3. A nucleus of doubtful motor cells. 4. A motor nucleus in the floor of the 4th ventricle. (2) The sensory nucleus and tract is found at a low level opposite the exit of the posterior roots of the 10th. This tract 9 *t* rapidly increases in size from the nucleus in the dorsal folds of the medulla, which is undoubtedly sensory. Anteriorly, this nucleus is replaced by the sensory nucleus of the 7th, and below it, in the angle of the medulla, (3) is a small nucleus of cells of different character which are probably motor, 9 *mn.* These doubtful cells have the same position as the nucleus of the lower root of the 7th pair, which is unquestionably motor. The fibres from these two nuclei constitute a single tract, and form the anterior root of the 9th nerve. (4) The motor nucleus in the floor of the ventricle, 9 *n*, is in exactly the same position as that of the 10th pair, and is composed of spindle-shaped, probably motor, cells. The fibres from this nucleus form the posterior root. (1) The fasciculus communis forms the middle root.

The 9th and 10th pairs have in common, first, the continuous and closely similar sensory nuclei and tracts arising from them which constitute the main sensory supply of the former nerve; second, the special motor nuclei in the floor of the ventricle; third, the fibres of the fasciculus communis, also sensory. The element of doubtful motor cells which is present in the 9th and absent in the 10th, may subsequently be found in the latter. The 9th, however, apparently lacks the fasciculus solitarius. The special motor nuclei, 9 *n* and 10 *n*, are seen to correspond in position to the lateral portions of the anterior horn, *i.e.* to the region dorsal to the extremity of the anterior horn.

The *Acusticus.* The nuclei and tracts of the 8th pair, as a nerve of special sense, do not in any degree repeat the features of the 9th and 10th, which to a certain extent are witnessed in the 5th and 7th. Of the *four* distinct roots of the 8th, I am in some doubt whether the first and last may not be given off out of place and ultimately join the 7th. The last of these roots may, however, at present be described as a portion of the 8th. (4) The fibres of the fourth, or posterior root, are received from the posterior longitudinal fasciculus, as beautifully shown in the floor of the ventricle of *Siren* and in sections of this level, Fig. 15. They suddenly turn out from the ascending bundle of the fasciculus and traverse the medulla at an oblique angle to join the nerve by two small roots. Whether studied in transverse or horizontal sections, this is clearly an *ascending* fasciculus, and connects the nerve with the lower regions of the medulla or spinal cord, not with the encephalon. This is an important point. (3) Shortly above the exit of the 9th pair, Fig. 14, a nucleus of large pale ganglion cells appears, which is quite distinct from the underlying motor nucleus of the 5th. This is the second source of supply of the auditory fibres, and probably corresponds to *Deiters* nucleus; it is sharply defined from the surrounding cells. (2) In the lower angle of the medulla is also seen a group of small cells which appears to contribute to this tract of the 8th, 8 *sn*, but cannot be positively determined. (1) On the dorsal side of this tract is the bundle of the fasciculus communis, which is here double, one-half, VIII., passing outwards to form the anterior root of the 8th. (5) As the nerve is given off, a large tract is seen which rises external to the sensory nucleus of the Trigeminus and constitutes the 8th encephalic tract, which is indicated by a contour above *fc'''* in Fig. 17, and by dotted lines in Fig. 21. It is possible that this tract sends fibres to the mesencephalic sensory cells which may thus form a superior nucleus.[1]

It is seen that, whatever may prove to be the peripheral distribution of the fibres of the fasciculus communis and posterior longitudinal fasciculus, whether to the 7th or 8th, two facts remain: first, that the 8th arises ventral to the 7th, although a purely sensory nerve; second, it is inserted in the centre of the Facial-Trigem-

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[1] It ascends to the midbrain, see Cerebellum

inal system, with no apparent homology in the arrangement of its nuclei to either.[1]

There is a strong ground for supposing that the fasciculus communis, although primarily given off with the Auditory, subsequently joins the Facial, since, first, it adjoins the lower motor bundle of the Facial, and second, it also joins the motor bundles of the 10th, 9th, and probably of the 5th, nerves, which fall into the same general category as the 7th. Still, this question can only be settled by following this tract peripherad beyond the passage of the 8th into the auditory capsule.

The posterior longitudinal fasciculus is stated by some authors to send a bundle to the 7th; I do not know that this has been positively determined. Spitzka regards it as highly improbable that this bundle enters the Auditory proper. It forms a close union with this nerve, VII.–VIII., 3–4, soon after its exit, at which point the two facial and four auditory roots have the relations, shown in Fig. 16, to each other and to the large Auditory ganglion. It seems improbable, from these relations, that this inferior bundle should unite with the facial bundle, and further, both Ahlborn[2] ('83, p. 262) and Fulliquet ('86, p. 81) have followed portions of these large fibres into the Auditory so that this tract is almost without doubt a portion of this nerve. There is also much similarity between the disposition of the 7th, 8th, and 5th tracts in *Cryptobranchus* and *Petromyzon* (op. cit., Taf XIV.).

Facialis and Trigeminus. As already stated, the nuclei and tracts of the upper and lower *Facial* bundles arise at a low level, opposite the exit of the 9th pair, somewhat lower, in fact, than represented in the scheme, Fig. 21. There is no difficulty in recognizing the upper tract as sensory, since it springs from the outer fold of the medulla in precisely the same manner as

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[1] Dr. E. C. Spitzka, to whom I am indebted for some valuable suggestions as to the identification of these tracts, questions the determination of the upper bundles, 7 *u–l*, in Fig. 15, as parts of the Facial, on the ground that the ventral position of the Auditory reverses the usual order. There can, however, be no doubt that these belong to the Trigeminal system, from the fact that 7 *u* passes directly to the Gasserian ganglion (see Fig. 5).

[2] Ahlborn distinguishes three groups of *Müllerian fibres* in *Petromyzon*, viz., lateral uncrossed, median crossed, and median uncrossed. The same groups are apparently present in *Cryptobranchus*. The first named corresponds in position with the posterior longitudinal fasciculus, and alone enters the Auditory root. See Appendix, Note 3.

the dorsal roots of the 9th, and from similar sensory cells, 7 *sn.* The lower tract begins at about the same level, and is distinguished from the upper by its larger fibres and by a distinct contour, but there is some doubt whether it is a motor tract. The nucleus, 7 *mn,* is at the angle of the medulla in the same position as the supposed motor nucleus of the 9th, and is composed of slightly larger cells than the sensory nucleus, but they are not distinctly of the motor character. As represented in Figs. 15 and 16, some of them are bipolar; but they have not the characteristic multipolar shape and large nuclei which are seen in the motor nuclei of the 5th, 5 *mn,* and 10th. There can be little question, however, from the peripheral distribution of this tract that it is motor.[1] The Facial is thus comparatively simple in its origin : unless it is reinforced by the fasciculus communis or posterior longitudinal fasciculus, or both, it has, so far as observed, no ascending bundle, and in this respect differs from the 9th, 10th, and 5th. It has, however, a small descending tract, rising towards the cerebellum above the descending 8th.

The Trigeminus. Five, or possibly six, tracts are observed to enter the Trigeminus, as follows: 1. The ascending tract from the cervical region, reinforced by, 2, fibres from the deep motor nucleus, representing two tracts. 3. Fibres from the sensory nucleus. 4. The descending tract from the mesencephalic nucleus. 5. The direct encephalic tract.

(1) The ascending trigeminus is first observed at the periphery of the cord, between the lateral and posterior columns, and increases rapidly in size, probably by accession of fibres from the lateral columns, so that at the exit of the 9th pair it is the largest of the tracts. (2) At this point we first observe fibres entering this tract from the motor nucleus, 5 *mn,* which immediately adjoins the motor nucleus of the 9th pair, and is external to the group of large ganglion cells which are continuous with those of the anterior horn. This nucleus increases in size to the level of the exit of this tract. (3) No sensory nuclear fibres enter the tract below the level of the exit of the 7th pair; at this point the sensory nucleus appears, 5 *sn,* continuous with that of the 7th, Fig. 17, and the motor nucleus, which is throughout composed of typical motor cells, immediately adjoins it ventrally. The sensory nucleus is very large,

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[1] See Appendix, Note 2.

and extends forwards beyond the level of the cerebellum. At this upper level, Fig. 18, the motor nucleus extends towards the centre, and sends fibres directly into the nerve root. (4) The descending tract is a large bundle from the more central region of the medulla. It rises obliquely, 5 t,^{4} from the root, Figs. 17 and 21, marked by its large, darkly stained axis cylinders, and is joined by another tract of similar fibres, the origin of which I have not observed, Fig. 21. The joint tract, thus formed, is very conspicuous and is followed without much difficulty. Opposite the cerebellum it splits into two bundles (see Figs. 23 and 24, 5 t^4). One of these passes into the cerebellum, Fig. 19, and, without crossing, enters the roof of the optic lobe at one side of the median line. The second bundle, 5 $t^{4'}$, passes forwards, and scatters into rays over the whole wall of the optic lobe, nearly as far forwards as the posterior commissure. These two bundles undoubtedly arise in the same manner from the large cells which constitute the nucleus.

The trigeminal mesencephalic nucleus has a remarkable extent in *Necturus*, reaching in two large masses of solidly packed cells, on either side of the median line of the roof, from the cerebellum to the posterior commissure. The posterior portion of this nucleus is shown, in Fig. 19, in which the cells lie, two or three deep, above the central gray of the ventricle. The cells are multipolar and spindle-shaped, Fig. 19 *a*, with large nuclei, the main processes being directed upwards into the tectum opticum. The actual connection of these processes with the cerebellar bundle of the descending trigeminal can be observed. It is also probable that these fibres are reinforced from other cells of the roof of the optic lobes, a point which is discussed later. This trigeminal nucleus is found in all the Amphibia, but is much larger in *Necturus* than in the other *Urodela*, and larger in the latter than in the *Anura*. It does not, therefore, appear to be directly correlated with the power of sight, although it appears to have an indirect connection with the mesencephalic roots of the optic nerve.

(5) In horizontal sections a large portion, 5 t^5, of the Trigeminus is observed passing forwards into the lateral portion of the medulla, but cannot be followed any great distance, owing to the similarity of its fibres with those of the main sensory

tract adjoining. This encephalic tract underlies the similar bundles from the Auditory and Facial, Fig. 18.

Abducens, Trochlearis, and Oculo-motorius. The most interesting facts observed in connection with these nerves is the close relation of their nuclei to the posterior longitudinal fasciculus and the relation of the oculomotor nucleus to the posterior commissure. Both of these observations have been made before, but in the Amphibian brain they stand out with unusual clearness. In vertical and longitudinal sections, Figs. 20 and 20 *a*, some of the large fibres of this fasciculus seem to pass directly into the larger processes of the cells of the oculo-motor nucleus, 3 *n'*. The larger processes seem to lie in the direction of these fibres; the smaller processes are partly directed towards the fibres of the posterior commissure, and actually extend into the lower portion of this commissure; they are partly directed towards the exit of the nerve. This group is figured with the camera as observed in *Cryptobranchus;* the posterior commissure also descends close to this nucleus in *Necturus* and *Rana*, as seen in vertical and transverse sections, Fig. 25.

The posterior longitudinal fasciculus also has close relations with the Abducens nucleus, as shown in Fig. 18, although I have not observed either in this or in the Trochlearis[1] the actual continuity of its fibres with any of the cell processes. The Abducens nucleus is directly opposite the exit of the 5th pair, but unlike all the posterior nerves of the medulla, it passes out close to the middle line, more in the manner of an anterior spinal nerve root.

The Oculo-motor nucleus is double, consisting of two small groups of typical motor cells, 3 *n* and 3 *n'*, the fibres of the posterior commissure descending between them. As found in *Necturus*, Fig. 25, the fibres all arise upon the same side of the brain, and the nucleus is placed at the edge of the central gray substance.

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[1] It is difficult to follow the Trochlearis from its nucleus to its exit. It is stated to contain sensory fibres in the Selachians and Amphibia. Gegenbaur, op. cit. p. 49. I have only observed a motor nucleus.

GENERAL CONCLUSIONS.

A general survey of the distribution of the nuclei, shown in Fig. 21, as described in the preceding sections, points to the natural division of the cranial nerves into three groups: Group A embraces the Vagus, Glossopharyngeus, Facialis, and Trigeminus. Group B embraces the Abducens, Trochlearis, and Oculo-motorius. Group C embraces the Acusticus.

The known tracts and nuclei possessed in common by each of these groups are distributed below: —

GROUP A.

X.–IX., VII.–V.

1. Dorsal[1] sensory nuclei (? wanting in the 10th).
2. Lateral motor nuclei (? wanting in the 10th).
3. Fasciculus communis[2] from sensory nuclei (not observed in the 5th).
4. Ventral[1] motor nuclei (wanting in the 7th).

GROUP B.

VI., IV., III.

1. Special ventral motor nuclei.
2. Posterior longitudinal fasciculus.

GROUP C.

VIII.

1. Special sensory nuclei.
2. (Fasciculus communis from sensory nuclei ?.)
3. Posterior longitudinal fasciculus.

The nerves of Group A are apparently closely homologous, in so far as their mode of origin is concerned. The dorsal sensory nucleus of the 10th, 9th, 7th, and 5th pairs shows the most marked continuity, and the nerve bundles are seen to issue directly from it. The ventral motor nuclei of the 9th and and 10th (10 *n* and 9 *n'*) are continuous, and occupy the same region as the great ventral motor nucleus of the 5th. The fasciculus communis, first appearing in the posterior horn, and all along in close contact with a small group of sensory cells, is given off to the 10th, 9th, probably to the 7th, and possibly to the 5th. The lateral motor nucleus, consisting of the cells in the angle of the medulla, contributes to the 9th, 7th, and probably to the 5th.

The absence of the ventral motor nucleus from the 7th nerve, and the large motor element in the 5th, may indicate that some

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[1] These adjectives, dorsal and ventral, are retained, since these nuclei are simply thrust laterad by the opening of the 4th ventricle.

[2] This is upon the probability considered on p. 00, that the fasciculus communis joins the 7th instead of the 8th.

of the motor portion of the 7th, as found in the higher vertebrates, takes its exit with the 5th in the *Urodela*, while some of the sensory portion of the 5th takes its exit with the 7th, probably as the upper or sensory bundle which immediately joins the 5th.

The roots of the Glossopharyngeus seem to be in a similar manner complementary to those of the Vagus, since the former nerve receives a large bundle from the dorsal sensory nucleus, as well as from the lateral motor nucleus, neither of which bundles, so far as I have observed, enter into the 10th.

Group B. The exit of the Abducens from the central region of the medulla, and the special connection of its nucleus and those of the other eyeball muscles with the posterior longitudinal fasciculus, seems to separate these three nerves sharply from the Vagus or Trigeminus system, and unite them closely into a group of their own. I am well aware that some grounds are found in the development and peripheral distribution of these nerves for considering the 4th or 6th as vagrant portions of the Trigeminal or Facial motor roots, but the internal origin certainly does not support this hypothesis; at the same time it cannot be said to disprove it.

Group C. The Auditory has been shown to differ widely from the 9th, 5th and 7th nerves by deriving no fibres from the dorsal sensory nucleus, although a purely sensory nerve. This can be stated with considerable certainty. One of its special nuclei is also composed of cells of a unique character, viz., pale ganglion cells. The reception of fibres from the ascending tract adjoining the posterior longitudinal fasciculus further distinguishes it from the nerves of group A.[1]

These considerations lead to the following provisional conclusions in regard to the *intra-axial* origin of the cranial nerves in the Amphibia.

1°. That there is a close similarity between the disposition of the nuclei and tracts of the IX.–X. and V.–VII. groups, the nerves of these groups being complementary to each other, and together apparently containing fibres from two sensory nuclei and from two motor nuclei. The extreme dor-

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[1] See Appendix, Note 3.

sal and ventral nuclei are composed respectively of unmistakable sensory and motor cells. While one of the lateral or intermediate nuclei is composed of less distinctively motor cells of smaller size (*e.g.* 9*mn*, 7*mn*), the other (fasciculus and nucleus communis) is clearly sensory.

2°. The nerves of the III.–IV.–VI. pairs form a special system with no apparent homology or connection with the motor elements of the Vagus or Trigeminus systems.

3°. The VIII. as a nerve of special sense has either no homology or an incomplete homology in the arrangement of its sensory nuclei and tracts with the sensory elements of the Vagus and Trigeminus systems.

If the fasciculus communis is found to enter the 8th instead of the 7th, this section must be modified to an incomplete homology.

I do not consider that these observations are sufficiently well tested to give sure support to theoretical deductions as to the homologies of the cranial and spinal nerve elements. It is clear that the Vagus and Trigeminus systems approach nearest the typical spinal nerve arrangement, and the apparent presence of two sets of sensory and two sets of motor nuclei in these systems is of great interest in its bearing upon Gaskell's theory of the compound nature, somatic and splanchnic, of the anterior and posterior roots. As frequently stated above, the motor or sensory character of some of the nuclei and tracts can only be determined by the study of their peripheral distribution, since the character and position of the cells themselves, as shown in the pale ganglion cells of the 8th and the small cells of the lower nucleus of the 7th, is an uncertain guide as to the nature of the fibres which spring from them. Even with this precaution it is a great advance to determine the presence of these two sets of nuclei for each of these systems.

III. THE ENCEPHALON.

THE CEREBELLUM.

As already observed, the cerebellum in the *Urodela* is widely different from that in the *Anura* in its size and internal structure. My observations relate principally to the former. The latter has recently been thoroughly investigated by Wlassak, in a memoir which I have not had an opportunity of studying, and independently by Köppen.

In an earlier paper upon the Cerebellum of *Cryptobranchus* I showed that it receives two lateral systems of fibres on each side, one from the medulla, one from the mesencephalon. Also a central system entering the mesencephalon. The latter, which I mistakenly compared ('84, p. 266, Plate VI., Fig. 7) with the superior peduncles of the mammalian cerebellum, I now find is composed of the cerebellar branch of the descending Trigeminus tract. The cerebellum of *Amphiuma* consists exclusively of these lateral and central tracts, containing no cells except the lining of ependyma ('83, Plate VIII., Fig. 3). The *Cryptobranchus* cerebellum contains, in addition, a small mass of round cells of the same description as those composing the central gray substance of the optic lobes. It thus consists of the following elements, as shown in Figs. 19, 23 and 28.

1°. Fine fibres from the extreme lateral portions of the medulla. It is clear that these fibres, *cbl.t'*, as shown in Fig. 18, do not arise from the central region of the medulla. They can in part be followed to the point of exit of the 7th and 8th pairs of nerves. Of these the larger portion seem to come from the 8th pair.

2°. Coarse fibres from the descending trigeminus tract. The course of these fibres has already been described on page 153, 5 t^4.

3°. Fine fibres passing laterally into the mesencephalon, *cbl.t;* these can be followed some distance into the lateral area of the central gray of the mesencephalon.

4°. A nucleus of small rounded cells, *cbl.n*, in the ventral area.

The passage of the fibres from the 8th pair through the cerebellum has also been observed by Ahlborn. It is somewhat difficult to determine positively, owing to the close similarity between the adjoining trigeminal and facial fine fibre bundles. In horizontal sections the fine fibres of the Trigeminus, 5 t^5, are, however, seen to pass directly forward into the lateral region of the mesencephalon. It is thus probable that the fibres entering from the medulla are mostly sensory fibres from the Auditory nerve which decussate to the opposite side of the brain through the cerebellum, and either enter the main sensory tract or terminate in some of the cells of the mesencephalon. The descending Trigeminus tract does not decussate, but enters the medulla on the same side.

The fine fibres of the Urodele cerebellum are in part decussating tracts of the Auditory nerve, and the coarse fibres are non-decussating descending tracts of the Trigeminus nerve.

This conclusion as to the connection with the Auditory nerve is supported by Köppen's observations upon *Rana* (op. cit., p. 13), and Ahlborn (p. 261). Ahlborn, however, considers that the fibres entering the cerebellum are commissural between the Auditory nuclei of opposite sides. This hypothesis is not supported by the fact that the superior and inferior tracts are subequal in diameter.

The passage from the medulla into the mesencephalon is accompanied by the compact disposition of the gray substance immediately surrounding the ventricle, Fig. 25. The fine fibres descending to the trigeminus and the great mass of fibres from the central region of the medulla become indistinguishable, and the only fibres which can be readily followed forwards in transverse sections are those of the descending trigeminal tract and the posterior longitudinal fasciculus. Anteriorly, in the region of the diencephalon, the so-called round bundle is sharply differentiated from the remaining fibres. In vertical sections, however, the tracts from the central region of the medulla can be followed with great ease, especially in the brains of *Amphiuma*, *Necturus*, and *Cryptobranchus*, in which the mid-segments are only slightly swollen and the sections fall in the plane of large bundles of fibres (see Fig. 30). These tracts have been carefully studied in *Necturus*, *Cryptobranchus*, and *Rana*, the former genera agreeing closely in all essential features.

THE NUCLEI OF THE ANTERIOR SEGMENTS.

The main masses of fibres from the spinal cord and central region of the medulla sweep forwards either directly into the central gray of the mesencephalon, diencephalon, or prosencephalon, while the secondary or more local tracts of the encephalon can in most cases be followed directly to certain nuclei. The latter are more numerous in the *Anura* than in the *Urodela,* at least they are much more sharply defined. The following nuclei have been observed in the brains of both classes (see Fig. 31).

A. The nuclei of the cranial nerves.

1°. The nuclei of the 3d, 4th, and 6th pairs, *3n, 4n,* and *6n,* are nearly upon the same horizontal level in the *Urodela.*

2°. The great mesencephalic trigeminal nucleus extends along either side of the entire roof of the segment in many of the *Urodela,* but in the *Anura* is much smaller and is mainly confined to the antero-lateral region (Fig. 26).

3°. Two special well-defined centres of the optic nerve fibres are observed: *a.* the roof of the mesencephalon on either side of the median line in the *Urodela;* in the *Anura* this extends into the widely expanding optic lobes. *b.* A distinct nucleus in the middle region of the walls of the diencephalon (corpus geniculatum).

B. The nuclei of the encephalic tracts.

1°. The most distinct of these are the ganglia habenarum, *gh,* just anterior to and partly traversed by the superior commissure. They are composed of small, rounded cells, like those of the central gray at the dorsal anterior angle of the thalami.

2°. In the floor of the mesencephalon, just posterior to the oculo-motor nucleus, is the ganglion interpedunculare, *gi,* composed of very small triangular cells.

3°. Just posterior to the posterior commissure is a small dorsal nucleus, in the course of the optic tract (see Fig. 24), the connections of which are undetermined.

4°. The corpus striatum is not well defined in the Amphibia; it consists of a mass of scattered cells, slightly anterior and ventral to the anterior commissure, Fig. 28, *cs.*

5°. Slightly posterior to the oculo-motor nucleus, on the same horizontal level, is a nucleus of pale bipolar ganglion cells quite distinct in character from the nucleus of the third pair, which consists of triangular deeply stained cells. This is figured, but not lettered, in Fig. 23, and is seen both in *Rana* and *Cryptobranchus* (? red nucleus).

6°. The most conspicuous nucleus in *Rana* is the nucleus magnus of Stieda. This is slightly below and in front of the cerebellum, *nm.*

7°. Another smaller but conspicuous nucleus in *Rana* is in the wall of the diencephalon, behind the corpus callosum, *n'*, Fig. 29.

The homologies of some of these nuclei are rather uncertain. The nucleus in the wall of the diencephalon which gives rise to the fibres of the optic nerve corresponds probably to the middle or lateral geniculate body.

The nucleus just behind the oculo-motor ganglion corresponds closely in position to the red nucleus of the tegmentum. Stieda and Köppen have suggested that the nucleus magnus corresponds to the dentate nucleus of the cerebellum, but this is also in the position of the red nucleus and presents many points of agreement with it in its relations to the surrounding tracts; its relations to the cerebellum are, however, by no means well ascertained.

THE MAIN SENSORY AND MOTOR ENCEPHALIC TRACTS.

There is no certain means of distinguishing the sensory from the motor tracts. In the ascending series of sections of the medulla oblongata, it has been shown that the posterior columns, which presumably contain unmixed sensory fibres, and the lateral columns of mixed fibres are thrust downwards by the superposition of the cranial nerve nuclei. As a result of this, we should expect to find the sensory tracts occupying the lateral portion and the motor tracts the median portion of the central region of the medulla, corresponding to the anterior columns of the lower levels of the cord. That such is actually the case is supported by two facts. First, it is found in *Cryptobranchus* that the median region consists of slightly larger and deeply stained fibres, more of the nature of motor fibres than those of the lateral region; and second, the fibres of the lateral region mostly terminate in the mesencephalon and diencephalon, while those of the median region, in large part at least, extend directly forwards into the prosencephalon. With this evidence I may at all events describe these lateral tracts as *sensory* and the median tracts as *motor.*

The Sensory Tracts. In successive sagittal sections of the brains of *Cryptobranchus*, *Necturus*, and *Rana*, we first pass through the fibres of the extreme lateral portions of the medulla, entering the cerebellum, *cbl.t*; then we observe large bundles of fibres from the lateral regions of the medulla, *mst*, ascending and spreading over the outer surface of the mesencephalon, Figs. 24 and 30. In sections slightly internal to these, the central gray of the mesencephalon comes into view, with rows of cells and bands of fibres alternating, and the continuation of the same medullary tract is observed spreading over the outer surface of the diencephalon in precisely the same manner, *dst.* These direct diencephalic and mesencephalic sensory tracts are beautifully shown in vertical sections of the brain of *Amphiuma*, in which these segments are very slightly differentiated from each other. In succeeding sections, still approaching the median line, the direction of the fibres is reversed; from the postero-lateral region of the mesencephalon and the lateral region of the diencephalon, the main trend of the fibres is downwards and forwards, *mst'* and *dst.'* The latter fibres pass directly forwards into the basal portion of the prosencephalon. The former, *mst'*, turn downwards, but their forward continuation into the prosencephalon cannot be so distinctly followed. The simplicity of these ascending and descending systems in the *Urodela* is interfered with in the *Anura* by the expansion of the optic lobes, but the arrangement is the same.[1]

In transverse sections of the optic thalami, the dorsal portion of the cerebral peduncles is composed of a compact round bundle of fibres, (Osborn, '84, Fig. 8, *l.*). The origin of this is somewhat uncertain. From the fact that it is first differentiated in the anterior portion of the mesencephalon and becomes more distinct in the thalami, we may infer that this bundle is composed of the prosencephalic sensory tracts formed from these segments.

In *Rana*, in which the corpus callosum and anterior commissure are somewhat separated, a portion of this bundle seems to pass between them (Fig. 29). There is room for error here in the fact that the basal fore-brain bundle from the medulla is reinforced by fibres both from the ascending diencephalic and mesencephalic tracts and from the infundibular tract.

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[1] See Köppen, op. cit., Taf. III., Figs. 27, 28.

The Motor Tracts. As the sections extend inwards the mass of fibres from the medulla does not ascend, but passes forwards directly into the basal portion of the prosencephalon as the basal prosencephalic tract (basal fore-brain bundle, Edinger). This is best followed in the *Urodela,* but is also readily followed in successive sections in the *Anura,* Figs. 28, 29. Upon reaching the corpus striatum, some of the fibres of this tract enter this body, as described recently by Edinger (Fig. 28), while others pass directly into the inferior portion of the mantle of the hemispheres; a third portion seems to terminate immediately below the anterior commissure: but in horizontal sections it is seen to pass to the other side.[1]

The tract thus consists of three parts: *a,* a direct bundle from the hemispheres; *b,* a bundle from the corpus striatum; *c,* a decussating bundle from the hemispheres. Two of these divisions were incidentally described and figured in my paper upon the *Corpus Callosum* (loc. cit., Taf. XIV., Fig. 8, *pm, pl*).

THE SECONDARY ENCEPHALIC TRACTS.

Under this head may be considered the tracts which, so far as observed, have no direct connection with the spinal cord or medulla.

Meynert's Bundle. This is a conspicuous tract in the brains of all the Amphibia, *mb.* It arises, in the usual manner, from the ganglia habenulæ and descends beneath the superior commissure as a compact bundle of darkly stained fibres, to the ganglion interpedunculare. I have followed it slightly beyond this point in *Rana,* Fig. 29, but not into the medulla, as Ahlborn has succeeded in doing, in *Petromyzon.*

The Infundibular Tract. From the infundibular lobes this large tract of fibres ascends, *it,* beneath the basal prosencephalic tract, towards the hemispheres. Köppen has described it as entering the thalami. It has this appearance in *Rana,* but not in the *Urodela,* where it appears to pass directly forwards and not upwards.

The Posterior Commissure. The relations of this commissure are threefold; first, to the oculo-motor nucleus and probably to the main sensory tract; second, to the pale ganglion

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[1] This decussation is described by many authors as a portion of the anterior commissure, but in my opinion should be considered as entirely distinct.

cells behind this nucleus; third, to the tectum opticum. As it descends, the fibres divide into two bundles (Fig. 25), of which the anterior surrounds the superior processes of the ganglion cells of the oculo-motor nucleus (Fig. 20, *pcs*): this connection is so close that some of these fibres seem to be actually continuous with the cells. The posterior bundle has a similar connection with the cell processes of the pale ganglion, which may in fact also belong to the oculo-motor nerve. None of the fibres of this commissure can be traced directly into the main (sensory) tracts adjoining these nuclei, as observed by Pawlowsky, although such a connection seems highly probable (tractus cruciatus tegmenti). Dorsally, the fibres of this commissure in *Rana* can be clearly followed into the peripheral white substance of the tectum opticum, as shown in horizontal sections.

The Superior Commissure. This is much less constant in size and development than the foregoing. It is extremely small in the *Anura* and apparently so in the *Proteida*,[1] but is large in *Cryptobranchus* and *Amphiuma*. It divides into two distinct bundles, one of which descends into the inner mantle of the hemispheres, *scs*, and finally disappears, after bending around into the outer portion of the mantle. The second bundle descends directly along the outer wall of the thalami. These bundles are clearly seen where the commissure is well developed, and I have fully described them elsewhere ('84, p. 268, Fig. 8). One fact militates against our considering the commissure as a purely decussational system; that is, the bundle entering the hemispheres is much larger than that entering the thalami. It forms either partly a commissural system between the posterior portions of the hemispheres and between the thalami, or partly a decussational system between the hemispheres and thalami.

Cerebral Commissures. I have seen reason to partly alter my views as to the nature of the commissures of the hemispheres which were described in detail in my paper on the corpus callosum. The more recent researches of Bellonci, with the aid of the Golgi method, upon these commissures, should be consulted.[2] They show that with the purely commis-

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[1] *Necturus.*

[2] I regret that I have not the opportunity at present to investigate thoroughly the interesting questions which Bellonci has raised in this valuable memoir in regard to

sural fibres, decussational fibres are intermingled. I have myself discovered that in the upper bundle or corpus callosum of *Menobranchus* there enter fibres from the diencephalon. *Proteus* agrees with *Menobranchus* in the entire separation of this bundle from the anterior commissure. I have seen no trace in the Amphibia of the fornix columns which I have found in the *Ophidia* ('86, p. 533, Fig. 20), and Bellonci has figured in the *Lacertilia*, ('87).

Other important commissures are the infundibular commissures which connect the infundibular lobes, dorsally and ventrally, and the extensive commissure of the tectum opticum.

THE ORIGIN OF THE OPTIC NERVES.

It has recently occurred to me that the presence of the two whitish bands seen upon the external dorsal surface of the optic lobes in many of the *Urodela* is partly due to the underlying optic tracts. It is certain that these tracts in the *Urodela* are principally confined to the median portions of the tectum opticum. They can be followed as far forwards as the cerebellum, II. *t* 1, Figs. 23, 24, and descend obliquely from this region to the nerve. In the *Urodela* there is no differentiation of cells into distinct layers.

The character of the cells of this region is shown in Fig. 25*a*, which illustrates an interesting observation upon the apparent connection of the fibres either of the optic nerve or of the direct sensory mesencephalic tract with the fibres of the descending Trigeminus tract. The peripheral cells of the central gray substance, II. *n*, have long single processes. These processes branch, one of the finer branches entering the coarse fibres of the descending Trigeminus, the other passing outwards into the fine layer of fibres of the tectum opticum. This observation has been confirmed at several points. It shows first that the fibres of the Trigeminus may have a compound origin, partly from the large cells, 5 *n*, partly from the small cells; second, that here is a possible centre between the optic and trigeminus nerves.

The second optic tract, II. t^2, arises from a mass of cells im-

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the complete structure of these commissures. I do not therefore at present feel in a position to reply to his courteous criticism of my paper.

bedded in the central gray of the thalamus, and not clearly differentiated as a distinct nucleus from the surrounding cells.

The third tract, II. *t* 3, enters the hemispheres directly. This observation, although made in both the *Urodela* and *Anura*, requires to be confirmed. The optic tracts have other sources of origin;[1] the above are the main centres contributing the principal portion of the nerve, and are the only ones which can be clearly made out by the carmine method.[2]

In *Rana* the roof of the optic lobes is divided into eight distinct layers, the fibres of the superior portion of the optic tract entering the outermost layer, 1 Fig. 26, and ramifying to the interior cells. The inferior portion of the optic tract enters the second fibre layer, 3. The tracts surround the whole circumference of each of the lobes.

The relations of the encephalic tracts in the general architecture of the amphibian brain is shown in Fig. 21, in which only the well-determined tracts are introduced. The designation of the tracts expresses my present views; as I have already stated, the efferent or afferent character of the main tracts is not by any means settled.

COMPARISON OF THE DIPNOAN AND AMPHIBIAN BRAIN.[3]

The recent memoir of Fulliquet upon the brain of *Protopterus* is the first contribution to the histology of the Dipnoan brain, and enables us to make some interesting comparisons. In the first place, as observed by this author and others, the general external resemblance between the Dipnoan and Urodele brains is very striking. The principal external features in common are as follows: the olfactory lobes are not well distinguished from the hemispheres; this is even more marked in *Protopterus* than in the *Urodela*. The mesencephalon of *Protopterus* passes imperceptibly into the diencephalon, as in *Amphiuma*, only a faint lateral constriction between these segments being evident.[4]

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[1] See the papers of Bellonci, Blaschko and Edinger.

[2] In my paper upon *Menopoma* ('84, p. 267, Fig. 8), I described a portion of the optic nerve as non-decussating. I am now inclined to consider these supposed uncrossed tracts, *b*, as the mesencephalic tracts which cross at a different level, or the basal optic root of Edinger. The sections at this point are deceptive.

[3] See also Appendix, Note 4.

[4] In distinguishing between these segments internally, Fulliquet has failed to take

The optic lobes form single, unpaired bodies, as in many of the *Urodela.* The infundibular lobes in both orders are large and functional. The cerebellum is small[1] and partly overhung by the mesencephalon.

In a few respects the brain of *Protopterus* differs: the *ganglia habenarum* are much larger than in the *Urodela,* resembling those of *Petromyzon.* The anterior portion of the metencephalon is greatly expanded by the hypertrophied nuclei of the 5th–8th nerves and a diverticulum of the 4th ventricle. The olfactory nerves arise from the dorsal aspect of the rhinencephalon.

The similarity in the internal structure is very significant. The general arrangement of the encephalic gray substance, as the *central gray,* immediately surrounding the ventricles, is the same; the dipnoan *ependyma* has the peculiarity, first observed by Stieda in *Rana,* of the thread-like extensions of its cells through the central gray into the white substance; we also observe the peculiarly modified elongate ependymal cells (Fulliquet, Pl. IV. Fig. 17, *cde*), in the region of the posterior commissure, so characteristic of the *Urodele* brain. As these observations were prior to the discovery of the true nature of the pineal gland, the author has naturally failed to identify this structure, mistaking the ganglia habenarum for it (Fig. 19). The relation of the dia- and procœliæ seem to resemble those of *Rana* more closely than those of the Urodeles, since, as far as I can judge from Figs. 19 and 20, the prosencephalic commissures are in the *lamina terminalis* proper, and not in a projection of the floor of the ventriculus communis, as in the *Urodela.* The space marked TM in Fig. 19 represents this ventricle.

The encephalic commissures of *Protopterus*[2] apparently agree

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advantage of the anterior and posterior boundaries of the Diencephalon (Entrencéphale), as defined by the posterior and superior commissures.

[1] As there is no sagittal section of the *Protopterus* brain given, it is somewhat difficult to determine the limits of the cerebellum. A portion of the brain designated *Cervelet* (Plate I.) is apparently a portion of the hypertrophied nucleus of the trigeminal nerve.

[2] Fulliquet has not distinguished the posterior or superior commissures as such; nor has he identified the upper bundle in the lamina terminalis with the corpus callosum, as seems highly probable. It follows that my determination of these commissures is largely inferential from a comparison with similar sections of the Urodele brain.

closely with those of *Cryptobranchus*. We first observe that the lobes of the infundibulum (Fig. 14) are united dorsally and ventrally by commissural fibres as in the *Urodela* (Osborn, '84, Plate IV., Fig. 4, *scm, icm*). The two sides of the tectum opticum are also united by an almost continuous band of transverse fibres, Fig. 11, *fcm*, as in the Amphibia, terminating anteriorly in a special enlargement, *fce*, Fig. 17, which I identify as the posterior commissure. The *bande fibrillaire laterale* of Fig. 15, *bfl*, is probably either the posterior commissure or Meynert's bundle. The bundle connecting the ganglia habenarum, in Fig. 18, *fgp*, is probably the superior commissure. The upper bundle *fih*, Fig. 19, and *pfh*, Fig. 20, in the lamina terminalis, is probably the corpus callosum; this is an important fact, if verified, since this commissure has not heretofore been definitely identified below the Amphibia.[1] This can only be verified by following the course of its fibres. The lower bundle, Fig. 19, *ca*, occupies a somewhat unusual position, upon the floor of the brain.

Two differences in the internal structure may be noted: first, the optic chiasma is intra-axial or central, instead of peripheral, as in the Amphibia; second, there is a single pair of large Mauthner fibres in the medulla oblongata, which are wanting in most of the *Urodela*,[2] although the posterior longitudinal fasciculus is apparently present, *fl, sp*, Fig. 1.

I cannot institute any satisfactory comparison in respect to the origin of the cranial nerves. Many minor points of resemblance and difference have been passed by in this resumé, the general conclusion being that there is a very close similarity between the Amphibian (Urodele) and Dipnoan brain, both in the external and internal structure.

COMPARISON WITH PETROMYZON.

One of the chief features of Ahlborn's memoir upon the brain of *Petromyzon* is the thoroughness with which he has in-

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[1] In concluding my paper upon the corpus callosum (Morph. Jahr., Band XII., p. 539), I had not seen Fulliquet's memoir, but anticipated from the embryology of the *Ceratodus* fore-brain, that this commissure would be found in the Dipnoi.

[2] They have been observed by Stieda in *Siredon*, see Appendix, Note 5.

vestigated the medulla oblongata, especially the origin of the cranial nerves and the fate of the Müllerian fibres. The arrangement of the latter, I have reason to believe, is very similar to that in the Amphibia, but this system has not been as yet well investigated.[1] His conclusions as to the origin of the cranial nerves are in many details supported and confirmed by my own, although I have discovered many additional structures which either do not exist or have been overlooked in the lamprey.

An important difference is seen as to the more primitive condition of the medulla in *Petromyzon,* in that the nerve nuclei are more central (Fig. 18), and not confined to the lateral regions of the medulla as in the *Urodela.* In the latter I have observed the large ganglion cells, *gc,* opposite the exit of the 8th, but cannot confirm the entrance of their processes into the Auditory roots as observed by Rohon and partly confirmed by Ahlborn. He places the 7th and 8th in one group, which I find cannot be done in the *Urodela,* the 7th being closely related to the 5th.

One chief point of agreement is that in *Petromyzon* the 7th nuclei and exit are dorsal to the 8th; this confirms my observations and undermines the hypothesis that the 8th is the sensory portion of a typical pair of nerves of which the 7th forms the motor element. Our observations agree further in respect to the connection of the posterior longitudinal fasciculus with the 8th (acusticus haubenbahn, p. 268); also as to the presence of a nucleus of pale ganglion cells near the exit of the 8th (p. 261), which I have found is one of the chief Auditory nuclei in the *Urodela;* further, the nuclei and tracts of the 8th have the same relation to those of the 5th, as I have described in Cryptobranchus; finally, in both genera the 8th sends a tract into the cerebellum.[2]

The resemblance of the main Trigeminal system is also close. I do not find the nucleus of the transverse motor tract as large as he describes it, but the motor nucleus adjoining the ascending tract is similar in form and position (Figs. 16–21). I do not find an upper and lower nucleus of the 8th,

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[1] See Appendix, Note 3.

[2] This determination of the Auditory nuclei as ventral to those of the Facial is confirmed by both Stieda's and Köppen's observations upon *Rana.*

consisting of small cells such as Ahlborn describes (see Fig. 19). His upper 8th nucleus, VIII., corresponds exactly with my lower 7th nucleus, 7 *mn;* this agreement raises a question whether Ahlborn's upper 8th root does not pass into the 7th nerve. If such is the case, the homology with *Cryptobranchus* is remarkably close.

In the upper portion of the encephalon in *Petromyzon* is found the posterior longitudinal fasciculus, approaching the Oculo-motor nucleus, and according to Ahlborn, not terminating with it, but decussating at this point to enter the thalami (p. 274). The descent of Meynert's bundle to the interpeduncular ganglion is also seen.[1] The taenia thalami optici, p. 285, with fibres entering both the hemispheres and the thalami, is homologous with the superior commissure.

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[1] Ahlborn has followed this bundle, asymmetrical in *Petromyzon*, into the medulla.

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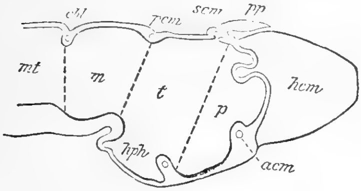
APPENDIX.

1°. Figure 2. A vertical section of the Brain of a *Rana* embryo, at the period of the formation of the encephalic commissures, *cbl*, *pcm*, *scm*. Lettering as in the Explanation of Plates.

Fig. 3. A horizontal section of the same, composed from two levels, showing the relation of the commissures to the encephalic vesicles.



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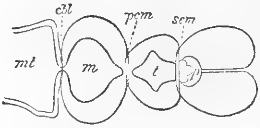

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2°. Fischer (op. cit., p. 135) upon the distribution of the Facial and Trigeminal Nerves in Cryptobranchus. The FACIAL divides into four main branches: R. palatinus; R. mentalis passes the *mylohyoideus* muscle and terminates in the skin of the lower jaw (sensory); R. alveolaris to the skin above the masseter muscle (sensory); R. jugularis to the *mylohyoideus posterior* and *digastricus* muscles (motor). The TRIGEMINUS has three branches: $5''$, *a*, *retractor bulbi*, *rectus externus* and *superior*, *obliquus superior* (motor, including Abducens); *b*, skin of forehead, olfactory chamber, snout and superior maxilla (sensory); $5'''$ to skin over premaxilla; $5''''$, *a*, to masseter and temporal muscles (motor); *b*, skin covering inferior maxilla (sensory). It will be observed that this distribution of the Facial is largely sensory and is consistent with the derivation of the main sensory elements of both nerves from the dorsal sensory nucleus, as I have described them. It also demonstrates that the lower bundle of the Facial is certainly motor.

3°. The Müllerian fibres and posterior longitudinal fasciculus. As shown in Fig. 11 (Plate V.), these two systems are apparently distinct. The Müllerian fibres are observed at the lowest medulla levels as a compact round bundle immediately below the anterior commissure; as we ascend, they multiply and form a crescent in the anterior median columns; at the exit of the *vagus* they separate into two strands, one, dorsal, below the sulcus centralis, the other, ventral, in the anterior columns; the ventral strands cross and disappear between the exit of the 9th and 8th nerves, entering large ganglion cells. The dorsal ascend to a higher level without apparently crossing; they are continuous with and apparently constitute the main portion of the posterior longitudinal fasciculus.

The Auditory tract of this fasciculus closely adjoins the dorsal Müllerian fibres, but may be distinguished from them by the slightly smaller diameter of its fibres; it is clearly distinguished opposite the exit of the 10th pair[1] and on all the higher levels; this leads me to the conclusion that this portion of the posterior longitudinal fasciculus is an ascending auditory tract apparently distinct from the Müllerian fibres. This further throws in doubt the supposed connection between this fasciculus and tract.

4°. Wilder upon the brain of Ceratodus. This description is macroscopic. In *Ceratodus*, like *Protopterus*, and unlike the lower *Urodela*, the ventriculus communis is very small. As in the *Urodela* there is a large *supraplexus*. The olfactory lobes, unlike those of *Protopterus* and the Amphibia, are pedunculated instead of sessile. The anterior commissure is mentioned, but the corpus callosum is not observed. Finally, an important distinction is seen in the fact that the extension of the hemispheres (secondary forebrain) is *ventral* from the primary forebrain both in *Ceratodus* and *Protopterus*, instead of directly anterior, as in the Amphibia.

I may express here my indebtedness to Professor Wilder for much of the terminology which I have adopted from his papers, and my regret that he has found it necessary to change his former terms in so many instances.

5°. Stieda's observations upon Axolotl include several points in which, if correctly described, this genus differs from *Cryptobranchus*. 1. Opposite the exit of the 12th nerve, on either side of the sulcus centralis, is a large Mauthner fibre, exactly as in *Petromyzon*. I think these fibres are not present in *Cryptobranchus*. 2. The ascending Vagus, or fasciculus solitarius, while arising in the same manner as in *Cryptobranchus*, is given off with the *anterior* roots, the Glossopharyngeus portion, instead of with the posterior. 3. A portion of the posterior longitudinal fasciculus makes its exit with the 8th pair, but is designated by Stieda as a portion of the Facial-Trigeminal system. This probably corresponds to the bundle which I have finally referred to the 8th nerve, Fig. 15, VII.–VIII. 3, 4. Another important observation is that a portion of this same fasciculus enters the Trigeminus. I am inclined to doubt this, as it has no parallel elsewhere, and it would be easy to mistake this for the posterior bundle which I have observed uniting with the descending trigeminus (see 5 t_4, Fig. 17). 4. Stieda describes the ascending trigeminus as *sensory*, probably from its relations in human anatomy; it is true this tract is first found in the sensory column of the cord, but it subsequently lies in the motor region and is reinforced by motor cells. It probably consists of mixed fibres.

Stieda's and Köppen's observations upon the brain of Rana. It is difficult to give a critical review of Stieda's results, first, because from the limitations

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[1] I regret that none of the figures represent the relations of this tract to the Müllerian fibres with perfect accuracy. I am not sure that this tract can be clearly distinguished at the level of the 12th pair, as represented in Fig. 11.

of his histological methods his observations were fragmentary; second, because the brains of *Rana* and *Cryptobranchus* differ so widely.

Stieda designates as the nucleus centralis the group of sensory cells in the floor of the ventricle on either side of the sulcus centralis. I cannot support his suggestion that this nucleus is in any way connected with the Vagus roots. As he has confused the Facial and Auditory nerves and nuclei, his results, so far as these are concerned, are invalidated.

Köppen, profiting by the Weigert method, has given a much more precise and full description of the *medulla,* although his description of the Facial-Trigeminal system is very incomplete. 1. He recognizes the posterior longitudinal fasciculus, p. 6, and its probable connection with the Auditory nerve. This adjoins the dorsal part of the Müllerian fibre system, the ventral part of which, after crossing, disappears, as in *Cryptobranchus,* in the great ganglion cells opposite the exit of the Auditory nerve. 2. He describes also, p. 7, a nucleus of large cells as probably belonging to the Auditory; this corresponds to my pale ganglion, 8*n*, Fig. 14. At this point he fails to distinguish between the Facial and Auditory elements, for his dorsal Auditory root, p. 9, is probably the main portion of the Facial. This error, if error it be, arises from the fact that he expects to find the facial a purely motor nerve, p. 10. 3. The Trigeminus, p. 10, is traced to two ascending bundles, and a large motor nucleus. No sensory nucleus or mesencephalic descending bundle is described. 4. Köppen makes many important additions to the higher encephalic tracts and nuclei in *Rana,* among which are the Auditory tract to the cerebellum, p. 13; the interpeduncular ganglion, p. 16; the posterior longitudinal fasciculus to the region of the III nucleus, p. 17; the infundibular tract to the hemispheres; the mesencephalic and diencephalic tracts from the medulla, and the tracts from these segments to the hemispheres, pp. 30–31; the ganglion habenulæ and Meynert's bundle. The hemispheres receive no direct sensory tracts from the medulla; these tracts first enter the optic lobes and thalami, from which fresh tracts rise to the hemispheres. With this conclusion, p. 31, I am inclined to agree, although I do not think it is absolutely demonstrated. 5. I differ from Köppen in his attempt to homologize the encephalic with the lower segments, p. 26; also, as I understand him, p. 30, he does not describe any direct motor tract, (basal forebrain bundle), to the anterior columns of the medulla. The agreement, in respect to the tracts mentioned above, is strongly confirmatory, since my observations were made independently, and the conclusions reached before the receipt of his paper.

6°. Methods. The methods of hardening and staining have been fully described in previous papers. The best staining results have been obtained with long *in toto* immersion in Ammonia Carmine. I have had the advantage, for purposes of comparison, of a full series of the brain of *Salamandra,* prepared after Weigert's Method by my assistant, Mr. J. Warne Phillips, in Dr. Edinger's laboratory. I find that brilliant as these preparations are, the carmine series give a fuller and more reliable field of observation. The late Professor Gudden, of Munich, told me, after long experience, that he had reached the same conclusion, and this is also the opinion of Dr. Spitzka of New York.

EXPLANATION OF PLATES IV.-VI.

INDEX LETTERS TO ALL FIGURES.

The Encephalic Segments. — *Rh,* rhinencephalon, olfactory lobes. *Pr,* prosencephalon, cerebral hemispheres. *Di,* diencephalon, optic thalami. *Me,* mesencephalon, optic lobes. *Mt,* metencephalon, medulla oblongata.

Ventricles. — *a,* aula, ventriculus communis. *prc,* prosocœle. *p,* porta, foramen of Monro. *di,* diacœle. *msc,* mesocœle. *mtc,* metacœle. *inf,* infundibulum.

The Commissures. — *cto,* commissure of the tectum opticum. *cal,* corpus callosum; *cal',* posterior division of same, (? comm. cornu ammonis). *icm,* inferior infundibular commissure. *pcs,* posterior commissure. *prcs,* anterior commissure. *scm,* superior infundibular. *scs,* superior commissure.

Cranial Nerves. — I.-IV., as usual. V.', opthalmic; V.'', superior maxillary; V.''', inferior maxillary, divisions of the Trigeminal. VII.', Facial, upper bundle, joining the Gasserian Ganglion; VII.'', lower bundle joining the Auditory and sending off the *R. mentalis* and *R. jugularis.* VIII., Auditory. IX., Glossopharyngeus. X., Vagus. XI., (XII.), Hypoglossal.

The Encephalic Nerve Tracts. — *bpt,* basal prosencephalic tract. *bft,* same. *cblt,* cerebellar tract entering optic lobes. *cblt',* cerebellar tract from medulla oblongata. *dst,* sensory (?) tract to optic thalamus. *dst',* sensory tract from optic thalamus to hemispheres. *fc,* fasciculus communis. *fs,* fasciculus solitarius. *it,* tract from infundibular lobes to hemispheres. *mst,* sensory (?) tract to mesencephalon. *mst',* sensory tract from mesencephalon to hemispheres. *mb,* Meynert's bundle. *plf,* posterior longitudinal fasciculus.

Cranial Nerve Tracts. Trigeminus. — 5 *t',* the ascending tract. 5 $t^{1\text{-}2}$, the ascending tract reinforced by the tract from the great motor nucleus. 5 t^{3}, the sensory tract. 5 t^{4}, the descending (mesencephalic) tract. 5 t^{5}, the encephalic tract.

Facialis. — 7 *tl,* lower, motor (?) tract. 7 *tu,* upper, sensory tract. 7 ?, encephalic tract.

Acusticus. — 8 *t,* tract from the pale nucleus, and special sensory nucleus. 8 ?, cerebellar tract.

Glossopharyngeus. — 9 *t,* sensory tract.

The Encephalic and Cranial Nerve Nuclei. — 3 *n,* 3 *n',* upper and lower Oculomotor nuclei. 4 *n,* Trochlearis, motor nucleus. 5 *sn,* dorsal sensory nucleus of Trigeminus. 5 *mn,* ventral motor ditto. 5 *n,* mesencephalic nucleus of Trigeminus. 6 *n,* Abducens nucleus. 7 *sn,* and *mn,* dorsal sensory and lateral motor nuclei of Facialis. 8 *n,* Auditory nucleus of pale ganglion cells. 8 *sn,* Auditory nucleus of small sensory cells. 9 *mn,* lateral motor nucleus ot Glossopharyngeus. 9 *sn,* dorsal sensory nucleus of same. 9 *n,* ventral motor nucleus of same. 10 *n,* ventral motor nucleus of Vagus. *cbl.n,* cerebellar nucleus. *cs,* corpus striatum. *dn,* superior diencephalic nucleus. *dn',* inferior diencephalic nucleus. *fcn,* nucleus of fasciculus communis. *gc,* nucleus of large ganglion cells opposite Auditory root. *gh,* ganglion habenulæ. *gi,* interpeduncular ganglion. *nc,* nucleus centralis. *nm,* nucleus magnus. *np,* pale nucleus.

EXPLANATION OF PLATE IV.

The figures of the brains were outlined with a Nachêt camera lucida, and the surface details inserted as studied in different lights. The vertical sections (Figs. 7–9) are reconstructions of the actual median plane by composition of a number of sections.

FIGURE 1. Brain of *Siredon* (*Axolotl*) *mexicanus*. The species is somewhat uncertain. Viewed from above. Enlarged 4½ diameters.

FIG. 2. Brain of *Necturus* (*Menobranchus*) *maculosus*. Viewed from above. Enlarged 4½ diameters.

FIGS. 3 AND 4. Brain of *Proteus anguineus*. Viewed from below and above. Enlarged 4½ diameters.

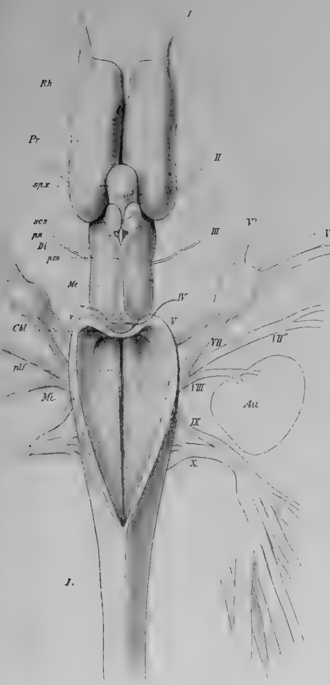
FIG. 5. Brain of *Siren lacertina*. Viewed from above. Enlarged 4½ diameters.

FIG. 6. Medulla oblongata of *Cryptobranchus alleghaniensis*. Viewed upon the ventral surface, showing the exit of the cranial nerves, as reconstructed from transverse sections.

FIG. 7. Sagittal section of the brain of *Cryptobranchus*, through an ideal median plane, as reconstructed from sagittal sections.

FIG. 8. Sagittal section of the brain of *Necturus*, drawn as above.

FIG. 9. Sagittal section of the brain of *Rana*, drawn as above.



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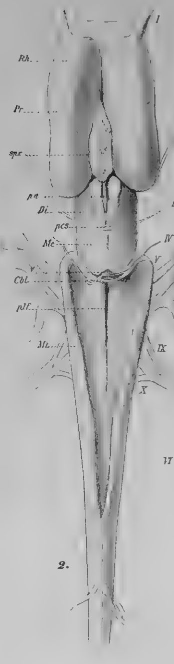

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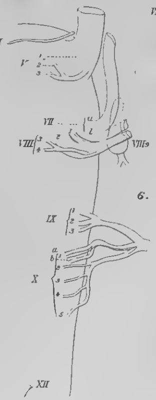

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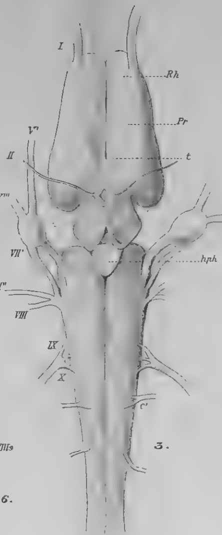

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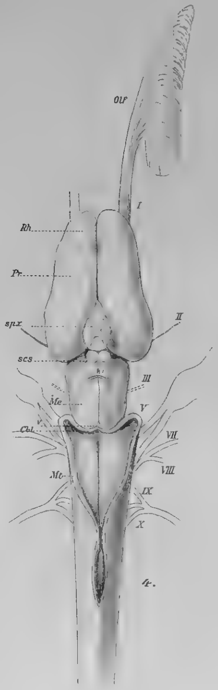

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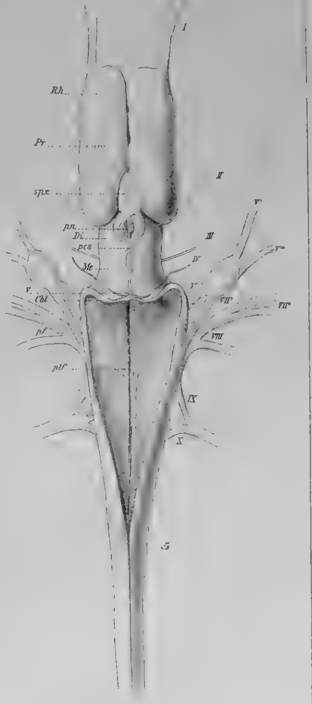

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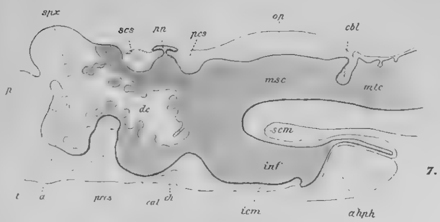

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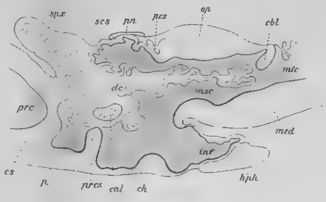

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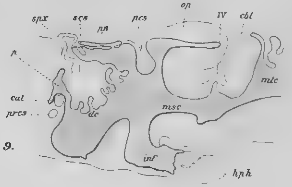

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H.F.O. and R. Weber del.

B. Meisel lith Boston

EXPLANATION OF PLATE V.

FIGS. 10 TO 18. A series of transverse sections through the medulla oblongata of *Cryptobranchus alleghaniensis*, from the exit of the 12th pair (XI.) to the exit of the 6th pair, enlarged about forty diameters. For the sake of clearness only a few cells of each nucleus are represented, and these are drawn to scale. Most of the sensory and motor cells of the *Central* region are also omitted. The cell area is represented in dark gray. The contours of the tracts are usually well defined, but have been exaggerated in several figures. The level of the transaction represented by each of these figures is indicated in the diagram, Fig. 21 (— f. 10 — f. 18).

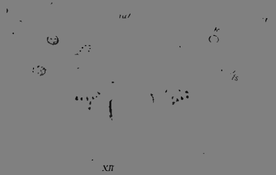
FIG. 19. Sagittal section through the tectum opticum (*opt*) and cerebellum of *Cryptobranchus*. This shows the posterior portion of the great trigeminal nucleus; the small nucleus of cells in the cerebellum, *cbln*; the decussating cerebellar tracts, *cblt*; and the descending trigeminus, $5\,t^4$. 19*a* represents the cells of the trigeminal nucleus enlarged.

FIGS. 20 AND 20*a*. Vertical and horizontal sections through the oculo-motor nucleus, as seen under a Zeiss D; camera drawing.

FIG. 21. Diagram of the cranial nerve nuclei of *Cryptobranchus*, as reconstructed from transverse and horizontal sections. The relative location of the 3d–6th nuclei, posterior commissure, Meynert's bundle, the main exits of the nerves and the posterior longitudinal fasciculus are all determined with the camera. The nuclei of the 5th–10th pairs are reconstructed from transverse sections. They overlap each other less closely than in nature. The *sensory* nuclei are distinguished by oblique lines; the *motor* nuclei by transverse lines; the pale ganglion nucleus of the Auditory by crossed lines. The external row, 5, 7, 9, are the dorsal sensory nuclei. The internal row, 5, 9, 10, are the ventral motor nuclei. The external intermediate, 7, 9, are the doubtful lateral motor nuclei, adjoining 8 and *f*, the lateral sensory nuclei.

The fasciculus communis f, f''' is represented in gray to indicate that it is apparently forming new bundles from a continuous sensory nucleus.

The dotted lines represent the descending, *i.e.* encephalic, tracts. The heavy lines, the descending trigeminus and the posterior longitudinal fasciculus. The pale lines, the tracts springing from the special nuclei.



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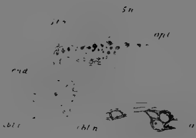

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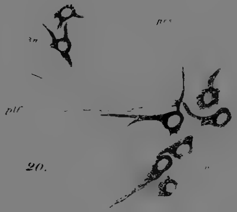

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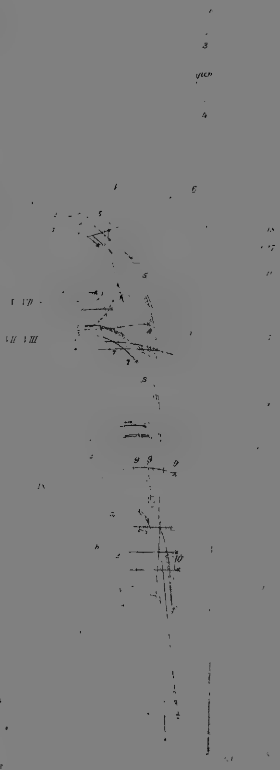

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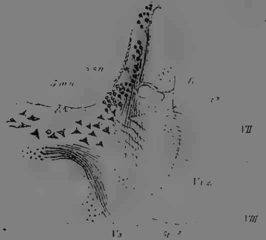

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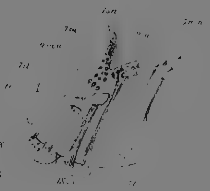

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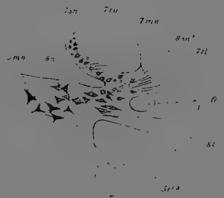

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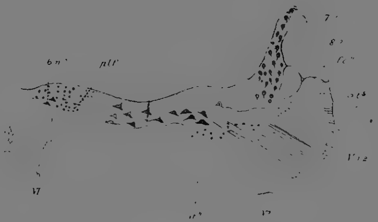

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EXPLANATION OF PLATE VI.

The figures, with the exception of Fig. 30, are composites of three or four sections, and thus present a larger number of fibres than are in view in any single plane.

FIGS. 24 AND 25. Sections of *Cryptobranchus.* The former is through the outer regions of the encephalic segments; the latter is just external to the mass of central gray matter.

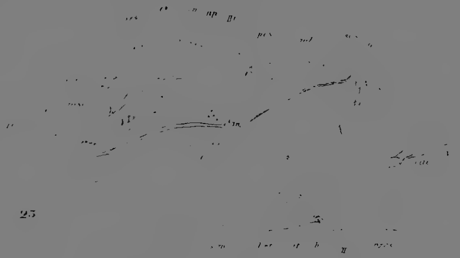
FIG. 25. Transverse section of the mesencephalon of *Necturus* at the exit of the 3d pair of nerves, 25*a*. An enlarged actual section of the roof showing the connection of the descending trigeminal fibres with the cells of the optic tract. Camera drawing.

FIG. 26. Sagittal section through the outer portion of the left optic lobe of *Rana.* Eight layers may be distinguished as follows: 1, the outer fibre layer which contains the superior portion of the optic tract; 2, the layer of scattered nerve cells; 3, the second fibre layer penetrated by the inferior portion of the optic tract; 4, the second layer of compact nerve cells; 5, the third fibre layer; 6, the third fine layer of compact nerve cells; 7, the fourth fibre layer; 8, the ependyma. The outer fibre layer is mostly homogeneous. The second and third fibre layers are traversed by radiating fibres which connect the three cell-layers.

FIGS. 27 TO 29. Outer, median, and inner sagittal sections of the brain of *Rana.* The latter is slightly external to the central gray substance.

FIG. 30. Sagittal section of the brain of *Amphiuma.* The dotted lines represent the actual contours in the lateral plane of this section. The plain lines represent the contours of the median plane.

FIG. 31. A diagram of the main encephalic tracts and nuclei as observed in the Urodele Amphibia, a composite of the figures upon Plates V. and VI. The distribution of the tracts is a matter of actual observation. The sensory or motor character of the tracts is in a measure inferential. *S,* main sensory tract. *M,* main motor tract.



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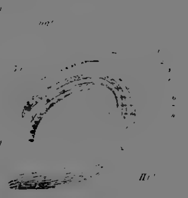

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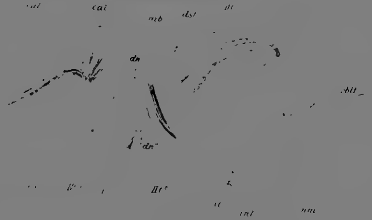

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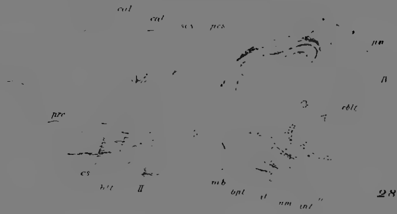

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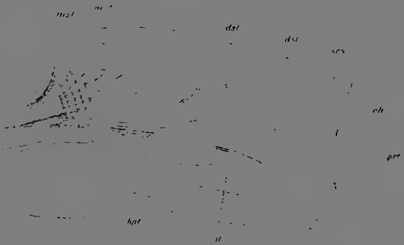

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STUDIES ON THE EYES OF ARTHROPODS.

WILLIAM PATTEN, PH.D.

II. Eyes of Acilius.

A COMPARATIVE study of the eyes offers, in my opinion, a promising field for the determination of the relationship between the different groups of Arthropods. To determine these relationships it is necessary to understand, (1) variations in the structure of the eyes, (2) their topography, and (3) the position and structure of the optic ganglia.

It is necessary first of all to obtain a thorough knowledge of some typical form. Comparison is then easy, for the problems solved in one case are already solved in others, while those left unsolved will torment the investigator in every succeeding study.

In following the development of the eyes of *Acilius* I was forced to consider their relation, and that of the optic ganglia, to the brain. This required a careful examination of the development of the whole head. But finding it impossible to treat of the head without considering the rest of the body, I decided to confine my attention to the eyes and optic ganglia. Some of the figures, however, will also serve to illustrate certain points in the "Development of Acilius," which will be the title of the paper I hope to publish in one of the next numbers of this Journal. I shall reserve till then a discussion of the relations which the eyes and optic ganglia bear to the head of Arthropods.

I. TOPOGRAPHICAL RELATIONS OF OPTIC PLATE AND OPTIC GANGLION TO CEPHALIC LOBES AND BRAIN.

The earliest stages of the eyes and optic ganglia are found before the appendages have made their appearance. The distal edge of each cephalic lobe is thickened to form the semicircular *optic plate*, distinguished on surface views by its opacity and the small size of its nuclei. The large ectoderm cells, on the inner edge of the plate, are infolded, forming an almost semicircular depression, the beginning of the invagination which subsequently gives rise to a large part of the optic ganglion.

The optic plate is soon divided into three segments (Pl. VII., Fig. 1). The anterior, or first segment, forms a kind of corner to the anterior, lateral edge of the cephalic lobe; the second occupies the median and larger part of the optic plate, with which its long axis is parallel; and the third forms the posterior edge of the cephalic lobes, its long axis being nearly at right angles to that of the second segment. The distal edge, and in some cases the whole, of the plate is buried in the yolk; it is then necessary, if one desires to obtain surface views, to cautiously pick the yolk away from the lobes with needles.

The ganglionic invagination soon deepens, and also shows traces of a differentiation into three parts, one of which lies on the inner edge of each segment of the optic plate (Fig. 1 $o.g.^{1-3}$).

From the median part of the cephalic lobes rise three pairs of thickenings, one pair opposite each ganglionic segment. They form the rudiments of the brain (Figs. 1–3, b^{1-3}), and appear to be direct continuations of the segments of the ventral chord.

The embryo is divided by transverse folds into a certain number of post-oral terga, *the first three of which are gradually drawn towards, and united with, the cephalic lobes.* The line surrounding the optic plate, after the rupture of the embryonic membranes, is not the old boundary of the cephalic lobes, but a new formation, which includes the cephalic lobes and the terga of the first three post-oral segments (Pl. VIII., Fig. 8). The indentation, $tg.^{5-7}$, appears in surface views like a newly developed eye. It was quite enigmatical until a more careful study showed it to be the boundary between the posterior edge of the cephalic lobes and the terga of the first three post-oral segments. The last trace of this fold disappears soon after the stage shown in Fig. 8.

While the optic plate is still in its semicircular form, two areas in each segment become visible in surface views, on account of the peculiar arrangement of their nuclei. From each of these areas is developed an ocellus, which I have numbered in the way shown in the plates. The growth of the embryo gradually forces the median, ventral part of the germ band forwards, leaving, as it were, the distal ends of the cephalic lobes behind, so that they are turned first posteriorly and then ventrally. This makes the ventral row of eyes assume an anterior and then a dorsal position, and also brings the first segment behind the other two (Figs. 1, 4, 8, 9, 10).

After the revolution of the embryo, eyes II. and IV. come to lie close together behind eye I., and eye VI. is wedged in between eyes I. and III. A comparison of the figures will show better than any description how the embryonic eyes develop into those of the larvæ. The reader who would follow the rather confusing changes in the optic ganglion and its nerves must have a clear mental picture of the way in which the eyes shift their position.

When the optic plate first appears, it is conspicuous on account of its dark color. Sections show that at this period it is composed of a single layer of closely packed cells, whose small, darkly stained nuclei are crowded together several rows deep. The nuclei in the brain and optic ganglion are large and spherical, and do not stain deeply. The optic plate is everywhere sharply demarked from the surrounding tissues, except on its distal, inner edge, where there is a gradual transition to the wall of the optic invagination (Pl. IX., Fig. 20, *p.n.*).

Occasionally one finds a large nucleus near certain clear areas of which we shall speak later. They are homogeneous and deeply stained, and, in some cases, contain a nuclear spindle (Pl. IX., Figs. 20 and 21; Pl. XI., Figs. 60 and 61). They often appeared like naked nuclei projecting above the level surface of the optic plate. I do not remember seeing them anywhere except in those parts of the optic plate that give rise to the eyes.

EYE V.

We shall now describe, by means of sections and surface views, the development of each eye. It is only with the aid of these surface views that the earliest stages can be understood.

While the optic plate is but a semicircular thickening of the lateral edges of the cephalic lobes, eye V. appears as a round, dark spot, surrounded by a clear area, on the inner edge of the third segment (Figs. 1–3, *V.*). During the earliest stages, the central area is conspicuous on account of its size and dark color. Later, it is reduced to a narrow band composed of a double row of darkly stained nuclei.

A large nucleus appears in the central area, which increases in size as the latter becomes more and more elongated. It finally lies in about the middle of the dark area, between the two rows of nuclei (Fig. 6*a*).

The explanation of the surface views will be found on examining Pl. XI., Figs. 61–63, which represent sections through the eye while in the stages shown in Figs. 2, 4, and 6. It will be seen that the median, dark area corresponds to a broad elevation of the ectoderm, in which the nuclei are crowded toward the surface, the superficial ones being slightly stained by my method of preparing surface views. On either side of the ridge the nuclei are deeply situated and unstained, hence the clear area surrounding the ridge. In order to save time and expense I have, in most instances, indicated the surface nuclei by shading. The elevation gradually narrows and sinks to the level of the surrounding ectoderm, or even below it, until it is reduced to a narrow ridge with a shallow furrow along its summit. On either side of this furrow a single layer of nuclei extends to the surface of the ridge (Fig. 63). The most superficial of these nuclei are the ones which appear as a double row in surface views.

The clear band surrounding the dark area soon loses its regular outline and becomes distinctly four-lobed (Figs. 6 and 6*a*), each lobe being a depression in the ectoderm, beneath which the nuclei are arranged much like those in the whole ocellus at a later period (compare Figs. 62 and 64), or like those found in separate sense organs. Each depression represents, in fact, a distinct sense organ, or eye. They form the greater part of the retina of the future ocellus. The two posterior pits are deeper and larger than the anterior ones, hence the whole clear area is somewhat conical.

There is a dark spot, with a clear area surrounding it, on the anterior dorsal edge, and one on the median ventral edge of the clear area (Fig. 6*a*, 5 *and* 6). These clear spots resemble the main clear area, with which they are continuous, in structure and general appearance.

All these clear areas and dark spots form one thickened patch of ectoderm, which soon becomes more regularly oval, and the pits and the dark streak disappear. The whole organ is being invaginated to form the floor of the deep depression seen in

Figs. 7, 7*a*, and 8*a*. The opening of the depression, or optic cup, is pear-shaped, the broad, posterior end indicating the position of the two posterior pits, which are the last to be enclosed on account of their greater size.

During the earliest stages a striated cuticular thickening appears over each pit of the clear area, the striations being apparently continuations of those in the clear space beneath (Pl. XI., Fig. 61, *ct.*). It terminates abruptly at the periphery of the central dark area, and as the latter decreases in width the edges of the cuticular thickening on either side of it come closer together, until only a narrow space, the median furrow, is left between them (Fig. 63, *m. f.*). When the whole sensory patch begins to invaginate, these edges unite, and the cuticula forms a continuous layer over the floor of the optic cup (Fig. 64).

From this cuticular layer the retinal rods are developed. In the stage shown in Figs. 62 and 63 it is apparently composed of stiff cilia, each of which has a minute, bead-like swelling at its base, while their outer ends are covered with a delicate membrane, which, in Fig. 64, is detached from the fibrous cuticula to form a delicate cover over the mouth of the optic cup.

The only evidence of the compound nature of the optic cup, after the disappearance of the median dark area, and the separate pits and cuticular thickenings, is to be seen in the optic nerve. In Figs. 62 and 64, the sections are at right angles to the line along which was developed the median ridge; consequently one part of the nerve goes to the ventral, and the other to the dorsal half of the clear area (Fig. 6*a*). A longitudinal, horizontal section would show that each half of the optic nerve was divided into two much less distinct parts, one going to the anterior pit, and one to the posterior. *Hence the optic nerve is composed of four, and perhaps more, nerve bundles. This fact, together with the presence of four pits in the clear area, the cuticular thickenings over each pit, and finally the constant and remarkable arrangement of the nuclei beneath each thickening, shows clearly that this ocellus is composed of at least four primitive optic pits.* The two clear areas, each with a dark spot in the centre, found on the dorsal and ventral side of the eye in Fig. 6*a*, form the two bands of inverted cells in the future ocellus. These patches resemble, both in sections and in surface views, the clear and dark areas in the centre of the eye, and there is the same absence of nuclei beneath their cuticular thickenings. I have not been able, however, to detect any evidence that they are supplied with separate bundles of nerve fibres, but this will not seem strange, when we consider their small size and transitory nature. I see no reason why they, like the sensory patches composing the centre of the eye, should not be regarded as remnants of distinct sense organs. This supposition will appear in a more favorable light, perhaps, when we consider similar patches connected with the rudiments of the remaining eyes.

The sensory spots, or primitive eyes, of which the clear area is composed, are comparable with those on the mantle edge of *Arca*, as described by me in "Eyes of Molluscs and Arthropods" (Pl. 30, Fig. 42). It was there shown that some of the eyes arose as simple, pit-like depressions covered by cuticular thickenings, into which the everywhere-present intercellular nerve fibres extended, producing the appearance of vertical striations. Such eyes contain the lowest stages in the development of visual rods. In more specialized eyes it was shown that the cuticula had broken up into blocks, one overlying each cell. The nerve fibres arrange themselves around these blocks in various ways, and a true retinal rod is the result.

In the embryos of *Acilius*, the eye passes through the stages permanently represented on the mantle edge of Molluscs, for the cuticular thickening over each optic pit, at first fuzzy and non-refractive, soon changes into a layer of stiff and refractive cilia-like bodies, which finally form a dense and almost homogeneous cuticular layer. As soon as the retinal cells become distinctly outlined, this cuticula breaks up into a number of minute rods, two being formed over each retinophora. The arrangement of the nerve fibres about the rods will be described later. It is sufficient for the present to state that it corresponds in almost every particular with that found in the more highly developed rods of Molluscs. Moreover, in *Acilius* as in Molluscs the cuticula overlying the sensory cells is divided into two layers: a thin outer membrane devoid of nerve fibres, *the corneal cuticula;* and a thicker, inner one, the *retinidial cuticula*, so called because it contains nerve ramifications, and gives rise to the rods. The development of the rods in Acilius, therefore, is in perfect harmony with the view concerning the phylogenetic development of visual rods, which I formulated from a study of the eyes of Molluscs. The harmony will be more perfect, when we consider the nerve endings, and compare the theory advanced to explain the intercellular nature of these nerve-ends with the origin of ganglion-cells.

THE LARGE NUCLEUS of eye V., which is wedge-shaped and filled with dark granules, is at first situated very near the surface, and usually projects some distance above it. It remains in this position until the dark area begins to disappear (Fig. 6). Sections of the eye after this period show that as the sensory patch is invaginated, the large nucleus withdraws from the surface and takes up a position among the other nuclei in the middle of the optic cup. I have not been able to find it after the stage represented in Fig. 65, but I presume it remains practically unchanged throughout larval life. Such is undoubtedly the case with similar nuclei in eyes I. and IV.

The mouth of the optic cup is gradually reduced to a narrow slit, the long axis of which is parallel with the median ridge, above which the thickened lips finally unite (Fig. 66). Although there is no duplication to form separate layers, there are three regions that can be identified as the three layers of the future eye. The closed lips of the optic cup are composed of radiating cells with deeply situated nuclei. Those over the centre of the eye are bent at right angles, their attenuated inner ends extending as far as the basement membrane on the sides of the eye. These bent cells, which give rise to the corneagen, are connected by intermediate forms with the short, straight ones of the surrounding ectoderm.

THE CORNEAGEN increases rapidly in thickness, and at the same time all its nuclei, except those on the periphery, become so indistinct that they seem to have disappeared. Even in very successful preparations it is only here and there that one can see, at the inner ends of the corneagen cells, the small, round nuclei with sufficient clearness to preclude all doubt as to their identity. In most cases, they are reduced to clear, colorless sacs, which can be recognized as nuclei only by a careful study of their position and the transitional stages by which they are connected with the undoubted nuclei of the periphery. In the full-grown larva, the corneagen cells are large and wedge-shaped, with distinct walls surrounding the coarsely granular, sometimes flocculent, cell contents.

THE IRIS contains pigment granules, varying in size from minute specks to large spherules, as large, or larger than the neighboring nuclei. The spherules are usually brown and contain a minute black dot in the centre. They are most abundant on the inner edge of the iris. The small granules are usually dull black.

When the pigment is dissolved by acids or alkalies, the iris-cells are left quite empty and colorless, so that even after the removal of the pigment it is easy to distinguish them from the adjacent non-pigmentiferous cells of the corneagen, for the latter are filled with deeply stained granular protoplasm.

THE LENS. — Immediately after the rupture of the embryonic membranes, and while the optic cups are still wide open, a delicate pellicle is formed on the outer surface of the hypoderm. This pellicle, which gives rise to the cuticula, usually covers the mouth of the optic cup (Fig. 65), but no part of the membrane is enclosed in the cavity of the eye, at least I have never been able to discover any traces of it in the newly formed vesicles. After the optic cups close, the pellicle is thrown into loose folds over the whole body, and is then cast off. At the same time, a new pellicle is formed beneath the old one, which is still present but widely separated from the surface of the embryo. The new skin is first visible above the unmodified hypodermis. Over the surface of the newly formed corneagen, it first appears as a thick, vertically striated layer much like that which gives rise to the rods (Fig. 67).

Soon after this stage, the corneagen cells increase in height and form an elevated cap to the optic vesicle, with a circular depression around it. The second pellicle becomes refringent and is thrown into minute folds everywhere except over the eye. There the non-refringent layer is transformed into a disc of clear, refractive cuticula (Fig. 68).

After hatching, the dome-shaped layer of cuticula over the eye increases in density and thickness until it forms the strongly biconvex lens of the adult, the curvature of the inner surface being much greater than that of the outer.

In the full-grown larvæ the cuticula surrounding the lens is composed of two layers: a dark brown, or quite black, outer one;

and a clear, transparent, tangentially striated inner one. The whole layer is divided into thick, imbricating scales, the tips of which are raised a little above the surface, producing according to the location either a notched, wavy, or serrated outline. The lens is composed of the same kind of scales, but they are thinner and higher, and concave like the leaves of an onion. In most cases they overlie one another so closely, and their outer surfaces conform so accurately with the general curvature of the lens, that it is difficult to distinguish their boundaries. But it sometimes happens that their outer edges curl upwards, producing a serrated outline to the lens, like that in Fig. 70.

THE RETINA.—The thick cuticular layer upon the floor of the optic cup is finally interrupted by a second median ridge, which appears in exactly the same place as that occupied by the first. It is formed by two rows of cells, the enlarged, projecting ends of which are bent so that the tips of all the cells in one row face the tips of those in the other (Figs. 66–70). At the tip of each cell is a minute rod, which at first sight might appear to be a product of the lateral wall of the cell; but this is not the case. *These rods are terminal and horizontal,* as we can see from the shape of the cells, and from a comparison with other eyes, where the homologous cells and their rods are much larger and can be more conveniently studied.

After the closure of the optic vesicle, some of the cells near the inner surface of the corneagen are distinguished by their large, deeply stained nuclei. The horizontal ends of these cells, which ultimately give rise to the *outer wall of the optic vesicle,* are frequently broken into loose, ill-defined, granular masses (Fig. 67, *o. w.*).

The innermost portion of the optic cup is composed of retinal cells, the greater number of which are placed so that their outer ends are at right angles to the median, vertical plane of the eye. Their rods are therefore horizontal, and those on opposite halves of the eye face one another. Only a few retinal cells on either side of the ridge are upright and parallel with the optic axis. The free ends of the cells which form the outer wall of the optic vesicle are finally bent inwards, and thus completely inverted (Figs. 68 and 69, *o. w.*); *at the same time they become more sharply outlined, and well-defined rods are formed at their tips.*

The ends of the peripheral retinal cells soon begin to draw away from the median plane of the eye, the cavity of the optic vesicle disappears (Figs. 67–70), the layer of rods becomes flattened out, and all the retinal cells and rods assume an upright position, except those of the median ridge.

THE RETINOPHORÆ. — I have shown that in Molluscs, the essential elements of the retina were colorless cells, bearing double rods, and containing two nuclei and an axial nerve fibre. These cells, or retinophoræ, I maintained were formed by the fusion of two rod-bearing cells, in one of which the nucleus degenerates. The nerve fibres between the two cells come to lie in the centre of the double one, to form its axial nerve. Each cell retains its own rod, hence the double rods of the retinophoræ. Resting on these facts, and upon the supposition that the primitive nerve fibres were intercellular, I maintained that when sensory cells were found with axial nerves and traces of two nuclei, they should be classed as retinophoræ, and must have arisen in the manner described above. In the Arthropods, I found the crystalline-cone cells had characteristics which led me to consider them as modified retinophoræ. My supposition was based on the expectation of finding in the ocelli of Arthropods, retinal cells, either very similar to the retinophoræ of Molluscs or intermediate between them and the crystalline-cone cells. A comparison of the text, and the diagrammatic figures in Plate 32 of "Eyes of Molluscs and Arthropods," will show that I expected to find the intermediate forms of retinophoræ in the posterior eyes of Spiders, and in the eyes of Scorpions and Limulus, while the Molluscan type might be looked for in the ocelli of Insects and Myriapods, and in the anterior eyes of Spiders.

The retinophoræ now to be described, show that these expectations have been realized, at least, as far as the ocelli of larval Insects are concerned.

The first stages in the formation of the retinophoræ are found during the open-cup period of the eye. In Figs. 63 and 64, we see that the inner wall of the optic cup is closely packed with five or six rows of deeply stained nuclei; all of which are alike except the median one already described, and those belonging to a few large ganglionic ones, to be described later. In the next stage (Fig. 65), they appear to be greatly reduced in numbers. This change is due to the fact that *the cells are uniting* *in twos to form retinophoræ; one half of the nuclei have degenerated into the non-stainable, apical nuclei of the retinophoræ, the other half form the deeply stained basal ones.* The first stages of this process are necessarily difficult to follow, since both kinds of nuclei are mingled in one confused mass, where one can distinguish only uncertain differences in the color and size of the nuclei. But during, and after, the stage shown in Fig. 65, they begin to arrange themselves in two layers, most of the non-stainable nuclei lying above the normal ones. I fully expected to find in the embryos and young larvæ, that the second nuclei would be, if not readily visible, at least much more distinct than in the adult. But my observations on Acilius do not support this expectation. Even as early as the stage shown in Fig. 65, the second nuclei are as faintly stained, and as difficult to see in section, as those of the adult eye. *This fact may indicate that the double cells are not the result of specialization in highly developed eyes, but that they are very ancient structures which we should expect to find in the simplest, as well as in the most specialized, sense organs.*

The large nuclei of the retinophoræ arrange themselves in a single row on the inner surface of the retina. The position of the smaller nuclei varies somewhat; sometimes they are just above the large ones, sometimes just below the inner ends of the rods, but usually about half way between these two points.

During the stage shown in Fig. 64, and in younger stages it is impossible to distinguish the shape of the retinophoræ as the cell walls are indistinct or absent, owing to the rapid division that is going on. In Fig. 65 the tissues are less dense, and the retinophoræ can be seen as spindle-shaped cells drawn out to a point at either end. The clear striated area beneath the cuticular thickening is composed of the rod-like, or fibrous, outer ends of the retinal cells mixed with nerve fibres. They are soon transformed into strongly bent columnar cells.

Although it is sometimes possible to see the *secondary nuclei of the retinophoræ* in sections, it is much easier to study their position and structure in isolated cells. It is also in this way that one obtains the most conclusive evidence of the double nature of the retinophoræ, for by carefully turning and rolling them, either before or after the removal of the pigment, one always obtains one view which shows that they are composed of two twisted cells (Pl. X., Fig. 58, *a. b.*). The inner end of one of the component cells is swollen, and contains a round, fairly well-stained nucleus; the outer end is quite small, and its contracted tip terminates in a flattened rod. The second cell is perhaps a little smaller; its broad outer end contains a very faintly stained nucleus, and also terminates in a flattened rod. Its opposite extremity fuses with the first cell to form the inward prolongation of the retinophora. Both cells supplement each other's irregularities so perfectly that a symmetrical and apparently single cell is the result (Figs. 57*a* and 58*a*).

When the cells are pigmented, the position of the second nucleus is often plainly indicated by a clear spot, but it would not be possible to identify it as a nucleus until the pigment had been removed.

The outer ends of the two component cells of the retinophoræ are widely divergent (Fig. 58, *g*). A similar condition occasionally obtains in *Arca* and *Haliotis*, and this fact affords excellent proof of the double nature of the retinophoræ.

Pigment. — Just after the rupture of the embryonic membranes, one can readily distinguish with the naked eye the bright red ocelli of the living embryos. The pigment of these stages is readily soluble in alcohol, the reddish-brown pigment found in the succeeding stages, much less so. It is the latter pigment that is first seen in sections, distributed in coarse granules through the iris. At about the same time, the outer ends of the retinal cells assume a diffuse reddish-brown color. This coloring matter was probably in distinct granules, and became diffuse through the action of the alcohol.

In the next stages, thin sections show a row of minute, pigmented blocks, arranged in pairs (Fig. 69). The blocks are cross sections of a pigmented collar surrounding the outer end of each cell.

In the fully developed eye, the pigment varies in color from brown to jet black, according to the method of preparation. Chromic acid, bichromate of potash, and Muller's fluid, partly dissolve the pigment, leaving it a light brown color. Picro-sulphuric acid has a similar, but much less effect. Eyes treated with alcohol alone contain great quantities of intensely black pigment, which in all stages is most abundant around the outer ends of the retinal cells.

A careful study of sections and isolated cells shows that the pigment is distributed in granules along the nerve fibres that cling to the walls of the retinophoræ. Toward the inner ends of the latter, the course of the external nerve fibres is often distinctly marked out by the pigment granules deposited upon them (Pl. X., Fig. 58). At the outer ends of the cells, the external nerves are straight and close together. Where there is little pigment, one can see that the granules are arranged in rows around each of these nerve fibres (Figs. 56 and 57). Usually, however, the pigment forms a continuous and uniform envelop around the outer ends of the cells, where it terminates abruptly, while the nerve fibres are continued onwards over the outer surface of the rods. If there is any pigment at all inside the cells, it must be deposited in a very thin layer in, or just beneath, the cell wall.

Just below the inner ends of the rods, cross sections show a mosaic of deeply pigmented, hexagonal blocks, from which we might conclude that here pigment was lodged inside the cell walls. But isolated cells show that pigment is deposited between the flattened and diverging ends of the two cells composing each retinophora; consequently we may not conclude from these solid blocks that the pigment is necessarily inside the retinophoræ. Again, when the larva had died a so-called natural death, or perhaps owing to other conditions of which I was ignorant, the pigment dissolved, staining the retinal cells dark brown throughout. Of course, in cross sections of such material, pigment would appear to be deposited inside the cell wall.

There is proof in the optic nerves, that some of the pigment, at least, is an intercellular product. For in sections and in loosened or isolated fibres, it is evident that the pigment granules are scattered about between the fibres, and not in them or in any distinct cells.

In the peripheral cells of the retina, and in those which constitute the outer wall of the optic vesicle, the pigment is coarser and less regularly arranged, resembling in general appearance that found in the iris. This fact enhances the deceptive appearance, already mentioned, that might lead one to think the retina was directly continuous with the iris and surrounding ectoderm. In the iris, the pigment is undoubtedly deposited inside the cell walls.

The Retinal Rods and Nerve Endings. — Since the retinophoræ are closely packed in the retina and the rods are on the periphery of their outer ends, it follows *that the rods of two neighboring retinophoræ are placed side by side so that they often appear like one rod, while those of the same retinophoræ are separated by a wide space.*

In eye V. (Fig. 54*a*) there is a beautiful mosaic of brilliantly refractive rods which form regular hexagonal figures, in the centre of which are the axial nerve fibres, and on opposite sides, the two rods belonging to the same retinophora. On two of the sides no rods are developed; only a thin membrane separates the adjoining hexagonal spaces at those points. Hence under a low magnifying power, the rods appear to be arranged in nearly parallel, zigzag lines.

It is impossible to see the axial nerves in the isolated retinophoræ, owing to the twisting of their component cells. But they are visible in cross sections as a single bundle in each retinophora. In the clear space between the two rods, the nerve breaks up into three or four fibres arranged in a plane parallel with the sides of the rods. In one of the spaces in Fig. 54*a*, they are at right angles to the normal position. Minute cross fibrillæ arise from these axial fibres, which probably penetrate the rods and unite with the external nerves. The cross fibrillæ constitute a *retinidium* similar to that of Pecten. In the latter, each pair of rods has completely fused to form a hollow cylinder containing a single axial nerve, from which arise radiating cross fibrillæ. In Acilius, the two rods are separate and flat, and the axial nerve is broken into smaller fibres placed in a row, so that a perfect radial arrangement of the fibrillæ is impossible.

The clear space between the rods is apparently filled with a non-refractive fluid in which the retinidial fibrillæ are suspended. It often contains fine granules, produced, I believe, by the coagulation or varicosities of the fibrillæ. The space is exactly like that in the centre of the rods of Pecten, and is undoubtedly an *intercellular one.*

That the cross fibrillæ penetrate the rods, I do not doubt, for they are marked with cross striæ continuous with the fibrillæ in the clear space. Neither do I see any reason to doubt that the fibrillæ in the clear space, as well as those in the rods, are equally essential elements. In Pecten, Acilius and Cephalopods, both the clear and the refractive parts of the rods are present. In the latter group, each retinal cell is probably double and has two rods separated by a clear space containing an axial nerve fibre. The rods are arranged in such a manner that four of them, each one from a different retinophora, come together to form compact groups, which Grenacher calls rhabdoms. Such rhabdoms, however, are different from those of the compound eye. They are more like the pairs of rods in Acilius. *In neither Acilius or Cephalopods have these groups of rods any morphological significance, for they are incidental results of the arrangement of rods in pairs, and this arrangement varies greatly in the different eyes of the same individual. The important fact to be borne in mind is that the pairs of rods belonging to one double cell are the units composing the layer of rods, and that the clear spaces containing the axial nerves form the centres of these units.*

In the rods of the convex eyes of *Arca*, in the crystalline cones of Arthropods, and in the rods of the Vertebrate eye, if I am right in my interpretation of these structures, there is no clear space between the two rods of the same retinophora. On the other hand, in *Mantis* and probably in most *Diptera*, the hard refractive part of the rods has disappeared, and the retinidial fibrillæ are suspended in a clear fluid. I think it is fair to conclude from these facts that *the essential element of the rods is the system of cross fibrillæ, or the retinidium, which may be suspended, in whole, or in part, either in a clear fluid or in a refractive and cuticula-like substance.*

In Acilius, the clear space between the rods is not covered by a cap of cuticular substance, as in Pecten, although in some cases I have clearly seen that it is covered by an extremely delicate, arched membrane, through which one of the axial nerve fibres projects, and, bending at right angles, unites with a similar fibre from an adjacent pair of rods (Figs. 57*a* and 59). Thus *axial-nerve loops* are formed much like those described in Pecten. In the latter case, the direction of the loops is more uniform than in Acilius, where they may be bent in any way, although there is a tendency to turn in some directions more than in others.

In Acilius, as in Molluscs, the retinophoræ are supplied with numerous pigmented nerve fibres that extend along the surface of the cells. At the outer ends of the cells, the fibres are straighter and slightly enlarged. The pigment stops at this place, but the fibres are continued onward, nearly parallel with one another, over the outer surface of the rods (Figs. 54 and 57).

The inner ends of the retinophoræ are continuous with coarse fibres composed of the inward prolongations of the external and axial nerves. There are in rare cases smaller bundles which, on their way to the more peripheral portion of the retina, pass over the inner third of some of the retinal cells at a sharp angle. Some of these fibres impinge upon a retinal cell near the primary nucleus and join the other external nerve fibres belonging to that cell. Such nerve fibres occasionally cling to isolated cells, and one might erroneously infer that they entered the cell opposite the nucleus.

About the time the clear area begins to be invaginated a number of deeply stained granules appear on the periphery of each ocellar thickening. They increase in size from the surface of the ectoderm inwards, and each one is surrounded by a clear area (Pl. XI., Figs. 63–66, and Pl. XIII., Figs. 82, 83, *ab. n.*). I have found similar products in the optic ganglia and in the ventral nerve chord. The manner in which they absorb coloring matter and their general appearance, together with the fact that they seem to be most abundant in tissues undergoing retrogressive changes, suggest that they may be degenerating nuclei.

EYE VI.

Eye VI. first appears in the posterior part of the third segment of the optic plate as a triangular depression, or clear area, the apex of which is directed dorsally and slightly forwards. On its ventral and posterior side, is a round dark area with a small clear spot in the centre. The depression soon becomes sickle-shaped, and finally circular, completely surrounding the dark area (Fig. 5*a*). In a little later stage (Fig. 6*a*) the furrows separating the eyes from each other have disappeared. The clear space is divided into two parts by a dark ridge, on the dorsal side of which is that part of the clear area that appeared first; it is now somewhat rhomboidal, contains a dark ridge composed of a double row of nuclei, and is divided into four pits, **1**, **2**, **3**, **4**. The ventral part of the eye is composed of an irregular clear area or depression, 6, deepest at the anterior end; it is connected with the dorsal part by a narrow furrow. The interpretation of these surface views is the same as that in eye V. The clear spaces represent slight surface depressions above a cup-shaped layer of deeply situated nuclei; the deeper the depression, the lighter it is in surface views; the darker parts are elevations where the nuclei come close to the surface (Pl. IX., Figs. 33 and 34, *VI.*). *It is evident that the structure of eye VI. is much like that of eye V, for besides the two peripheral spots it contains four separate pits, or sense organs, divided by a transverse ridge, containing a large median nucleus, into two parts.*

The whole sensory patch is soon changed into one uniformly clear area, which finally sinks below the surface to form the floor of a deep, circular-mouthed pit, or optic cup (Pl. X., Fig. 47). The nuclei no longer show by their arrangement that the patch is composed of separate groups of cells; the cuticular thickenings have united to form a uniform layer over the floor of the optic cup, and the median ridge has disappeared. I have not represented many sections of the earlier stages of eye VI., since with the exception of certain modifications readily understood from an examination of surface views, they are exactly like those of eye V.

There are considerable differences, however. between the later stages of the two eyes.

Just before, and during, the rupture of the embryonic membranes, the circular opening of the optic cup is converted into a transverse slit (Fig. 8*a*). As soon as the lips meet, their cells, by assuming different curvatures, form the *corneagen,* and the *outer wall of the optic vesicle.* On the anterior, dorsal side of the eye, the retina is curled over in such a way that it forms a part of the middle layer of the eye, although it does not extend far enough to meet a similar, but larger fold on the opposite side (Pl. XII., Figs. 72 and 73, *o. w.*). In the still later stages, it is folded down on to the rods, and is apparently continuous with a very delicate membrane, — in which I believe I have seen nuclei, but so small and indistinct as to leave me in some doubt, — that extends over the outer surface of the retina till it meets the mass of inverted cells on the opposite side (Fig. 74, *o. w.*).

When the sensory patch which formed the rudiment of eye

VI. was invaginated, the large clear spot, **6**, (Fig. 6*a*) came to lie on the ventral and posterior edge of the optic cup (Figs. 8 and 9, **6**). The cells of this sense organ become more and more bent and elongated as the cup closes, until they finally form a great tongue of cells projecting into the space between the corneagen and the retina (Figs. 71 and 72, *t. i. c.*). As it increases in length, it reduces the optic cavity to an oval space in the dorsal and anterior portion of the eye. The cavity is finally completely obliterated by the increase in length of the corneagen cells (Fig. 73).

The free ends of the cells belonging to the sixth sense organ bear inverted retinal rods, the same as those belonging to the upright ones, except that they are less regular in shape. Cross sections show that they are cylindrical with a clear central portion in which runs an axial nerve. The nuclei are at first situated near the free ends of the inverted cells, and are somewhat larger and differently stained from those in the remainder of the retina. When the pigment, which is scattered through these cells in coarse granules like that in the iris, is removed, they appear almost colorless, with here and there a few coarse granules.

Figs. 71–74, represent semi-transverse sections of the head, at right angles to the nerve *n* VI., Fig. 9, and parallel to the dark area of eyes III. and I., Fig. 8. When the sections are cut in most other cross planes, the retina appears perfectly symmetrical, its periphery being bent over and continuous with a very thin membrane in the same way that the left-hand edge is in Fig. 73. But if any of these cross sections should pass a little posterior to the median plane of the eye, the tongue of inverted retinophoræ would be seen, which might readily be mistaken for the cut end of a large number of nerve fibres, such as one finds in retinas with inverted cells, as in *Pecten* for example.

That we should have eyes with both upright and inverted retinophoræ, as in eye V., is remarkable and, so far as I know, without parallel. The condition in eye VI. is still more extraordinary, for there only a comparatively small cluster of rod-bearing cells is inverted, while all the rest are upright.

The sense organ, **5**, has either united with **1–4** to form the floor of the optic cup or disappeared; at any rate after invagination it is no longer distinguishable.

In eye V., the two groups of inverted cells arise from the dorsal and ventral sense organs, **5** and **6**, in the same way that the tongue of cells in eye VI. is derived from its ventral sense organ, **6**.

In the full-grown larva, the group of inverted cells is proportionally as well developed and conspicuous as in the younger stages. It is not shown in Fig. 75, since the section is a semi-transverse one passing through the optic nerve *n* VI., (Fig. 10*a*). The direction of the cells in the inverted sense organ is at right angles to that of the optic nerve, consequently it is impossible to cut a longitudinal section of both structures at once.

THE CORNEAGEN forms a thick cap to the eye, above which a lens is formed, as in eye V., from a striated layer of non-refractive cuticula.

In Fig. 73 there is a temporary indentation in the corneagen which seems to mark the place where the lips of the optic cup came together.

THE RETINA. — Just before the closure of the cup, the retinal nuclei suddenly appear to decrease in number, owing to the formation, in the manner already explained, of the retinophoræ, which soon arrange themselves in a single layer, with all their primary nuclei at about the same level. The retinophoræ are the same as those in eye V., except that they are a little shorter, and the primary and secondary nuclei are often situated so close together as to appear like one nucleus.

In the full-grown larva the retina is almost a hollow hemisphere, and consequently the rods on the periphery are very nearly at right angles with those in the centre.

THE RODS are remarkably uniform in structure. On the posterior edge of the retina they are not quite so long as elsewhere. Each pair forms a thin-walled, hexagonal tube, which when isolated shows distinctly its two component rods. Cross sections show a mosaic of closely packed, hexagonal figures without the regularly arranged thin places so conspicuous in the rod-mosaic of eye V. (Fig. 45*b*).

EYE III.

Eye III. appears very early as an oval, dark area in the middle of the second segment of the optic plate. It is soon surrounded by a circular clear space, and then both parts become considerably elongated, the latter assuming a figure-8 shape, and the former being reduced to an elongated ridge composed of a double row of nuclei (Figs. 1–6). The explanation of surface views given in the description of eye V. will serve equally well here.

In both eyes I. and III. there are two broad and poorly defined light areas, one on the dorsal and the other on the ventral side of the eyes, which extend almost their whole length. These areas are well developed in the stages shown in Figs. 5 *a* and 4. But they soon disappear, and the eye assumes the appearance shown in Fig. 6*a*.

Although this eye is considerably longer and larger than eye V., it is evidently constructed on the same plan. The figure-8 shaped clear area is composed, as in eye V., of four sensory pits. In the centre is the elongated ridge, and on either side of its anterior end is a small, round, dark spot, surrounded by a faint depression. In surface views we see that the dark area is bent in the middle, and at the apex of the bend, which is directed dorsally, is situated the large nucleus. In some cases this configuration of the dark area is more conspicuous than that shown in Fig. 6*a*, which represents about the average condition. This bend is similar to that in the retinal furrow of eye IV., to be described later, but it does not, as in this last case, remain throughout life. The invagination and general structure of the eye is almost exactly like that of eye I., only it has no dorsal appendage or vertical retina. See *infra.*

Eye I.

The early stages of this eye, which arises from the first segment of the optic plate, are much like those of eye III. After the light area has assumed a figure-8 shaped contour, it increases in extent at the anterior end until a large oval patch, in reality a shallow depression, is formed. This depression is finally separated from the remainder of the clear area by a dark ridge, leaving only a narrow connecting streak on the ventral side of the eye. Figs. 11–16 represent surface views of the first segment as seen from the anterior dorsal side of the embryo. In Fig. 13 a light streak, or furrow, is seen on the ventral side of the eye, united at its anterior end with the main clear area. At this point appears a round dark area (*d. a.*^{4} Fig. 14).

The main dark area, *d. a.*[1], which at first was very broad and surrounded by a narrow furrow, formed by the abrupt termination of the cuticular thickening overlying each sensory area (Figs. 11, 12), is gradually reduced to a narrow ridge composed of two rows of nuclei, between which is the large median one, *nc.*[1]

The dark area becomes strongly bent at the anterior end, and at the angle appears a second large nucleus, *nc.*[2], Fig. 14. Finally a third smaller and much less distinct nucleus appears where the area **7–8** joins the main eye.

After this stage, the round spot, *d. a.*[4], and the ventral clear area, **10**, together with the nucleus, *nc.*[3], disappear. The dorsal appendage grows smaller but more conspicuous, and contains an oblong dark area divided in halves by a narrow light streak, in the centre of which I thought I could detect a nucleus like that found in the dark areas of the other eyes (Fig. 18). The main part of the eye is reduced to a narrow, bent band, with a light or dark streak, according to the method of preparation, in the middle.

The main part of eye I. differs from all others in containing at least two large nuclei and eight sensory pits. The dorsal appendage represents at least one more pit, perhaps two, if we can place any reliance upon the indication of a retinal furrow as shown in the faint, light streak seen in surface views. As in eye V., the large nuclei are situated in the centre of a group of four sensory pits. The structure of the sensory area is seen from sections (Pl. XIII., Figs. 82 and 83) to be like that of eye V. The former section corresponds with Fig. 63, in which the cuticular thickenings are still separate; and the latter, to Fig. 64, where they have united and the median furrow has disappeared. In describing the invagination, we will leave out of consideration the dorsal appendage *c. e.*, of which we shall speak separately by and by.

Nothing like an optic cup is formed by the invagination. As fast as the median ridge sinks below the surface, the outer faces of the clear areas on either side are brought together like the leaves of a book, and the distal ends of the sensory cells meet one another in the median longitudinal plane of the eye.

But this is not the only direction in which invagination takes place. In Fig. 8 the sensory area is still seen lying lengthwise on the surface; but during the succeeding stage, its anterior end is pushed into the tissues of the head, as though the whole plate swung on a pivot at the posterior end, through an angle of ninety degrees. The long axis of the retina then lies at right angles to the surface, and in a semi-transparent preparation, like that shown in Fig. 9, we look along the retinal furrow, not down into it as in Fig. 8. It is not easy to form a clear mental picture of the way in which the retinas of eyes I. and III. are invaginated. To make matters clearer, let us suppose the head to be made of soft india-rubber. Then if a slender but inflexible rod be laid between the two rows of nuclei of the median ridge, as fast as it is pushed below the surface, the lips of the indentation that will tend to form, come together, conceal the rod, and prevent the formation of any cavity. If this process is continued until all the sensory cells on either side of the rod are invaginated, a long narrow pocket will be formed, composed of two thick walls, whose originally outer surfaces touch each other, bringing their cells end to end and at right angles to the opening of the pit (Fig. 85). There are no transitional cells connecting the inner edges of the two walls, so that, strictly speaking, there is no floor to the pocket. This completes the first stage of the invagination. Now, in eye III., suppose the posterior end of the rod is fixed and the opposite extremity swung inwards through an arc of ninety degrees; the retina will then be brought with its long axis at right angles to the surface, and the second stage will be finished. Finally carry the rod in this position backwards a distance equal to the height of the future corneagen, and, without considering minor details, the third and last stage is completed.

In eye I. the pocket has a bend like that of the dark area (Figs. 14–16) which divides the retina into two unequal parts. Between the lateral walls of the posterior portion, or that which gives rise to the *horizontal retina*, is situated the first large nucleus (*nc*^{1}., Figs. 17 and 85), and in a corresponding position in the anterior part, which gives rise to the vertical retina, is the second large nucleus, *nc*.^{2} The whole pocket is of nearly uniform depth, as shown in Fig. 17, which represents a digrammatic outline of the whole eye seen as a transparent object. In order to continue the invagination by means of our rod, it must be cut at a point a little back of the second nucleus, *nc*.^{2}, and that part of the rod lying in the future vertical furrow, removed. Now if, as in eye III., the posterior end of the rod is fixed, and its anterior extremity swung inwards through an angle of about ninety degrees, and then carried backwards a distance equal to the height of the future corneagen, the invagination of eye I. will have been completed, and a condition obtained like that in Fig. 18, Pl. VIII. When we began to carry the posterior part of the furrow inwards and backwards, of course the anterior part was gradually pulled into a vertical position and extended along the inner lateral edge of the flattened optic cup, where it remains through life as the *vertical retina.*

Figs. 79–81, Pl. VII., represent longitudinal vertical sections of eye I. (semi-transverse sections of the head, parallel with the long axis of the retinal furrow, see Fig. 8), showing three successive stages in the invagination of the retina.

CORNEAGEN. — As soon as the early stages of invagination have carried all the clear area below the surface, the surrounding ectoderm cells are drawn in, in the same way, to form the corneagen. But these cells, instead of meeting end to end above the retinal furrow, take an outward curve, so that their long axes are parallel with the plane of invagination. The first direction of the invagination is towards the brain, and as the long axes of the corneagen cells are parallel with the direction of invagination, they naturally point inward and are at right angles to the long axis of the vertical and horizontal retinas (Fig. 79). But when the invagination is directed backward, the inner ends of the corneagen cells are pulled backward also, so that they finally have their long axes at right angles to the horizontal retina, and parallel with the vertical one (Figs. 80 and 81).

The shape of the corneagen cells shows the way in which they were formed. In all cross sections of the horizontal retina, — sagittal sections of the head, — the nucleated ends of the corneagen cells bend away from the median plane to either side, and in such a way as to leave no conspicuous boundary between them and the retinal cells. For some time after the closure of the flattened optic vesicle there is a line in the middle of the corneagen marking the place where the lips of the invagination united. The difference in curvature between the cells belonging to the corneagen and to the retina gives rise temporarily to a small triangular space between these two structures (Fig. 85). After the lens has appeared, and even in the fully developed eye, the ends of the cells lying in the middle of the corneagen are so compressed and filled with fine granular protoplasm as to form a distinct, deeply stained core.

The nuclei of the corneagen are at first arranged in two great lateral masses (Fig. 85), but as it increases in depth, they form a single layer that at first sight appears to be a direct continuation of that formed by the retinal nuclei. But the inner ends of the median corneagen cells, although slightly bent away from the median plane, do not reach the periphery of the eye. One can see the nuclei at their expanded inner ends almost over the centre of the retina (Pl. XIII., Figs. 90, 91). The inner ends of the remaining corneagen cells are situated at the periphery of the eye, and are filled with a dense layer of black or dark brown pigment granules which completely envelop and conceal the nuclei. In stained, depigmented sections, the formerly pigmented ends of the corneagen cells are quite colorless and empty, with the exception of a few coarse granules and the deeply stained nuclei.

RETINA. — As we have already said, the horizontal retina is composed of two long strips of thickened ectoderm with their originally outer surfaces brought face to face (Fig. 85). In the early stages, the cells nearest the corneagen are indistinctly defined, and contain large oval nuclei with a few coarse, deeply stained granules. The position and general character of these cells is much like that of the inverted ones in eye V., and I believe them to be of the same nature. However that may be, they soon disappear. There is no evidence that, in the later stages, they form an outer wall to the optic vesicle.

Throughout the greater part of embryonic life the free ends of all the retinal cells are at right angles with the optic axis (Fig. 85); but the outermost cells finally draw away from the middle line and assume a more upright position. This process goes on until only a few rows of small horizontal cells are left overlying the gigantic ones which form the innermost walls of the furrow. In cross sections the layers of rods now form a Y, the diverging arms being composed of nearly upright rods, and the stalk, of the double rows of horizontal ones (Fig. 86).

In the full-grown larva the anterior wall of eye III. is quite straight, and most of the retinal cells of that side are horizontal

(Fig. 90). The posterior wall, however, is strongly convex, and the retina on that side is composed of a broad layer of nearly upright cells, whose short rods decrease in length from the furrow toward the posterior periphery of the retina. This remarkable asymmetry is correlated with the position and inclination of the lens, which looks upwards, inwards, and forwards, so that its optic axis falls about in the middle of this posterior layer of horizontal rods, and not, as one might expect, upon the retinal furrow. In eye I. the horizontal retina is also asymmetrical, but to a less degree, and in an exactly reversed manner, for the greatest expanse of horizontal rods is on the anterior side of the furrow instead of the posterior (Fig. 91). There is a similar asymmetry in the retinas of eyes II. and IV.

The *gigantic retinal cells,* arranged with great regularity in two rows, one on either side of the retinal furrow, are very broad and thin at their free ends. At their opposite extremities, there is a slight swelling containing a large oval nucleus. These cells are similar in nature and arrangement to those at the bottom of eyes II., IV., and V. (Figs. 70–78), except that they are much larger, and, owing to the way in which they receive their nerve supply, somewhat differently shaped. Those on the side of the furrow with the greatest number of upright rods are longer than those in the opposite part of the retina. The important point is, that, except in size and shape, they do not differ from the remaining retinal cells. They must be regarded as horizontal retinal cells with very wide and short rods; compare the isolated cells *d, e,* and *i,* Fig. 58, Pl. X. When these cells first become distinctly outlined (Fig. 85), there is only a small space between the primary nucleus and the rod, while the outer edge of the cell shelves steeply inwards to the level of the almost horizontal inner edge. They are also much darker than the smaller cells, and their free ends being concave, a space is formed between the two rows of rods. But the latter are soon brought more closely together, their terminal edges become as straight and ridged as though crystallized, and the narrow space is filled with a mass of densely pigmented nerve fibres.

In order to economize space without disturbing the arrangement of the rod-bearing portion, the thick nuclear ends of the cells are turned alternately toward and away from the median plane. Hence it happens that in vertical cross-sections of the eye, four or five rows of large nuclei are seen near the middle of the retina, although the outer ends of the cells to which these nuclei belong are arranged with the utmost precision in two rows.

The giant cells have, in the early stages (Fig. 76), short rods extending the whole length of their distal ends. In the full-grown larva these rods are longer but narrower, the protoplasm of the cells having pushed its way under the inner edge of the rod to form a deeply pigmented heel that excludes the rays of light from the underlying nerve fibres (Pl. X., Fig. 56).

The *large nucleus*, nc^1, conspicuous in surface views, remains throughout life unaltered, except that it is perhaps a little larger and flatter in the older stages. It lies a little inside the middle of the horizontal retina, between the deep edges of the two rows of large cells (Figs. 81 and 86).

The *vertical retina* differs principally in size from the horizontal one. It is deeply buried in the pigment at the periphery of the corneagen, and might be easily overlooked. It arises, as already pointed out, from the short bent portion of the dark area (Figs. 14, 15, 16). There is a second large nucleus that marks, in surface views, about the point where the horizontal and vertical retinas are continuous; but when the eye is well invaginated, this nucleus has changed its position to about the middle of the vertical retina. In the next stage (Fig. 80), the vertical retina is reduced in size at the angle of the bend, so that it has apparently lost its connection with the horizontal one. At its outer end the retinal cells are well developed, and form a projecting mass that shelves off abruptly toward the dorsal appendage (Pl. XIII., Fig. 80).

In the still later stages the furrow is relatively smaller and more uniform in size. At the bottom of the furrow is a double row of large, flat cells, bearing short, broad rods placed end to end against those on the opposite side (Fig. 84). Outside of them is a single row of smaller, cylindrical ones, bent in the form of a semi-circle and bearing short terminal rods. These retinal cells are filled with coarse, black pigment granules, so that only a narrow slit is left through which the light can pass to the circular space containing the large rods (Fig. 84).

Longitudinal vertical sections of the eye expose the arrangement of the cells on one side of the furrow (Fig. 81). It is there seen that the terminal edges of the broad rods trend toward the centre of the newly developed lens. The latter is placed so as to throw light upon the vertical furrow. But this condition is not permanent; in the adult, the lens is horizontal, and its axis is directed toward the bottom of the eye. By this change, the amount of light that falls upon the vertical furrow is very much reduced.

The nucleated ends of the corneagen cells never lie in front of the furrow, but always to one side of it.

The *retinophoræ* of eyes I. and III. are like those of eye V. The secondary nucleus is always situated beyond the primary one, in the terminal quarter of the cell.

It is not so easy to detect the secondary nucleus in the gigantic cells as one might suppose. Their flattened ends make it difficult to roll them when isolated, so that one cannot view the same cell from different points. Moreover, they have a tendency to stick together in great flakes that appear, owing to the excessive thinness of the cells, to consist of but one retinophora, when they may contain half a dozen or more. But in spite of these difficulties, I have seen enough to convince me that they are double cells and that the secondary nucleus is situated in their expanded and flattened ends about half way between the primary nucleus and the rod.

Although I have not made any extended observation on the structure of the retinophoræ in the vertical furrow, their intimate connection with those of the horizontal retina, as shown by the early stages of development, and the presence of the double rods, leave no room to doubt that they have the same structure as the other retinophoræ.

In only one instance have I seen anything like ganglion-cells in the retina. It was a small tripolar cell, with an outward prolongation extending along the sides of a retinal cell. Both cells were firmly united with each other, and were found among a great many isolated ones from all the eyes, so that it was impossible to determine to which retina it belonged. It was (Pl. X., Fig. 58, *h*) very much like the tripolar cells found by me in the retina of Haliotis.

I have looked for these cells in sections, but have never found any trustworthy evidence of their presence. I regard them as half-formed ganglion-cells which have not succeeded in separating themselves from among the sensory cells, by transformation of which they arose.

NERVE ENDS. — The manner in which the nerves terminate in the retina is practically the same as in eye V., while owing to the large size of the inner retinal cells, some points are brought out with great clearness. But the layer of pigmented nerve fibres between the rows of gigantic cells is a feature only found where these cells are especially well developed.

In Fig. 56, Pl. X., is represented a section through the horizontal furrow of eye I. The sides of the cells are thickly covered with nerve fibres that converge toward the inner end of the cell to form a large bundle that might readily be mistaken for a continuation of the cell substance. The fibres follow, as nearly as possible, the contours of the outer and inner edges of the cell. This point is of importance, for it furnishes additional evidence that the rods belonging to these cells are terminal, and consequently developed at what is morphologically the free end of the cell; for in the smaller retinal cells the nerve fibres always run parallel with the longitudinal axis; hence the direction of the fibres shows in which way the cells have been bent.

At the distal end of the cell all the nerve fibres become roughly parallel, and develop refractive, spindle-shaped swellings, densely coated with pigment, the granules of which often form distinct lines, showing clearly the position and direction of the nerve fibres around which they are arranged; or the granules may be collected in shapeless masses near the inner end of the rod, showing no traces of the arrangement of the nerve fibres they so effectually conceal.

At the opposite extremities of the cells the pigment granules are arranged in lines similar in direction to the nerve fibres; they are also found on the nerve fibres after they have left the cell to form the optic nerve.

Beyond the spindle layer described above, the nerve fibres emerge from the pigment and extend over the surface of the rods in nearly parallel lines. At certain intervals these fibres expand into spindles, which were a sore puzzle to me before I had made a careful study of depigmented sections. They seemed to indicate quite clearly the division of the broad rods into segments, about the width of the smaller rods, a condition that it was of course impossible to reconcile with the great size of the cells to which they belonged, unless we assumed that each of these cells possessed many rods.

In the smaller cells, the nerve fibres and pigment granules are also distributed in the manner just described, but their course and arrangement is less easily followed.

The small retinal cells contain an *axial nerve* which, between the two rods of each retinophora, breaks up into a fan-shaped bundle of fibres, that in cross sections appear like a row of dots midway between each pair of rods, and usually parallel with their broad surfaces (Fig. 55).

In the gigantic retinophoræ, the axial nerves are arranged in a sheet as broad as the ends of the cells. In longitudinal vertical sections, they are consequently seen as a row of dots between each pair of rods (Fig. 55).

Most of the nerve fibres supplying the retinal cells come from two bundles that extend along the edges of the horizontal retina (Figs. 90 and 91). A third group extends along the middle of the under surface of the retina. *From it arise two sheets of densely pigmented nerve fibres which extend upward into the space between the two rows of gigantic cells* (Pl. X., Fig. 56, *v. n.*). These fibres are very straight and arranged with almost as much regularity as the large rods, with whose terminal edges they are parallel. I suspect that the number of these nerve fibres bears a pretty constant relation to the number of large rods. In some of my preparations I could see that a single nerve fibre lay in or near a shallow furrow which marked the point of union of each pair. From this I judge that in the living, normal condition, one of these vertical fibres extends along the terminal edge of each pair of large rods. But evidence of this condition is not often found in sections, owing to the action of the reagents, which cause a contraction that draws the fibres away from the rods towards the middle of the furrow. Hence in horizontal sections, these nerve fibres are seen in cross sections as two rows of dots, a little distance from the terminal edges of the rods (Pl. X., Fig. 59, *v. n.*).

From the vertical nerve fibres arise a great many fine fibrillæ which extend at right angles to the main fibres towards the rods and apparently become continuous with the external nerve fibres. Others extend in an opposite direction where, *between the two* *sheets of vertical fibres, they form a mass of the finest, interwoven fibrillæ, that presents the same appearance as the medullary substance in the optic ganglia.* It cannot be that this enigmatical mass of nerve fibres is nothing but a flake of coagulated serum. The latter is frequently present and is especially abundant after some modes of treatment, filling all the cavities of the head with a finely granular substance. At other times it is altogether absent, or at any rate the cavities appear quite empty. But under both these conditions, this mass of nerve fibres, unenclosed by any membrane and devoid of nuclei, maintains such a constant shape and uniform appearance as to preclude all thought of its being a product of coagulation. It may be remarked, also, that the coarse pigment granules, so abundant about this fibrous mass, are completely dissolved by acids, and consequently leave no granular residue that might be mistaken for nerve fibrillæ. We have already pointed out that in the iris the pigment is also completely dissolved by these reagents.

One occasionally finds, among the fragments of cells isolated by maceration, what appear to be large flakes of pigment with parallel striations. They are fragments of the sheets of vertical nerve fibres covered with pigment, the fibres being united with one another by the innumerable fibrillæ that arise from them.

Between the outer ends of the vertical nerve fibres is an oval space devoid of pigment, quite constant in shape and size (Figs. 90 and 91, Pl. XIII.). I have no suggestion to make concerning its significance.

The vertical fibres, and the pigment surrounding them, do not extend beyond the outer edges of the large rods.

The Rods in eyes I. and III. develop in the same way as those of eyes V. and VI.; and although their arrangement in the fully developed eye differs in some important and interesting particulars from that in the last-mentioned eyes, their general structure is the same in both cases.

The horizontal rods are arranged with great precision and regularity edge to edge in vertical rows. The broad sides of two rods belonging to adjacent retinophoræ lie so close together as to look like one rod with a faint vertical line in the middle. The rods belonging to the same retinophoræ are separated by a clear space, a little smaller in diameter than that of the retinophoræ to which they belong. In the centre of the clear space is the vertical row of axial nerve fibres (Pl. X., Fig. 55). At the lower end of each double row of rods are two pairs of much larger ones belonging to the large retinophoræ at the bottom of the retinal furrow. They are arranged in pairs like those of the small retinal cells, except that the clear space between each pair is alternately wide and narrow.

The rods in the rows just above the gigantic ones differ from all others in that their free ends are united in pairs *opposite the centre of the retinophoræ* (Fig. 60).

Toward the periphery of the retina, where the rods are upright, the rod-mosaic is composed of zigzag lines like those in eye V. (Fig. 54*a*).

Dorsal Appendage. — Besides the vertical, and horizontal retinas of eye I. there is a third part that up to this time we have left out of consideration. It is what in a former paper I have called the dorsal outgrowth of the large posterior ocellus. The observations recorded in this paper throw new light on that remarkable organ.

We have already described how the changes seen in surface views gave rise to an oval sensory patch constricted off from the anterior, dorsal end of eye I., but with which it was still connected by means of a narrow furrow (Pl. VIII., Figs. 14–16). While the main portion of eye I. is being invaginated, the dorsal appendage is depressed, forming a deep pit, at first round, then oval, and finally slit-shaped, the long axis of the depression being at right angles with that of the main eye (comp. Figs. 8 and 14–16). In Fig. 79 is shown a longitudinal section of the main eye with a cross section through the middle of the dorsal appendage, during a stage corresponding to that shown in Fig. 16. In a similar section of a later stage, the pit is closed and three layers of cells are formed very much like those in eye V. (Fig. 80). The outer ends of the retinal cells soon lie close against the corneagen. The outer wall of the vesicle is flattened and probably forms an imperfect middle layer; at least I have seen in several cases one or two nuclei just beneath the corneagen, which, I believe, must be referred to the outer wall of the vesicle. Fig. 16 shows that the sensory cells connecting the ocellus with its dorsal appendage are joined to the latter at its anterior edge, consequently only those sections that pass through the anterior edge of both these structures — and not those shown in Figs. 79–81, which pass through the middle of the appendage — will show the continuity of their retinal cells. After the stage shown in Fig. 81, I have not been able to detect evidence of this continuity, although the vertical furrow contains retinal cells up to the very outermost edge of the eye.

Surface views indicate that the peculiar structures found in all the other eyes, such as the median rows of cells and the large nucleus, are probably present in the dorsal appendage, although imperfectly developed. My failure to detect them in sections may be due to the difficulties of observation.

In longitudinal vertical sections of eye I., the dorsal appendage is seen to be somewhat thickened in the middle, the rod-bearing ends of the retinal cells converging toward an imaginary centre some distance above the corneagen.

The appendage is never sharply limited from the surrounding ectoderm; it is less so in the older stages than during the period when it is an open cup or newly closed vesicle (Figs. 80 and 81). The basement membrane is continued without interruption from the surrounding ectoderm, over the inner surface of the appendage, and this tends to obscure still more the limits of the parts in question.

The retinophoræ of the appendage are much like those of the other eyes. They are long, spindle-shaped cells with double rods, and hence probably contain two nuclei and an axial nerve fibre.

The observations recorded in this paper were made entirely upon material collected in a small pool near Milwaukee. In all these specimens the appendage was entirely devoid of pigment.[1] In the larvæ that formed the basis of my preliminary note on the "Eyes of Acilius," in the first number of this Journal, and which were collected near Boston, Mass., the retinophoræ of the appendage contained large blotches of pigment just below the rods.

Grenacher has described, without figures, the dorsal appendage in the larva of *Acilius sulcata* as being pigmented. He failed to recognize that it was composed of two distinct layers; and while he thought it was in all probability some kind

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[1] In some of my sections I have noticed, since this was written, mere traces of pigment at the base of the rods in the Milwaukee species.

of a sense organ, perhaps one in course of development, he apparently had grave doubts about its being a visual organ; at any rate he is careful not to call it such.

EYES II. AND IV.

Eyes II. and IV. arise from the distal edge of the first and second segments of the optic plate. They are so much alike that it will not be necessary to describe them separately. I have not been able to follow the very earliest stages in the development of these eyes, owing partly to their small size and partly to the fact that during these stages they are situated on the infolded edge of the optic plate, so that it is almost impossible to study them in surface views. Nothing in the sections indicates that they differ in any important points from the corresponding stages of eyes V. and VI.

The eyes are first seen in surface views (Figs. 5*a* and 5*b*), as round clear spaces containing an elongated dark area composed of a double row of nuclei nearly parallel with those of eyes I. and II. Between the rows of nuclei is a single large nucleus. The similarity between the structure of these eyes and the remaining ones makes it probable that the large nucleus, as in all the other eyes, is situated in the centre of four sense organs.

Eyes II. and IV. are not invaginated to form either optic cups or vesicles. Just as in eyes I. and III., as fast as the sensory areas on either side of the median ridge are tipped over, the ends of their cells meet in a vertical plane above the median ridge, and thus obliterate the cavity that tends to be formed.

Toward the close of invagination the cells on the outer edges of the sensory area curve outward and their sides meet in the median plane of the eyes to form the corneagen (Pl. XII., Fig. 76), whose nuclei form a row continuous with those of the retina, so that the latter appears to be directly continuous with the unmodified hyperdermis. This deceptive appearance is due to the fact that the nuclei of the corneagen cells over the centre of the eye stain very faintly, so that, in most cases, they escape, or even defy detection. In Fig. 76 there is no trace of a middle layer of cells between the retina and corneagen. But in two cases, one or two cells were seen, with rather large and deeply stained nuclei, wedged in between the periphery of the retina and corneagen. They were like the similarly placed cells described in eyes I. and III. (Pl. XIII., Fig. 85, *o*, *w*), and I do not doubt they are of the same nature, *i.e.* cells that have been pushed between the retina, and the corneagen, forming the rudiments of a middle layer. They never form groups of inverted sensory cells, as in eyes V. and VI., or a continuous layer of non-sensory ones, as in a part of eye VI.

The retinas of both eyes are asymmetrical, as in eyes I. and III., in that there are more upright rods on the dorsal side of the retina than on the ventral (Figs. 77, 78).

Eye II. contains a greater number of horizontal rods than eye IV., and the median space in which they lie is considerably deeper.

The outer retinophoræ are long and semi-circular, and nearly uniform in size throughout. The innermost ones are broad, scimetar-shaped cells, arranged with great regularity in two rows that extend the whole length of the longitudinal axis of the retina. Their free ends, which are bent at right angles, are almost as broad as the remainder of the overlying retina. In the younger stages, the terminal edges of the large rods are concave, and a considerable space is left between the two rows (Fig. 76). In the later stages they are rigidly straight, and the space is filled with a layer of densely pigmented, vertical nerve fibres, like those in eyes I. and III. (Fig. 78).

In all essential particulars, the finer structure and arrangement of the retinophoræ and their rods, and the distribution of nerve fibres, is the same as in eyes I. and III.

After the corneagen has formed a continuous layer over the retina, the *large nucleus* lies just below and between the inner edges of the two rows of giant retinophorae. It stains deeply on the periphery, and contains a few coarse, deeply stained granules. It is always oval, with its long axis parallel with the long axis of the retina, and is somewhat compressed, as though forceably flattened between the two rows of cells. It remains in this position, unaltered, through larval life.

Eyes II. and IV. are somewhat canoe-shaped, the retinal furrow being at first nearly parallel with that of eyes I. and III., below which they lie in the earlier stages; but they finally change their position for one behind the deep end of eye I. During this change, they rotate on their optical axis through an angle of about ninety degrees, so that by the time the embryo is ready to hatch, their retinal furrows are at right angles with those of eyes I. and III. (compare Figs. 5*b*, 8, and 10*a*). Surface views of eye IV., in its younger stages, show that its retinal furrow is bent, a condition which is retained through life (Fig. 8*a*).

The Lens of eye II. (Fig. 77) is asymmetrical, in that the radius of curvature of its strongly convex inner surface is greater on the dorsal, than on the ventral side. The axis of the lens falls upon the layer of short, nearly upright rods on the dorsal side of the retinal furrow. The latter, which is the most specialized part of the retina, lies, therefore, very much to one side of the apparent optical axis of the eye. The same fact was observed in eyes I. and III. This extraordinary condition is difficult to account for satisfactorily. There is every reason to believe that the retina has not been moved by shrinkage from its normal position in relation to the lens. The greater depth of the iris on the dorsal side, the extension of the rods in that direction, the slight flattening of the dorsal, inner surface of the lens, and the whole history of development, show too clearly that these diverse parts are modified in this manner in order that the optical axis might have the direction indicated.

Although in eye IV. the lens is more symmetrical, its axis falls upon the retina some distance above the furrow.

In the larva, the optical axis of eye II. is directed upward and backward, that of eye IV. downward and backward.

II. The Optic Ganglion.

As soon as the cephalic lobes have assumed their characteristic shape, a slight depression, the future mouth, appears in the median line between them. On either side of this depression are three ectodermic thickenings from which the brain is subsequently developed; they appear to be direct combinations of the segmental thickenings of the ventral nerve chord (Fig. 2, b^{1-3}). On the lateral edge of the third pair of thickenings, b^3, are the antennae, a^2. On the inner edge of the second pair are two appendage-like outgrowths of the ectoderm, that finally unite in the middle line above the mouth to form the labrum, a^1.

Between the brain and the optic plate (Fig. I.) is a broad expanse of ectoderm composed of faintly stained cells containing coarsely granular, or even flocculent, protoplasm and large spherical nuclei.

In Pl. IX., Fig. 19, which represents a cross section through the middle of the cephalic lobes of an embryo considerably younger than that shown in Fig. 1, there is no thickening to form the brain, although the distal edges of the lobes have already given rise to the optic plate, on the inner edge of which is a depression, containing large wedge-shaped cells quite different in appearance from those on either side of them (*o. g.*). This depression, the beginning of the invagination of the optic ganglion, is fairly uniform in depth, and in surface views appears like a semi-circular furrow on the inner edge of the optic plate.

The ectoderm that gives rise to the optic ganglion divides into three segments, or lobes, each of which is united on the one hand with a segment of the brain, and on the other, with a segment of the optic plate (Fig. 1, $o.\ g.^{1-3}$).

The semi-circular groove is soon deepened to form two distinct pits with slit-like openings (Fig. 1, $g.\ v.^{1-2}$). There is no infolding between the third segment of the optic plate and the third segment of the optic ganglion, but there is, as shown in sections, a distinct inward proliferation of ganglion-cells at this point. Each segment appears in some cases to be divided by a faint line into two parts, a condition that may have some connection with the fact that it belongs to a part of the optic plate provided with two eyes.

Figs. 20–23, Pl. IX., represent four cross sections of the cephalic lobes during the stage shown in Fig. 1. The first section passes through the first ganglionic invagination, $g.\ v.^1$, the lateral wall of which is composed of a single layer of loosely connected cells, continuous, at the opening of the pit, with the edge of the optic plate. There is no infolding between the anterior edges of the optic plate and first ganglionic segment (Fig. 1). The invagination appears just behind this point as a slight furrow that increases in depth backwards as far as the anterior end of the second segment of the optic plate.

The section shown in Fig. 21 passes through the bridge of ectoderm separating the first invagination from the second. Beneath the uninfolded layer is a V-shaped mass of ganglionic cells, the cavity of which is continuous with that of the first ganglionic invagination.

In the next two sections there is a solid chord of cells in the place of the V-shaped mass of Fig. 21. It connects the cells of the first ganglionic invagination with those of the second.

The succeeding section (Fig. 22) passes through the second pit, *g. v.*^{2}

That shown in Fig. 23 passes through the base of the antenna and the point marked *g. v.*^{3}, Fig. 1. It shows at *g. v.*^{3} a cross section of a thick chord of ganglion-cells extending from the third ganglionic segment to the under surface of the third ocular plate. It is produced by an inward proliferation the direction of which is parallel with the long axis of the antenna.

The invaginated part of the optic ganglion now forms a continuous semi-circular mass of cells tucked beneath the optic plate. *It is directly continuous along its inner edge with the distal inner edge of the optic plate, p. n.*

This fact may possibly throw some light on the inexplicable presence of an optic, and ganglionic invagination side by side. My studies on Molluscs and Arthropods led me to suppose that ganglion-cells were derived from sensory cells that had wandered into the underlying tissues, leaving their outer ends, transformed into nerve fibres, sticking in the epidermis. Confirmation of this supposition was found in Pecten. Much better evidence will be given in describing the origin of the large tripolar cells in the optic ganglion of Acilius.

But the point I wish to emphasize now, is, that from the earliest stages, the inner surface of the optic plate is continuous with the optic ganglion (Figs. 20–23, *p. n.*), and from what takes place later, it is highly probable that ganglion-cells are formed at this period by an inward proliferation of the optic plate.

My idea is that an increase in the width of the optic plate, since its distal edge is fixed, would produce a fold like that in Fig. 20. The main part of the optic ganglion of this period may be regarded as a formerly sensory area with an underlying plexus of ganglionic cells continuous with a similar plexus underlying the eyes. With the great development of the latter, all the cells of the sensory area were converted into ganglionic ones, which were then overgrown by the optic plate and added to the plexus arising directly from the eyes. The general character of the invagination points to this conclusion, and it seems hardly possible to reconcile, by an explanation along any other line, the independent development of such dependent structures as the eye and the optic ganglion.

The sections shown in Figs. 24–27 belong to a little younger stage than those shown in Figs. 20–23. They were cut from an embryo somewhat abnormal, the antennæ being lodged in a great depression, on the floor of which was the mouth. There was nothing abnormal about the parts belonging to the eyes. The first and second ganglionic invaginations are shown particularly well.

All these sections and those described above are instructive from the fact that there cannot be a shade of doubt that the ganglionic invaginations have nothing whatever to do with the formation of optic vesicles, for the peculiar way in which the eyes develop makes it possible to determine, even at this period, just what parts develop into the eyes and what into the optic ganglion.

These two series of sections show pretty clearly that *there are two distinct, and one obscure, invaginations to form the optic ganglion. This fact is of especial interest when we consider that there are three segments to the brain and three to the optic plate, and three distinct parts to the optic ganglion of the convex eye.*

In Fig. 3 *a* the three ganglionic segments, $o.\ g.^{1-3}$ are still visible in surface views, and at the anterior ends of the first two are seen the openings of the ganglionic invaginations, $g.\ v.^{1}$ and $g.\ v.^{2}$

In a later stage (Fig. 4), nearly all the eyes, as well as the mouths of the two invaginations, are visible. Still later (Figs. 5 *a* and 6) the invaginations have disappeared, and all but a small part of the optic ganglion is concealed by the optic plate.

Just after the rupture of the embryonic membranes, the optic ganglion is completely shut off from the surface, and the ectoderm of the optic plate becomes continuous with that over the brain.

Figs. 28–34, Pl. IX., represent seven sections of an embryo about the age of that in Fig. 4.

The optic ganglion now forms a great, complex mass of cells, the most of which is not yet overgrown by the optic plate. It requires careful attention, not only to recognize its parts, but to distinguish them from the brain.

The first section (Fig. 28) passes just above the anterior edge of the plate, and shows the proximal ends of each ganglionic segment, *o. g.*$^{1-3}$

The next (Fig. 29), passes through the first invagination, *g. v.*^{1}, and the anterior end of eye V.; compare Fig. 4. At this niveau, the third ganglionic segment, *o. g.*^{3}, is separated from the third lobe of the brain by the cephalic infolding, *z.*

In Fig. 30, the section passes through the centre of the third segment, which is not separated by any epithelial layer from the exterior. At *x. y.* is a section of the second segment of the optic plate, where it dips down towards the second ganglionic invagination. The underlying cells, *o. g.*^{1} and *o. g.*^{2}, connect the main part of each ganglion with the segment of the optic plate to which it belongs.

In Fig. 31, the section passes through the upper edge of eyes V. and III., and in Fig. 32, through about the middle of these eyes. The scattering fibres uniting the eyes with the optic ganglion indicate the position of the future nerves.

In Figs. 33 and 34, the sections pass through the upper and lower edges of eye VI., and show how the optic ganglion is here reduced to a chord of cells continuous with the retinal cells of the eye.

After the rather confusing condition shown in the last series of sections, it will be a relief to find in the next (Figs. 37–39), a simpler arrangement. These sections are taken from a head a little older than that shown in Fig. 4. The first section (Fig. 37) passes through the site of the first ganglionic invagination. It is now closed, but there is a depression above an inwardly projecting core of cells, which marks its former position, *g. v.*^{1} It also cuts the anterior edge of the first ocular plate, showing a small part of the first ganglionic segment, *o. g.*^{1} Two or three sections below this we find one (Fig. 38) which passes through the point *g. v.*^{2}, Fig. 4, and consequently through about the middle of eye I. and the anterior edge of the second ocular segment. The third segment of the optic ganglion is still exposed to the exterior, *o. g.*^{3} The outer wall of the ganglionic invagination has completely disappeared by this time, and the edge of the optic plate comes squarely against the outer surface of the third ganglionic segment. The only part of the brain seen at this niveau is a section of the anterior end of the antennary lobe.

It is separated from the optic ganglion by the invaginated ectoderm, *z*. After three or four more sections, we come to one (Fig. 39) that passes through the middle of the fifth eye and the lower end of the first. It should be remembered that the sections are cut from an embryo a little older than that in Fig. 4, and that the posterior end of eye I. is on a level with eye V. We see that the continuity of the optic plate with the optic ganglion is now interrupted everywhere except along three lines directly beneath, and parallel with, the median furrow of the eyes. These three connectives are short and nearly as broad as the optic plate. Compare Figs. 4 and 5*a*. They are the rudiments of the optic nerves, and are composed of a mixture of nerve fibres and ganglionic cells.

If we refer to Fig. 1, and the sections of that age, Figs. 20–23, we shall see that the first cross section passes through the first ganglionic invagination, with whose direction of ingrowth it is nearly parallel. Now if we suppose a section to be cut through the long axis of the optic plate at that stage, we should then see three bands of cells — the optic plate, the middle wall of the ganglionic fold, and the optic ganglion itself. Owing to the way the cephalic lobes have developed, a cross section of the head shown in Fig. 4 will give a picture something like our imaginary one, only the middle wall of the fold has disappeared, and the inner one, the optic ganglion, is bent so as to appear like a thick, imperfect ring (Fig. 39).

The brain at this period consists of a medullary core enclosed in a thick layer of ganglion-cells. The latter are continued, without any perceptible modification or break, into those which constitute the optic ganglion, which, up to this time, contains no medullary core. From this time up to the latest stages, there is no way of distinguishing the parts of the optic ganglion except by their position, and the nerves which go from them to their respective ocular segments.

I have represented two more sections from a head a little younger than that in Fig. 6. The first (Fig. 35) passes through the upper edges of the first and second ocular segments, and shows, besides eyes I. and III., the anterior edge of the optic ganglion. In the next section below, not represented in the plate, the optic ganglion is seen in section as a circular mass of cells, apparently cut off from the brain by the invaginated ectoderm, *z.* It contains in the centre a round medulla, the downward continuation of the fibrous mass, *m. b.* in Fig. 35. The second section (Fig. 36) passes through about the middle of the first and second ocular segment, and just above the third. The ring of ganglion cells is now interrupted on its median edge, forming a narrow inlet into a central space lined with the cut ends of medullary fibrillae. The whole cavity is soon filled with a mass of fibres which develop into the medullary stalk of the optic ganglion, *s. o. g.*, which afterwards serves to connect the different ganglionic centres with the brain.

In all sections of the optic ganglion during the younger stages, its inner face is sharply defined, as though bounded by a delicate membrane, something like the basement membrane on the inner surface of ectodermic layers. In the older stages this membrane disappears, and the optic ganglion becomes a mass of loosely connected cells.

In the section shown in Fig. 36, and in those of the same series below it, the short bundles of nerve fibres connecting the optic ganglion with the eyes, pass completely through the ganglionic layer, at the inner surface of which they bend upwards, and pass through the centre of the ganglion into the brain.

MEDULLÆ OF THE OPTIC GANGLION. — It is necessary to understand the position and arrangement of the larval medullæ in order to comprehend the structure of the optic ganglion of the imago. They become definitely established soon after or during the rupture of the embryonic membranes, and may be studied in a series of sections (Figs. 42–47) cut from a head like that in Fig. 8.

The first section (Fig. 42) passes through the upper ends of eyes I. and III. and cuts through the optic ganglion at its junction with the brain, showing the cut ends of the medullary fibres as they bend from the brain down into the centre of the optic ganglion. After four more sections, we come to one (Fig. 43) passing through the upper end of the optic ganglion, in the centre of which is a circular mass of medullary substance bounded by a layer of minute dark cells, continuous with those surrounding the medulla of the brain.

In the fourth next section (Fig. 44) the optic ganglion appears as an oval mass of cells close beneath the optic plate. The roots of nerves I. and III., seen in longitudinal sections, are somewhat swollen and divided into two parts.

The fibres at the ends of the nerve roots turn upwards and pass into the stalk of the optic ganglion. Their cut ends do not lie on the inner surface of the ganglion, as during the earlier stage (Fig. 39), but in the centre. On the ventral side are seen medulla 3 and sections of the roots of the nerves supplying eyes V. and VI.

The next section (Fig. 45) passes through eye V., and shows its double nerve in longitudinal, and that of eye VI. in cross section. It is below the level of eyes I. and III., but shows eye II. and its minute nerve root with its adjacent large ganglion cell.

Fig. 47 represents a section passing through eye VI. and its nerve just as the latter bends at right angles. It is clothed with nerve cells up to the very base of the eye.

This series of sections shows the principal features of the optic ganglion at this stage. The parts are lettered in a way to show at once their relations to the eyes. They should be carefully examined and compared with Fig. 8, for a better understanding of the parts will be obtained in this way than by a long and tedious description.

Toward the close of embryonic life most of the nerve cells are situated on the dorsal surface of the ganglion, where the latter joins the brain.

In Fig. 48 is represented the optic ganglion as seen in a cross section of an embryo about ready to hatch. The section passed through the head between eyes II. and IV. showing a little of both. Fig. 8 represents a younger embryo than the one we have in mind, but it serves perfectly well to show the level of the section. As the head is bent at right angles to the body in such embryos, the section would be the same as a longitudinal, horizontal one of the larval head, Fig. 10. Again, the section we are about to describe would cut that shown in Fig. 49, taken, however, from an older head, just below the crown of ganglionic cells on its dorsal surface. At this period, the shape of the medullæ and the characteristic arrangement of the fibres in them can be studied to best advantage.

Suppose the side of the head to which belongs the optic ganglion we are describing, laid flat on the paper, opposite the section of the optic ganglion. An outline drawing of the eyes in this position would then be almost the exact mirror-image or "Spiegelbild," as the Germans call it, of the medullæ of the optic ganglion (Fig. 1, wood-cut).

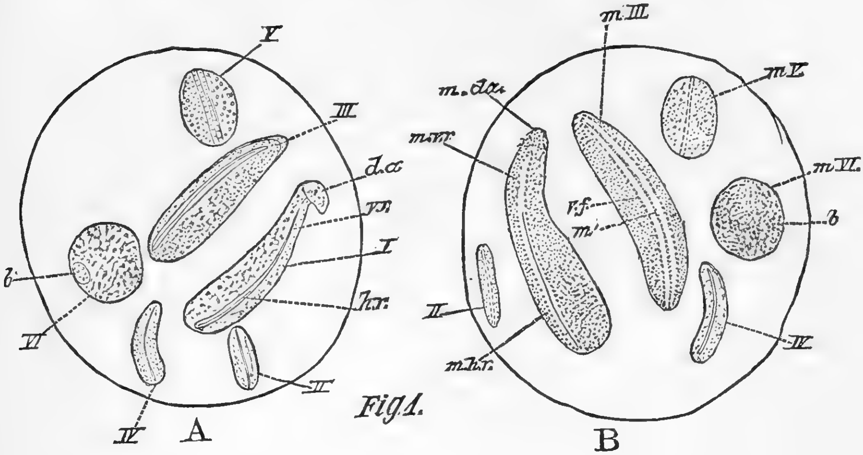


Figure 1. — A. Projection of the retinas just after the rupture of the embryonic membranes. B. Horizontal section of the optic ganglion during the same period. I.–VII. = eyes. 6 = cluster of inverted cells derived from sixth sense organ of eye VI.; *d. a.* = dorsal appendage; *h. r.* = horizontal retina; *v. r.* = vertical retina; *v. f.* = vertical fibre; m^1 = plate of medullary substance between the vertical fibres, corresponding to a similar plate in the retina. *m.* III. = medulla of eye III.; and *m. d. a.* = medulla of dorsal appendage, etc. The two cuts illustrate the correspondence between the structure of the medullæ and that of the retinas.

Medulla 3 (Fig. 48) is long and flat in section and somewhat pointed at the outermost end. It is divided into two unequal parts by a double row of coarse fibres. Between them is a clear space containing a long line of extremely fine medullary substance, which I have not succeeded in dissolving into fibrillæ, although I do not doubt it has such a structure from its great similarity to the medullary substance on either side of it. If we compare this part of the medulla with a horizontal section of the retinal furrow of eye III., we shall see (Fig. 59) that in both, there is a double row of coarse fibres seen in cross sections; the rows are separated by about the same distance, and between them is a thin layer of interwoven fibrillæ which in the retinal furrow are deeply pigmented.

On either side of the double row of cut fibres, there is a layer of felted fibrillæ, that on the posterior outer side being much thicker than the other. If we turn again to the retina of eye III., it will be seen that the part on the posterior side of the furrow is much broader than that on the opposite, and exceeds it in width by about as much as the posterior layer of fibrillæ in the medulla exceeds that on the anterior side. That this extraordinary correspondence between the structure of the eye and its medulla is no fanciful one, may be proved by referring to any other medulla. In each case, we shall find that *the structure of the medulla is like that of the retina to which it belongs.* For instance, in eye V. there are remnants of a median row of peculiar cells which undoubtedly represent the gigantic cells, such as those in eyes I. and III. In the embryos just ready to hatch, the medulla of eye V. is divided in the middle by a layer of coarse fibres, the cut ends of which are distinctly visible in cross sections, so that the outline of the medulla, with its median row of cross fibres, is the mirror-image of eye V. with its median row of cells. In the full-grown larva, the latter are much smaller and less conspicuous, and we find on turning to a section of the medulla that the median row of coarse fibres has degenerated in a corresponding degree.

In eye VI. the upright retinal cells are uniform in structure throughout, the median ridge seen in surface views of the younger stages having disappeared. But there is a remarkable bundle of inverted cells on the ventral side of the retina, and this peculiarity is expressed in the medulla of that eye by a small bundle of fibres in a corresponding position. Still again medulla I. shows by its configuration that it belongs to eye I. There is the narrow bent portion belonging to the vertical furrow, the broad inner part to the horizontal retina, and at the outermost end of the medulla is a small bundle of fibres belonging to the appendage. To complete the correspondence there are the three rows of fibres in the middle, just as described in medulla III., and on either side a layer of medullary substance, the thicker layer being on the anterior edge, corresponding to the greater width of the retina on that side of the furrow.

All the optic nerves are composed of coarse fibres arising from the medullæ. So far as it is possible to determine, each fibre is composed of the prolongation of the external and internal fibrillæ of the cell with which it is united. The latter are probably continued into the medullæ without losing their identity. *There is reason to believe, from the similarity in structure of the retina and the medullæ, that the fibrillæ of the latter are rearranged in a manner corresponding with that of the fibrillæ in the retinal cells.* Now if my supposition is correct, we ought to find in the medullæ of eye I., for example, systems of fibrillæ similar in number and arrangement to the retinidia of the retina. We find indications of such a condition, for there is a furrow in the medulla containing a double row of fibres, between which is a layer of very fine medullary substance. To make the comparison complete, the cross fibrillæ arising from the fibres ought to unite with distinct clusters of fibrillæ corresponding in composition and number with the retinidia on either side of the retinal furrow. But although we cannot distinguish these *medullary retinidia,* since all are united to form one continuous mass, there is reason to suppose they really exist, for, as we have shown above, where there is a break or any marked peculiarity in the arrangement of the retinal retinidia, we find a corresponding change in the structure of the medullæ. For example, if there are more rods and consequently more retinidia on one side of the retina, there is an increase in the thickness of the medulla on its corresponding side. If there is a bend in the retina, there is a similar one in the medulla. If there is a furrow in the retina, containing a double row of coarse fibres, there is a space in the medulla that also contains a double row of coarse fibres, and if the furrow is absent, the space is absent also; and we might enumerate a number of other peculiarities in the structure of the retina that had their counterpart in the medulla.

I am not prepared to discuss the conflicting hypotheses that have been advanced concerning the significance of the medullary substance, but I desire to call attention to the fact that its peculiar structure in *Acilius* may throw some light upon its function.

I venture to suggest the idea that occurred to me. The medullæ may be regarded as the retinas of the mind, the inner eyes, in which are reacted the nerve changes produced in the external ones. The whole apparatus may be compared to a telephone in which a vibration of the air produces a movement of the receiver, an intermittent flow of electricity follows, and finally, at some distant point, perhaps, a second vibration is produced exactly like the first. We may suppose that in the eye, light causes some change — it may be vibrations of the retinidial fibrillæ which are transmitted, not as vibrations, but as chemical changes, along the fibres of the optic nerve to the medullæ, where they give rise to other vibrations exactly like those produced in the eye. The changes aroused in each retinal cell are transmitted along a bundle of wires to the medullæ, where they are united in a proper sequence of time and place, which if we could see or hear, we should recognize as the same symphony of activities produced in the eye. An essential feature of the telephone is the similarity in structure and action of the two ends. It was the similarity in structure between the retina and the medullæ which led me to infer that the activities aroused in one must produce similar activities in the other.

The fibrillæ at the proximal ends of the medullæ unite to form the medullary stalk to the optic ganglion, which is continuous with the medullary substance of the brain. The medullæ of those eyes belonging to the same segment unite first, that is, medulla I. with II., III. with IV., and V. with VI., so that three stalks are formed, which almost immediately unite with one another to form the common stalk of the whole optic ganglion. Thus another intimation of the threefold structure of the optic ganglion is given.

On the dorsal surface of the young larval optic ganglion are some small, deeply stained cells, crowded together to form three ill-defined clusters, one on the side and dorsal surface of each of the three branches of the medullary stalk. The nerve cells send downwards single fibrous prolongations, which, after uniting with one another to form ill-defined bundles (Fig. 48, *p. n. f.*), pass to the sides of the medullæ where they appear to break up into fine fibrillæ. The latter issue from the distal end of the medullæ and immediately unite to form coarse fibres about the size of those which arise directly from the ganglionic cells. These fibres then unite in large bundles to form the optic nerves.

Between the medullæ are scattered cells, which in the younger stages cannot be distinguished from other cells in the brain and optic ganglion.

In the larvæ, however, after some modes of treatment, they appear to be much smaller and stain more deeply. They then resemble the small dark cells which immediately surround the medullæ of the brain and the ventral nerve cord.

The optic ganglion of the late embryonic, or early larval, stages does not undergo any noteworthy change until toward the beginning of the pupal period. I never succeeded in finding or raising pupæ, but feel confident that the oldest larvæ obtained had about reached that stage. A view of the dorsal surface of part of the brain and optic ganglion at this period is shown in Pl. IX., Fig. 40; and sections of it in Pl. X., Figs. 49 and 53.

In Fig. 40 we see beneath the crown of ganglion cells the faint outline of the medullæ, and still further below, the continuation of their distal ends into the optic nerves. The ganglion cells of the second segment, *o. g.*^{2}, now form a semicircular band that almost encloses the other two. They are recognized in sections by the clear protoplasm of their columnar cells (Figs. 49 and 50).

The cells of the third segment are crowded toward the brain, where they form a narrow collar around the stalk of the optic ganglion. Above the middle of the stalk, the band lies at the bottom of a cavity, the roof of which is formed by over-arching ganglion cells (Fig. 50, *o. g.*^{3}). Towards its anterior end it is wider and folded double (Fig. 49, *o. g.*^{3}). It is directly continuous on the one hand with the cells of the second segment, and on the other, with a broad layer of large scattering cells that fill up the space between it and the third segment (Figs. 40, 49 and 50).

Horizontal sections below the crown of nerve cells have a wedge-shaped outline in which the medullæ have much the same arrangement as in Fig. 48. Fig. 51 represents such a section at the posterior edge of which is shown a part of the second ganglion segment. A section a little above this (Fig. 52) shows part of the second and first segments, and finally a still more dorsal section (Fig. 53) shows the second and third.

In Figs. 49 and 50 the optic ganglion is seen in two vertical sections, the first, near the anterior edge, the second, near the middle. By comparing these sections with the surface view in Figs. 40 and 41, a fair idea will be obtained of the structure of the optic ganglion at the close of the larval period.

OPTIC NERVES. — In the younger embryonic stages, the fibres connecting the eyes with the optic ganglia are so intermingled with ganglion-cells that it is not easy to distinguish them from the optic ganglion. Even in the larval stages, when the optic ganglion is situated behind and some distance away from the eyes, the optic nerves are in places so ill-defined that it is difficult to follow them to the medullæ from which they arise.

The nerve to eye V. descends from the outer anterior edge of the optic ganglion, and after reaching the inner lower edge of eye III. turns nearly at right angles and runs forward to join the eye on its posterior dorsal face.

Nerve 6 is the most compact of all. Its root lies on the inside of that belonging to eye V. The two nerve roots extend downwards nearly parallel with each other to the lower edge of the ganglion; and then nerve 6 bends backwards, and sweeping around the lower posterior edge of eye I., terminates on the posterior edge of eye VI.

Nerves 1 and 3 extend downward and forward from the lower anterior edges of their respective medullæ as two great sheets of loose fibres. At the lower, inner edge of eye I., those of nerve 1 unite to form a more compact mass which suddenly bends outward and divides into five bundles, two of which run along the under side of the eye on either side of the retinal furrow. Two other bundles extend upward on either side of the vertical furrow. The fifth bundle extends upward to the dorsal appendage (Fig. 18).

The nerve to eye III. is similar to that of eye I. in shape and in the direction it follows. On reaching the eye it divides into two branches which extend parallel with each other along the under side of the retina.

In both eyes I. and III., fibres extend along the median under surface of the horizontal retinas, and finally bend upward to form, between the rows of gigantic cells, the vertical fibres.

There is nothing noteworthy about the course of nerves 2 and 4.

The relative positions, in the full-grown larva, of the nerves, the medullæ, and the eyes, throw some light on the relation of the eyes to one another.

It will be seen that in the later stages the medullæ show more clearly their primitive relations to one another than do the eyes. At this period, it is impossible to recognize which eyes belong to the same segment, or that there is any paired arrangement at all.

NEURILEMMA. — The brain, optic ganglion, nerves, and eyes are suspended or enclosed in a common envelope continuous with the basement membranes and derived from the ectoderm. During the youngest embryonic stages, the inner surface of the ectoderm, especially of the thickenings that give rise either to the eyes or nervous system, is covered by a delicate membrane which in the majority of cases is quite devoid of nuclei. When the eyes are invaginated, the membrane is pushed in likewise, but it is unaffected by the shifting of the cells to form the corneagen and the outer wall of the optic vesicle, and is continued from the indifferent ectoderm over the bulb of the eye to the optic nerve.

The neurilemma of the brain and optic ganglion is formed in a similar manner. As the ectodermic thickenings that give rise to these organs separate from the parent layer, they are suspended in a sort of sling formed by the basement membrane, which is distinctly nucleated where it surrounds the developing organs. As the latter separate from the ectoderm, the membrane surrounds, but does not completely enclose them, for at quite late periods one sees at certain places the two limbs of the membrane close together, suspending the brain, as the intestine in its mesentery, to the wall of the head (Pl. X., Figs. 43 and 44). Wherever the membrane is still attached to the surface ectoderm, the cells are drawn out into long fibres with nuclei at various heights. Some cells are entirely separated from the others, taking up a position on the outer surface of the membrane, in the formation of which they seem to take a part. As the outer surface of the basement membrane becomes the inner one of the neurilemma, we find that the nuclei of the latter, during embryonic life at least, are on its inner surface (Figs. 42 and 47).

In the adult larvæ, the suspending membranes are reduced to cords of fibres mixed with nuclei extending from the posterior, median edge of each brain lobe to the roof of the head.

In Figs. 42–47, are shown different stages in the formation of the neurilemma as seen in different parts of the head. In Figs. 42 and 43, its continuity with the basement membrane, and the drawn-out ectoderm cells are well shown, and in Fig. 45, the double membranes suspending each lobe of the brain.

The same membrane forms a common envelop for the distal end of the optic ganglion and the roots of the nerves, but beyond this point each nerve has a separate sheath.

In the full-grown larvæ, the neurilemma is thicker and laminated, with small flattened nuclei in the middle of the layer. I have seen some cases when it appears to be composed of two thin membranes with nuclei between.

ORIGIN OF GANGLION-CELLS.

During the earliest embryonic stages, the whole inner, distal edge of the optic plate is connected with the optic ganglion by a mass of tissue composed of fibres mixed with ganglion-cells. The connection is gradually broken everywhere except beneath each eye, where broad bands of tissue remain forming the rudiments of the optic nerves. It will be more convenient to follow the development of the ganglion-cells in eye V., since the different stages of this eye have been described and illustrated in most detail.

Near the connecting bridge of cells in Pl. XI., Fig. 61, *n. g. c.*, the ganglionic nuclei are smaller, cell boundaries have disappeared, and the tissue assumes an appearance more like that in the optic thickening. In fact, there is a gradual transition from the retinal cells to those of the optic ganglion. A careful examination shows that among the half-ganglion, half-retinal cells, are many fibres of varying size, some large enough to be parts of slender cells, others so minute that they are seen with difficulty. The larger fibres are the outer ends of newly formed ganglion-cells; the minute ones are similar parts of cells whose outer ends have been converted into true nerve fibres. Such a condition as this may be seen in sections of eyes from the stage shown in Fig. 4, Pl. VII., down to that in Fig. 1. In the older stages the tissue connecting the eyes and optic ganglion has become almost devoid of cells and is composed of closely packed fibres. The migration of sensory cells from the eye has nearly ceased, but one or two cells may still be seen, which, owing to their enormous size, offer special facilities for following the process in detail. In Fig. 62 is shown one of these cells just as it has reached the inner surface of the eye. It arose from one of the large nuclei found among the closely packed retinal ones, from which they are distinguished by their large size and coarsely granular contents. As these nuclei descend into the clear space at the inner surface of the eye they increase rapidly in size, and a great mass of finely granular protoplasm collects around them so that they become very conspicuous objects in sections of the eye at this period. The cells are distinctly tripolar. One of the prolongations is always directed outwards. Its base, which is broad and filled with protoplasm like that in the cell, is continuous with a tube-like prolongation. Owing to its wavy course and to its clear contents, which cause it to stand out clearly against the dark protoplasm of the retinal cells, it is not difficult to follow this tube a considerable distance into the tissues of the eye, where it is finally reduced to a thin refractive fibre that disappears between the retinal cells. The two inner prolongations do not become visible until the cell has reached the innermost part of the eye. They are less conspicuous than the one just described, for they are smaller, and the dark protoplasm extends into them a short distance only. They usually arise from opposite sides of the inner surface of the cell and extend in opposite directions at right angles to the outer fibre. But there is considerable irregularity in the position of the fibres. In some cases it looks as though the nucleus moved inward faster than the rest of the cell, leaving the inner fibres behind. It frequently happens that the latter are directed at right angles to the section plane; the cell then assumes a shape like that in Fig. 82. One often sees a cluster of four or five enormous cells midway between the eye and the optic ganglion (Fig. 63, *n. g. c.*). Most of these cells are converted by rapid division into small pear-shaped ones which gradually move inwards along the optic nerve, forcing a way for themselves between the fibres, until they are finally lost among the similar cells of the optic ganglion. But one of the cells retains its great size. When it reaches the optic ganglion, it is pushed to one side, out of the nerve root; its inner end is swung outward toward the periphery of the ganglion and the outer prolongation, which is now more conspicuous than ever, is bent almost double. Between the bend and the cell itself, the prolongation is filled with dark granular protoplasm. Beyond the bend it is reduced to a coarse, colorless, and refractive fibre that may be followed outward into the eye. As development goes on, the bend of the fibre is carried more and more into the optic ganglion until it reaches the medulla, where it becomes hyaline and refractive and breaks up into a tuft of a dozen or more fibrillæ that extend along the sides of the medulla and then turning inward, disappear (Fig. 48).

The outer end of the cell is somewhat flattened, and on either side is continued into a tube-like prolongation with clear, homogeneous contents. In the centre of the tube, I have seen on several occasions what appeared to be a small fibre, but cannot say positively that it was such. The protoplasm of the cell protrudes a little near the mouth of the tube, but is not continued into it.

These tubes, or fibres, are difficult to follow, and I have only succeeded in doing so in a few cases, and then not very far. They extend, at right angles to the great inner stalk, in opposite directions along the under surface of the neurilemma, and I should judge they served to connect the ganglion-cells with one another. I see no reason to suppose they extend into the medullæ; they do not run in that direction, and no fibres were seen running into the medullæ that could not be referred to the stalk-like prolongations of the ganglion-cells.

The gigantic ganglion-cells continue to divide, but with decreasing frequency, up to about the time of hatching. At that period, there is usually but one cell of enormous dimensions on the side of each medulla. Their position, size, and shape, as shown in Fig. 48, are very constant. In rare cases, there may be in the larvæ two large cells side by side, one a little smaller than the other. In the full-grown larvæ, the cells are proportionally smaller and less conspicuous.

In Fig. 48 is shown a pair of ganglion-cells placed end to end, and easily distinguishable from the surrounding ones by their peculiar shape. There was an exactly similar pair in the optic ganglion on the other side of the head, and I have also seen them in one or two other cases, so that I do not doubt that they are usually present during these stages.

There is a singular modification of the sixth gigantic ganglion-cell, in that its inward prolongation is divided into two branches, one of which is continued half way across the optic ganglion to the fifth medulla.

There are some minute fibres scattered about among the cells of the cortical layer, that I cannot trace to distinct cells. They are seen running in an irregular manner from one cell to another, or from the cortical layer to the neurilemma. They often extend over the surface of the large cells branching in all directions (Pl. X., Fig. 48). They are not numerous enough to form a sheath or envelop about the cells, such as that so frequently described in the Annelids, although it is not improbable that they belong to the same category. They may possibly arise from the small, dark cells, sometimes called the inner neurilemma, that form an investment for the medulla, and which are specially well developed in the brain and ventral nerve chord.

The fact that a not inconsiderable number of the ganglion-cells arise directly from the gigantic, tripolar ones might lead one to suppose that all the cells of the optic ganglion were tripolar and differed from the large ones only in size. All that one can actually observe points towards this conclusion.

In my paper on the eyes of Vespa, page 198, attention was called to certain conical or pear-shaped ganglion-cells at the inner edge of the middle lobe of the optic ganglion, and it was stated that some of the conical ones were possibly tripolar, for indications of two prolongations at the broad distal ends of such cells had occasionally been seen. A re-examination has led me to believe that all of them are tripolar, like the large ones in Acilius. Their deceptive, unipolar habitus is due to the great size of the inner prolongation as compared with the very delicate outer ones.

As there is no reason to suppose that more than one kind of cell is present in the cortical layer of the optic ganglion, — we do not include the minute, dark cells surrounding the medullæ, or those interspersed among the fibres of the optic nerves, concerning whose minute structure we are ignorant, — and in consideration of the facts we have presented concerning the origin of ganglion-cells, we have arrived at the following conclusion: *The cortical layers of the optic ganglia are composed of large and small tripolar ganglion-cells. The large, inward prolongation of each of these cells is filled with granular protoplasm continuous with that in the cell body, and represents a part of the outer end* *of a formerly sensory cell lodged in the ectoderm, or of one derived by division from such a cell. In passing through the medulla this prolongation breaks up into a bundle of fibrillæ. The other two prolongations are small, and contain no granular protoplasm; they arise from the opposite sides of the broad end of the pear-shaped cells and, extending in opposite directions, probably serve to unite the ganglion-cells with one another.*

COMPARATIVE ANATOMY OF THE OPTIC GANGLION.

Although some work has recently been done on the development of the Arthropod eyes, the optic ganglion, both of the convex eyes and ocelli, has received little notice. It has been stated that it arises either as an invagination of the ectoderm near the eyes, or as an outgrowth of the brain. Both Bobretzsky and Reichenbach have failed to produce satisfactory evidence to show that what they regarded as the developing optic ganglion really was such. Reichenbach made the fatal mistake of neglecting to follow his optic invagination up to a point where its real nature would be apparent. Had he done so, he would not have mistaken the retinal ganglion for the layer of rhabdoms and retinulæ, and he would have seen that his crystalline-cone layer was the whole ommateum. In my paper upon the eyes of Vespa, I maintained that Reichenbach had misinterpreted the facts. I have recently examined, by means of sections and surface views, the head of *Astacus*, and find my objections sustained.

It is not my intention to enter here into a long account of the comparative anatomy of the optic ganglion of Arthropods, for the subject is worthy of separate consideration. I merely desire to state the main conclusions to which I have been led by a study of the development of the optic ganglion in such groups of Arthropods as the Isopods, Decapods, Hymenoptera, Lepidoptera, and Coleoptera.

In Vespa, it was shown that on the dorsal edge of the optic thickening a great mass of cells was pushed inward to form the rudiment of the optic ganglion. This mass of cells, which from the very earliest stages is connected with the ventral edge of the optic thickening, after invagination divides into three lobes, which immediately arrange themselves in a line connecting the eye and brain. The middle lobe develops into the optic ganglion of the adult; the outer, into a layer of cells which, during the earlier stages, form, around the outer edge of the median lobe, a semicircular band, conspicuous on account of the peculiar character of its cells (Fig. 2, wood-cut). The inner lobe, which likewise disappears during the later stages, forms a characteristically shaped layer of dark cells on the proximal side of the median one. It is over-arched by the cells of the brain in such a way that it appears to form the floor of an oblong cavity. Each lobe, except the outer one, contains a great medullary core.

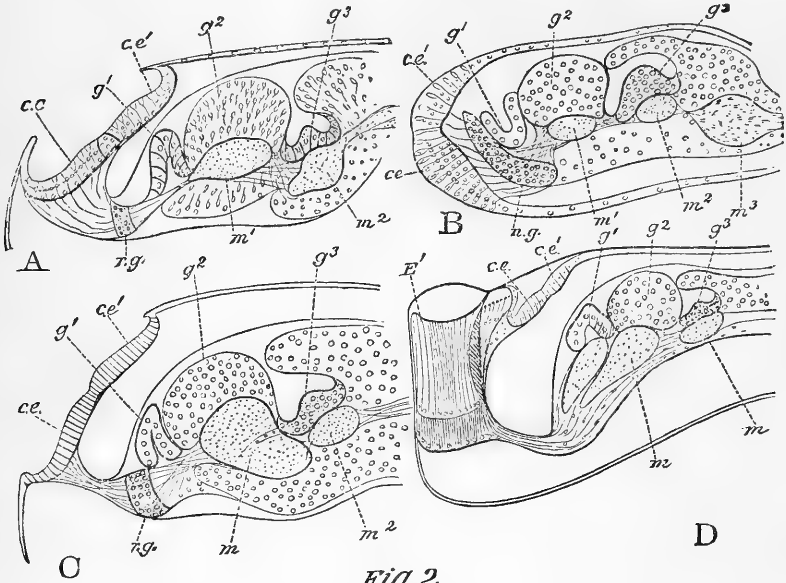


Fig. 2.

Figure 2.— Semi-diagrammatic views of the optic ganglion of:

(*A*) *Vespa*, towards the close of the larval stage, (*B*) *Astacus*, (*C*) *Cecropia*, beginning of pupal stage; (*D*) *Acilius*, close of larval stage,— showing the position of the retinal ganglion and the three lobes of the imaginal optic ganglion.

E. Eye I. of *Acilius*; *c. e.* ventral half, *c. e.*^{1} dorsal half of convex eye; g^{1-3} lobes of optic ganglion; m^{1-3} medullæ of same; *r. g.* retinal ganglion.

The retinal ganglion arises at a comparatively late period, not by invagination, but by the formation of a layer of ganglion-cells among the fibres connecting the optic ganglion with the eye.

In Astacus (Fig. 2, B.), the optic ganglion, after invagination, breaks up into three lobes. The outer one is formed of a folded layer of clear cells, Reichenbach's "*Augenfalte.*" The shape, position, and structure of this fold, and the manner in which it degenerates and disappears, leave little room to doubt that it is homologous with the outer lobe of the optic ganglion of Vespa. The fact that in Astacus this layer is folded as if formed by invagination is an incidental and secondary condition. In Vespa, Cecropia, and Acilius the direction of the infolding is reversed.

The middle lobe is relatively smaller in Astacus than in Vespa; from it arises the epiopticon of Hickson, or the second optic ganglion of Carriere. This lobe contains an oval medulla, from the outer end of which arise decussating fibres that extend into the retinal ganglion. The inner lobe of Astacus, unlike that of Vespa, develops into a distinct ganglion, with a medulla and cortical layer of ganglion-cells like those in the median lobe, but darker colored. It is over-arched by a thick layer of cells arising from the cortical layer of the stalk of the optic ganglion.

The distal end of the stalk is enlarged, and apparently forms a third medulla, the minute structure of which is quite different from that of the other two.

On the outer side of the first lobe is a layer of small, dark ganglion-cells, which Reichenbach regarded as the outer wall of his "*Augenfalte,*" and which he maintained gave rise to the layer of retinulæ and rhabdoms. But this layer of cells is really the *retinal ganglion,* and is formed, as in Vespa, by the development, some time after the ganglionic invagination, of a layer of cells among the fibres connecting the optic ganglion with the eye.

Among *Isopods* I have examined the optic ganglion of *Cymothoa,* and find that in development and structure it does not differ from that of Astacus in any particulars that concern us at present.

No extended observations were made on the optic ganglion of the larvæ of *Cecropia.* I can only say that it has a superficial resemblance to that of Acilius, but it is much smaller and less perfectly developed. Toward the beginning of pupal life, the optic ganglion increases enormously in size and assumes a structure very much like that of *Vespa* (Fig. 2, C.). The resemblance between the optic ganglion of Vespa and Cecropia is sufficiently evident to render a detailed description unnecessary. In the later stages both the inner and outer lobes disappear or are reduced to mere insignificant appendages, and the cells at the base of the optic nerve develop into a large retinal ganglion. The main portion of the optic ganglion arises from the middle lobe.

The similarity in the structure of the optic ganglion of these distantly related genera shows that the optic ganglion of the convex eye of Insects is homologous with that of Crustacea, and that in both groups its structure may be reduced to the same plan. *The variations in the structure of the optic ganglion of Arthropods may be referred to the modification, development, or suppression of one or more of three lobes, to which may be subsequently added the retinal ganglion.* What is the meaning of the three lobes so constantly present, at one stage or another, in the optic ganglion of Arthropods? It would be difficult to form a fruitful hypothesis of their significance from a study of forms that do not pass through an active larval existence, for we now know that the optic ganglion of the imago is derived from a larval ganglion, which in some cases is highly complicated, and has itself a long story to tell. In Astacus, Cymothoa, etc., the convex eye and its optic ganglion appear at a period corresponding with the end of the larval stage. Hence we must look for the preliminary stages of the optic ganglion in the larvæ and embryos of such forms as Acilius; and there we may expect to find a solution of the three-lobed structure of the ganglion of the convex eye.

We have already seen how, in the earliest stages of Acilius, the optic plate is composed of three segments, each bearing a pair of eyes, and on the dorsal side of each segment there is a ganglionic invagination.

The three masses of ganglion-cells thus produced unite to form the larval ganglion. Toward the close of larval life, each segment increases rapidly in size; the third segment grows around the proximal side of the ganglion to form the inner lobe, the second forms the fold around the anterior edge of the ganglion, or the outer lobe, and the first forms the posterior inner mass of the ganglion, or the middle lobe of the future ganglion of the convex eye.

At the beginning of pupal life, the ocelli are drawn towards the brain, and are replaced by the convex eye, which unites with the larval ganglion in a way that I do not yet understand.

From these facts we may infer that *the three-lobed optic gan-*

glion of the convex eye of Arthropods is derived from a three-segmented, larval ganglion, each segment of which belongs to a pair of larval ocelli.

III. SUMMARY AND COMPARISON.

The great nucleus that figures so prominently in the early stages is not the least remarkable feature of the eyes of Acilius. So far as my knowledge goes, it is without parallel and inexplicable.

In eyes II., III., IV., and V., there is a single nucleus in the middle of the retina, between the two rows of gigantic cells, that remains unaltered through life. In eye I. there are at least two of these nuclei, one in the horizontal, and one in the vertical furrow. In eye VI. the nucleus is only present a short time during the earliest stages. In all the eyes the large nucleus seems to be situated in the centre of a group of four sensory pits.

Kleinenberg has described in *Asterope* a gigantic, flask-shaped cell that secretes the vitreous substance filling the cavity of the optic vesicle. But there is probably only a superficial resemblance between this cell and that in the eye of Acilius.

The reader has no doubt been impressed by the presence of horizontal rods in the eyes of Acilius, as well as by the fact that *the rod mosaic varies in a constant manner, according to the inclination of the retinal cells.* All the horizontal rods, large or small, are flat, and arranged in long, parallel rows. The semi-upright ones form, in cross sections, zigzag lines, and the upright rods are bent so as to form the sides of regular hexagonal figures. Why are the horizontal rods invariably arranged in parallel lines? As the rods are mere frames for the support of nerve fibrillæ, it must be, no doubt, because in this way the fibrillæ are most advantageously arranged for the reception of light stimuli. In my paper upon the "Eyes of Molluscs and Arthropods," page 652, the statement was made that the perfection of a visual organ was dependent, among other things, upon the degree to which the retinidial fibrillæ have become perpendicular to the rays of light. At that time I did not think it probable that there were horizontal rods, as stated by Grenacher, in the eyes of Myriapods. It must be evident now from my description of horizontal rods in Acilius that there is no longer any reason for me to doubt the accuracy of that part of Grenacher's account.

When I became convinced that most of the rods of Acilius were horizontal, it seemed at first as though the above-mentioned view concerning the direction of the retinidial fibrillæ would have to be abandoned, for here were undoubtedly highly specialized eyes in which as many retinidial fibrillæ were parallel with the rays of light as at right angles to them, provided they radiated in all directions from an axial nerve. In *Pecten, e.g.*, (Fig. 5, A.), we have cylindrical vertical rods containing axial nerves, from which radiate nerve fibrillæ in all directions. All the fibrillæ are consequently at right angles to the rays of light. But put the rod in a horizontal position, and just as many fibrillæ will be vertical as horizontal. In order to bring these horizontal rods into harmony with my theory of nerve endings, it is requisite that the rods should be flattened, and of course so that the long diameter is vertical. Then if the axial fibres, instead of forming a single bundle, as in the cylindrical rods, should form a transverse row (Fig. 5, B.), fibrillæ could arise from them, nearly all of which would be at right angles to the rays of light. If the rod were broad and very much flattened, and the upper and lower sides disappeared, then all the fibrillæ would be at right angles to the rays of light (Fig. 5, C.). In *Acilius all the horizontal rods fulfil the above requirements; they have exactly the structure they ought to have, and the only one they could have, to bring their retinidial fibrillæ at right angles to the rays of light; therefore, instead of horizontal rods being fatal to my theory of nerve endings, they afford by their arrangement convincing evidence in favor of it.* For those who believe that the nerve fibres described by me are the product of coagulation, or, perhaps of the imagination, may not be so ready to push lightly aside the evidence which the structure of the horizontal rods affords. It certainly is remarkable that in Acilius, whose eyes show as wide differences in structure as we could expect to find between any larval ocelli of Insects, the horizontal rods should invariably assume the only shape that would permit all the retinidial fibrillæ to be at right angles to the rays of light.

A vertical section of a pair of broad horizontal rods would give an outline exactly like that formed by a similar section of upright ones, except that in the first case between each pair would be the cut ends of a row of axial nerves, and in the second, a bundle of vertical nerve fibres (Fig. 5, C. and D.).

Some observations have been made upon the eyes of other insect larvæ. With one or two exceptions, nothing was found that I care to speak of here. When enough material has been obtained, it is possible that I may be able to give a more extended comparative account of the larval ocelli of insects than I desire, or am able, to do now.

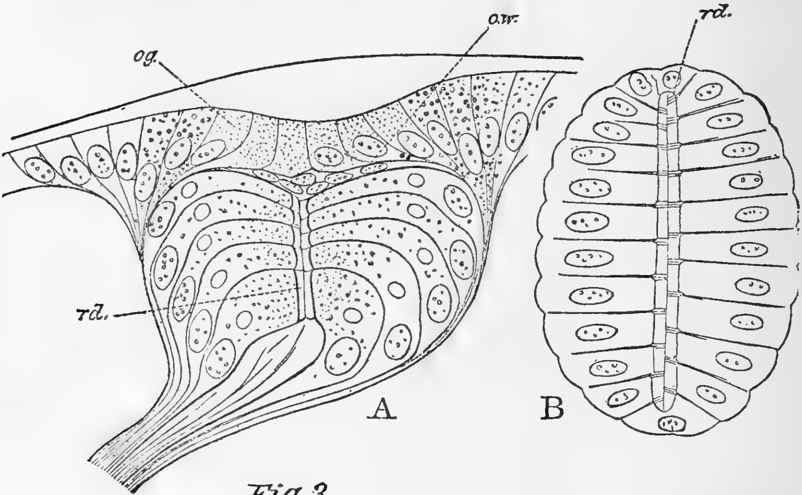


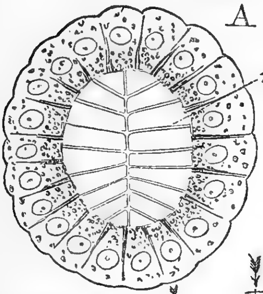
Fig. 3.

Figure 3.—Vertical (*A*) and horizontal (*B*) section of a Hydrophilus larva about 7 mm. long. *cg.* corneagen; *o. w.* outer wall of the optic vesicle; *rd.* rods.

The eyes in the young larvæ of both *Hydrophilus* and *Dytiscus* are much alike. In the woodcut (Fig. 3) is represented a section of the eye of a Hydrophilus larva about 8 mm. long. We perceive at once the fundamental differences in the construction of this eye and that shown in Grenacher's well-known figure of the young larval ocellus of Dytiscus. First, there are three distinct layers in my figure produced by the invagination of an optic vesicle. The outer wall of the vesicle is represented by a cluster of small, deeply stained nuclei over the centre of the retina. The latter is composed, not of upright cells, as Grenacher has it, but of horizontal ones, bearing short horizontal rods. The latter form a thin oblong and vertical plate in the middle of the retina. In this respect also, Grenacher's figure is incorrect, since it represents a broad layer of long upright rods, whereas no such structures are present.

The eye of Hydrophilus, as shown in the woodcut, is much like that of eyes II. and IV. of Acilius, even to the presence of the large retinal cells at the bottom of the furrow.

Fig. 4.



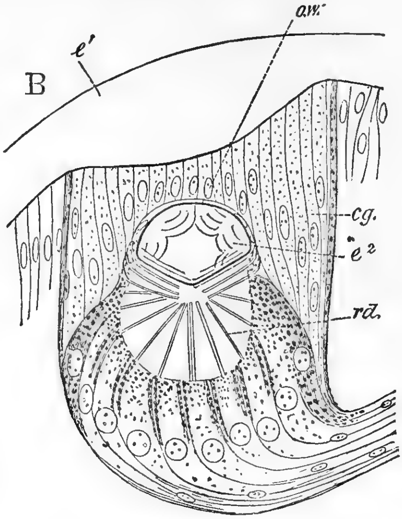


Fig. 5.

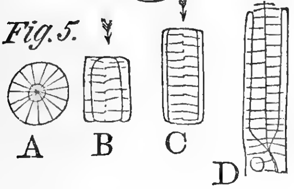


Figure 4. — Horizontal (*A*) and vertical (*B*) section of the larval eye of a neuropterous larva, *Chauliodes* (?). *cg.* corneagen; l^1, l^2, inner and outer lenses; *o. w.* outer wall of the optic vesicle; *rd.* rods.

Figure 5. — Diagrammatic views of the retinidial fibrillæ in upright and horizontal rods. *A.* cross section of rods of *Pecten; B.* same of small horizontal rods of *Acilius; C.* same of large rods, and *D.* longitudinal section of upright rods in eye V. The arrows indicate the direction of the light.

In Fig. 4 is shown a section through the eye of what I took to be a full-grown larva of *Chauliodes*, but I am by no means certain that it is such. Expecting to obtain more material, all but the heads were thrown away, and now I have no means of identifying the larvæ.

I have represented a section of the eye because it showed an interesting modification of the three-layered ocellus. There seem to have been present both upright and inverted retinal cells, as in eyes V. and VI. of Acilius, but the latter, instead of retaining their inverted rods have converted them into a cuticular, nerveless mass that has assumed the function of an inner lens something like that in *Peripatus.* On the inner surface of the lens, we can still see some of the inverted rods that have not quite lost their identity. The outer surface of the lens is surrounded by a membrane, between which and the lens are a few scattered nuclei. The latter are continuous with those of the retina. In vertical sections, the rods appear to be upright, but cross sections show that they are horizontal and arranged in a double row in a nearly circular space surrounded by the pigmented ends of the retinal cells.

The optic vesicle is covered by a corneagen composed of a thick layer of colorless, columnar cells with distinctly stained nuclei. On the periphery of the corneagen is a thin layer of pigment.

MYRIAPODS. — There are many important points in which the larval ocelli of Insects resemble those of Myriapods, and I venture to assert we shall find a still greater resemblance when a better knowledge of the structure and arrangement of the rods in the latter group has been obtained.

The material upon which Grenacher made his observations had been hardened in alcohol only, and as he himself had occasion to repeat, there was much to be desired, especially in the preservation of the rods. In only two instances was a clear picture of the rod mosaic obtained: in Cormocephalus, where they were cylindrical tubes; and in Scutigera, where they were flattened much like those of Acilius. If, after re-examination of properly prepared material, the first case should still stand, it would offset the significance that I attached to the flattened rods in Acilius. But there are not inconsiderable reasons for doubting that it will stand, for in Acilius the flattened rods when hardened in alcohol sometimes appear like cylindrical tubes. In other cases the rods were so poorly outlined that Grenacher was always in doubt as to their structure; indeed, in some instances he could go no farther than to assert that they were rods.

Besides the similarity in the possession of horizontal rods, one that is all the more striking since these remarkable structures are at present only known in the two groups we are discussing, there are many minor points in which the ocelli of Insects resemble those of Myriapods. The resemblance is striking when we compare eyes II. and IV. of Acilius with those of Iulus or of Heterostoma.

The retinal pigment is in both cases most abundant at the outer ends of the retinophoræ, and is confined to the outside of the cell. At least on p. 437 Grenacher states that in the Scolopendriden, if we may regard the condition in Cormocephalus as normal, the pigment appears "in der Mantelfläche der Zellen abgelagert zu sein, und die innern Theile derselben freizulassen." My sections show just such figures as he represents in Fig. 6, except that in my judgment the pigment in Acilius and Dytiscus is outside the cell wall instead of inside.

A peculiar feature of Acilius is that in the younger stages all the eyes are elongated in the direction of the retinal furrow, and this condition is more or less conspicuous in the larvæ of Dytiscus, Hydrophilus, Colymbetes, Psephenus, and Gyrinnus. There is a similar elongation of the retina in Iulus.

One of the most striking points in the less specialized eyes of Acilius is the great notch at the bottom of the eye containing the broad rods of the gigantic cells. Grenacher has shown in Scolopendra a similar notch, and there are strong reasons for believing that it contains a double row of large cells. I think it probable that in Scolopendra, as in the first four eyes of Acilius, all the originally horizontal retinal cells, except the large ones at the bottom, have gradually withdrawn from the median plane of the eye to form a concave layer of nearly upright rods.

When it is urged that Grenacher saw no such gigantic cells, and that there is no indication of them in his drawings, we shall answer that the same thing might be said of his description of the eyes of Acilius, and yet a casual examination of depigmented sections will show at once that such cells are there.

When we compare the retina of Heterostoma (Fig. 4) with that of eyes II. and IV., we cannot withhold the suspicion that in the retina of this Myriapod there is also a double row of large cells, and that their gigantic rods were provided with horizontal external nerve fibres which had been mistaken for the dividing lines between many small superimposed rods.[1] If this be so, then Grenacher's "*Haarzellen*" are probably ordinary retinal

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[1] At one time I also regarded these markings in Acilius as the divisions between small rods.

cells with double horizontal rods, and the so-called hairs are the external nerves of these rods. In sections parallel with the broad surface of the rods of Acilius, the external nerves are conspicuous, and in alcoholic material they appear like hairs, or at any rate might give rise to the impression that each cell was provided with a number of slender rods. That these external nerves are probably present in Myriapods is shown by the fact that Grenacher, p. 456, has himself described in the large flat rods of Scrutigera a set of cross striations which he says recall the "*Plättchenstructur*" so frequently described in the rods of Arthropods, and he even hints that there may be some connection between this fact and the hair-like rods in the eyes of Myriapods.

Finally, in his Fig. 14, is shown a semi-transverse section of the retina of Glomeris, where the hair-like rods are united in groups that would correspond very closely to the flattened rods of Acilius, and even in his vertical sections we see indications of the same thing.

The bodies projecting beyond the pigment layer in his Fig. 1, look more like a layer of short rods than the ends of cells, as he calls them. There is no other instance to my knowledge where only the outer ends of retinal cells are free from pigment. I regard them as rods, and support this interpretation mainly on the fact that Grenacher represents them as extending into the notch at the bottom of the eye.

But what shall be done with the layer of rods in his first figure? I should regard it as a corneagen, which like that in Acilius had lost its nuclei, if in Fig. 2 both a corneagen and this striated layer were not present. If we do not accept Grenacher's interpretation, no course appears to be open except to consider the outer layer of Fig. 2 as a corneagen, and the middle one, if it is really a separate layer, as the outer wall of an optic vesicle, which forms in this case a vitreous, striated body comparable to that in Chauliodes (Fig. 3) or with that in the cavity of the optic vesicle of Peripatus.

That there is a tendency to form two kinds of rods in Myriapods is clearly shown in Grenacher's drawing of the eye of Heterostoma (Fig. 4). We might expect to find the outer rods short and upright as in the eyes II. and IV. of Acilius, although

Grenacher maintains that they are horizontal like the others, but much longer.

Eye I. of Acilius is the largest and most complicated, and as there are several instances in which the posterior dorsal ocellus of other Insect larvæ is conspicuous on account of its greater size, it may be well to mention that a similar condition is to be found in Lithobius, for Grenacher says, p. 441, "Die Einselaugen sind unter sich nicht völlig gleich gross ; auffällig ist freilich nur die uberwiegenden Grösse der jenseite am meisten nach hinten gelegenen."

We have tried to show above: *That there is a striking resemblance between the eyes of Myriapods and those of larval Insects,* (1) *in the pigmentation of the retinal cells ;* (2) *in the shape of the retina ;* (3) *in the presence of a retinal furrow, and* (4) *and* (5) *in the probable presence of dimorphic retinal cells and rods, some of which are horizontal and others upright. This similarity is all the more important since we seek in vain for any special points of resemblance between the larval ocelli of Insects and those of Crustacea or Arachnids.* Even if it should be shown that the retinal cells in Spiders and Scorpions are upright, there would still be a great difference between the ocelli of Insects and those of these groups, for the presence of upright rods in both instances is in itself too general a feature to be of much importance in determining affinities, and there is no trace whatever in Scorpions, Crustacea, or Spiders of those peculiar features, such as horizontal rods, retinal furrow, and dimorphic retinal cells, that are common to Insect larvæ and Myriapods.

SPIDERS AND SCORPIONS. — Although both Graber and Sograff maintain that the eyes of Myriapods and the ocelli of Insects and Spiders have essentially the same structure, it is probable that both writers based their opinions solely on the fact that in all these cases the eyes were composed of two layers. But granting that such a condition prevails, very little is gained thereby, for it leaves out of account altogether the fundamental differences in the structure of the retinas.

In spite of the recent contributions to our knowledge of the eyes of Arachnids, by Schwemkewitz, Bertkau, Locy, Mark, and Parker, we are still much in the dark concerning the structure and development of these eyes.

Locy maintained that the ocelli of Spiders were formed of invaginated vesicles, the outer walls of which became the retinas.

Mark, in discussing the various theories that had been advanced to account for the origin of the retina and its method of formation, says, p. 54, that Locy's observations "seem adequate to settle these conflicting views — so far at least as regards the spider-like type." Great stress is laid upon the inversion of the retina in Spiders, for he says (p. 54), "The inversion of the retina proper is a fact of broader significance than would at first sight appear, and it affords a satisfactory explanation of some of the points in the anatomy and histology of simple eyes which have been so earnestly discussed during the past few years." And a little farther on he intimates that it is doubtful if any Monomeniscus Arthropod eyes contain upright retinas. In fact, the main purpose of his paper is to show that the Arthropod ocelli are constructed on the "Spider-like type," that is, of three layers, the inverted middle one forming the retina. Wherever in the ocelli of Arachnids, Myriapods, and Insects there is evidence of a post-retinal layer and a "*lentigen*" with a retina between, Professor Mark would infer that the eye originated as in Spiders, and he seems to have found evidence of one or more of these structures in the eyes of Myriapods and Scorpions and in the larval and frontal ocelli of Insects.

In the present state of our knowledge, the larval and frontal ocelli of Insects cannot be made to fit this theory; certainly not in Acilius and Vespa, the two cases to which Professor Mark gives especial attention. In Vespa, I have shown since his paper was published that the frontal ocelli were derived from open-mouthed pits, the inner wall of which gave rise to the retina.

The eyes of Myriapods are so much like those of Coleopterous larvæ that there is every reason to suppose they develop in the same way.

It would not be safe to conclude from Parker's observations that the retina of the median eyes of Scorpions is inverted, since they do not extend to sufficiently young stages. But, according to his observations, the lateral eyes are single-layered, and consequently the retinal cells are upright. Professor Mark regards the retinal cells in the median eyes as inverted, and since the rods and nerve fibres do not indicate any such inversion, he is forced to assume not only that the nerve fibres have shifted their attachment from one end of the cell to the other, but that new rods have been developed at those ends of the cells where, according to all experience, rods are never found. His supposition, which implies that inverted rods are not favorable to perfect vision, which pretends that, in some unexplained manner, upright rods get into an unfavorable position, and then forces us to assume a fundamental upheaval of primitive relations in order to bring them back to what is practically their original condition, is, in my opinion, at present unnecessary. Even after making this sacrifice of preconceived ideas, the way is no clearer than before, since we have imposed upon ourselves the difficult task of explaining why these supposed inverted retinal cells are exactly like the upright ones of the lateral eye!

I may be permitted to call attention to one or two facts that will perhaps be of service to those who think it necessary to make further observations on the eyes of Spiders. My observations on the eyes of Astacus, Cymothoa, Vespa, and Acilius leave no room to doubt that there are two invaginations connected with the eyes: one to form the optic vesicle; another, the optic ganglion. The presence of two such invaginations in types so widely separated suggest that a similar condition prevails in Arachnids. If this be so, where is the ganglionic invagination? Is it possible that the ganglionic and optic invaginations have been confused as in Astacus and Crangon, and the conclusions vitiated thereby?

The second point I wish to mention is more of a theoretical nature, and has to do with the causes of inversion. Professor Mark has suggested that the primitive eye was a laterally flattened cup, with a lens over the slit-like opening, and that either the cup was bent to one side, so that the broad surface of one wall was folded against the lens, or a second lens had been formed, bringing light to the retina from a new direction, and this led to the development of the retina from that wall of the pit next the new lens. In either case the final result would be the formation of a three-layered eye, the middle layer of which developed into the retina. A simpler explanation is suggested by the condition in eye V. of Acilius, where there are both inverted and upright rods; in such an eye it would be a simple matter to develop the inverted cells at the expense of the upright ones. The degenerated retinal cells could then be transformed into the tapetal matrix, the retinal cells producing tapetal scales instead of rods, as the inverted retinal cells in Chauliodes give rise to the inner lens. If this be true, then the tapetal slit might be compared to the median furrow in the retinas of Acilius.

A probable instance of such a method of inversion is found in Pecten, whose inverted rods I derived from the outer wall of an optic vesicle, by supposing that partially inverted and upright rods existed at the same time; eye V. of Acilius furnishes us with a needed example of such an eye. Moreover, in Pecten there is evidence that the inner wall was derived from a retina, the retinophoræ of which were transformed into the argentea or reflector, and the ganglion-cells into the red pigment layer. Such a transformation of the optic vesicle of Spiders would harmonize with Bertkau's description of the tapetal eyes, or "*Nebenaugen.*" The anatomy of the non-tapetal ones, as far as known, would lead one to believe the retina is composed of upright cells, while embryology says they are inverted.[1]

In the earliest stages of Acilius, the eyes are composed of several sensory pits, each with its cuticular thickening and nerve. It is possible that in the Arachnids the numerous nerve bundles supplying the eyes, such as figured by Grenacher for Lycosa (Pl. III., Fig. 22), might owe their existence to the fact that these eyes also were formed by the fusion of several sense organs.

We might change the eyes of Acilius into the Aranean type by suppressing the eyes of the third segment and inverting the retinas in all but the large posterior pair. The latter would then become the "*Hauptaugen*" of Spiders, and the smaller ones with inverted retinas the "*Nebenaugen.*"

The failure to form, either by speculation or observation, an adequate notion of the origin of the retina in Arthropods has long stood in the way of a satisfactory explanation of the various structural forms these eyes assume. It was not possible to treat the subject comprehensively and systematically while still in

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[1] It is difficult to understand Bertkau's statement that his observations confirm those of Grenacher. There certainly is a great difference between his drawings of the tapetal eyes and those of Grenacher.

doubt as to whether the retina arose from the hypodermis or from the brain, or from neither; or while that organ sometimes called the optic ganglion, in the absence of all evidence, might be regarded as a retina, a retinal ganglion, the brain, an outgrowth of the brain, or an optic nerve, or whatever else might commend itself to the imagination of the investigator.

There were the one-layered, the two-layered, and the three-layered eyes, one with upright, another with inverted, another with horizontal rods. The structure of one eye was as intelligible as that of another; no more, no less. There was no unit of measure.

It was inferred in "Eyes of Molluscs and Arthropods" that the ground plan in all these confusing variations of structure was a three-layered eye, an invaginated optic vesicle, the inner wall of which became the retina, and an overlying layer of hypodermis the corneagen. Such an eye would be much like that of Peripatus; flatten the vesicle vertically, reduce the outer wall to a thin membrane, and you have the ocelli of some Insects and Spiders. The observations recorded in this paper confirm the supposition mentioned above. We may now go still farther and say that a lateral flattening would produce the larval Insect, and Myriapod eyes, with horizontal rods; that the outer wall of the vesicle may, in some cases, develop inverted retinal cells side by side with the upright ones of the inner layer; and that the rods of these inverted cells may be converted into a lens inside of the optic vesicle, as in Chauliodes and perhaps Peripatus, or they may take the place altogether of the upright ones, as in the tapetal eyes of Spiders.

It can no longer be affirmed that there is a wide difference between the so-called Molluscan and Arthropod eye; both belong to the same type, as I formerly maintained. This difference it has been urged was due to the presence in the former of an optic cavity filled with an inspissated, refractive substance. But there is just such a cavity in the early stages of eyes V. and VI. of Acilius and one in Chauliodes which is filled with a lens like that in Peripatus and some Molluscs and Worms.

Professor Mark maintains that "none of Locy's predecessors have in the least foreseen the true course of events" concerning the origin and method of formation of the retina of Arthropods.

But it cannot be denied that I foresaw in my paper on the "Eyes of Molluscs and Arthropods" not only the origin of the retina and its method of formation, but, to a great extent, that of the optic ganglion as well. The observations on the development of Vespa and Acilius now furnish a substantial support for the theoretical views advanced in that paper, and this confirmation does not lose any of its value in consideration of the inversion of the retina in the tapetal eyes of Spiders, for that can most readily be explained, as already shown, by referring to the condition in eyes V. and VI. of Acilius; or by the fact that Reichenbach's and Kingsley's observations point to the conclusion that the sensory part of the convex eye is inverted, for in both instances the misconception undoubtedly arises from a confusion of ganglionic and optic invaginations; and finally the inference lies close at hand that the supposed inversion of the retina in the eyes of Scorpions and in the non-tapetal ones of Spiders is due to a similar confusion of the two invaginations.

CONVEX EYE.—In my paper on the "Eyes of Vespa," an attempt was made to throw some light in the phylogeny of the "convex eye." It seemed to me that a solution of the problem might be obtained by explaining its double nature; for as shown by the embryology of Vespa and by the permanent condition in such forms as the Libelluliden, Ephemeriden, Gyrinnus, Astacus, Phronima, Schizopods, and others, it is probably composed throughout the Arthropods of a distinct ventral and dorsal part.

I attempted to explain this double condition by supposing that it was a modified larval ocellus like the posterior dorsal one of Acilius and Dytiscus, which I maintained was also composed of a dorsal and ventral part: the latter was the ocellus proper; the former, an appendage whose structure and general appearance indicated that it was a secondary and younger part subsequently added to the ocellus; and it was maintained that if such an ocellus developed into the compound eye, a needed explanation would then be furnished of its double nature. But there was no evidence to show that the posterior ocellus with its dorsal appendage really did develop into the convex eye. I determined to obtain such evidence, if possible, by studying the history of the eye of Acilius during the larval and pupal stages. But all my efforts to obtain pupæ were unsuccessful. I have shown, however, that the appendage is not, strictly speaking, an outgrowth of the posterior dorsal ocellus, as I formerly supposed, and I do not now see any reason to suppose that the ocellus proper develops into any part of the compound eye. The appendage is, I now believe, one or two of the primitive sense organs of which the ocellus is composed, that have not completely united with the others, and have undergone a special modification in the direction we have already explained.

Toward the close of larval life, the convex eye appears as a thickening of the ectoderm immediately around the appendage. At this time it is difficult to distinguish any line of demarkation between the appendage and the thickening. In the latest stages I possess, it forms an enormous, thickened band that almost encircles the six ocelli. The band is narrow in the middle, but expanded and rounded at either end. Its ventral edge is deeply invaginated, especially near the appendage where the invagination first appears, and is connected with the adjacent ectoderm by a thin vertical layer of cells (Fig. 1, wood-cut). At first it seemed probable that the appendage developed into the ventral half of the convex eye, and the thickened band into the dorsal half. If the band itself should be divided into two parts, this interpretation would be, so far as I can see, untenable, and I must admit that there is an indication of such a division, though so indistinct and unaccompanied by any difference in the development of the ommatidia on either side of it, that I am still in doubt as to its meaning.

It is difficult to believe that the appendage of the posterior ocellus has nothing to do with the convex eye, since the latter is, in the early stages, so intimately connected with the former. One thing is certain, that a great part of the compound eye arises suddenly at the close of larval life as a thickening in a previously indifferent layer of hypodermis; hence that part at least cannot be considered a modification of any functional larval organ.

The development of the *frontal ocelli* points to the conclusion that they are widely different from the larval ones, and perhaps closely related to the compound eyes.

One of the things that impressed itself most deeply upon me, after studying the embryology of Acilius, was the threefold structure of the head as shown in the three segments of the optic plate, optic ganglion, and brain. The same feature is also shown in the arrangement of the eyes in the imagines of those insects supplied with frontal ocelli, for in such cases it is evident, since I have shown in Vespa that the median unpaired ocellus is double, that the imagines have three pairs of eyes, and it at once suggests itself that there is some intimate connection between this fact and the presence of the three larval segments. It is possible that the solution of the problem, to which I shall return in my next paper on the "Development of Acilius," may lie in an explanation of the pupal stage.

NEUROEPITHEL CELLS. — My studies on the "Eyes of Molluscs and Arthropods" led me to believe that ganglion-cells were modifications of sensory ones. This belief was based upon the presence of intermediate stages between sensory and ganglionic cells, upon the constant occurrence of intercellular nerve ends, and upon the embryological evidence afforded by the fact that in Pecten the ganglionic cells of the eye and sensory papillæ were derived from the cells of the hypodermic thickening that gave rise to these sense organs. This supposition further led to the conclusion that the optic ganglion of Arthropods could not be an outgrowth from the brain toward the eye, but one from the eye toward the brain. This conclusion is now in a measure confirmed by the history of the development of the optic ganglion of Acilius.

When we review the semi-ganglionic cells described by me in Haliotis, "Eyes of Molluscs and Arthropods," Pl. 30, Fig. 68, and in Acilius, Pl. X., Fig. 58, *h*, and the myoepithelial cells of Cœlenterates as described by Hertwig, we perceive that nearly all these cells have three prolongations, one of which is directed outwards, and terminates between, the cells of the ectoderm; the other two extend, from the opposite pole of the cell, inwards, and probably unite with similar prolongations from other ganglionic cells. There is no sharp line of demarkation between the tripolar cells described by me in the retina of Haliotis and the neuroepithelial cells of Cœlenterates as figured by the Hertwigs. In the case of Haliotis and Pecten, the origin of some, at least, of the ganglion-cells is beyond question, for they still form a part of the ectodermic thickening that gave rise to the sensory part of the eye. In Acilius we have temporarily represented the condition that prevails in the sense organs of Cœlenterates and Molluscs; for, while many ganglion-cells arise from the invagination on the side of the eye, others wander inward from the optic thickening itself. The details of the latter process are best studied in the great cells that are the last to form. While these cells are still in the optic thickening they are distinctly tripolar, one prolongation being directed outward to form the rudiment of a nerve end. Such cells would correspond to the tripolar neuroepithelial cells of Cœlenterates, or those tripolar ones already mentioned in Haliotis and Acilius.

In Acilius there is no reason to suppose that a ganglion-cell once established in the above manner ever loses its direct connection with the ectoderm. According to Hertwig, those connected by an outward prolongation with the ectoderm are intermediate between fully developed ganglion-cells and sensory ones, and we are to infer that they are intermediate because of this outward prolongation. I fail to see the necessity for this conclusion, for there is reason to suppose that most, if not all, ganglion-cells, have some connection with the outer world, consequently the existence of such a connection would not indicate the age of the ganglion-cells.

The history of the giant ganglion-cells of Acilius, together with a consideration of the neuroepithelial cells of other groups, it seems to me, warrant the conclusion *that the primitive ganglion-cells were tripolar, and were derived from tripolar neuroepithelial cells. The outer extremities of these neuroepithelial cells were reduced to intercellular nerve ends, the bases of which, in Acilius, became the protoplasmic prolongations of the ganglion-cells, and are probably homologous with the axis-cylinders of Vertebrates.*

SUMMARY.

The more important results of the foregoing study are as follows: —

(1) The larval optic ganglion is composed of three segments, each of which is united on the one hand with a segment of the brain, and on the other, with a segment of the optic plate.

(2) Each segment of the optic plate bears a pair of eyes.

(3) The ocelli are composed of four or more sensory spots, or pits, each pit being supplied with a separate cuticular thickening and nerve.

In the centre of each group of four sensory pits, is a single large nucleus of doubtful significance.

(4) The pits of each eye finally unite to form a thickened patch of ectoderm, with a median double row of gigantic cells and a common cuticular thickening.

(5) The thickened ectoderm is invaginated to form an optic vesicle, the inner walls of which form the retina, while the surrounding indifferent ectoderm forms a third layer of cells over each vesicle, thus producing a typical three-layered eye.

(6) In the embryonic stages of eyes I.–IV., the retinas of which are invaginated without the formation of a cavity in the optic vesicle (unless the space between the median row of gigantic cells can be called one), all the rods are horizontal.

(7) In the full-grown larvæ, the smaller outermost rods become upright; the larger and deeper ones remain in a horizontal position.

(8) In eye V., there is at first a strong tendency to form horizontal rods. But the laterally flattened optic vesicle expands, forming a spacious cavity in the vesicle, and all the rods become upright except those of the median row of gigantic cells.

(9) In eye VI., which has no median row of giant cells, no horizontal rods are formed.

(10) The outer wall of the optic vesicle in eyes I.–IV. seems to be absent. In the embryos, its presence is indicated only by a few characteristic nuclei between the retina and the corneagen.

(11) In eye V., the outer wall of the optic vesicle is represented by two great masses of inverted, rod-bearing cells, probably derived from the two sensory spots, **5** and **6**, seen in surface views of the eye before invagination.

(12) In eye VI., the outer wall is composed of a thin nucleated membrane, and a cluster of inverted retinal cells, derived from sense organ number **6**.

(13) Eye I. is composed of at least nine sensory spots, four of which with their central nucleus and median row of giant cells give rise to the horizontal retina; four more, exactly like the first, to the vertical retina; and the ninth, to the appendage. All these sense spots unite to form a single homogeneous organ; but, during the later stages, the three groups of sensory spots become greatly modified, so that in the adult eye the parts they give rise to, the vertical, and horizontal retinas, and the appendage, are widely different in structure.

(14) All the retinas are composed of retinophoræ, formed by the union of two cells. They contain two nuclei and two rods, and are supplied with axial, and external nerve fibres.

(15) In very rare cases one finds ganglionic cells in the retina of Acilius.

(16) The rods are arranged in pairs, which form a mosaic of hexagonal figures when upright, and straight vertical lines when horizontal.

(17) In the horizontal, as well as in the vertical rods, the retinidial fibrillæ are at right angles to the rays of light.

(18) All the larval ocelli of Acilius and Dytiscus contain more or less distinct dimorphic, retinal cells. The giant cells always form a double row along the bottom of the furrow. Their free ends are bent at right angles, and bear short but broad horizontal rods.

(19) The ends of the smaller retinal cells, and consequently their rods, may be horizontal, upright, or inverted.

(20) Between the two rows of giant rods are two sheets of coarse, vertical nerve fibres and a layer of medulla-like substance.

(21) The pigment granules are deposited on the surface of the retinophoræ and around the external nerve fibres.

(22) All the eyes are developed from the optic plate, the thickened distal edge of the cephalic lobes. On the proximal edge of this optic plate is a semi-circular furrow, which gives rise to the optic ganglion. The furrow is deepened to form two distinct pockets, that give rise to the first and second segments of the optic ganglion; the third segment is formed by an inward proliferation on the proximal side of the third segment of the optic plate.

(23) The innermost walls of the ganglionic segments are from the earliest stages connected with the inner face of the optic plate.

(24) Numerous ganglionic cells arise from the optic thickening, and wander along the optic nerves into the optic ganglion.

(25) Toward the close of this process, about the time when the invagination of the sensory areas begins, enormous, tripolar cells are formed in each eye, which pass along the optic nerve, from the eye to the optic ganglion, dividing rapidly on the way, and producing small, tripolar ganglion-cells. But one of the proliferating cells retains its great size throughout life, and finally takes up its position on one side of the medulla belonging to the eye from which it arose.

(26) The history of these cells affords excellent evidence in proof of the theory which explains the presence of intercellular nerve fibres, by supposing them to be the outer ends of sensory cells, now converted into ganglionic ones.

(27) The optic ganglion of the convex eye of Arthropods is composed of three lobes: the first always, and the third sometimes, disappears; the second gives rise to the optic ganglion proper. The retinal ganglion is a secondary product, and is not formed by invagination.

(28) The three-lobed optic ganglion of the convex eye of Arthropods is derived from a three-segmented larval ganglion, each segment of the latter belonging to a pair of larval ocelli.

(29) The first, second, and third segments of the optic ganglion of Acilius larvæ are respectively homologous with the second, first, and third lobes of the optic ganglion of the compound eye.

(30) Hence, from the first segment of the larval ganglion, or that segment which is united with the large, posterior, dorsal ocellus, is developed the optic ganglion proper of the compound eye.

(31) The optic ganglion contains six medullæ, each of which corresponds in structure to that of the retina to which it belongs, and this indicates that the arrangement of the medullary fibrillæ is as near like that of the retinidial fibrillæ of the retina, as the existing condition will allow.

(32) The structure of the retina in the larval ocelli of Insects is much like that of Myriapods, and the whole eye is constructed on the same plan as that of *Peripatus* and most Molluscs.

MILWAUKEE, June 1, 1888.

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EXPLANATION OF LETTERS USED IN THE PLATES.

a.^{1}	first pair of antennæ; labrum.
a.^{2}	second pair of antennæ.
ab. n.	nuclear-like bodies.
a. l.	antennary lobe.
am.	amnion.
a.^{2} *n.*	nerve to second antenna.
ap.	appendage to eye I.
ap. n.	nerve to appendage of eye I.
ax. n.	axial nerve.
b.$^{1\text{-}3}$	brain.
bd.	bridge over ganglionic invagination.
bm.	basement membrane = outer neurilemma.
c. a.	clear area.
ce. & ce.^{1}	convex eye.
cg.	corneagen.
cg.^{1}	corneagen; median part with faint nuclei.
cg. a.	corneagen of appendage.
cl.	cuticula that gives rise to lens.
c. g. v.	cavity of ganglionic invagination.
c. o. t.	corneal cuticula.
c. o. v.	cavity of the optic vesicle.
c. t.	cuticula thickening = retinidial cuticula.
d. a.$^{1\text{-}4}$	dark areas.
d. n.	dividing nuclei.
e.$^{1\text{-}6}$	eyes.
en.	endoderm.
en. c.	cavity in endoderm.
ex. n.	external nerve fibres.
f. g.	frontal ganglion.
g.$^{1\text{-}6}$	great ganglion cells of optic ganglion.
g. c.^{1}	double ganglion cell of optic ganglion.
g. c. r.	ganglion cell of retina.
g. r. d.	great rods.
g. v.$^{1\text{-}3}$.	ganglionic invagination.
h. g. c.	heel of great retinal cells.
h. m.	medulla of the horizontal retina.
h. r.	horizontal retina of eye I.
h. rd.	horizontal rods.
i.	iris.
i. n.	inner neurilemma.
i. o. g.	infra-œsophageal ganglion.
i. rd.	inverted rods of outer wall of optic vesicle.
l.	lens.
l. a. n.	loops of axial nerve.
l. n.	lateral nerve of horizontal retina.
m.	mouth.
m. a.	medulla of the appendage to eye I.
mc.	muscles.
m. c.	median chord.
m. b.	medulla of the brain.
md.	mandibles.
md. n.	mandibular nerve.
m. h.	medulla to horizontal retina.
m. i. c.	medulla to inverted cells.
m. f.	median furrow.
m. g. c.	median row of giant cells.
m. g. r.	median row of giant rods.
m. o.	œsophageal muscles.
m. r.	median ridge.
ms.	mesoderm.
m. v.	medulla of vertical retina.
mx.$^{1\text{-}2}$	maxillæ.
n.$^{\text{I-VII}}$	nerves to the eyes.
n.$^{1\text{-}8}$	nerves to the sense organs in eyes.
nc.$^{1\text{-}3}$	large nuclei.
n. f.	nerve fibres.
n. fl.	nerve fibrillæ.
n. g. c.	newly formed ganglion cells.
n. g. c.^{1}	outer ends of ganglion cells that have passed inwards.
nr.	primary nuclei of retinophoræ.
nr.^{1}	secondary nuclei of retinophoræ.
n. s.	nerve spindles.
œ.	œsophagus.
œ. c.	œsophageal commissures.
o. g.$^{1\text{-}3}$	optic ganglion.
o. n.	outer neurilemma.
o. op. c.	opening of optic cavity.
o. p.	optic plate.
o. w.	outer wall of optic vesicle.
o. w. g.	outer wall of optic ganglion.
pg. n.	pigmented nerve fibres.
p. n.	place where optic ganglion is continuous with the optic plate.

p. n. f.	primitive nerve fibres.
rd.	rods.
$rd.'$ & $rd.''$	rods of primary and secondary cells of the retinophoræ.
rn.	retinidium.
s.	segments of nerve chord.
s. o.	segments of optic plate.
s. o. g.	stalk of optic ganglion.
s. r. c.	small retinal cells.
s. rd.	small rods.
$t.^{1-3}$	tentorium.
$tg.^{3-8}$	tergæ.
t. i. c.	tongue of inverted cells.
tn.	tentorium.
v. n.	vertical nerve fibres.
v. r.	vertical retina.
x.	dark nuclei in young eyes.
y.	yolk.
y. c.	yolk cells.
z.	first cephalic invagination.
$z.^1$	second cephalic invagination.
1–10.	sense organs of the eyes.
x. y.	upper edge of eye III.

EXPLANATION OF PLATE VII.

Fig. 1. Surface view of the head of a young Acilius embryo. × 110.

Fig. 2. The same. × 110.

Fig. 3. The same. × 110.

Fig. 3*a*. Side view of the same. × 110.

Fig. 4. Side view of the head. × 110.

Fig. 5. Ventral view of head. × 110.

Fig. 5*a*. Side view of same head. × 110.

Fig. 5*b*. Dorsal view of dorsal edge of optic plate of same head. × 110.

Fig. 6. Ventral view of head. × 110.

Fig. 6*a*. Side view of optic plate of the embryo in Fig. 6, showing arrangement of surface nuclei around the sense organ of each eye. × 190.

Fig. 7. Ventral view of head just before rupture of embryonic membranes.

Fig. 7*a*. Side view of same. × 110.


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b²
b³
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og¹
og²
og³
op.
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mr²
ms¹
tq¹
tq²
tq³
qr¹
qr²
I
II
III
IV
V
VI

EXPLANATION OF PLATE VIII.

FIGS. 8 AND *8a*. Ventral and side view of head just after rupture of embryonic membranes. × 86.

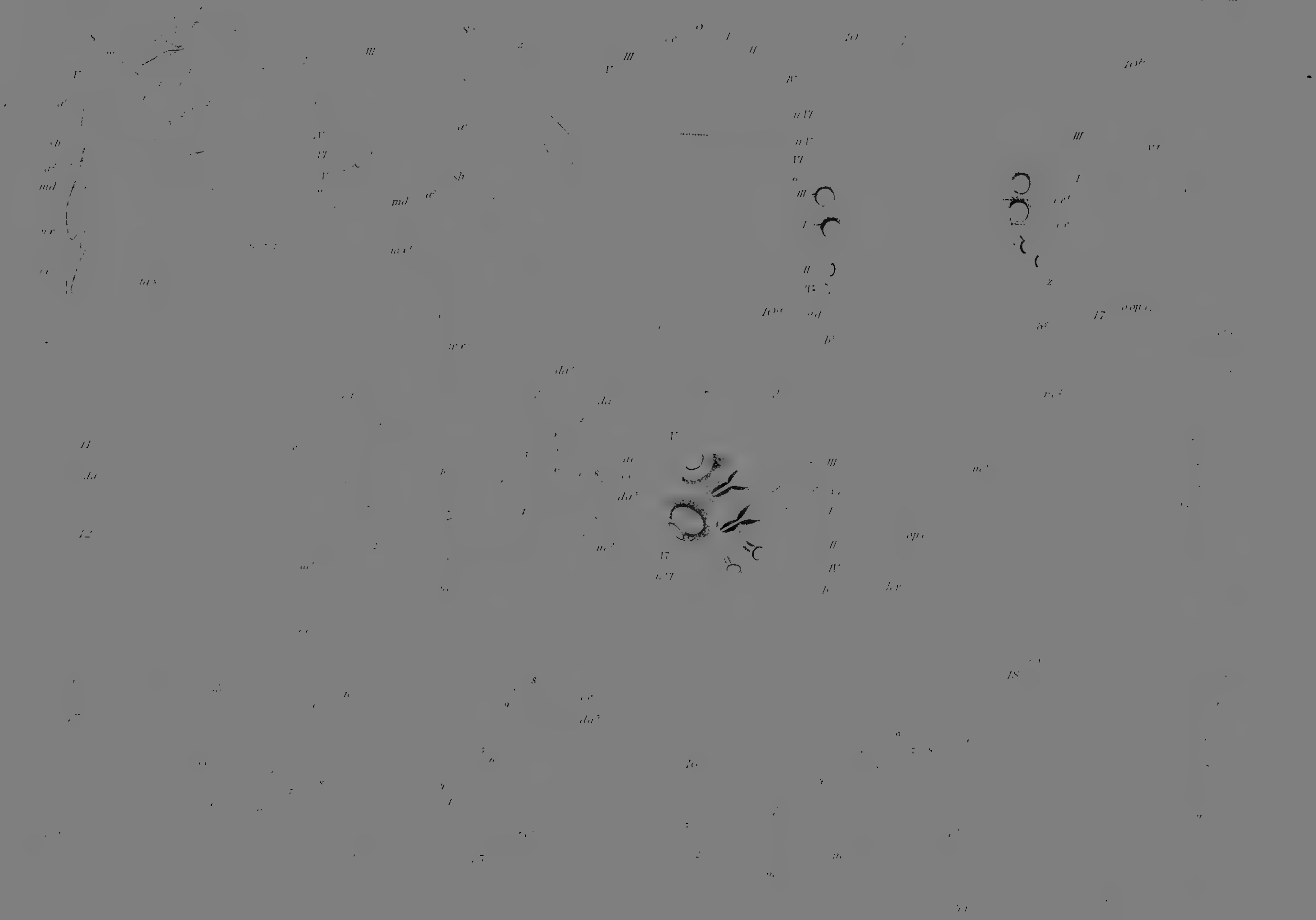
FIG. 9. Side view of head of an embryo almost ready to hatch. Semi-transparent. × 96.

FIGS. 10 AND *10a*. Dorsal and side view of the head of a full-grown larva.

FIGS. 11–16. Surface views of the dorsal, anterior edge of the optic plate, showing successive stages in the formation of the first eye. In order to economize time and labor, the surface nuclei are shown only in Figs. 14 and 16. × 260.

FIG. 17. Semi-diagrammatic and transparent side view of eye I., in the stage shown in surface view in Fig. 16.

FIG. 18. The same, in a later stage, showing the bend in the middle of the sensitive area, to form the vertical and horizontal retinas, and the sense organs and nerves to each part.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EXPLANATION OF PLATE IX.

Fig. 19. Cross section of the cephalic lobes of an embryo somewhat younger than that in Fig. 1, Pl. VII. × 360.

Figs. 20–23. A series of cross sections through the cephalic lobes of an embryo like that in Fig. 1; showing the three ganglionic invaginations. × 360.

Figs. 24–27. Cross sections of an embryonic head about same age, perhaps younger, as that in Fig. 1. This head was abnormally shaped. It was deeply invaginated along the median line; on the sides of the invagination were the antennæ, and at the bottom, the mouth. × 360.

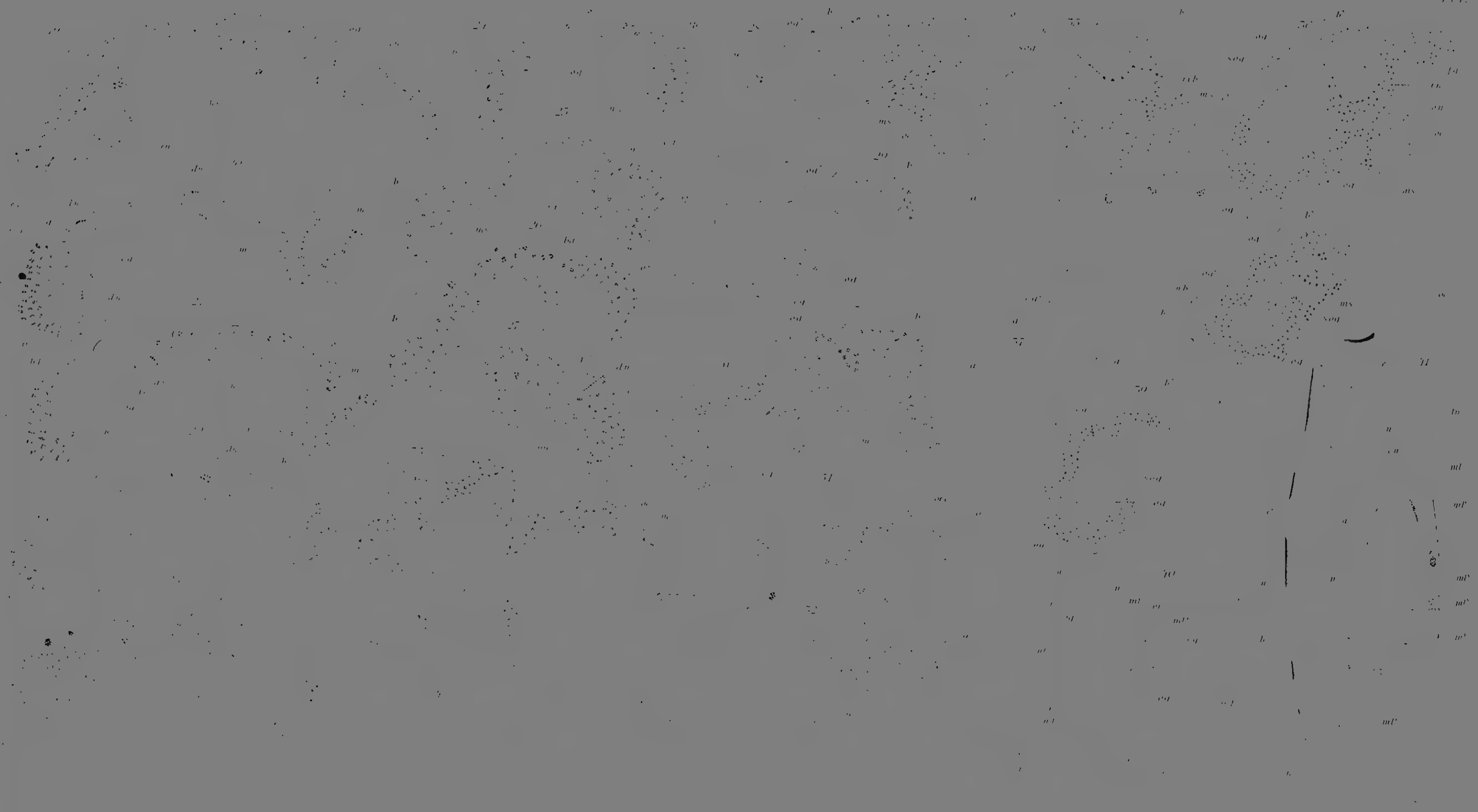
Figs. 28–34. A series of cross sections through the head represented in Fig. 5. They show the structure of the brain, optic ganglion, and optic plate. × 360.

Figs. 35, 36. Cross sections of a head like that in Fig. 6, just after the optic ganglion is completely shut off from the exterior. × 190.

Figs. 37–39. Cross sections of a younger stage than that in the preceding figures, showing the last stages in the enclosure of the optic ganglion, etc. × 138.

Fig. 40. Semi-transparent surface view of the optic ganglion and one side of the brain; showing the three lobes of the optic ganglion, the medullæ, and the nerves.

Fig. 41. Semi-diagrammatic horizontal section through the medullary portion of the optic ganglion; showing the position and shape of the medullæ and the nerves that unite them with their respective eyes.



EXPLANATION OF PLATE X.

FIGS. 42–47. A series of sections through the head of an embryo just after the rupture of the embryonic membranes. See Fig. 8. They show the structure of the brain and its envelop, optic ganglion and eyes, as well as the tracheal invaginations of the head. For explanation of last-named structures, see my next paper on the "Development of Acilius." × 138.

FIG. 48. Horizontal section of the optic ganglion, from an embryo just ready to hatch. The break in the outer neurilemma is on the side next the eyes. It is important to notice the remarkable similarity between the structure of the medullæ and the retinas to which they belong.

FIGS. 49, 50. Two vertical sections through the optic ganglion of a full-grown larva; showing the medullæ and nerves, and the three lobes of the ganglion. × 170.

FIGS. 51–53. Three horizontal sections of the optic ganglion of a full-grown larva. Shows same as preceding sections. × 170.

FIG. 54*a*. Cross section of the rods in the fifth Eye; showing axial nerves, retinidia, etc.

FIG. 54*b*. Same from the sixth eye; showing loops of axial nerves, etc.

FIG. 55. A vertical section through the furrow of eye I.; showing the ends of the giant, and small rods. Compare Fig. 56.

FIG. 56. Vertical section of the horizontal retina of the first eye; showing the double row of giant cells with their external nerve fibres, the layer of vertical fibres, with their fibrillæ, and the ends of the small horizontal cells, etc.

FIG. 57*a*. Semi-diagrammatic view of a retinal cell from the fifth eye; showing the double retinophoræ, and the position and shape of the rods belonging to each cell of the retinophora, etc.

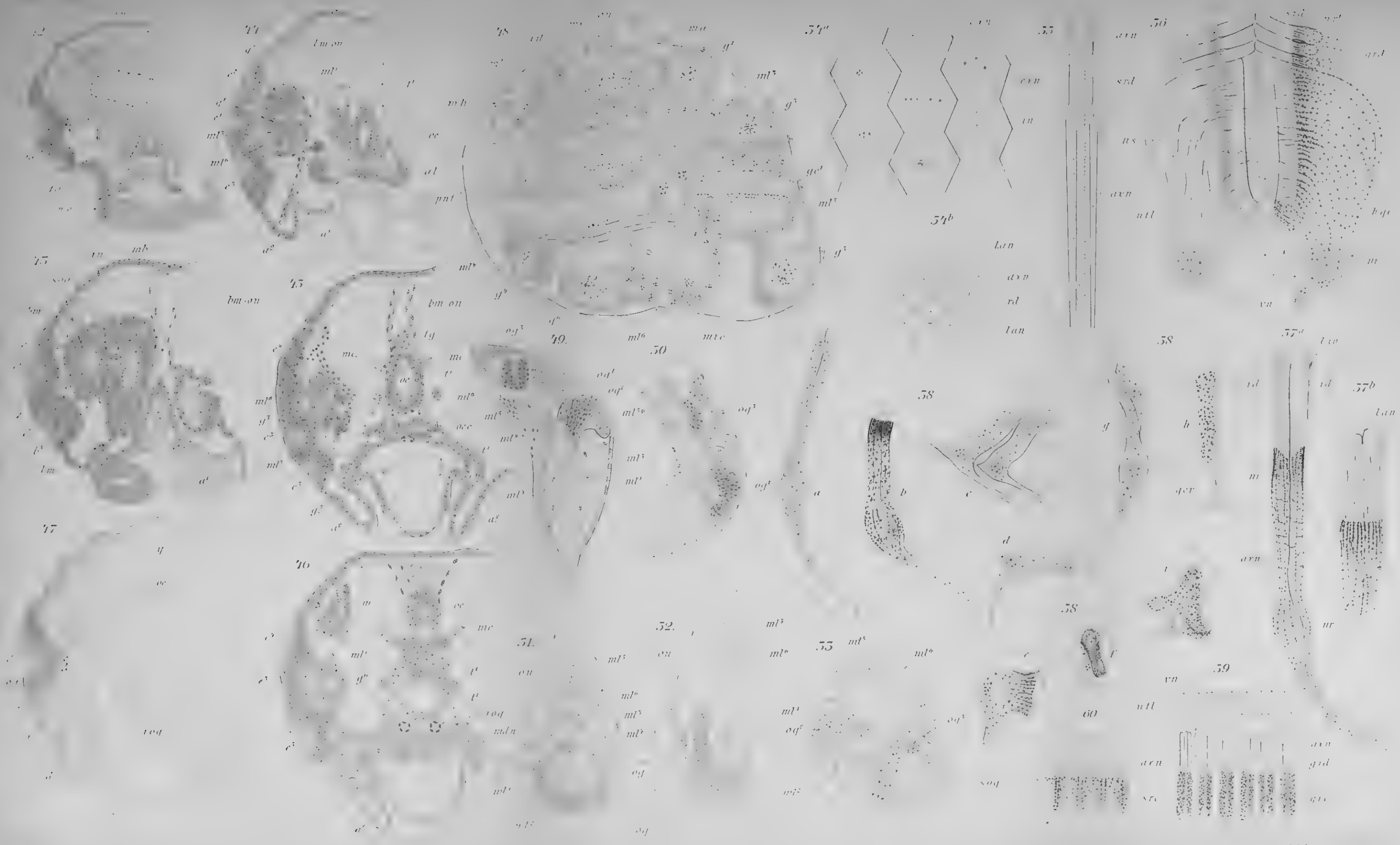
FIG. 57*b*. Same, in side view.

FIG. 58. Retinophoræ isolated by maceration.

- *a*. A double cell, decolorized, from the fifth eye.
- *b*. Isolated cell from the sixth eye. The primary and secondary nuclei are situated close together.
- *c*. Two double cells, depigmented, from the sixth eye; showing the nerve fibres and the deceptive shape of the inner ends of the retinal cells.
- *d*. Same.
- *e*. *f*. Two views of a small retinal cell with horizontal rods, probably from the second or fourth eye.
- *g*. Decolorized retinophora that showed especially well the shape of its component cells.
- *h*. A fragment of a retinal cell with a tripolar ganglionic cell attached to it.
- *i*. Two giant cells from the first eye; showing how the light and dark cells overlap.

FIG. 59. Horizontal section of the first eye; showing one of the rows of giant cells and the two layers of vertical fibres with the medulla-like substance between. Compare Fig. 56.

FIG. 60. Horizontal section of the row of small retinal cells just above the giant cells in the horizontal retina of the first eye. It shows how the rods of each retinophora unite with each other above the centre of the cells, and not with the rods of neighboring cells, as in all other cases. See Fig. 57*a*.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EXPLANATION OF PLATE XI.

Development and Structure of the Fifth Eye.

FIG. 61. Cross section of the head in Fig. 3; showing the large median nuclei and two of the sensory pits of which the eye is composed, etc. × 430.

FIG. 62. Same, in a little older stage; showing formation of a large ganglion cell. × 560.

FIG. 63. Section of the eye in the stage shown in Fig. 6*a*. It shows a large cluster of newly formed tripolar ganglion cells, wandering from the retina to the optic ganglion. × 560.

FIG. 64. Section of the eye before the rupture of the embryonic membranes. The pits and their cuticular thickenings have united to form a single sensory layer, and the large nucleus has sunk into the retina. The formation of ganglionic cells from the retina has ceased. The last one formed is now seen in the optic ganglion on one side of the optic nerve. × 560.

FIG. 65. Section of the eye just after the rupture of the embryonic membranes.

FIG. 66. Section of the eye just after the closure of the optic cup. The median row of giant cells, although small compared with those in the other eyes, is very conspicuous on account of the manner in which it protrudes above the level of the surrounding cells. × 560.

FIG. 67. Section of the eye in a later stage, showing the first steps in the differentiation of the corneagen, and the outer wall of the optic vesicle.

FIG. 68. Section from an embryo about ready to hatch. The outer wall of the optic vesicle is formed by two great masses of inverted rod-bearing cells, derived from the sense organs 5 and 6. See Fig. 6*a*. We can now see the minute rods of which the cuticular thickening is composed. Most of the reddish brown pigment has been dissolved by the alcohol. × 560.

FIG. 69. Section of the eye one or two days after hatching; showing the distribution of pigment, and the well-developed inverted rods of the outer wall of the optic vesicle. × 520.

FIG. 70. The eye as shown in a longitudinal horizontal section of a fully developed larva. × 220.

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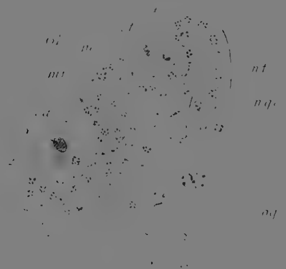

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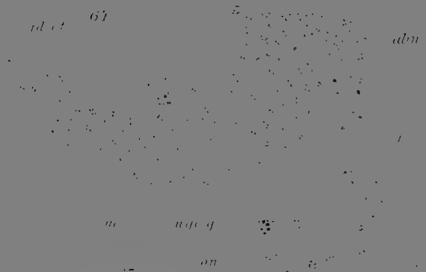

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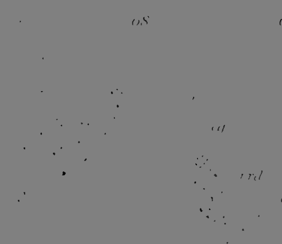

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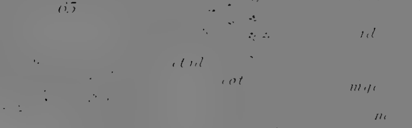

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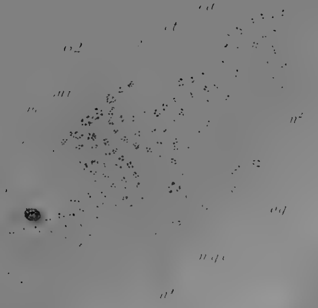

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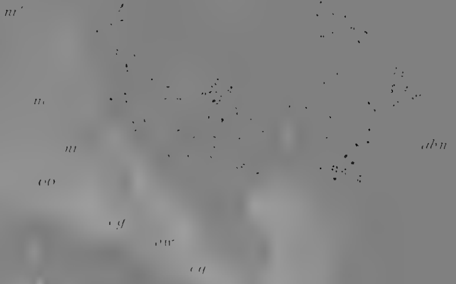

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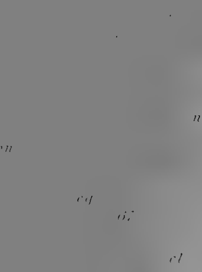

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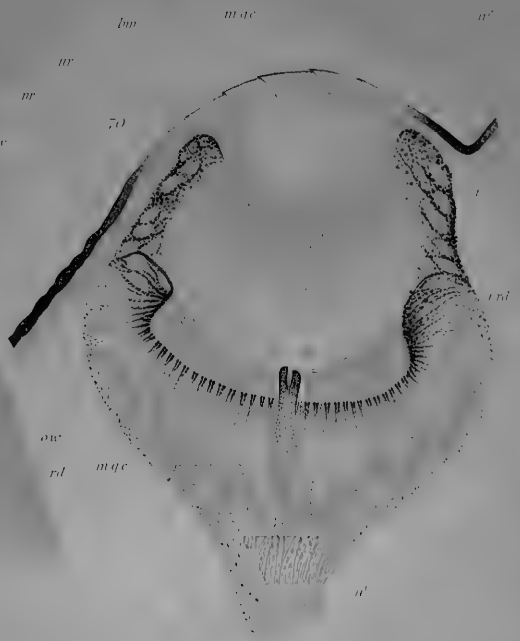

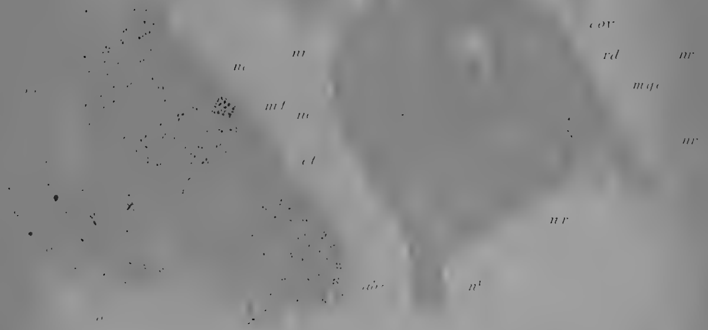

EXPLANATION OF PLATE XII.

Structure and Development of Eyes II., IV., and VI.

FIG. 71. Eye VI. as seen in a cross section of the head just after the closure of the optic cup. × 430.

FIG. 72. Same in a little later stage. × 430.

FIG. 73. Eye VI. of an embryo about ready to hatch. Compare Fig. 9. The section is semi-transverse, cutting through the inverted sense organ 6 = *t. i. c.*, and the longitudinal vertical axis of eye III. × 430.

FIG. 74. A similar section through the same eye of a one-day-old larva. × 430.

FIG. 75. Eye VI. of a full-grown larva, as seen in semi-transverse section. Compare Fig. 10 *a*. The section passes through the optic nerve of this eye, but does not show the tongue of inverted cells. It passes just on the dorsal side of it. × 350.

FIG. 76. Eyes II. and IV. = *A* and *B*, as seen in a longitudinal horizontal section of an embryo, some time after the rupture of the embryonic membranes. Compare Fig. 9. × 430.

FIGS. 77 AND 78. Eyes II. and IV. of a fully developed larva, as seen in a semi-transverse section, nearly parallel with the vertical axis of the first and third eyes. × 430.


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rc
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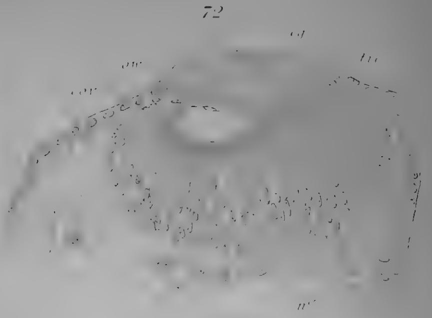
n^{IV}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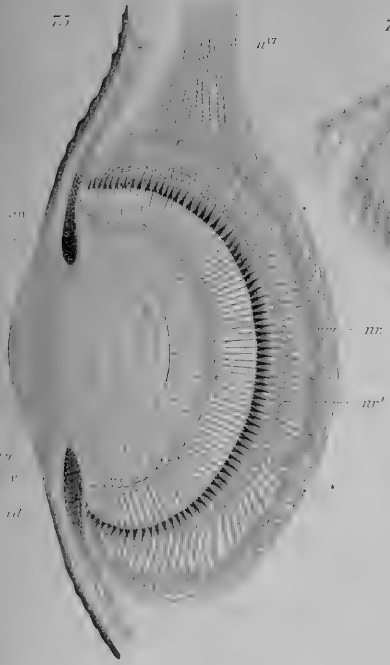
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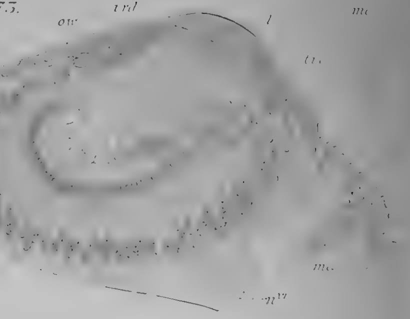
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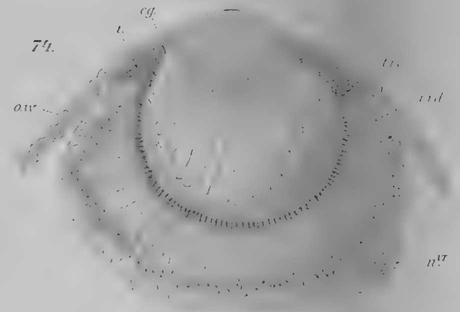
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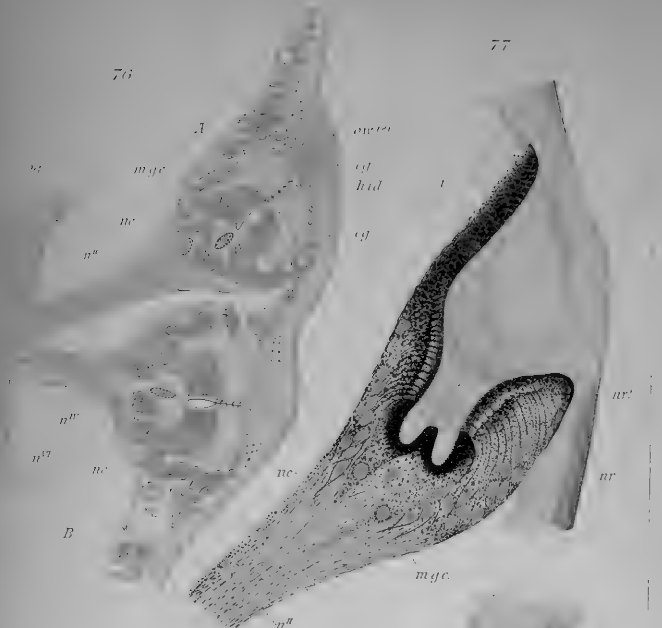
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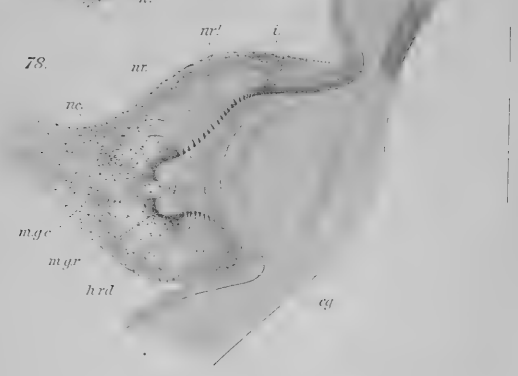
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EXPLANATION OF PLATE XIII.

FIG. 79. Eye I. as seen in a semi-transverse section of an embryo just after the rupture of the embryonic membranes. Compare Figs. 8 and 16. × 520.

FIG. 80. The same, after the sensory area is differentiated into the vertical and horizontal retinas.

FIG. 81. The same, from an embryo some time before hatching.

FIG. 82. Transverse section of the sensory area of Eye I. in the stage shown in Fig. 14. × 560.

FIG. 83. Same, of Eye III. in a later stage. The median furrow has disappeared and the invagination of the sensory area has commenced. × 560.

FIG. 84. Cross section of the vertical retina of Eye I. in the full-grown larva. × 430.

FIG. 85. Eye I. as seen in a tangential section of the side of the head. The section is at right angles, and from an eye in the same stage, to that shown in Fig. 80. × 415.

FIG. 86. Section, in same direction as the preceding, of Eye I. just before hatching. × 260.

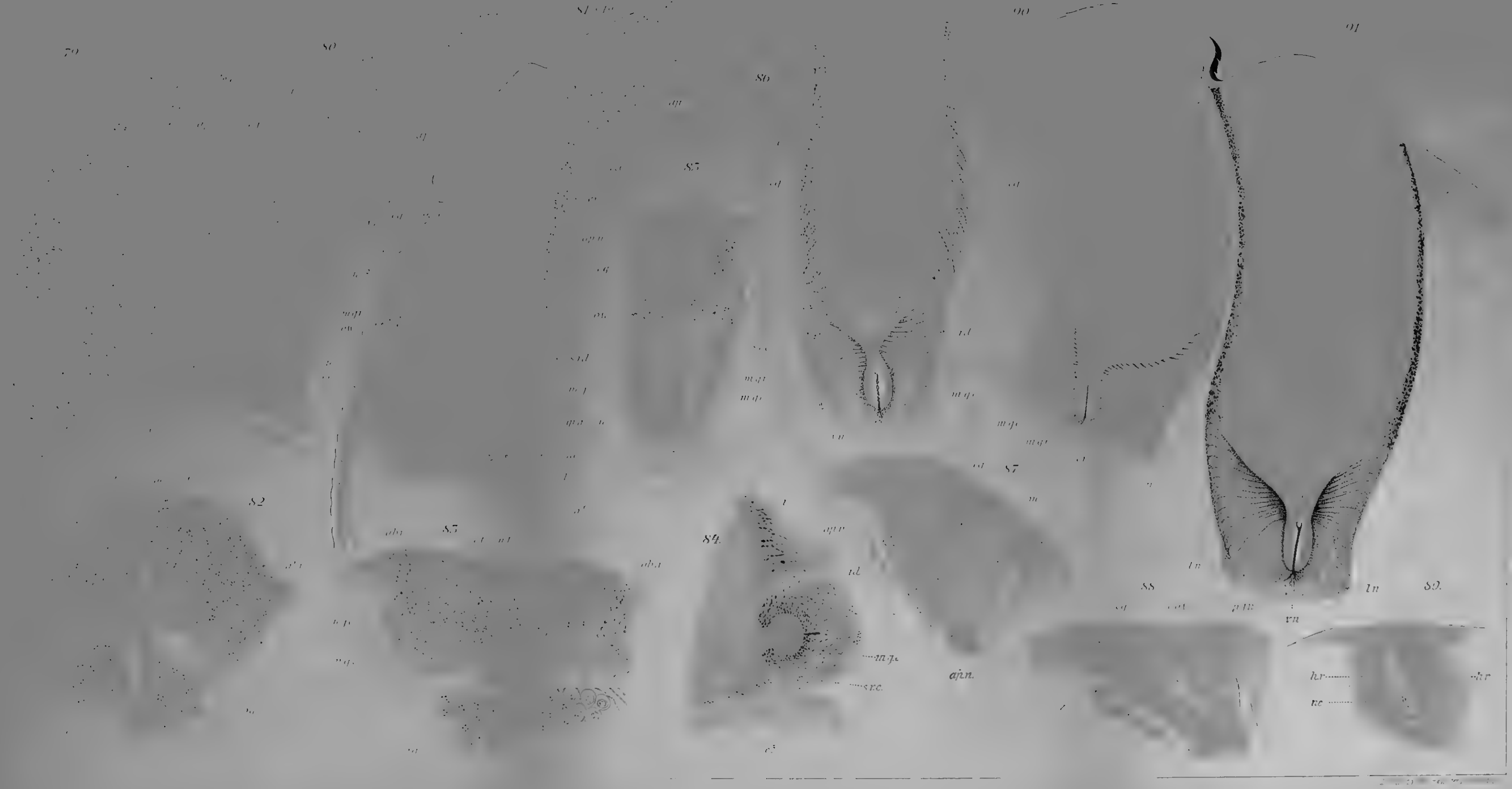
FIG. 87. Transverse section of Eye I. in same stage as shown in Fig. 79. The section passes through the large nucleus of the horizontal retina.

FIG. 88. Section similar to the preceding one, through the vertical retina of the same eye. × 430.

FIG. 89. Horizontal section through the horizontal retina of Eye I. during a little earlier stage than that shown in Fig. 85. × 430.

FIG. 90. Eye III. as seen in a tangential section of the head of a full-grown larva; partly depigmented. × 240.

FIG. 91. Eye I. in same section as the preceding. × 240.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Volume II. *November, 1888.* *Number 2.*

JOURNAL

OF

MORPHOLOGY

ON THE DEVELOPMENT OF MANICINA AREOLATA.

A thesis for the degree of Ph.D., accepted by the Board of University Studies of the Johns Hopkins University, May, 1888.

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FELLOW OF THE JOHNS HOPKINS UNIVERSITY.

DURING the spring of 1887 the Marine Laboratory of the Johns Hopkins University was stationed on the island of New Providence, Bahamas. As soon as possible after my arrival, March 10, I endeavored to find out what corals were breeding. Of half a dozen species examined only one was with eggs. This was the so-called Chenille stone, or *Manicina areolata,* one of the commonest corals in the Bahama waters. The breeding continued to be very active until the middle of April, when it began to decline, coming to a close before the first of May.

The coral is found in large numbers in water of easy wading depth, lying with its pedicel buried in the sand. It lives very well in small aquaria, if care be taken to change the water twice a day. In rearing the larvæ I was compelled to employ the same tedious method as Lucaze Duthiers: every morning and evening I transferred them, one or two at a time, by means of a pipette, to a dish of fresh water. When once the larvæ had become attached, the matter was simplified by transferring the entire dish to a bucket of fresh water. For preserving the larvæ, Perenyi's fluid proved the most generally useful reagent. Osmic acid specimens were also of very considerable value in elucidating special points. For the anatomy of the adult, absolute alcohol gave the most satisfactory results. I take this opportunity of thanking Professor Brooks, the director of the Marine Laboratory, for his advice and constant suggestions, which have been of the greatest value to me during the course of this work, both at the seaside and in the Baltimore laboratory. I am also indebted to Mr. C. S. Hodge, of this laboratory, who very kindly took upon himself a part of the task of cutting the sections.

I. Systematic Description of Manicina.

Milne Edwards makes Manicina the sixty-fourth genus in the family Astræidæ. Like Meandrina, this coral grows by incomplete fission, the calicles remaining connected so as to form meandering valleys, in which the limits of a calicle are not distinguishable. The shape of the colony ordinarily met with is subturbinate (see figures on Plate I), there being a well-marked pedicel. With increasing age the pedicel becomes less and less evident, until the corallum finally assumes the shape of a convex mass with a flat basal surface. The basal surface has two diameters, the longer about three inches, the shorter two inches, and the vertical height of the corallum is about equal to the shorter diameter. The distinguishing features of the genus, besides its growth from a pedicel, are as follows: The columella is spongy and very well developed. The septa are thin, closely set, and have strongly marked granulations on their sides. The edges of the septa, both within and over the exterior of the calicles (costæ), are finely and regularly toothed. "The genus was instituted by Ehrenberg for certain of Lamarck's Meandrinæ, characterized by growing from a pedicel or central point of attachment" (Dana). In the species Manicina areolata, the septa can be divided into three cycles, and each septum has in the neighborhood of the columella a large and rounded lobe.

The animal is of a brownish color, and when expanded, extends high above the skeleton. In this condition the tentacles are moderately long, and are closely set round the periphery of the oral surface. In the pedunculate forms, both in the expanded and contracted condition of the animal, the upper part of the lateral surface of the skeleton is covered by the polyp. The pedicel, which includes the skeleton below this region, is usually disfigured by small annelid tubes and other incrustations.

The young, after the swarming life is over, affix themselves to some solid substratum, such as a piece of rock or a shell. To this they remain attached until they have reached a diameter of about half an inch. Until the diameter is one-third of an inch, the animal remains a single polyp, circular or oval in transverse section, and with a flat or irregular surface of attachment. The multiplication by fission then begins, and with it the formation of the pedicel. When the latter has become apparent, the coral is broken off from the rock to which it was attached, and henceforth lives free in the sand.

II. General Sketch of the Development from Surface Views.

Lacaze Duthier's figures of Astroïdes (1) apply so well to Manicina, that I have thought it unnecessary to give a series of such views. The chief point of difference is that the larvæ are red in the former genus, but colorless in the latter.

Manicina is hermaphrodite. Normally, it would appear, the mother gives birth to larvæ, which pass out by the mouth. But the first two batches of corals I kept poured out an abundance of eggs and semen. Each batch numbered eight corals, was distributed into four aquaria, and was kept for only a day. The first set laid on the night of the 15th, the second, on the 17th of March. I was not able to try a third batch until the 20th, when I was surprised to find that all the corals had given birth to larvæ a little more advanced than the planula stage. The throwing out of eggs and spermatozoa was probably abnormal, as the eggs which I watched underwent very irregular changes, and finally broke up. In connection with this ejection of eggs and semen, it may be interesting to note that though after March 20 the corals always ejected larvæ when kept in aquaria, the stage of development in which the larvæ were born became much more advanced as the season grew older. The larvæ born March 20 and 21 were without cilia, and at the stage represented in Fig. 4, Pl. II. Those born April 5 were ciliated and as far advanced as Fig. 20, Pl. IV.

The larvæ I obtained during March lay, for a day or two after birth, motionless on the surface of the water. They then acquired cilia, and began to swim feebly about at the surface, often collecting in rows at the sides of the vessel or in groups away from the sides. Lucaze Duthiers noticed the same habit in Astroïdes. At the end of a week the larvæ are rapid swimmers, now spending most of their time below the surface of the water. Often they creep along the bottom and sides of the dish like little worms. Though they are constantly lengthening or shortening their bodies, the general shape is that of a pear, with the mouth at the small end. The broad end is usually, though not invariably, directed forwards in swimming. While creeping over the glass they frequently fasten themselves by their broad ends for from one to ten minutes, becoming free again of their own accord. The larvæ continued to swim about without any change in form until the middle of April. By this time, as subsequent examination showed, they had acquired six mesenteries (three pairs) and two long mesentrial filaments (Fig. 19, Pl. III.). A large number now began to attach themselves. Supported on the broad end, they stood nearly erect, spinning slowly around. The long axis began to shorten, and by the time they had assumed the shape of an oblate spheroid, eight meridional constrictions had appeared, marking the number of mesenteries. The long or, rather, oral-aboral axis continued to shorten until the little coral had assumed a disk-like shape with a flat basal surface and a convex upper surface, the latter marked with the meridional constrictions (a transverse section of this stage is shown in Fig. 34, Pl. V., and a longitudinal in Fig. 38). The whole process of fixation occupied several hours. All the larvæ did not become attached at the same time. On the contrary, many continued to lead a free life until the first part of May.

The lot of larvæ I got on the fifth of April were born in a more advanced state than their predecessors, and developed after birth more rapidly. So much so, that by the middle of April as many of this batch became attached as of the larvæ born March 20. Indeed, the first fixed larvæ I obtained, April 9, were from this lot, and had taken only four days to go through the metamorphosis, which in all the other larvæ required from two to four weeks. This great amount of difference amongst the larvæ, as to the time required to reach a certain stage of development, made it a matter of some trouble to pick out a consecutive series of stages. When I began to section, I found that inferences based on the length of the larva's life were only true within wide limits.

The stage with eight mesenteries is followed in a day or two by the stage with twelve. At this period the first deposition of the skeleton makes its appearance as a circular patch of calcareous matter on the basal surface of the attached polyp. I was not able to rear the young corals beyond this point; though I kept a few alive until the first of June. The death rate increased very much as soon as the larvæ became attached.

III. Early Stages, including the Formation of Layers.

The diameter of the unsegmented egg was about two-thirds the long diameter of the blastosphere (Fig. 2, Pl. II.). There was a very large centrally-placed nucleus, and the body of the egg was filled with vesicles, resembling in this respect the endoderm of the subsequent planula. The only observations on the segmentation were made on the eggs accidentally (?) discharged March 21. The spermatozoa played round each egg in large numbers. After fertilization the spherical egg became oval, and then divided into two equal blastomeres, which remained connected by a bridge of tissue. The division into four then followed. So far the segmentation was quite regular, but irregularities now began to crowd in, which led to the production of a grotesquely shaped mass comparable with the irregular planula described by Metschnikoff for Oceania (2). (I have observed a precisely similar segmentation and planula in an allied medusa, Turritopsis.) The irregular mass did not develop any further.

The normal segmentation which goes on in the body of the parent results in the formation of a blastosphere with a very large cavity (Fig. 1). The blastosphere is markedly bilateral, and is without cilia. The cells contain a large number of very distinct vacuoles, pretty evenly distributed through the cell body. In older blastospheres, Figs. 2 and 3, the formation of the larval or primitive endoderm has begun. The blastosphere cells are columnar, the nucleus is peripherally placed, and the vacuoles are concentrated in the central end of the cell. The cells are evidently delaminating, the inner vacuolated ends being split off to form the endoderm. The nuclei of the endoderm segments are very hard to make out. The delamination takes place irregularly over the general surface of the blastosphere, and is of a peculiarly complex character in certain spots. In the cell groups *m* and *m'*, Fig. 2, for instance, the lines of the transverse divisions of the several cells are continuous, and seem to indicate that the whole group must have divided transversely while it was yet a single cell: before it had been split up by the longitudinal divisions. But the latter show that the transverse divisions did not precede them. Such a cell as *n*, Fig. 3, throws light on the matter. This cell has begun to divide longitudinally, but even in the peripheral part of the cell, though the longitudinal constrictions are evident enough, the segments are far more intimately connected than are, say *n*, and the adjacent cells. In another cell, *n'*, the longitudinal division is apparently perfect; but on comparing the close apposition of the new segments with the marked space between *n'* and the adjacent cells, I am inclined to believe that the halves of *n'* are still connected by bridges of tissue, much as the blastomeres in many segmenting eggs remain connected after they are clearly marked off. In the group *m'*, then, Fig. 2, it is probable that the longitudinal constrictions were the first to appear in the mother cell, but that before they became complete divisions a general transverse constriction took place.

Delamination appears to be the exclusive means by which the endoderm is formed. I looked in vain for cells migrating from the surface. Whenever there appeared to be such, examination of the next sections showed that the cells in question had been cut obliquely, the peripheral end with the nucleus having been severed from the rest of the cell body. The cell *a*, Fig. 2, for instance, is merely the central portion of a constricted cell like *b* in the same figure. The delamination and accompanying longitudinal division often give rise to spheroidal cells, such as *x*, Fig. 3. These cells are always at the surface of the blastospheres. Whether their fate is different from that of the general ectoderm cells, I do not know.

The cavity of the blastosphere having been filled up by the endoderm segments, a solid planula, Fig. 4, is formed. On studying this figure, a median longitudinal section, we see that the longitudinal division of the superficial cells, which was active in the blastosphere, has given rise to a layer of columnar cells, the ectoderm. The inner ends of these cells are not distinctly marked off from the solid endoderm. The endoderm, when the living larva is compressed or when pretty thick sections are examined, appears made up of a quantity of vesicles, which look something like fat cells. When thin sections are examined (Fig. 4), it is found there exists a continuous protoplasmic matrix binding the vesicles together, which are now seen to be identical with the vacuoles present in the endoderm segments of the blastosphere cells. There is, however, a difference in their appearance, which is best shown in Figs. 9 and 10. In the blastosphere cell, the protoplasm in which lie the vacuoles is pretty uniform; but in the endoderm of the planula, the protoplasm immediately round each vacuole is denser than the intervening stroma, and forms a more or less differentiated shell for the vacuole. The shell stains much more deeply than the stroma. What the contents of the vesicle is, I cannot say. Carmine and hæmatoxylin do not affect it, and in these young stages I did not try osmic acid.

The endoderm contains, besides the vacuoles just mentioned, a number of "yellow cells" and scattered nuclei. No cell boundaries can be made out, and there is every indication that the layer is a plasmodium. A stage between Figs. 2 and 4 would go far towards elucidating the intricate structure of the solid endoderm, but I did not succeed in obtaining such.

While the embryo is still solid, the œsophageal invagination makes its appearance, Fig. 4. The larva is very narrow except at its base, where it is slightly dilated. At this stage it swims feebly about, the cilia having commenced to develop.

The formation of the permanent layers is illustrated in Fig. 5. In the region *d* the layers are in the condition characteristic of the earlier larva. But in the neighborhood of *c* the ectoderm cells have become much more clearly marked off from the endoderm. Their inner ends form a ragged line which gradually becomes more uniform, until the ectoderm is bounded internally by a smooth limiting surface, as at *a*. Though the bounding surface is smooth in this region, the supporting lamella has not yet formed. A little later it appears as a delicate membrane between the two layers (from *a* towards the mouth). While it is still very thin it resembles an ordinary cuticle. It appears between the layers, and is not formed by the direct metamorphosis of the ends of ectoderm or endoderm cells. As to the much-discussed question of which layer secretes the membranes; in early stage, such as Fig. 5, it is impossible to decide whether the secretion is the peculiar property of either layer. But in later stages, it is found in places where it can only be endodermic, and in others where it is evidently ectodermic. I shall return to this point further on. The various steps in the formation of the permanent layers can often be observed, with but few gaps, in a single section. Fig. 5 is such a section, with a few additions from another.

The permanent endoderm is formed from the larval endoderm by a differentiation of a peripheral layer from the central portion, Fig. 5. The peripheral layer is not formed continuously over the whole surface, but in spots here and there. It is at first marked off from the central portion only by its somewhat greater density, but it gradually breaks its connection with the latter by the acquisition of a smooth limiting surface, Figs. 5 and 10. Cell boundaries soon appear. The permanent endoderm as thus formed is a single layer of vacuolated cubical cells, except in the immediate neighborhood of the œsophagus, round the sides of which the cells are massed so as to fill up, more or less completely, the space between it and the body wall. This is especially noticeable on the left side of Fig. 5.

The œsophageal invagination as seen in Fig. 5 is much dilated at its base. Here the ectoderm has preserved its intimate connection with the endoderm, the ectoderm cells not even having acquired a smooth bounding surface. In Fig. 6 this even surface has been acquired, but at no time is a supporting lamella secreted over this area. The absence of the lamella clearly facilitates the absorption by the endoderm (or yolk) of the base of the invagination. The details of the absorption are as follows. The dilated bottom of the invagination, shown in transverse section in Fig. 10, is broken through at one point. Through this breach the yoke passes into the lumen, Figs. 8–10, and the base of the œsophagus thus enclosed above and below by yolk is absorbed. It is, I think, possible to recognize the base after it has passed into the yolk, though of course the histological structure is gone. In Fig. 8 is seen a curved mass of tissue extending from the left side of the œsophagus nearly to the right. Though in structure like the yolk, it stains a much deeper hue, and is therefore well defined. On comparing this figure with Figs. 6 and 10, there seems to be no doubt that the mass in question really represents the ectoderm base of the œsophagus.

The central portion of the larval endoderm remains as a food-yolk. In Fig. 5 it still exists as a continuous structure, but as more and more of the protoplasm is drawn into the layer of permanent endoderm, the vesicles lose their connection with each other. By the time the layers are definitely established, Figs. 6 and 8, the yolk is a loose mass of vesicles, the shells of which have begun to disintegrate. The shell is extremely dense, and in this and subsequent stages seems to be fatty, as it stains very dark with osmic. Remnants of the yolk are found in stages as late as Fig. 19.

Though the formation of the supporting lamella and the differentiation of the permanent endoderm very often take place at about the same time, this is not always the case. In many larvæ the supporting lamella is entirely formed, and the œsophagus has opened centrally, while the endoderm is still solid, Figs. 10 and 12.

The "yellow cells," which later are found in such abundance, appear for the first time in the planula, Fig. 4. I have not seen them actually entering the planula, but in this and slightly older stages, Fig. 5, a few occur in the surface ectoderm, whereas in older larvæ and in the adult they are confined to the inner layer of the body.

COMPARISONS.

a. Germinal Layers.

Among the many ways in which the germinal layers are formed within the Cœlenterates, Metschnikoff (2) has decided that one represents the manner in which the earliest metazoa were formed. In this so-called "mixed delamination" a solid endoderm is built up both by delamination and by the migration of superficial cells into the interior. *Polyxenia* (Metschnikoff) and, better, *Aurelia* (Götte) are good examples of this process. Accepting this type as ancestral, *Manicina* has diverged along the same path as certain Trachomedusæ (Geryonia, Liriope);

i.e., none of the blastosphere cells migrate into the interior, but the endoderm is formed exclusively by delamination.

Though the way in which the solid larva was originally formed seems preserved in but a few species, the solid larva itself may fairly be considered as typical for the Cœlenterates. It is especially well preserved in the Hydroids and Anthozoa. In the latter group it is nearly universal among Alcyonarians, and occurs in the majority of the Zoantheria. The Alcyonarian which comes nearest to *Manicina* in the formation of its layers is Renilla (3). In this genus, though the blastosphere has a very small cavity, the endoderm is formed by delamination, as in the coral. As regards the structure of its larval endoderm, however, Renilla differs from Manicina. In the former the endoderm is made up of a mass of cells, of which the peripheral layer becomes the permanent endoderm, while the central cells go to pieces, and are probably eaten, amœboid fashion, by the peripheral cells. In Manicina, on the other hand, the larval endoderm is a plasmodium, and in the entire process which leads up to the formation of the adult endoderm it would seem that a prominent physiological part is played by the "vesicles," which in all probability contain some kind of yolk. Owing to the plasmodial nature of the solid endoderm, the complete transformation of the latter into the permanent layer must require less time in Manicina than in Renilla. For in Manicina there is no large accumulation of yolk cells which must slowly be devoured, amœba fashion, by the peripheral cells. On the contrary, when the time for the formation of the permanent endoderm has arrived, the general protoplasm is merely drawn towards the periphery, and after it has there broken up into cells, there remains but little nutriment in the loose yolk mass. Just how the yolk is ingested after the cellular endoderm is formed, I am unable to say. It is not devoured, amœba fashion, by the endoderm cells at large, though in the region of the œsophagus, Figs. 6 and 8, connection is maintained for a considerable time between the yolk and the endoderm, which elsewhere is completely formed.

Amongst the corals and actinias, two or three forms have been described as undergoing invagination, notably *Cerianthus* (Kowalevsky 4) and *Actinia* (Jourdan 5). While the mere recurrence of invagination in a cœlenterate group can scarcely be said any longer to have a phylogenetic significance, these two forms are especially interesting, as E. B. Wilson has remarked (3), because in each of them a yolk mass appears after the layers have been completely formed. I have not seen Kowalevsky's figures, but the yolk shown in Jourdan's figure 119 is precisely like the yolk of a young Manicina (making allowance for difference in thickness of the sections). The *à priori* improbability that the endoderm would first secrete a yolk (Kowalevsky) and then swallow it again, taken together with the similarity of the yolk in question to that of Manicina, might tempt one to believe that both authors had mistaken a stage like Fig. 12, Pl. I., for a true gastrula. But Kowalevsky's statements on this head are so definite as to preclude this supposition.

b. Supporting Lamella.

The only two authors who have described in detail the formation of the supporting lamella are Jourdan (*l.c.*) and Wilson (*l.c.*). Jourdan's observations were made on a coral, Balanophyllia, and an actinia, Actinia equina. He draws a sharp distinction between the "membrana propria" and the jelly.

The former answers to the German *Stutzmembran.* It is a firm limiting membrane which appears between the two layers and extends into the mesenteries to form their axial bands. This is what I have spoken of as the supporting lamella (comp. any of figures on Pl. IV.). Its origin Jourdan was unable to trace with any certainty. The jelly, on the other hand, which eventually becomes fibrous, is formed outside the membrana by the superficial ectoderm cells. The inner ends of these cells break off and fuse together to form a granular mass, in which fibres subsequently appear (*l.c.* Figs. 119 and 129).

The supporting lamella described by Wilson is evidently the same thing as Jourdon's membrana. Its origin according to Wilson is double. In the mesenteries it is a simple cuticular secretion of the ectoderm cells. But in the body wall it is formed in a manner similar to that just described for the jelly: the inner ends of the ectoderm cells become swollen, constrict off, and form a granular layer which condenses to a smooth membrane.

In Manicina there is first formed a very distinct membrane as described. In later larval stages, at various spots, especially in angles, a thin fluid jelly accumulates. This is noticeable in

Figs. 16 and 17, beneath the right-hand mesenteric filament, and in Figs. 44 and 45 at the angles of the œsophagus. It is always to be found in the axis of the larval filament, Fig. 26. The distinction between the supporting membrane and the more fluid jelly, which is noticeable in larval stages, is lost later in life. In the older larvæ, Fig. 39 for instance, the supporting membrane throughout its whole extent has become considerably thicker than in younger stages, though the jelly in the axis of the filament is still to be distinguished from the more membrane-like band of the mesentery. In the adult the axial band of the mesentery is so much wider, while the jelly in the axis of the filament is at the same time denser than in larval stages, that all distinction between the two structures is lost. Compared with an actinia the whole mesodermic skeleton of the adult Manicina is very scanty and membrane-like, but in certain places it reaches a more generous jelly-like condition, for example, in parts of the mesenteries, Fig. 51. Here the supporting substance is merely the thickened primitive membrane.

There indeed seems to be no difference between the supporting membrane proper and the jelly, except in the mere quantity of the secreted substance and in the percentage of water. What applies to the origin of one should explain the origin of the other. Now as regards the membrane proper, I am quite sure that in Manicina it is formed as a cuticular secretion, and not by the direct conversion of the ends of ectoderm cells into granular matter, which subsequently condenses to a membrane. Turning now to the question as to which layer secretes the membrane, we see from the figures (14, 17, 26, 45) that after the mesenteries are formed, the lamella is much more intimately connected with the endoderm than with the ectoderm: where the layers are forced apart, it always sticks to the endoderm. But even here the ectoderm is provided with a well-defined limiting membrane, which if thinner than the lamella, is essentially like it. I conclude from this and other facts to follow that when the lamella lies between the two layers, both layers share in secreting it. That the endoderm cells can secrete the lamella, is plain from its occurrence in the axis of the mesenteries, and in the axis of the genital bands of a Cubomedusa (6). On the other hand, the same argument can be used to prove the ability of the ectodermal cells to secrete this substance, for in the velum of Hydromedusæ there is a well-defined lamella, which is formed *in situ.* In Cunocantha (7) I have pointed out that when the velum is developing, the ectoderm cells range themselves so that their bases will secrete a continuous membrane.

IV. FORMATION OF THE FIRST PAIR OF MESENTERIES AND FILAMENTS.

I was led to pay especial attention to the filaments by E. B. Wilson's interesting discovery that the dorsal pair of filaments in the Alcyonarian polyps are ectodermal lobes (8). Relying on the histological similarity between this pair of filaments and the *flimmerstreifen* of an actinian filament, Wilson suggested that perhaps in the latter the *flimmerstreifen* were ectodermal, and only the median *nesseldrusenstreif* was endodermal. I find, however, that the filaments of *Manicina* are as to origin like the dorsal pair in the Alcyonaria. They are simple ectoderm lobes which grow down from the œsophagus.

The œsophageal invagination in the earliest stages is symmetrically placed, Figs. 4 and 5. It very soon, however, begins to travel towards one side of the larva. This is shown in the transverse section, Fig. 7, and still better in the longitudinal section, Fig. 6 (the endoderm in these two larvæ is in different stages of development). The lateral motion of the œsophagus has compressed the endoderm on its left into a compact mass, which completely fills the space between the œsophagus and body ectoderm. On the right hand the endoderm has been stretched, until it forms a single layer of cells. The narrow lumen of the œsophagus is bilateral (it is doubtful whether this is true in all larvæ at this stage), and its dilated extremity has no longer the symmetrical bulb-like shape of Fig. 5. In Fig. 8 the lateral movement has gone a step farther, and meanwhile the œsophagus has opened centrally. The movement of the œsophagus is continued until in one meridian there is nothing left between the œsophageal and superficial ectoderm but the supporting lamella, Figs. 11 and 12. (In Fig. 11 the lamella has not yet appeared, but both stomadoeal and body ectoderm have smooth, limiting surfaces.) The intermediate stages show that the lateral movement of the œsophagus travels from above downwards, and that the endoderm has consequently been pushed down in this meridian. This is proved by Figs. 9 and 10, transverse sections from a larva in which the œsophageal movement had gone farther than in Fig. 8. Fig. 9 is about at the level *a* in Fig. 8, and Fig. 10 is at the level *b*. In this larva then the œsophagus was closely pressed against the ectoderm at the level *a*, but was separated from it by endoderm at a lower level *b*. In the later stage, Fig. 11, the lowest part of the œsophagus has completed the journey. The meridian in which the œsophagus is thus pressed against the ectoderm, is that of the first mesentery. (Though Figs. 9 and 10 are from the same larva, both the supporting lamella and endoderm are much farther advanced in the lower section than in the upper.)

The larva from which the longitudinal sections, Figs. 12 and 13, were cut, was very backward in forming the permanent endoderm. Fig. 12 is taken through the line *a* and *b* in Fig. 11, and is in the plane of the first pair of mesenteries. It is only on the left side that the œsophagus is in contact with the body ectoderm. But the right side is following suit, and in a slightly older stage, Fig. 12, is in the same manner applied to the surface ectoderm over a narrow tract. Fig. 13 is to one side of *a* and *b* in Fig. 11, and is consequently out of the plane of the mesenteries.

My next stage after Fig. 12, is the larva from which the series of transverse sections, Figs. 14 to 17, was taken. It is this stage which proves the meridians, along which the œsophagus is applied to the body ectoderm, to be really those of the first pair of mesenteries. Fig. 14 is the uppermost of the series, and is through the body of the œsophagus, the lumen of which is exceptionally large. On the right side the œsophagus is separated by jelly alone from the surface ectoderm. Following down the series of sections, we see that in this meridian the œsophageal ectoderm sends down a slender lobe, which, like the œsophagus above it, divides the endoderm and rests on an accumulation of jelly (right side of Figs. 15, 17). This lobe is a mesenterial filament. It is considerably shorter than the filament on the opposite side, Fig. 17, and is probably the second one of the first pair. The right side of this larva is practically in the condition shown in Fig. 12, except that the œsophagus has formed a filament.

On the left side of the larva, Fig. 14, matters are more advanced. On comparing this side with Fig. 12, we see the œsophagus has moved away from the surface ectoderm, but while doing so has remained connected with it by a band of supporting lamella. Running through the series of sections, it is found that in this meridian also an ectoderm lobe has grown down from the œsophagus. This lobe is the primary filament. It is much wider at its start, near the œsophagus, than its fellow on the opposite side, but soon dwindles to about the same size. Like the œsophagus above it, this filament is in a more advanced condition than the filament on the right side. Since we know that the left side of the œsophagus itself has passed through the condition which exists on the right side, we are pretty safe in believing that the left filament has likewise passed through the condition in which the right filament is found. The lack of a fairly intermediate stage between Fig. 12 and the larva we are studying, is to a certain extent supplied by the larva from which Fig. 11 was taken. In this individual, which was sectioned transversely, the œsophagus extended so much farther down in the meridian of the first mesentery than round its general lip, that in this meridian it formed a very evident though not a very long lobe. This lobe, which becomes the primary filament, is shown in Fig. 11, and is to be found in the sections immediately below the one figured, growing smaller towards its end.

On comparing the first and second filaments in Fig. 17, it is clear that the endoderm, which at a higher level grew in between the œsophagus and body ectoderm, has likewise forced its way beneath the primary filament, and thus given rise to the first mesentery. The mesentery is continued from the level of Fig. 17 downwards, as a very slight endodermic ridge on which rests the filament. The axial band of supporting lamella is continuous with a thinner lamella, separating the filament from the endoderm. Immediately beneath the opening of the œsophagus the mesentery is much more elevated than at a lower level. The elevation of the mesentery in this region is connected with the first appearance of an intermesenterial chamber.

In the larva we have been studying the first pair of intermesenterial chambers has been marked off. Round the œsophagus, however, they are still solid, Fig. 14, though at a lower level the hollowing out of the solid endoderm has begun. At this level, Fig. 15, which is just beneath the opening of the œsophagus, the endoderm on one side of the first mesentery exhibits a small cavity. The cavity, when traced through the series of sections, is found to open into the cœlom in Fig. 16, forming, as it does so, the cave or bay which underlies one-half the primary filament in the figure. It is thus (comp. Figs. 14 and 15) in the larger of the two primary chambers that the excavation of the solid endoderm begins, and, as I learn from other series, the excavation of this chamber is nearly completed before that of the smaller begins. The excavation starts, as we have just seen, in the immediate neighborhood of the first mesentery. From this spot it gradually extends across the chamber to the second mesentery, travelling all the while from the lip of the œsophagus upwards.

The second mesentery, which exists in its embryonic condition in Fig. 14, follows the example of the first. In Fig. 18 it is completely formed, and in the series of longitudinal sections, Figs. 20–23, which I shall describe later, the second mesentery is in the condition in which the primary is in Fig. 14; *i.e.*, in the immediate neighborhood of the second mesentery the larger of the two intermesenteric chambers is solid, while the smaller chamber is entirely solid.

In the larva from which the transverse section, Fig. 18, was made, the various processes which have been described are now completed. The œsophagus is swung by two complete mesenteries. Both intermesenteric chambers — the larger on the left, the smaller on the right — have been hollowed out. Below the œsophagus, the mesenteric ridges extend the whole length of the larva, and the first pair of filaments about half the length. The section is slightly complicated by other features, of which I shall now speak.

In the larger of the two chambers, Fig. 18, the second pair of mesenteries, 3 and 4, has appeared. The axial bands of supporting lamella as yet cause no elevation of the endoderm, and at a level slightly below the œsophagus are entirely lost. In Fig. 18 *a*, above Fig. 18, the axial band numbered 4 stretches across to the œsophagus, and still higher up 3 does likewise. In this section the position of the œsophagus is eccentric. This is very often the case at the extreme upper limit (the appearance is not due to oblique sections), and hence one mesentery usually runs out before its fellow (2 before 1). The mode of origin of the second pair of mesenteries is thus entirely different from that of the first pair. All the subsequent mesenteries are formed after the fashion of the second pair.

The outer wall of the larger intermesenterial chamber in Fig. 18 is made up of unmistakable endoderm, but the inner or œsophageal wall has an ephithelium precisely like that of the œsophagus. Both are composed of very slender elongated cells with a median thickening, in which lies the nucleus; the peripheral end is enlarged and flattened, so that by the juxtaposition of many such cells a continuous cuticle can be formed. The cells in question resemble the well-known "supporting cells" of the Hertwigs (9). Besides the supporting cells, glandular cells are found. These are slender and full of granules, the latter staining very deeply with hæmatoxylin. The epithelium of the œsophageal wall of this chamber is, moreover, sharply marked off from the rest of the epithelium. It is directly continuous with the œsophageal ectoderm round the lip of the œsophagus, and is evidently a tract of ectoderm. Any doubt which might cloud this point is removed by later stages, such as Figs. 44 and 45, where the epithelium, which is claimed as ectoderm, overlaps, at its upper limit, the endoderm. It is clear that in this stage, Fig. 18, the œsophageal ectoderm has been reflected round that portion of the lip (free edge of œsophagus) which belongs to the larger chamber, and has then run up along the outer surface of the œsophageal tube, driving the endoderm before it. The direction of growth is reversed, but otherwise the ectoderm is acting in precisely the way which it chose in forming the first pair of filaments. In the smaller chamber of Fig. 18, the epithelium forming the œsophageal wall does not differ from the rest of the endoderm. In a later stage, when the third pair of mesenteries has appeared, the ectoderm is also reflected round the lips of this chamber, and runs up along the œsophageal wall, Figs. 36 and 39.

The reflection of ectoderm, which leads to the condition shown in Fig. 18, commences as soon as the excavation of the primary (larger) chamber begins, and follows close on the heels of the latter process. The object of the reflection of ectoderm, as will be shown later, is to provide filaments for the young mesenteries before the latter are complete; *i.e.*, continuous from body wall to œsophagus. Bearing this in mind, it is probable that the reason why the ectoderm is reflected into the primary chamber at such an early date, is that the second pair of mesenteries will be formed in this chamber. The series of longitudinal sections, Figs. 20–23, illustrates the early reflection of ectoderm round the lip of the larger chamber. The larva from which this series was made was at a stage intermediate between Figs. 14 and 18. The supporting lamella of both of the first pair of mesenteries were complete, as in Fig. 18; but the intermesenterial chambers were far from perfect. The smaller chamber was entirely solid, and the cavity of the larger was only partially formed. In spite of the difference in age, it will do to refer the planes of the longitudinal sections to Fig. 18. The section, Fig. 20, thus is taken through the mesenteries 1 and 2, and the corresponding filaments. The next three figures represent a series of sections to the left of this plane, the one farthest to the left lying in the plane *a–b* of Fig. 18. Finally, the left-hand mesentery in Fig. 20 is the primary mesentery, 1 in Fig. 18. With this orientation it is seen, on glancing through the series 20–23, that only in the neighborhood of the primary mesentery has the intermesenteric chamber been hollowed out. In all the sections the endoderm is solid on the right side of the œsophagus. Now, in Fig. 23, the intermesenteric chamber (to the left of œsophagus) is in the state in which it was formed. The ectoderm has not yet been reflected round the œsophageal lip. But in the sections nearer to the mesentery, Figs. 21 and 22, the ectoderm *has* been reflected, and has driven the endoderm before it. The reflection of ectoderm, as I have said, follows very closely the excavation of this chamber. As the latter proceeds from mesentery 1 to mesentery 2 (Fig. 18), so does the former; and by the time the chamber is completely established, the ectoderm is reflected all the way from 1 to 2, as is seen in Fig. 18.

In the larva which was used to show the earliest appearance of the primary intermesenteric chamber, Figs. 14–16, the reflection of ectoderm had already begun to take place round one edge of the primary œsophageal lobe (Fig. 16, left).

To sum up the more important events described in this section:

To form the first mesentery the whole œsophagus moves laterally, until in the meridian of the mesentery there is only supporting lamella between the œsophageal and surface ectoderm. The œsophagus now grows downward in this meridian as a lobe of ectoderm, which represents the primary filament, and which pushes the endoderm before it. On the opposite side of the animal, along the line of the second mesentery, the œsophagus becomes applied to the body ectoderm in the same manner, and a lobe grows down from it to form the second filament. The mesenteries as such are formed by the ingrowth of the endoderm between the body ectoderm and œsophagus above, and between the body ectoderm and the filaments below. The primary pair of intermesenterial chambers are at first solid. The larger chamber acquires its cavity before the smaller, the excavation travelling from the lip of the œsophagus upward, and from the first toward the second mesentery. The excavation of the primary chamber is closely followed by the reflection of ectoderm into this chamber, the reflected ectoderm running up the œsophageal wall, and driving the endoderm before it. The second pair of mesenteries appear in the larger chamber as longitudinal ridges of the supporting lamella, which cause no elevation of the endoderm.

V. Histology of the Larvæ.

It may now be advisable to describe the histology of the larvæ, going when necessary beyond the stages already studied.

a. The Surface Ectoderm.

The ectoderm at the time when the supporting lamella is formed, Figs. 5 and 6, consists of columnar cells, the protoplasm of which shows a great tendency to break into small polygonal balls. While the ectoderm is in this condition the mucus cells appear (*m*, Fig. 6, Figs. 7, 8), as pear-shaped bodies in the peripheral ends of the columnar cells. The contents of the pear-shaped body stains a deep blue with hæmatoxylin, and is thus distinctly marked off from the surrounding cells. It appears to be fluid from the start, as even in such young stages as Fig. 7, many of the mucus cells have poured out their contents, which adheres to the mouth of the cell as a little mass of a blue color. This tendency of the mucus cells to eject their contents, presumably when the killing fluid touches the larva, is very noticeable in older stages such as Fig. 27, which are often completely covered by a thin layer of mucus. The mucus cells increase in size and number, until they become the prominent feature of the ectoderm (Figs. 7, 20, 27). In their final condition, Fig. 27, they are large, clear sacs, in which a few strands of protoplasm may be seen in carefully prepared osmic specimens. The nucleus of the original cell in which the sac developed cannot be made out in sections.

The mucus cells develop over the general surface of the larva, but are not found at the aboral end. Here their place is taken by a slender elongated cell, full of granules which stain even deeper with hæmatoxylin than does the mucus cell. The granular gland cell is easily recognized in its earliest stage, and is formed from the embryonic ectoderm cell by a deposition of granules throughout the length of the cell. The granular cells, though especially grouped at the aboral end of the larva, are found here and there over the general surface.

The remaining cells of the embryonic ectoderm become for the most part transformed into slender "supporting cells." Thread cells, *n.c.*, are first noticed in larvæ at about the stage of Fig. 14. Whether the ectoderm contains any muscle cells, I do not know. The larvæ can alter their shape to a great extent, but the fibres are probably all endodermal.

For the study of nervous elements, *Manicina* in all stages is a very unfavorable subject. Even the ganglion cells which show so plainly in sections of actinian larvæ, I was not able to make out in the coral. There is, however, a finely granular stratum at the base of the ectoderm, which is very thin over the general surface, Fig. 26, but at the aboral end of the swimming larva is thick and easily seen, Fig. 20. When the living larva is compressed, this accumulation of granular substance is very noticeable. It is perfectly clear, and until I began to section I thought it was jelly. When carefully examined, the granular layer in this region is found to consist of a mass of fine fibrils. It is very probably nervous. The fact that the cœlenterate planula in general swims with its aboral end in front, taken together with the occurrence of a bunch of long cilia on this end of many actinian larvæ, suggests the existence of some such primitive nervous centre as I take this accumulation of granular matter to be.

When the various elements of the ectoderm have been completely differentiated, Fig. 26 (from a stage a trifle older than Fig. 29), a finely striated cuticle is secreted, in all respects like that described by the Hertwigs for the actinias (9. Taf. III.). The cilia with which the body ectoderm is completely covered, and with which the œsophagus and filaments are likewise provided, I have not represented in the figures.

b. Œsophagus and Filaments.

The œsophagus and young filaments, Fig. 20, have the same structure as the superficial ectoderm, except that mucus cells are absent, and the granular gland cells more abundant than over the general surface. As a rule it is only in the youngest stages that the reflected ectoderm, Fig. 18, contains gland cells, and even then they are rare. In later stages, Fig. 24, mucus cells are found in the upper part of the œsophagus immediately round the mouth, and very large thread cells, Figs. 24 and 27, appear in considerable numbers in the œsophageal epithelium, extending down into the filaments. The histology of the filaments will be treated in detail in a special section.

c. Endoderm.

The endoderm, after it has once formed, remains about the same during larval life. I am not sure whether it is ciliated. The cells are cubical or columnar, and contain one or more large and distinct vacuoles. The protoplasm is granular and coarsely reticular. The cell outlines can only be distinguished with a little care. The number of yellow cells steadily increases with age. A few very fine muscle fibres can be made out here and there, especially in the mesenteries, and a continuous layer probably exists.

In closing, the general similarity between the ectoderm of the coral larva (practically the same in the adult *Manicina*) and the actinian ectoderm, as described by the Hertwigs, may be noticed. In particular, the two kinds of gland cells in the actinias are exactly represented in the coral. The Hertwigs suggested that possibly the granular gland cell was but a stage in the development of the mucus cell; but this appears not to be the case, as the two are distinguishable from the start, and have also a different distribution.

VI. MESENTERIES AND FILAMENTS FROM THE SECOND TO THE SIXTH PAIR.

Before proceeding to the detailed description of the reflection of ectoderm, which, as I conclude, leads to the formation of all the filaments except the first pair, it will be convenient to give an account of the order in which the mesenteries appear.

The first appearance of the second pair of mesenteries has already been described, Fig. 18. In a later stage, Fig. 27 (transverse section) this pair is complete at the level of the figure. At a lower level, just above the lip, Fig. 28, one of the pair, 3, is still complete, while the other, 4, is incomplete. The difference in growth between the two mesenteries of the second pair is an exception; they usually develop at the same rate. Below the œsophagus, Fig. 29, both mesenteries exist as slight ridges, which extend the length of the larva.

The third pair of mesenteries have appeared in Fig. 27. They remain insignificant during the swimming life of the larva. After the larva has become attached, the third pair is prominent; and the fourth pair is also found, in the position shown in Fig. 34 (a transverse section taken below the œsophagus — the primary mesenteries are supplied with large and coiled filaments). According to Lacaze Duthiers, the fourth pair appears between the first and second pairs. The Hertwigs suggested (?) on general grounds of symmetry that the order of appearance was as I have figured. As regards the fifth and sixth pairs, however, the old account of Lacaze Duthiers holds for *Manicina* as against the figures given by the Hertwigs for Adamsia (Taf. 1, f. 3). This is seen on referring to Fig. 39, a transverse section through the œsophagus of a stage with twelve mesenteries. The fifth and sixth pairs develop simultaneously on opposite sides of the primary mesenteries. In *Adamsia*, according to the Hertwigs, the two pairs of mesenteries appear on opposite sides of the long axis of the œsophagus, in the chambers between the first and second pairs.

Fig. 39 represents my oldest larval stage, and I was consequently not able to trace the development of the muscle plates and the rearrangement of the twelve primary mesenteries. According to the accepted account, the pairs 3 and 4, in Fig.

39, become the directive pairs, and on each side of the long axis of the œsophagus, 5 and 1 unite to form one pair, and 6 and 2 another pair.

In this connection it may be observed that after the larvæ became attached, the lumen of the œsophagus was decidedly bilateral in the living animal, and bore the relations to the mesenteries shown in Fig. 39. The shape of the lumen is, however, susceptible of great changes, and in many of the sections through attached larvæ the typical shape is not retained (Fig. 36), or the œsophagus is compressed in the (normally) long axis, and drawn out in the short (Fig. 45). In the swimming larva the small size of the mouth will not permit one to decide as to the shape of the œsophagus in the living animal. After examining a large number of sections I conclude that in stages as old as Fig. 27, the arrangements are as in the attached larva: the lumen is bilateral and has one of the first pair of mesenteries on each side of its long axis. In earlier stages, such as Figs. 7, 14, 18, I could not decide whether the œsophagus had acquired its ultimate shape.

We now come to the formation of filaments for the second and subsequent pairs of mesenteries. In Fig. 18 the reflected ectoderm which forms the œsophageal wall of the larger chamber extends horizontally from 1 to 2. The mesenteries of the second pair, 3 and 4, are extremely incomplete. In Fig. 27 these mesenteries are complete, and now the reflected ectoderm does not extend from 1 to 6, but is represented by the patch *R.E.* between 3 and 4. In sections of the same larva (Figs. 28 and 29, below the level of Fig. 27) a certain irregularity makes its appearance, which is connected with the formation of the third mesentery, and of which I shall speak later. In the typical larva of this stage the sections below Fig. 27, between it and the lip of the œsophagus, are precisely like Fig. 27. This means that the mesenteries 3 and 4 are both complete throughout the length of the œsophagus, and that the œsophageal wall of the chambers inclosed between 2 and 4, and 3 and 1 respectively, is endodermal. At the very lip of the œsophagus in some larvæ the œsophageal walls of these chambers are ectodermic. In a section just below the œsophagus it is found that the mesenteries 3 and 4 have short filaments. Further, the tract of ectoderm *R.E.* only extends upwards for about one-third the length of the œsophagus, while it will be remembered that in this stage (Fig. 18) the reflected ectoderm extends nearly the whole length of the œsophagus. Now what has taken place in the transition of the stage Fig. 18 into the stage Fig. 27? Plainly it is that the mesenteries 3 and 4, as they grew down and gradually became complete, carried along with them the reflected ectoderm, part of which came to lie along the mesenteries as short filaments, while the remainder was divided into three portions. Of these, the two lateral, which originally extended from 2 to 4 on the one side, and from 1 to 3 on the other (Fig. 27), were carried all the way down to the lip of the œsophagus, while the middle portion *R.E.* was not carried the whole way down.

A couple of longitudinal sections will further elucidate the series of changes which separate Fig. 18 from Fig. 27. The sections given in Fig. 25 were made from a larva at about the same stage as Fig. 27. The two mesenteries of the first pair had long filaments, and the mesenteries of the second pair were complete and equally advanced. The section *b* is a radial half-section through one of the second pair of mesenteries, say 4 in Fig. 27. The mesentery is complete, and to its edge clings a short filament. The other mesentery of the second pair, with its filament, is the exact counterpart of the one figured (in cutting the larva, radial sections of one mesentery and equally true transverse sections of the other were obtained). The precisely horizontal plane in which the filament of *b* lies, is probably due to the sudden expansion of the larva, on being killed, in the direction of the shorter transverse axis of the œsophagus (the transverse section would be elongated in a direction at right angles to the long axis of Fig. 27). The half-section *c* in Fig. 25 is reversed so as to complete the œsophageal lumen. It is the second section to one side of *b*, and *a* is the second or third on the other side. Comparing all these figures with Fig. 27, *b* is through mesentery 4, *a* is on the far side of 4, and consequently cuts the reflected ectoderm *R.E.*; *c* is on the near side of 4, and the ectoderm is not reflected round the free edge of the œsophagus.

Fig. 24 is a single longitudinal section from a stage slightly older than the one just described. On the right it is through one of the second pair of filaments, and on the left through an intermesenteric chamber. Referring the section to Fig. 27, the right half is through mesentery 4, and the left through the chamber opposite at about the point *x*.

Having now described the ordinary way in which the first and second pairs of mesenteries and filaments are formed, I will take up an exception, which has more bearing on the relationship between the Anthozoa and Scyphomedusæ. Figs. 30–33 are transverse sections, numbered from above down, of a larva in which the first pair of filaments extended about half the length of the body. The œsophagus throughout its vertical extent is apposed to the surface ectoderm over a wide tract, *a* to *b* in Fig. 30. On running through the series of sections it becomes evident that the tract *a–b* is not the meridian of a single mesentery, as it would be in a normal larva like Fig, 14, but is the space between two mesenteries. The first section below the œsophagus, Fig. 31, shows that a rather wide lobe of ectoderm is growing down, and also that between *a* and *b* this lobe has been forced apart from the body ectoderm. In Fig. 32 (two sections omitted between 31 and 32) a lobe of endoderm has grown in between *a* and *b*, and has thus given rise to two mesenteries, which are provided with a common filament. In the section below, Fig. 33, the lobe of endoderm is hollowed out, and the two mesenteries definitely established. In a section (not figured) below Fig. 33, the mesenteries *a* and *b* exist as separate ridges, and the common filament has split into its constituent parts, 1 and 3. The filament 3 extends a very short distance down, and the mesentery *b* only reaches the equator of the larva. The mesentery *a*, with its filament 1, is the fellow of 2, on the opposite side of Fig. 32. These two mesenteries belong to the first pair. I have assumed that *a* is the primary mesentery, since its filament is larger than that of 2.

Bearing in mind the normal development as illustrated in Figs. 12 and 14, the exceptional character of this larva is due to the fact that one of the second pair of mesenteries is formed at the same time and in the same manner as the mesenteries of the first pair. This aberrant member of the second pair, *b*, Fig. 30, etc., may be called the third mesentery. We may suppose that the œsophagus, applying itself to the body ectoderm along the line not only of the first *a*, but also of the third mesentery *b*, was unable to force down the endoderm in these lines without carrying down at the same time the endoderm between *a* and *b*. Thus came the condition shown in Figs. 30 and 31. When the time came for the mesenteries as such to be formed, the endoderm which had been pushed down between *a* and *b* was compelled to grow up again, becoming excavated so as to form the intermesenteric chamber. It is in this process that we see the endoderm in Figs. 32 and 33. The irregularity of the larva, it will be noticed, is confined to one side: the right side of the sections is normal, and doubtless the other member of the second pair of mesenteries would have developed in the usual way.

The larva just described was the only young specimen I observed, which exhibited this peculiar variation. I found a few older individuals, however, in which one of the filaments of the first pair was so intimately connected with one of the second pair, as to render it probable that the two were simultaneously formed from a common lobe in the manner shown in Figs. 30–33. The larva, Figs. 27–29, to which I have already referred several times, comes under this head. Though the section, Fig. 29, is an appreciable distance below the œsophagus, the filaments 1 and 3 are still united, and bear evidence of their common origin. The other mesentery of the second pair, 4 in Fig. 28, has itself been formed, and is gaining its filament, in the normal manner. The reflected ectoderm only extends from 2 to 3, and if the latter mesentery has been formed in the manner suggested, the ectoderm never was reflected between 3 and 1.

Returning to the normal development we have now to trace the origin of the filaments for the third pair of mesenteries. These filaments are derived from a lobe of ectoderm, which is reflected into the smaller of the two primary chambers. The reflection takes place after the larvæ have become attached. In a stage with twelve mesenteries, Fig. 39, the lobe is marked *x*. The section is taken at a level higher than that reached by the lobe belonging to the chamber *c* (marked *R.E.* in Fig. 27). In a section just above Fig. 39 the third pair of mesenteries bury themselves in the lobe *x*, much as 4 does in Fig. 28. In the uppermost sections, where the mesenteries are complete, *x* is not found. After a great many trials I succeeded in getting a radial section through one of this pair of mesenteries, which had forced down the reflected ectoderm so that the latter lay along its free edge as a tiny filament (Fig. 38, left half; the right half is through chamber *c*, Fig. 39). The lobe for the third pair of filaments is almost always present in larvæ with eight mesenteries: in Fig. 36, a section just above the lip, it is marked *c*. In this larva the mesenteries of the second pair are backward in development; they are not yet perfectly complete, though on one of them a very small filament is seen.

As the fourth pair of mesenteries continue to increase in size, the tract of ectoderm, which belongs to the chamber *c*, in Fig. 39, extends farther upwards. In Fig. 39 it reaches about the same level as in Fig. 27 (*R.E.*). In a slightly more advanced stage, Fig. 38 (right half), it extends nearly the whole length of the œsophagus; and in the series of transverse sections, Figs. 43–45, it likewise extends to nearly the uppermost limit of the chamber. The latter series is a very good one, as the polyp was killed in its natural shape. In life, when the young coral is expanded, there is a very distinct oral cone, indicated by the line *m–m* in Fig. 38. In dying, the oral surface is almost always retracted, and the median longitudinal section is then as in Figs. 37 and 38. The transverse section, Fig. 43, is taken through the line *x–y*, in Fig. 38. Figs. 44 and 45 lie above it. In the larva from which the series was taken, both the third and fourth pairs of mesenteries were very well developed below the level of *x–y*, but above this level they were not perceptible. Judging from all my other sections I should say that this rapid development of the mesenteries along the side-wall of the polyp, as contrasted with their backwardness in the upper œsophageal region, was exceptional. In the sections figured the first and second pairs of mesenteries are complete. The chambers *a* and *b*, together with *c*, represent the larger of the two primary chambers. The walls of *a* and *b* are endodermal except for a short distance above the œsophageal lip, but in *c* and in *d* (the smaller of the two primary chambers) the reflected ectoderm extends very far up. As the third pair of mesenteries lie in chamber *d*, the ectoderm of this chamber, as might be expected, extends farther up than in *c*, in which lie the fourth pair. In the ectoderm of *d* there are a few large nettle cells, a rare occurrence. At the upper limit of each tract of ectoderm, the overlapping of the layers, previously referred to, is shown. This overlapping of the layers, while uncommon, is noticed in a good many specimens. In Fig. 37 the left half of the section, through an intermesenteric chamber, exhibits this phenomenon. The right half of the section is through one of the second pair of mesenteries.

The fifth and sixth pairs of mesenteries appear simultaneously, but it is convenient to speak of one pair as the fifth and the other as the sixth. They are still very small in my oldest larval stage. The filaments for the fifth pair are probably formed from the lateral portions of the lobe *x*, Fig. 39, after it has been divided by the completion of the third pair of mesenteries. The filaments for the sixth pair, it seems, will be formed from the tracts of ectoderm, which belong to the chambers *a* and *b*, Fig. 39. These tracts, it will be remembered, were in most larvæ pushed completely back to the free edge of the œsophagus, where the second pair of mesenteries become complete. In stages with twelve mesenteries, however, such as Fig. 39, they have again appeared, though they usually extend but a very short distance above the lip. In a couple of larvæ as old as Fig. 39, they were unusually well developed, reaching as far up as the tract for the chamber *c*.

In summing up the facts of the reflection of ectoderm it will be convenient to refer to Fig. 39.

The ectoderm reflected into the larger of the two primary chambers is pushed down by the growth of the second pair of mesenteries. From it are formed the filaments for these mesenteries, while the remainder of the original tract splits into three divisions. The middle division, chamber *c*, is not pushed entirely to the edge of the œsophagus ; later in life, when the fourth pair of mesenteries is well developed, this tract grows once more nearly to the upper limit of the œsophagus. The lateral divisions *a* and *b* are pushed to the edge, but after the sixth pair of mesenteries has appeared they begin to grow up again. When the mesenteries of the third pair are well advanced, the ectoderm is reflected into the smaller of the two primary chambers, and runs up the œsophageal wall nearly to the top of the chamber. The mesenteries, when they begin to grow down, carry a part of the ectoderm along their free edges as very slender filaments. The growth of the various tracts of reflected ectoderm is thus seen to follow in general the order of development of the mesenteries.

VII. ORIGIN OF THE FILAMENTS IN THE ADULT.

After studying the larval development it seems very sure that the filaments of the first twelve mesenteries are ectodermal. Further, I think the stage with twelve mesenteries holds the key to the condition in the adult. In this stage, Fig. 39, etc., there are complete (first and second pairs) and incomplete mesenteries (third pair), both provided with ectodermal filaments. Both kinds of mesenteries are exactly comparable with the two kinds in the adult, and if the incomplete mesenteries of the larva are successively supplied with filaments by the reflection and upward growth of the ectoderm, it seems probable that the incomplete mesenteries of the adult are supplied in the same manner.

The gap between my series of larval stages and the adult is partially bridged over by the transverse sections, Figs. 41 and 42. The young *Manicina* from which these sections were made was one-eighth inch diameter. I found a couple of about the same size on a piece of coral rock. In hardening these two specimens I was not fortunate, and they were consequently of no value for the study of such fine points as the reflection of ectoderm. Fig. 41 is through the œsophagus, and disregarding the skeleton, shows six pairs of complete and six pairs of incomplete mesenteries. The twelve complete mesenteries represent the mesenteries present in the larva, now rearranged in pairs and with simple muscle plates (only shown in the directive mesenteries). The incomplete mesenteries have appeared according to the general law governing the mesenteries above twelve.

Manicina remains a single polyp until it has reached a diameter of about one-third of an inch. In this condition it has all the characters of the adult, except those dependent on asexual multiplication. It is, moreover, not sexually mature. Such a coral has, disregarding local irregularities, twelve pairs of mesenteries of the first order (complete), twelve of the second order (incomplete), and twenty-four pairs of the third order (much more incomplete). Fig. 50 gives a median longitudinal section of the coral at this age. The polyp was in a state of complete contraction, the oral surface or peristome, *Pr*, pulled down, the mouth, *Mo*, widely open, and the tentacles, *T*, retracted. The section on the right is through a mesentery of the first order, on the left through one of the second order. The line 3 marks the position of the free edges of the tertiary mesenteries. The latter are not provided with filaments. On each side of the section, the mesentery is divided into a central and peripheral part (*R.P.*) by the calcareous theca, *Th.* (When the animal is expanded, the peristome is lifted high above the level of the skeleton. It then embraces the whole width of the animal, the tentacles forming a dense ring round its edge, while the mouth is narrowed to a slit-like opening.)

On the right side of Fig. 50 the epithelium of the œsophagus, Œ, is directly continuous with the filament 1, the mesentery being complete. On the left side the mesentery being incomplete, the œsophagus has a free edge. Now if my view is correct, not only the lining epithelium of the œsophagus is ectodermal, but the epithelium *x*, which forms the gastric covering of the œsophagus and peristome between the complete mesenteries, is likewise ectodermal: the ectoderm here, as in the larva, is reflected round the lip of the œsophagus, and extends upwards until it reaches the secondary mesentery, down which it courses as the filaments. Fig. 55 is a more highly magnified view of the lower part of the œsophagus, as shown in the left half of Fig. 50. The lining epithelium of this part of the œsophagus, the lower third, is composed of slender supporting cells. The upper two thirds contain large nettle cells, and in the region of the mouth mucus cells. The epithelium on the outer surface of the œsophagus, is for some distance (compare Fig. 55 with Fig. 50) exactly like the lining epithelium, except that it contains a few yellow cells. Then comes a region of vacuolated cells, which is followed by a very low epithelium made up of exceedingly small cells, the exact shape of which I could not determine. The low epithelium is continued up the œsophagus and over the peristome, and is continuous with the filaments on the secondary mesenteries. These filaments, though of large size at a lower level, gradually become very small as they approach their upper limit, and by this means run without any break into the low epithelium covering the peristome. The filaments on the third pair of mesenteries in the larva were likewise very small in the upper part of their course, though, to be sure, in my oldest larval stage they as yet only existed in this part.

The view that the gastric lining of the œsophagus and peristome is ectoderm can only be held by supposing the epithelium in question to have suffered a great histological change. (It is possible that a very careful histological examination of the epithelium, *x*, would show that it does not differ so much from the ectoderm as appears to be the case.) But though this tract of epithelium cannot be said to resemble the ectoderm, it differs quite as much from the undoubted endoderm. The endoderm of the adult, Figs. 51 and 52, is made up of large irregularly columnar cells, packed with "yellow cells," the vacuoles present in the larval endoderm being confined to special localities. The only apparent alternative to the view offered is that while the first twelve mesenteries are provided with ectodermal filaments, the filaments of all subsequent mesenteries are endoderm. Since the several orders of filaments in the adult differ only as regards size, and since even this difference is a transient one, owing to the constant transformation of incomplete into complete mesenteries during the growth of the coral, it seems improbable that such precisely similar organs should be formed by both layers.

On the other hand, E. B. Wilson (8) came to the conclusion that the dorsal pair of filaments in the Alcyonaria were ectodermal lobes, but that the remaining six filaments were purely endodermal. The two kinds of filaments in these polyps have, however, a very different histological structure, with which is associated a division of labor.

Von Heider (11) several years ago decided that the filaments of *Cerianthus* were ectodermal. He reached his decision by a histological study of the adult, and though this method is inconclusive, I am not surprised after studying myself some immature specimens of *Cerianthus*, that he came to this view. The Hertwigs in their classical work on the actiniæ pointed out that embryological deductions based on adult histology are not very reliable, and also brought forward as an objection to von Heider's view, the existence of filaments in the actiniæ generally on incomplete mesenteries.

VIII. HISTOLOGICAL STRUCTURE OF THE FILAMENTS.

The very young mesenteric filament is shown in cross-section in Fig. 17. In this larva, the first pair extend about half the length of the body. In Fig. 29, though the mesentery is elevated above the general endoderm, the filament retains its simple character. It is roughly hemispherical in section, and is separated from the mesentery by a thin sheet of supporting membrane. Besides supporting cells, there are present granular gland cells. In most larvæ in which the first pair of filaments reach the aboral end of the body, the filament is no longer separated from the mesentery by supporting lamella. Fig. 19 gives a surface view of such a larva, and Fig. 26, a cross-section of one of the long filaments. In the latter figure the sheet of supporting lamella, on which the filament formerly rested, has given place to an accumulation of jelly at the apex of the mesentery. Though the cells of the filament are practically continuous round this gelatinous axis with the cells of the mesentery, the line of demarcation is very evident on each side owing to the different histological characters of the endoderm and ectoderm cells. In the filament there are now numbers of large nettle cells, and the gland cells are far more numerous than in earlier stages. Nervous elements are very probably present, as there is a granular stratum in the deepest part of the filament. As is shown in Fig. 19, the filament increases in size towards its lower end. Near the close of the swimming life the first pair of filaments begin to get slightly curved and twisted in the lower part of their course. The young filament before its cells become continuous with those of the mesentery, is very loosely attached to the latter; in a number of cases I observed that the mesentery and filament had entirely separated from each other (Fig. 29, Mes. 3), owing, no doubt, to the contraction caused by the killing fluid.

Fig. 35 is through one of the first pair of filaments, and its mesentery, of an attached larva with eight mesenteries. In the attached larva these filaments pursue a straight course for a short distance below the œsophagus. In the lower part of their extent, they are curved and twisted as in the adult, and in this region sections like Fig. 34 are obtained. Fig. 35 is through the straight portion of the filament. On comparing this figure with Fig. 26 (magnified to the same degree) it is seen that the mesentery has become more elevated, and at the same time thinner; also, that where the endoderm cells end and the filament cells begin there has been a pinching in, which, added to the actual bulging out of the filament, has very distinctly worked off the latter from the mesentery. The bulging out of the filament is due to the lateral expansion of the axial jelly shown in Fig. 26. The expansion of the jelly has so taken place that the filament, Fig. 35, is divided into three portions: the main body to which are confined the nettle and gland cells; and two tracts, *v.l.*, which may be called the ventro-lateral tracts. The latter are composed exclusively of slender supporting cells. As in the swimming larva, the filament cells are sharply marked off from the cells of the mesentery. In spite of the twisted condition of the lower part of the filament, sections show that the structure is the same as in the upper part.

In the adult the upper portion of the filament on a complete mesentery is comparatively straight, but the main portion is twisted, Fig. 50. The filaments of the incomplete, are less twisted than those of the complete mesenteries. The filaments are attached their whole length to the mesenteries, there being no free acontium; they are, however, capable of extrusion both through the mouth and (though I could not find the apertures) through pores (cynclides) in the body wall.

Unlike the larval filament, that of the adult has a different structure at different levels. Figs. 52, 53, and 54 are sections through the different parts of a filament on a complete mesentery. Fig. 52 is through the upper third. The filament itself has almost exactly the shape shown in Fig. 35, but the mesentery is swollen out and forms two lateral lobes, *m.l.*, between which the filament rests. The ventro-lateral tracts are much better marked in the adult than in the larval filament. This is due to the continuation of the pinching in process which had already gone some distance in Fig. 35, and to the outgrowth of the mesenteric lobes, *m.l.* By these means the slender "waist" is produced, which indicates the separation of filament and mesentery.

The ventro-lateral tracts of the filament, both in the upper portion of its course, Fig. 52, and lower down, Figs. 53 and 54, are made up exclusively of supporting cells. The main body of the filament in Fig. 52 contains a large number of granular gland cells and numerous nettle cells. The mesenteric lobes are composed of cells which do not differ essentially from the rest of the endoderm; they are only much elongated and contain a number of very large vacuoles. The passage of the filament into the œsophageal epithelium is effected in the following manner. Immediately below the œsophagus, the "waist" in Fig. 52 becomes gradually wider until the ventro-lateral tracts no longer exist, and the filament cells are continuous with the mesentery cells round the horns, *h*, of the supporting lamella of the filament. At this level, the filament or œsophageal lobe is much flatter and wider than it is below (Fig. 52), and the supporting lamella of the filament is also nearly flat. The latter passes directly into the supporting lamella of the œsophagus, and the filament into the lining epithelium of the œsophagus.

Fig. 53 is through the middle third of the filament. The gland cells are absent in this region, but the nettle cells are very large and exceedingly abundant. The mesenterial lobes are not so well developed as in the region above.

The lower third of the filament, Fig. 54, contains neither nettle cells nor the typical gland cells. The body of the filament is here made up of very large granular cells, between which are scattered a few supporting cells. The granules are much more numerous in the peripheral than in the central halves of the large cells, and at the sides of the filament where the main body passes into the ventro-lateral tracts, they become gradually restricted to the peripheral ends of the cells. The granules are chemically different from those in the ordinary granular gland cell: they do not stain especially well with hæmatoxylin, but become dark brown with osmic acid. In a number of filaments these peculiar granular cells contained large, irregular concretions, which stained dark red with borax carmine, while the cell body stained but faintly. The mesenteric lobes in this region are slightly less pronounced than in the rest of the filament. In a transverse section through the filament of *Sagartia*, Von Heider (10) has figured the lateral parts of the simple filament (according to the Hertwigs, the section is through the acontium) as composed of just such large granular cells as I have described. The Hertwigs do not speak of these tracts.

From Fowler's brief description (15, II.) it would seem that the filaments of *Madrepora* are essentially like those of *Manicina.* The condition of the specimens, however, as the author states, did not permit a detailed study.

The filaments on the secondary are somewhat smaller than those on the primary mesenteries. The mesenteric lobes, too, are less pronounced, not reaching a development greater than is shown in Fig. 54. It has been mentioned that in the upper part of their course the secondary filaments become very small. Though the diminution in size is so great in this region, that it was impossible for me to make out the histological structure, I was able to trace the filament as a darkly staining and compact mass of tissue into the epithelium of the peristome. The filaments of the young coral, from which Figs. 41 and 42 were made, were like those of the adult, except that the mesenterial lobes were less developed.

I did not study the living filaments, but from the histology it is evident that the function of the ventro-lateral tracts is that of ciliated bands, while the digestive functions and nettle cells are distributed over the three portions of the main body of the filament. The mesenteric lobes I regard merely as a device to support the filament.

Before comparing the mesenteric filaments of *Manicina* with the actinian filament as described by the Hertwigs, I will give a brief account of the filaments of *Cerianthus*, this being the only actinia I have been able to study by way of comparison. In Nassau harbor the larval or free-swimming Cerianthus was common. All the individuals I obtained were at about the same stage of development. They were oval light brown bodies about one-fourth inch long, and had eight or nine very short, stubby tentacles. On sectioning the larvæ, I found they confirmed the theory advanced by the Hertwigs (*l.c.*) as to the mode of origin of the mesenteries. Fig. 49 is a section through the upper part of the œsophagus. The number of complete mesenteries is fifteen. At one end of the œsophagus is the ventral or directive pair of mesenteries, *D.M.* At the other or dorsal end are two incomplete mesenteries, 1 and 2, of which the former is the younger. The mesentery 3 becomes incomplete not far above the œsophageal lip, and 4 follows its example just above the lip. From these four mesenteries it may be gathered that each new mesentery appears along the dorsal meridian between the two last formed, and in such a way that the successive mesenteries come to lie on opposite sides of the dorso-ventral plane. The directive pair, *D.M.*, corresponds to the directive pair which the Hertwigs have figured (Taf. I., Fig. 8). These authors state, however, that this pair is the longest of all, extending to the anal pore. In the young specimens I have studied, this pair disappears some distance above the pore, and is exceeded in length by two or three mesenteries on each side of the dorso-ventral plane. Von Heider (11) made the discovery, which the Hertwigs confirmed, that in the adult there is a much shorter pair enclosed between the two directive mesenteries. This short pair only extends the length of the œsophagus. It must appear in stages later than Fig. 49, so that besides the formation of mesenteries which takes place dorsally, at least one pair is formed ventrally.

Filaments were found only on the complete mesenteries. Fig. 47 is from a section just below the œsophagus. The mesentery is composed of very large cells with immense vacuoles.

At the edge of the mesentery, just beneath the filament, the tissue is becoming more compact. This process has gone much farther in Fig. 48 (from the same mesentery at a lower level). The whole mesentery, as may be seen by comparing my figures with Hertwigs' Taf. VIII., gradually suffers this change as the animal becomes adult. In Fig. 47 the filament has a central body provided with gland and nettle cells, and two lateral ciliated tracts *m*, composed of supporting cells, which are gradually assuming the shape of distinct lobes owing to the subjacent growth of the jelly. The central body passes directly into the epithelium of the œsophagus, the lateral tracts becoming indistinguishable from the body of the filament just before the transition. This figure is but slightly different from the section of the adult filament given by the Hertwigs. At a lower level, Fig. 48, the ciliated tracts are no longer found. On many mesenteries the filament has almost no connection with the endoderm, as in the figure. In such figures as Fig. 48, it need hardly be said that violent contraction has had much to do with producing such complete separation of filament and mesentery; but this only shows how loose the connection is in early life. On other mesenteries the filament is continuous at its sides with the cells of the mesentery. None of the filaments in these young specimens of *Cerianthus* ran the whole length of the mesentery. Most of them stopped at about the equator of the body.

In the actinias, studied by the Hertwigs, the mesenterial filament in the upper part of its course is in section tri-lobed. There is a median secretory tract and two lateral ciliated tracts. The mesoderm extends into each lobe. On all the mesenteries the ciliated tracts are lost in the lower portion of the filament. On the incomplete mesenteries the median tract disappears towards the upper limit of the mesentery, the lateral ciliated bands remaining. On the complete mesenteries the median tract merely gets smaller towards the œsophageal end, but does not disappear.

The description I have given of the filaments of *Cerianthus* is, barring slight differences due to age, like the account the Hertwigs give for this actinia. From this description it is seen that the filament of *Cerianthus* corresponds in the main to a typical Hertwig filament, such as is on a complete mesentery. But the lateral lobes, *m*, Fig. 47, are very small even in the adult when compared with the lateral wings of the *Sagartia* filament (H., Taf. V., Fig. 10).

The filament of *Manicina* is a much simpler structure. It is not trifid, though the mesenteric lobes, *m.l.*, Fig. 52, give such an appearance to the edge of the mesentery. But on referring to Hertwig's figure of *Sagartia* (Taf. V., Fig. 10), it is evident that the mesenterial lobes of *Manicina* do not represent the ciliated bands of *Sagartia*. They are totally different histologically, and do not contain prolongations of the mesoderm. On the other hand, the ventro-lateral tracts of *Manicina* do correspond histologically with the ciliated bands in the Hertwig filament, and the glandular lobe of the latter is in general similar to the median stripe of the *Manicina* filament. As I take it, all three tracts of the Hertwig filament, taken together, are homologous with the simple filament of *Manicina*. They must all, therefore, be ectodermal: in the young *Cerianthus*, Fig. 47, the lateral lobes evidently belong to the median lobe, and are not modified parts of the mesentery; and since the median lobe at a lower level, Fig. 48, shows its independence of the mesentery, the conclusion seems to be that the whole filament is ectodermal. Though the filament of the adult coral is a much simpler form than the trifid filament, it would be difficult to derive the latter from the former, owing to the presence of mesenteric lobes in the coral. It is easy, however, to derive the trifid from the larval filament, Fig. 35. In this form the ciliated tracts, *v.l.*, and the median secretory tract, are already differentiated; to produce the trifid filament it is only necessary for these tracts to become separated by the division of the mesoderm into three lobes. By this division, while the median stripe gains but little, the ventro-lateral tracts are put in a position where it is possible for them to reach a high development.

The number of Actinozoa in which the mesenterial filaments have been carefully studied is very limited, but from the data at hand it seems probable that the ancestral filament, like the filament of the larval *Manicina*, was a simple undivided body, in which, however, the originally uniform ectoderm had become split up into three physiologically distinct tracts: a median tract, in which were concentrated the nettle and glandular elements, and which embraced most of the filament; and two lateral ciliated portions which were but slightly developed. The belief that the division of labor in the Zoanthorian filament dates very far back, is supported by the existence of a similar division of labor in the Alcyonaria. But in these polyps, as Wilson (8) has shown, the functions are not distributed over different parts of the same filament, but amongst the several filaments. The dorsal pair are ciliated bands, having no gland or nettle cells, while the remaining six filaments contain gland and nettle cells, but have no ciliated tracts.

IX. THE SKELETON.

Until the time of Von Koch's researches the skeleton of the Madreporaria was regarded as calcified mesoderm. The theca, or coral wall, according to this view, represented the supporting lamella of the lateral body wall of an actinia; and where, as in most corals, the theca was largely uncovered by animal substance, the explanation was that the ectoderm had atrophied. In 1879 Von Koch (12) showed that the theca is independent of the lateral body-wall, and projects into the cœlenteron of the polyp in such a way as to divide the cavity and mesenteries into central and peripheral parts. This conclusion, though not universally accepted, is, I think, now incontestable. Von Heider in 1882 (14) published the important observation that the skeleton is not only covered by supporting lamella and endoderm, but that between the calcareous matter and the supporting lamella is another layer of cells, to which was given the name of calycoblasts. Von Koch in 1883 (13) made the whole matter clear by showing that in the young *Asteroïdes* the skeleton is secreted by the ectoderm and is at first entirely outside the body. The ectoderm of the basal surface of the attached larva secretes a calcareous basal plate. Radial folds of the basal ectoderm then grow up between the mesenteries into the cavity of the polyp, lifting up, as they grow, the supporting lamella and endoderm. The cavity of the fold is filled with calcareous matter, which is the septum. The secreting ectoderm becomes the calycoblast layer of Von Heider. The origin of the basal plate and septa is thus clear enough, but Von Koch's account of the development of the theca is not satisfactory. As far as his observations went they appear to have confirmed his belief, gathered from a study of adult corals, that the theca is formed secondarily from the septa; the originally simple septa become bifurcate at their peripheral ends; the lateral processes of adjacent septa grow towards each other, pierce the mesentery, and, fusing, form the theca. Von Koch's account of the relation of the skeleton to the soft parts in the adult has recently been confirmed on a number of genera by Fowler (15) and Bourne (16), though as regards the extra-thecal part of the cœlenteron Fowler differs from Von Koch in the interpretation of his sections. From these papers it is also evident that the *Madreporaria* exhibit great variety in the details of the relation between the soft parts and skeleton. My own very incomplete observations on the skeleton of *Manicina* are for the most part a confirmation of Von Koch's statements.

In the newly attached larva, Fig. 37, the ectoderm of the basal surface is made up exclusively of supporting cells. The granular cells present at the aboral end of the swimming larva have all disappeared. Some time after attachment a small patch of calcareous matter is found on the basal surface, and sections through such larvæ, after the lime has been removed by acid, give figures like Fig. 38, though in many individuals the ectoderm was torn in freeing the larva from the bottom of the dish. In Fig. 38 the cells of the basal ectoderm radiate toward a common centre. There seems to be an effort on the part of the more peripheral cells to share in the secretion of the central patch of homogeneous substance shown in the figure. This homogeneous substance is the animal basis of the nascent basal plate. It exhibits no structure, but stains deeply with hæmatoxylin, and in its general appearance impresses one as a very much thickened cuticle. I was not able to trace the development of the skeleton any further.

The fully formed skeleton may very conveniently be studied in young polyps, which have not begun to multiply asexually. Ground sections of the skeleton are of some use, but with a little care the polyps may be decalcified so that the skeletal layer of tissue retains with great exactness the shape of the skeleton. Figs. 46, 50, and 56 are from young *Manicinas* about one-third inch in diameter. Fig. 46 is part of a transverse section through the line *a* in Fig. 50 (*oe. ec.* is the ectoderm of the peristome; *ec.* that of the lateral body wall). Were the section complete, it would show twelve primary, twelve secondary, and twenty-four tertiary pairs of mesenteries. At this level the secondary mesenteries are complete; a little lower down they are incomplete.

In going down through a series of sections, the tertiaries run out before the lip of the œsophagus is reached. In Fig. 50 the line 3 marks the free edge of a tertiary mesentery. The theca, *Th.*, divides the mesenteries and cœlenteron into peripheral and central portions. The septa, *S.*, are all entocœlic; *i.e.*, lie between the two mesenteries of one pair, and not between two adjacent pairs. The size of the septa varies with the rank of the mesenteries between which they lie. On the outer surface of the theca are the longitudinal ridges, *C.*, or costæ, which appear to be merely the peripheral prolongations of the septa. The edges of the septa are finely and regularly toothed. This is shown in the radial section, Fig. 56, which is taken through one of the coral septa. In Figs. 50 and 56 the relations of the columella, *Col.*, to the theca and septa are shown. In the former figure, through a mesentery on each side and consequently between two septa, a deep depression separates the columella from the theca. The primary mesenteries extend to the floor of the depression; the secondaries end some distance above it. The columella is circular in section, and the depression surrounds it as a trench. But the trench is not continuous, being completely divided in the radius of each primary septum, as is gathered from Fig. 56, which is taken through such a septum. In this figure the septum and columella are directly continuous with each other. The columella in reality is not solid, as it is drawn in the figure, but is spongy, being full of portions of the body cavity which it has cut off during its growth. Whether an originally simple and solid columella is formed as a central elevation of the basal plate, is an open question. But the subsequent growth of the columella takes place by the constant incorporation in it of the lower portions of the inner edges of the primary septa. The teeth on the edge of the septa, and the granulations found on their sides, sufficiently explain the spongy nature of the columella.

The skeleton inside the polyp is everywhere covered by the three layers of the body wall, of which the skeletogenous ectoderm or calycoblast layer is next the skeleton. In Fig. 46 and the radial sections these layers are not represented, but they are shown in Fig. 51, a more highly magnified portion of one of the peripheral entocœlic chambers of Fig. 46. The superficial ectoderm is marked *ec.*; the peripheral parts of the mesenteries *mes.* The calycoblast layer covering the costa, or, more exactly, the costal tooth, is as elsewhere a layer of flattened cells. The skeletal endoderm is likewise very flat, and markedly different from the endoderm of the body wall and mesenteries. In radial sections the calycoblast layer is found to be continuous with the superficial ectoderm round the edge of the extra-thecal part of the polyp, or *randplatte*, *R.P.* in Fig. 50.

That portion of the polyp, *R.P.*, that lies outside the theca, has been called by Von Heider the *randplatte*. It has been claimed (Moseley, 18; Fowler, 15) that this part of the polyp ought not to be regarded as normally on the outer surface of the skeleton; but that when the expanded polyp, which extends high above the skeleton, contracts, while most of the body is drawn into the interior of the theca, a portion is pulled down over the outer surface of the skeleton. However plausible this belief may be in the case of those adults in which the extra-thecal part of the polyp is confined to the upper edge of the theca, it is at once found to be untenable on examining a small number of young *Manicinae* of the size of Fig. 50. In the polyp, for instance, from which this section was made, the randplatte covered more than one-half of the lateral surface of the skeleton, and this was true both in the expanded and contracted condition of the animal. Further, in every dozen such young *Manicinas*, one or two asymmetrical ones will be found, in which, while the randplatte is confined to the upper half of the lateral surface on one side of the polyp, on the other side it covers the whole wall down to the surface of attachment. What puts the matter beyond dispute, in this genus at least, is that in the very young *Manicina*, Figs. 41 and 42, the whole skeleton is practically inside the polyp. I also found two or three older specimens (single polyps) in which the entire lateral surface of the skeleton was covered by the randplatte. One of these which I sectioned, was oval in transverse section, long axis about $\frac{2}{5}$ in.; short axis $\frac{1}{4}$ in. The skeleton had a flat surface of attachment, and was $\frac{1}{3}$ in. in height. The randplatte (on rather extra-thecal polyp) in this individual was unbroken, down to the piece of rock to which the coral was fastened; here its ectoderm turned in to form the calycoblast layer.

It appears, then, that up to a certain age, which varies much in individuals, the lateral surface of the skeleton is entirely covered by the polyp. The transformation of the originally large extra-thecal part of the polyp into the relatively small rand platte may possibly take place in many cases gradually, by the constant dying off of this part of the polyp at its free edge, and subsequent disappearance of the dead tissue. But in some instances this is not the case. I found a number of small single polyps in which I first thought the randplatte covered the entire lateral wall of the skeleton, but on looking again, I saw that a very definite line extended all round the lateral surface at about the level of the edge of the randplatte in Fig. 50. Above this line the soft parts looked perfectly healthy, but below it dull and sickly. On sectioning I found that above the line the randplatte was normal, but that the tissue below it was a membrane with scarcely a trace of cellular structure and made up for the most part of plant filaments. In some asymmetrical specimens the portion of the skeleton left uncovered by the randplatte was covered by a precisely similar membrane, which was marked off from the randplatte by a deep furrow. In all such specimens the ectoderm of the randplatte was continuous at the edge of the latter with the calycoblast layer. These peculiar membranes gave every indication of having been originally continuations of the randplatte; and I conclude that in the individuals possessing them, the extra-thecal part of the polyp had remained intact up to a certain time, but that then the whole lower portion of this part of the animal was cut off from the general gastric cavity. Deprived of its nutriment, this portion became membranous, and was infested by plant filaments. As the coral increases in size, the membranes are shed, leaving a large part of the theca bare. After the randplatte once becomes restricted to the upper part of the skeleton, there is no more shedding of large pieces of tissue. But as the skeleton is constantly growing in height, we have to suppose that the randplatte as constantly dies at its free edge, unless, indeed, we assume that the connection between the calycoblast layer and the skeleton is so slight that the randplatte is merely carried up with the growing skeleton.

In the young *Manicina*, Figs. 41, 42 ($\frac{1}{8}$ in. diam.), the skeleton is very immature, though the various parts of the adult skeleton can all be recognized. In this specimen there was a thin, flat, basal plate, uncovered at its periphery by the body wall. The skeleton above the plate was internal except at the points *a* and a′, where the lower edge of the extra-thecal part of the polyp was notched, so that at these points the skeleton was bare for a short distance above the basal plate. Fig. 41 is through the œsophagus, Fig. 42 is below, and strikes the apex of the columella. Though some of the septa are still independent at as low a level as Fig. 42, at a still lower level they all unite to form a theca, which on the right side of the directive mesenteries is very slightly developed, but on the left side is prominent. Two or three of the septa in the region where the theca is so slightly developed, exhibit the bifurcation of their peripheral ends which Lacaze Duthiers and Von Koch have described. In Fig. 42 indications of six primary septa are more or less evident, and in lower sections where the septa fuse with the columella they are easily distinguished. There are also six secondary septa to be made out in Fig. 42. These twelve septa, which are entocœlic, extend as high and higher than Fig. 41. Further, in Fig. 42 it is evident that twelve tertiary septa have started to develop, though only a few of them extend an appreciable distance above the theca. As only twelve pairs of mesenteries have been formed, the tertiary septa are temporarily exocœlic. Transverse and longitudinal sections through such a polyp as this show very clearly that the growth of the theca is continuous and from below upwards. Nowhere are two septa found which actually pierce a mesentery to form the theca, but everywhere the growing theca pushes the tissues of the mesenteries upwards. Where the theca is formed in such a manner as this, it is out of the question to believe, after Von Koch, that the radial cracks found in ground sections of the theca are due to the existence in these radii of the atrophied remains of the lower portions of the mesenteries.

The costæ in Figs. 41 and 42 are very feebly and irregularly developed. Each septum has, however, three or four teeth along its outer edge, and also a few on its inner edge. All the teeth on the outer edge of the septa open directly to the exterior over the side wall of the coral. In Fig. 41 the septum included between the near pair of directive mesenteries is cut just below the point at which it thus opens. Fig. 40 gives a more highly magnified view of the same septum cut at the level of its opening. In Fig. 42 a tooth has opened at *m*, and another at *n* is sectioned just beyond its opening. The apertures are of good size, and through them the external ectoderm is continuous with the calycoblast layer. This peculiarity of the teeth is no longer found in *Manicina* after asexual multiplication has begun, and only a few teeth open to the exterior in single polyps with the full complement of septa. In one such polyp, however, all the teeth opened in this way. From this it would seem that the connection of the calycoblast layer with the surface ectoderm at these points is a characteristic of youth which is gradually lost. It is possible that this peculiarity may have been acquired in order to bind the little polyp and its simple skeleton firmly together.

X. Origin of the Anthozoa.

As is well known, the reigning view as to the origin of the Anthozoa is that advanced by Claus and Haeckel, according to which the Anthozoa are descended from hydropolyps with gastric ridges. This hypothesis, which considers the distinguishing feature of the Anthozoa (and Scyphomedusæ) to be the possession of tænioles, or endodermal ridges (mesenteric ridges), has recently been attacked by Professor Götte in a very interesting paper (17) on the development of the Scyphomedusæ (Aurelia). The author conclusively proves the Anthozoan nature of the Scyphostoma larva, showing it to possess four complete mesenteries and an ectodermal œsophagus. Unfortunately, no observations were made on the origin of the mesenterial filaments, which in all probability are ectodermal lobes. Regarding, then, the Scyphomedusæ as an offshoot from the older Anthozoan stem, Götte argues that the manner in which the mesenteries and intermesenterial chambers are formed in the larva of the former, is directly opposed to the old view of the hydroid origin of the Anthozoa. The mesenteries and chambers are formed in the following manner: the planula is bilateral, and the permanent layers are formed before the invagination of the œsophagus takes place. The latter is invaginated in such a shape that in the shorter transverse axis of the larva the endoderm is pushed down, while in the other transverse axis two endoderm sacs are formed. The woodcut, Fig. 1, is a transverse section of this stage, through the œsophagus, and Fig. 2 is a longitudinal section through the shorter transverse axis. In a subsequent stage,

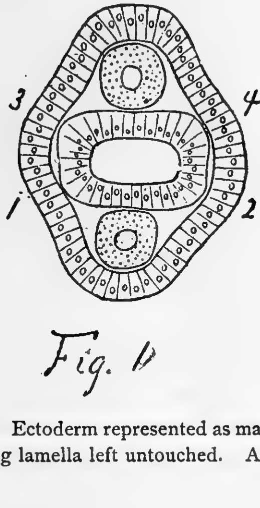

Fig. 1

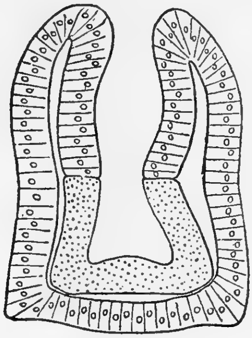

Fig. 2

Ectoderm represented as made of columnar cells. Endoderm is dotted. Supporting lamella left untouched. After Götte, Pl. II., Figs. 20 and 24.

two endoderm sacs grow up from the cœlenteron in the shorter axis, and the œsophagus is then surrounded by four sacs. The sacs are the intermesenteric chambers, and their partition walls form the mesenteries. Götte concludes that in this development there is no stage which corresponds to the hypothetical hydropolyp ancestor. The young Scyphostoma itself, which has hitherto been regarded as a hydropolyp with tænioles, is in reality an Anthozoan with four complete mesenteries; and the development previous to the Scyphostoma does not pass through a hydroid stage, but, on the contrary, jumps directly from a hollow planula to the larva provided with two (later four) endodermal sacs. This larva is called the Scyphula, and from *Kowalevsky's* account of the development of *Cerianthus* (4), Götte believes it to be common to both the Scyphomedusæ and Anthozoa, and consequently an ancestral form. In *Cerianthus* according to the abstract given by Hoffman and Schwalbe of Kowalevsky's paper, the œsophageal invagination does push down the endoderm along two opposite meridians; but though the abstract is not definite on this point, the implication is that the meridians are those of future mesenteries. If this is so, *Cerianthus* agrees essentially with *Manicina*, and not with *Aurelia*.

The ancestral Scyphula form was derived, according to Götte, directly from the hollow planula, the invagination of the œsophagus *necessitating* the simultaneous formation of endoderm sacs. The infra-œsophageal mesenteric ridges, from this point of view, are not of any phylogenetic importance, and have nothing to do with the endoderm ridges of Tubularian or Siphonophore polyps; they have come into existence merely as the after-result of the formation of endodermal sacs. This theory contains in itself an obvious difficulty: the sudden and direct transformation of such a simple form as the planula into such a complex form as the Scyphula. What could have caused this complex group of changes, Götte does not suggest. But aside from this objection it seems clear that the development of *Aurelia* is a highly modified form of the development of *Manicina*, and the manner in which this peculiarly symmetrical modification was brought about is suggested by the variations shown in Figs. 30–33.

If Fig. 30 is compared with the woodcut Fig. 1, it is seen that as far as the left halves of the sections are concerned, they are identical in all essential respects. In each the œsophagus is opposed to the surface ectoderm along the meridians of two adjacent mesenteries (*a* and *b*, 1 and 3), and also over the intervening tract. In a later stage an endoderm lobe grows up between *a* and *b* in Fig. 30, and between 1 and 3 in the woodcut, and in each this lobe becomes an intermesenteric chamber. If, now, in the larva, Figs. 30–33, the right side had followed the example of the left, that is, if the second and fourth mesenteries had been formed in the same manner as the first and third (*a* and *b*), there would have resulted an exact counterpart of the condition in the *Aurelia* larva.

The four mesenteries of Scyphostoma would thus seem to correspond to the first and second pairs of mesenteries in *Manicina*. We may suppose that in the primitive Scyphostoma the mesenteries were usually formed in the gradual way which is normal in *Manicina*, but that the Scyphostoma had inherited from the parent stock (probably Anthozoa with a large number of mesenteries) a tendency towards the variation illustrated in Figs. 30–33, and that this variation gained ground and finally became the normal process. There is, of course, an alternative to this hypothesis, namely, to regard the variation found in *Manicina* as a case of partial reversion to the ancestral condition as presented by *Aurelia*. But the derivation of the Anthozoa from such an ancestor as the young Scyphostoma (or Scyphula with four endoderm lobes) is beset with the greatest difficulties; for instance, the formation of the first before the second mesentery, and the very general occurrence of a primary tentacle in actinia larvæ and in the Scyphostoma itself. Moreover, the Scyphula larva has not been found in any Anthozoa, unless, indeed, the case of *Cerianthus* be really, as Professor Götte seems to have considered it, similar to *Aurelia*.

Having shown that it is possible to derive the so-called Scyphula larva from the larva of *Manicina*, and that it is consequently in all probability an instance of secondarily acquired symmetry, I consider Götte's objection, based on the existence of this larva, to the hydropolyp ancestry of the Anthozoa, as no longer valid. The question whether or not the Anthozoa are descended from hydropolyps must be argued out on the ground of some more primitive Anthozoan development, such as that of *Manicina*. And here it is at once seen that, contrary to Götte's idea, the invagination of the œsophagus does not necessitate the formation of endodermal sacs. In Figs. 5 and 7 the œsophagus is already formed, but is still surrounded on all sides by endoderm. The apposition of the œsophagus to the surface ectoderm along the lines of the first and second mesenteries takes place later; and though, since this process occurs in the Scyphomedusæ as well as the Zoantharia, it must date very far back. I am inclined to believe it was secondarily acquired and was not a peculiarity of the primitive Anthozoa. This belief is supported by the entire absence of the process in the Alcyonaria (Wilson, 3). The explanation of the process is possibly connected with the early development of the first pair of filaments.

Baltimore, March 25, 1888.

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DESCRIPTION OF THE FIGURES.

In the larvæ, the supporting membrane is represented as a heavy black line; the jelly, where present, as light brown. In the adult, and in the complete section of *Cerianthus*, the supporting substance is uncolored. All the sections were drawn with the camera. Zeiss lenses are referred to, and the figures are reduced to one-half the size of the original drawings.

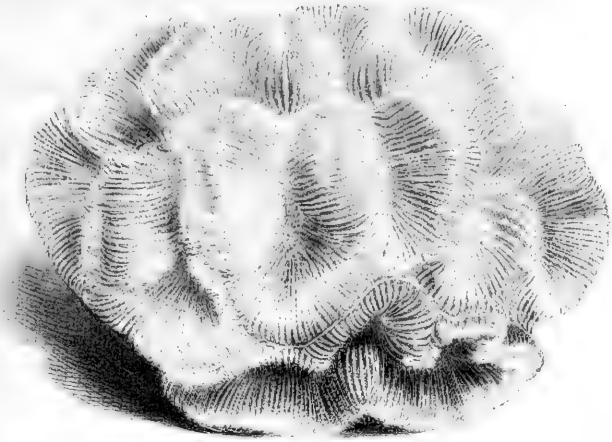
The following letters have been used uniformly in the figures: —

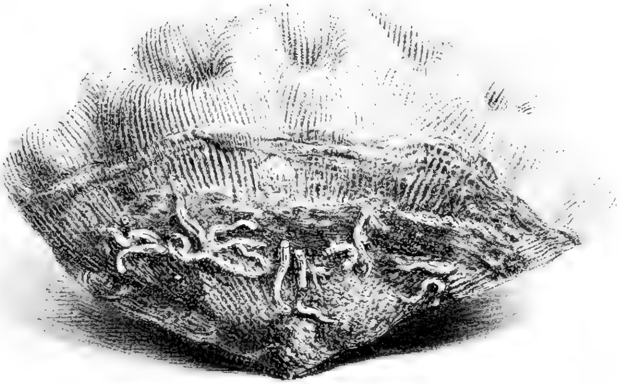
c.b.	Calycoblast Layer.
C.	Costa.
Col.	Columella.
D.M.	Directive Mesenteries.
ec.	Ectoderm.
en.	Endoderm.
Mo.	Mouth.
Mes.	Mesentery.
m.l.	Mesenterial Lobes.
Oe.	Œsophagus.
Pr.	Peristome.
R.P.	Randplatte or Extra-thecal Part of Polyp.
S.	Septum.
T.	Tentacle.
Th.	Theca.
v.l.	Ventro-lateral Ciliated Tracts.

DESCRIPTION OF PLATE I.

FIG. A. Corallum of a Manicina colony, viewed from above. Natural size.

FIG. B. Side view of same, to show the pedicel. The randplatte extends but a short distance below the rim of the theca; its lower limit is marked by a slight accumulation of irregular laminæ.





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DESCRIPTION OF PLATE II.

Fig. 1. Section through a blastosphere. C, 4.

Fig. 2. Section through delaminating blastosphere. C, 4.

Fig. 3. Part of another blastosphere such as Fig. 2. D, 4.

Fig. 4. Median long. sec. through a solid planula with commencing œsophagus. C, 4.

Fig. 5. Long. sec. through a larva in which the permanent layers are forming. C, 4.

Fig. 6. Long. sec. of slightly older stage. Position of œsophagus is eccentric. C, 4.

Fig. 7. Trans. sec., through œsophagus, of larva at about the stage of Fig. 5. The formation of the permanent layers is not so far advanced as in the latter figure. D, 4.

Fig. 8. Long. sec. through a larva in which the œsophagus has opened centrally. D, 4.

Fig. 9. Trans. sec. through a larva in which the œsophagus is still more eccentric than in Fig. 8. The section is through line *a* in Fig. 8. D, 4.

Fig. 10. Trans. sec. of same larva at lower level, through line *b* in Fig. 8. D, 4.

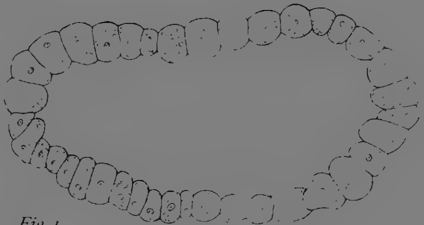

Fig 1

Fig 2

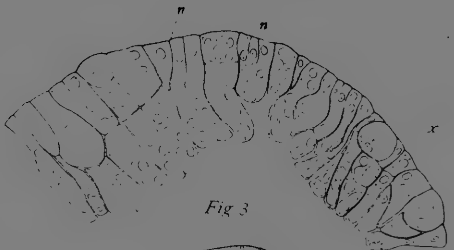

Fig 3

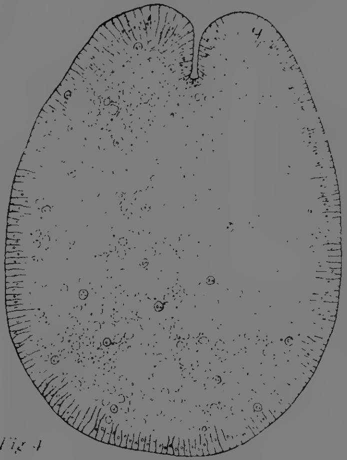

Fig 4

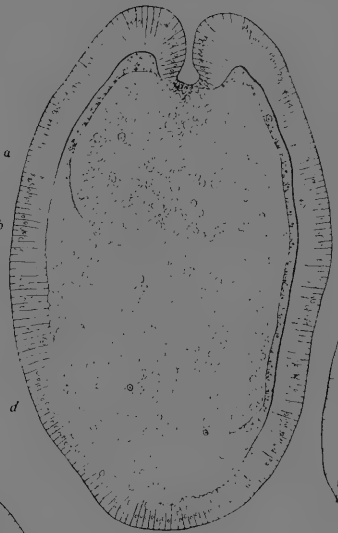

Fig. 5

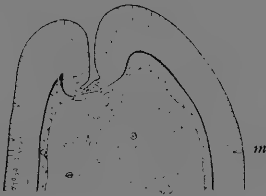

Fig. 6

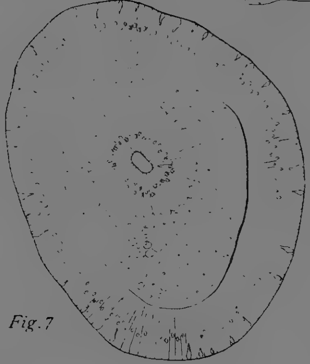

Fig. 7

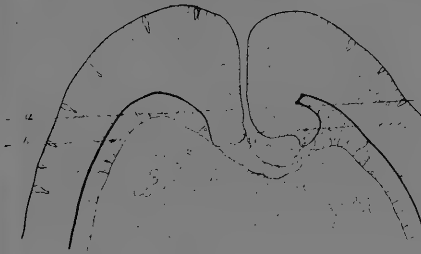

Fig. 8

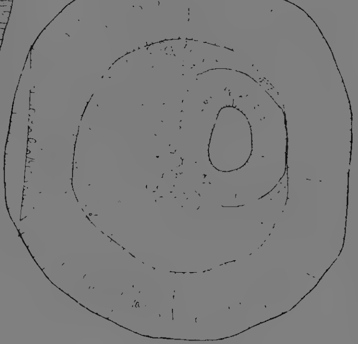

Fig. 9

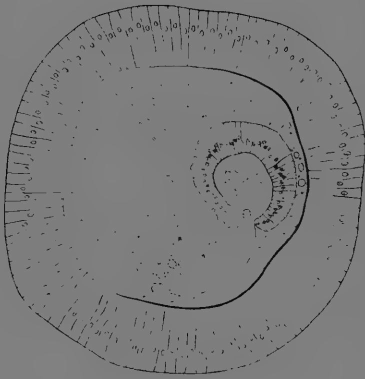

Fig. 10

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DESCRIPTION OF PLATE III.

FIG. 11. Trans. sec., through lowest part of œsophagus, of a larva in which the œsophagus along its whole length is apposed to the surface ectoderm. D, 4.

FIG. 12. Long. sec. of larva at about the same stage as Fig. 11 in the plane of the first two mesenteries. D, 4.

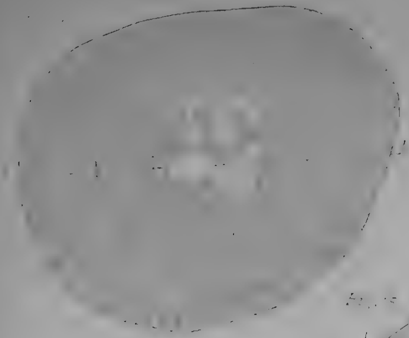
FIG. 12′. Median long. sec. of a larva, in which the œsophagus is applied to the surface ectoderm along the lines of the first and second mesenteries. An older stage than Fig. 12. D, 4.

FIG. 13. A section to one side of Fig. 12, through future intermesenteric chambers. D, 4.

FIGS. 14, 15, 16, 17. Series of transverse sections, numbered from above down (Fig. 14 is through the œsophagus), from a larva in which the first pair of filaments and the first mesenteric ridge are present. Along the line of mesentery 2, the œsophagus is still applied to the surface ectoderm. D, 4.

FIGS. 18, 18 *a*. Trans. sec., through œsophagus, of a larva with two complete mesenteries and a pair of filaments. Fig. 18 *a* is the upper of the two. D, 4.

FIG. 19. Surface view of balsam preparation. The larva has two long, and one (possibly two) short filaments. C, 2.



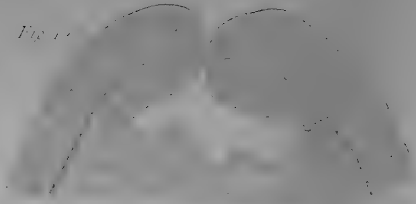
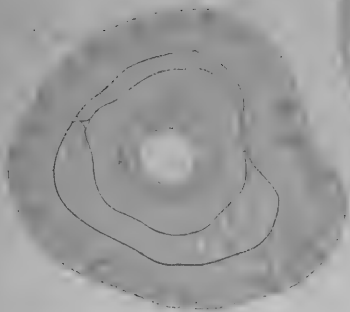


Fig. [illegible]

Fig. 15



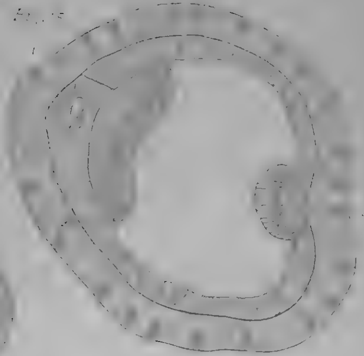


Fig. [illegible]

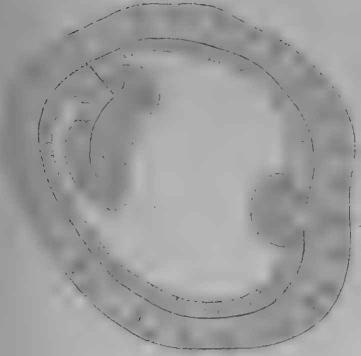


Fig. 16

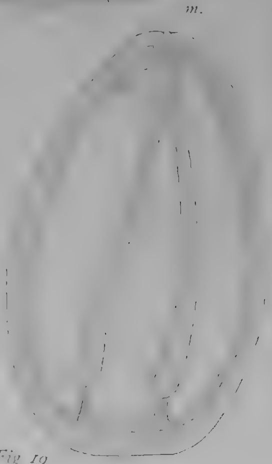


Fig. 19

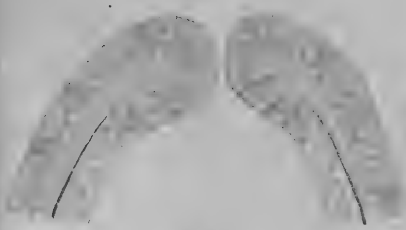


Fig. [illegible]

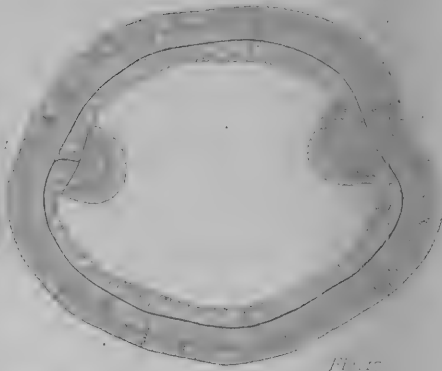


Fig. 17

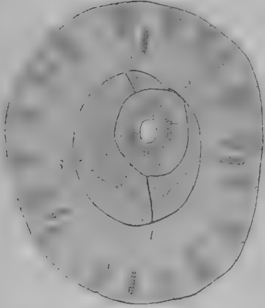


Fig. 18 a

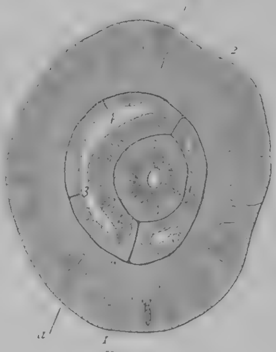


Fig. 18

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DESCRIPTION OF PLATE IV.

FIGS. 20, 21, 22, 23. Series of long. sec. from a stage somewhat younger than Fig. 18. Fig. 20 is through the first pair of mesenteries and filaments; Fig. 23 is through the line *a*, *b* in Fig. 18; and the other sections fall between. C, 4.

FIG. 24. Long. sec. through a larva such as Fig. 19; on the right, through one of second pair of filaments, on the left through an intermesenteric chamber. D, 4.

FIG. 25. From a larva with two long and two very short filaments, *a*, *b*, *c*, are three half-sections from the same side of the larva. *b* is through one of second pair of mesenteries with its filament; *a* and *b* are on opposite sides of this mesentery. D, 4.

FIG. 26. Trans. sec. through one of primary pair of filaments and mesenteries of a stage like Fig. 19. F, 4.

FIGS. 27, 28, 29. Series of trans. sec. from a larva like Fig. 19. Fig. 27 is through the œsophagus, 28 is just above the lip, and 29 is below the œsophagus. The sections are very slightly oblique. The third pair of mesenteries exist as longitudinal ridges of the supporting lamella. *R.E.* is the reflected ectoderm. D, 4.

Fig. 20

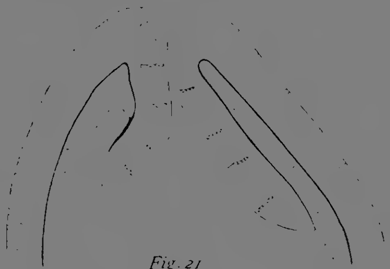

Fig. 21

Fig. 22

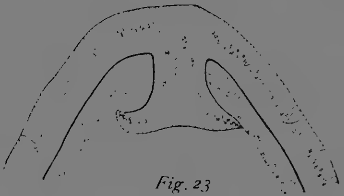

Fig. 23

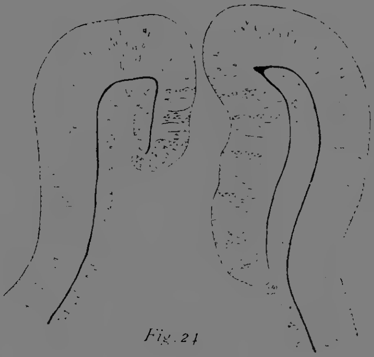

Fig. 24

Fig. 25

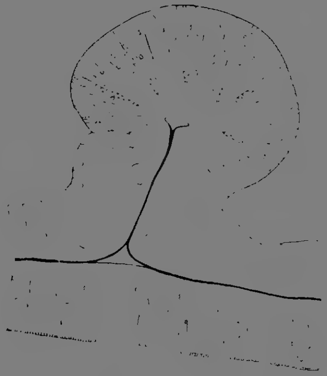

Fig. 26

Fig. 27

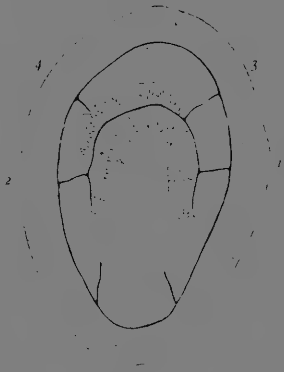

Fig 28

Fig. 29

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DESCRIPTION OF PLATE V.

FIGS. 30, 31, 32, 33. Series of trans. sec., numbered from above down, from a larva with two pretty long (half the length of larva) and one very short filament. The first and third filaments have been formed from a common lobe, and the third mesentery (*b*) has been formed at the same time and in the same way as the first (*a*). D, 4.

FIG. 34. Trans. sec., below œsophagus, of attached larva with eight mesenteries. B, 4.

FIG. 35. Trans. sec. through upper part of one of the primary filaments of an attached larva. The large clear cells are nettle cells. F, 4.

FIG. 36. Trans. sec., through œsophagus, of attached larva with eight mesenteries. The second pair of mesenteries is not quite complete, and consequently at this level (just above the lip) the reflected ectoderm is found all round the œsophagus. B, 4.

FIG. 37. Long. sec. through attached larva; on the right through one of second pair of mesenteries, on the left through an intermesenteric chamber. C, 2.

FIG. 38. Long. sec. through attached larva in which the basal plate has appeared; on the left through one of third pair of mesenteries with its filament, on the right through an intermesenteric chamber. The line *m*, *m* indicates the outline of the polyp when expanded. C, 2.

FIG. 39. Trans. sec., through œsophagus, of attached larva with twelve mesenteries. B, 4.

FIG. 40. A more highly magnified view of one of the septa of Fig. 41 (that lying in the near "directive" chamber), sectioned at the level of its opening. *c.b.* is the calycoblast layer.

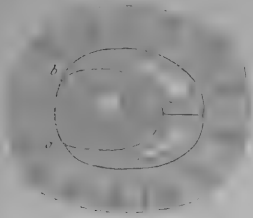

Fig. 30

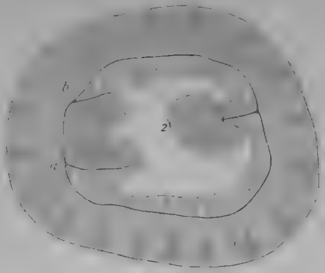

Fig. 31

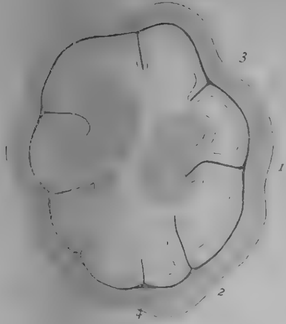

Fig. 34

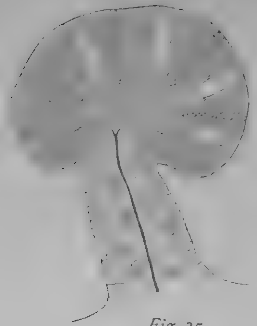

Fig. 35

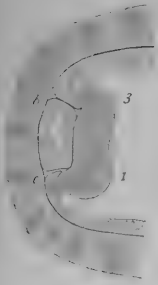

Fig. 33

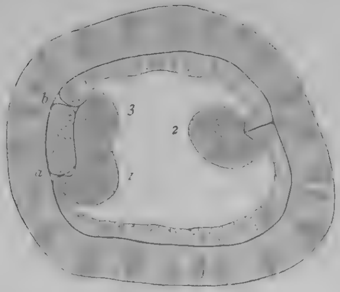

Fig. 32

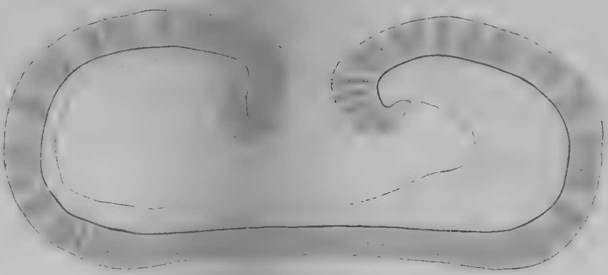

Fig. 37

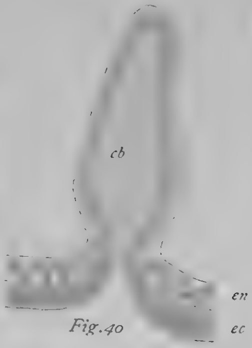

Fig. 40

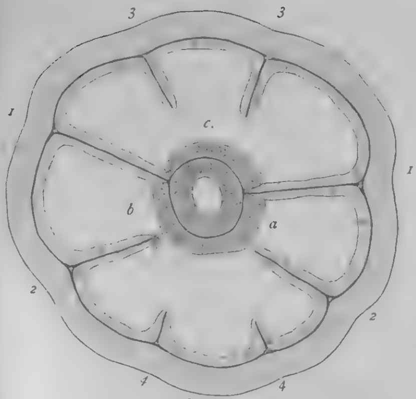

Fig. 36

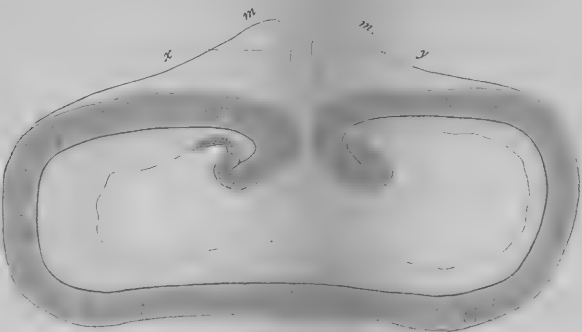

Fig. 38

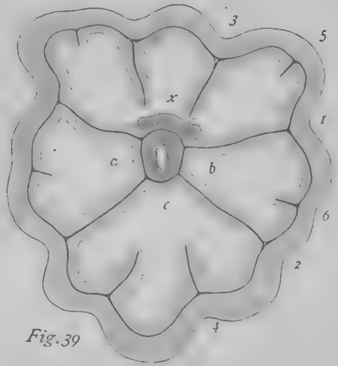

Fig. 39

DESCRIPTION OF PLATE VI.

FIG. 41. Trans. sec. through œsophagus of young Manicina, $\frac{1}{8}$ in. diam. *D.M.*, the directive mesenteries. X, 60.

FIG. 42. Section of same specimen, below œsophagus. Skeleton is bare at *a* and *a'*. The tip of the columella lies in the cœlenteron. X, 68.

FIGS. 43, 44, 45. Series of trans. sec., numbered from below upwards, through the oval cone of a larva like Fig. 38. Fig. 43 is through the line *x, y* in Fig. 38. Only the first two pairs of mesenteries extend into the uppermost part of the cœlenteron. The overlapping of the reflected ectoderm and endoderm is well shown. D, 4.

FIG. 46. Part of a trans. sec. of adult single polyp, through line *a* in Fig. 50. The ectoderm of the peristome is marked *oe.ec.*; that of the lateral body wall, *ec.* X, 30.

FIG. 47. Trans. sec. of filament and mesentery of a larval *Cerianthus.* Level of section is just below the œsophagus. *m* is the commencing ciliated band (flimmerstreif). F, 2.

FIG. 48. Section of same filament lower down. The violent contraction has caused the halves of the mesentery to spring apart, leaving the coagulated supporting lamella partially free. F, 2.

FIG. 49. Trans. sec., through œsophagus, of a larval *Cerianthus. D.M.*, the (larval) directive mesenteries. The numbers 1, 2, 3, 4, mark the four youngest mesenteries, in the order of their age, 1 being the youngest. X, 60.

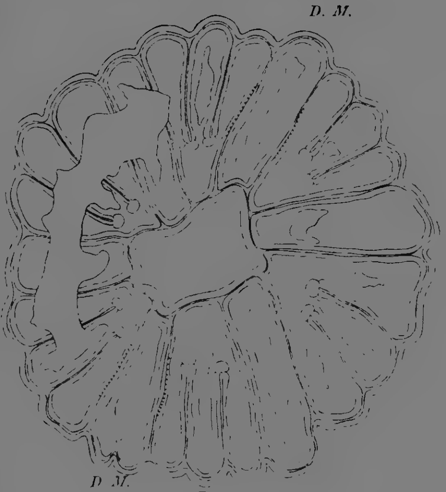

Fig. 41

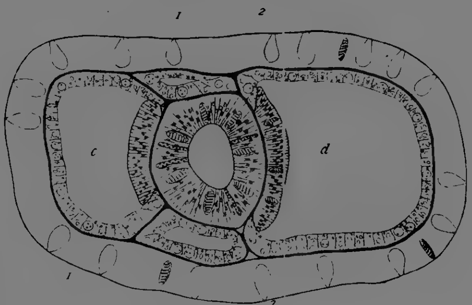

Fig. 43

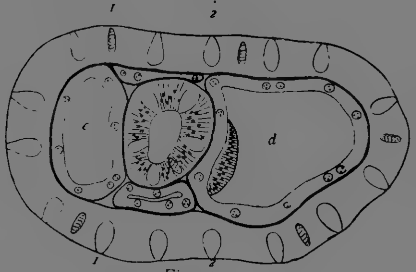

Fig. 45

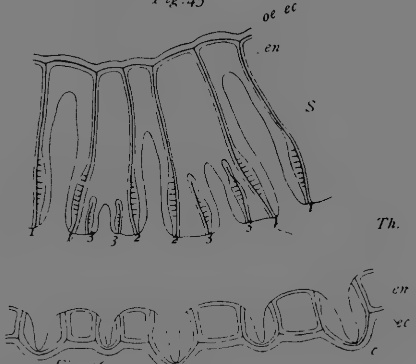

Fig 46

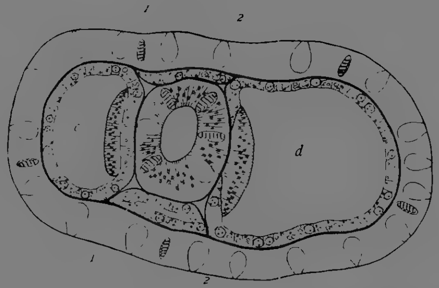

Fig 44

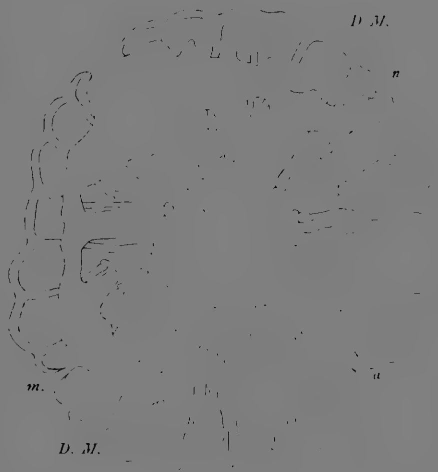

Fig 42

Fig. 48

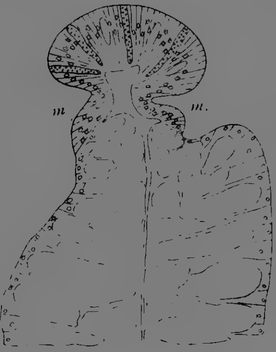

Fig. 47

Fig. 49

H. V. Wilson, Del.

A. Hoen & Co. Lith., Balt.

DESCRIPTION OF PLATE VII.

Fig. 50. Median long. sec. through an adult single polyp; on the right through a primary, on the left through a secondary mesentery. The line 3 marks the position of the free edge of a tertiary mesentery. The surface of attachment was irregular, but the corallum extended only a very short distance below the limit of the skeleton in the figure. X, 30.

Fig. 51. One of the extra-thecal entocœlic chambers of Fig. 49 more highly magnified. *Mes.* is the peripheral portion of a mesentery.

Figs. 52, 53, 54. Trans. sec. of an adult primary filament. Fig. 52 is through the upper, 53 through the middle, and 54 through the lower portion. The large clear cells in Fig. 53 are nettle cells. D, 4.

Fig. 55. A more highly magnified figure of the lower portion of the œsophagus, as shown in the left half of Fig. 50. *Oe.ec.* is the lining epithelium of the œsophagus.

Fig. 56. One-half of a median long. sec. of an adult single polyp. The section is through one of the primary septa. X, 30.

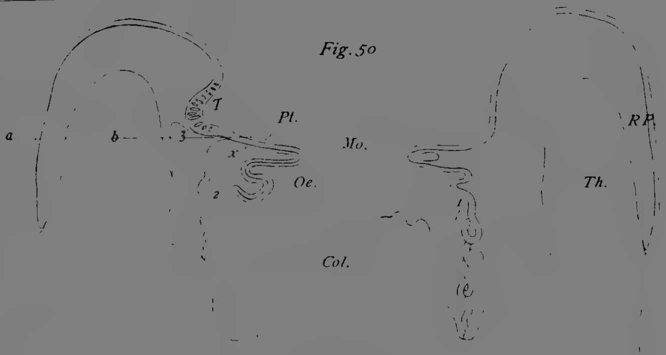

Fig. 50

Fig. 51

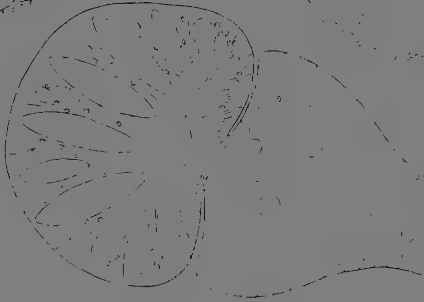

Fig. 53

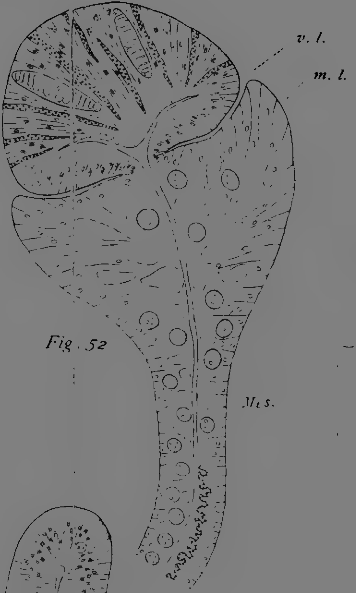

Fig. 52

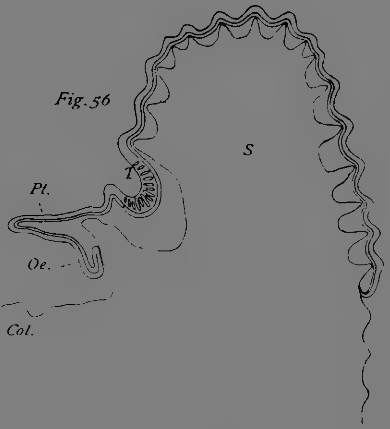

Fig. 56

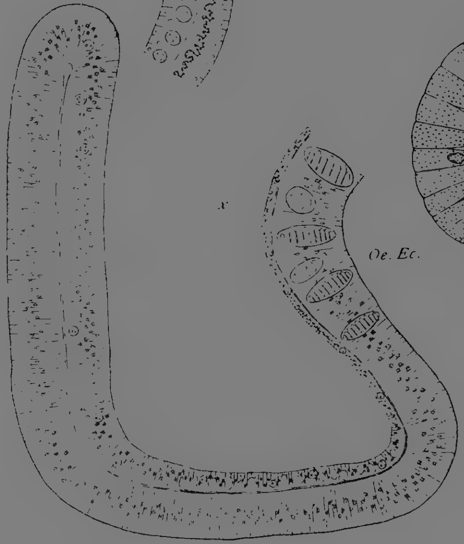

Fig. 55

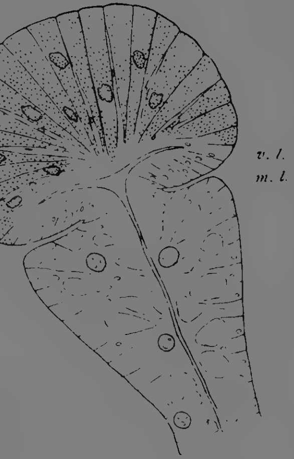

Fig. 54

H. V. Wilson, Del.

A. Hoen & Co. Lith., Balto.

THE STRUCTURE AND DEVELOPMENT OF THE VISUAL AREA IN THE TRILOBITE, *PHACOPS RANA*, GREEN.

By JOHN M. CLARKE.

To students of the fossil Arthropoda it should be a matter of congratulation that so great success has been achieved by palæontologists in solving the problem of anatomy and development in the extinct crustacean order, the Trilobita. Though much may remain to be done, too great esteem cannot be accorded to those who have contributed to what has been accomplished; Eichwald, Burmeister, Volborth, Quenstedt, Richter,[1] Barrande, Hall, Billings, Ford, Walcott, Woodward, Mickleborough, Matthew, Packard. To the labors of these men is due our knowledge of the development of the trilobite from the ovum to maturity; of its delicate locomotive and respiratory apparatus; and somewhat of its reproductive, alimentary, and muscular anatomy.

The present paper endeavors to throw some light upon the structure and development of the eye in a typical representative of an extensive group of trilobites, *Phacops rana*, Green. In the study of this organ abundant material consisting of several thousand specimens has been accessible, in the majority of instances only those being utilizable in which the lenses of the eye

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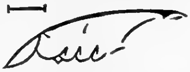
[1] It may be well to call attention to the fact that Richter's single observation upon the ventral anatomy of *Phacops*, which has been overlooked by later investigators, is of much greater significance than the author himself accorded it. In the *Beitrag zur Paläontologie des Thüringer Waldes*, 1848, Pl. 2, Fig. 32, is given an enlarged view of a transverse section through one-half the thorax of a Devonian *Phacops* (species not given). As this work may not be generally accessible, the figure is here reproduced; and although the author states (*op. cit.* p. 20) that the section serves to establish Burmeister's conception of the ventral anatomy of the trilobite, in the light of Walcott's demonstration of the spiral branchiæ in *Calymene senaria* it appears that what is represented here is a section of one of these appendages. I may add that I have also detected evidence of these spiral branchiæ in *Phacops rana*.



have been so perfectly retained as to allow of enumeration. These specimens have been derived from the shales and limestones of the Hamilton group at various localities in Western New York, those best adapted for the purpose of sectioning being from the basal limestones near Centerfield, Ontario County.

THE CHARACTER OF THE VISUAL AREA in the trilobites is twofold; (*a*) it may be covered by a smooth, continuous epithelial film or cornea, through which the lenses of the ommatidia are visible by translucence, and (*b*) the cornea may be transected by the protrusion of the sclera[1] and limited to the surfaces of the ommatidia. To the first group belong species of the genera *Asaphus*, *Illænus*, *Calymene*,[2] *Homalonotus*, *Proëtus*, *Cyphaspis*, *Acidaspis*, *Lichas*, and others; to the second, the single extensive family, *Phacopidæ*, with its genera, *Phacops* and *Dalmanites* (? *Harpes; vide* conclusion). The first group may be designated by the term *Holochroal;* the second group by the term *Schizochroal.*

PHACOPS RANA is one of the most abundant and characteristic species of the Hamilton faunas. Though widely distributed in the formations of this age throughout the United States and Canada, it is not known with certainty to have been present in faunas older than those of the Hamilton, and it does not appear to have continued its existence after the displacement of the Hamilton faunas. A detailed and very complete description of the species, accompanied by copious illustration, is given in the

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[1] I have found the term *ommatidium*, proposed by Carrière for the little eyes or ocular elements in the compound eyes of Arthropods and Mollusks, a very convenient and significant term, but may use it with a little license, as I do not regard the eyes included in the second of the above groups as properly compound. The term *sclera* as here used may be open to some objection. It is applied to the interstitial test between the ommatidia, and is preferable to the expression *cornée opaque* of Barrande.

[2] Professor Edward Orton, of Columbus, Ohio, has allowed me to examine a very young individual of *Calymene senaria* in which the lenses are relatively very large, and are strongly suggestive of the character of the lenses in *Phacops*, although in the adult of this species they are so small as scarcely to be detected. This specimen suggests the query whether in the holochroal eyes the lenses may, with the advancing growth of the animal, become apparently smaller, from close juxtaposition or other cause, and also indicates the possibility that the difference in the holo- and schizochroal eyes is not as great as it now appears.

monograph of North American Devonian crustacea, constituting Volume VII. of the Palæontology of New York. In this place are also to be found satisfactory figures of the eye in various modes of preservation.

Composition of the Visual Node.

The eye is composed of the visual surface, which is normally a lunate segment of the surface of a cone, but often in senile individuals is inclined to sphericity; this surface is buttressed on the glabellar side by a strong palpebral lobe, which is produced to and slightly beyond the upper edge of the visual surface, forming a distinct *palpebrum*. The lower edge of the visual surface is bordered by a ridge, which becomes broader and more conspicuous outwardly, and may be called the orbital ridge.

The lenses as seen from the upper surface are convex, sometimes being translucent, especially when they have been filled with crystalline calcite, or have been slightly separated from the matrix; they are circular in outline, although the cavities in which they lie (*lensal pits*) appear in old individuals to be hexagonal. This appearance is due to the undiminished growth beyond maturity of the sclera, which crowds upon and overlaps the edges of the lenses on all sides, deepening the lensal pits. The general arrangement of the lenses is in alternating vertical rows or quincunx. For convenience, however, in the accompanying statements of enumeration, the lenses are regarded as arranged in diagonal rows parallel to the lower posterior margin of the visual surface, and are numbered from this line consecutively. It appears probable that this is also the order followed by nature in increments to the number of lenses, from the time of the formation of the primary row of ommatidia (*vide seq.*) onward to maturity. Under this arrangement the last row in enumeration is that ending in the upper anterior angle of the visual surface.

The number of these rows is variable, in the majority of cases being *nine,* in comparatively few individuals of average size and richly supplied with lenses, being *ten,* in extremely rare instances *eleven,* only a single example of average size showing so many; in very young individuals the number of rows is but *eight.* The youngest specimens observed show no less than this number, and it seems probable from other considerations that in still earlier stages of growth the number of diagonal rows was not much less than eight.

The number of lenses constituting the visual surface of each eye is variable, but not irregularly so. The smallest number noted is thirty-three, in a very young individual having but *eight* rows; the greatest is eighty-eight, occurring in the single example mentioned, which bears *eleven* rows.

Again, *the number of lenses in successive rows is variable, but only so within certain well-defined limits.* In order to make this point clear, the following ten enumerations are presented, taken at random from a list of above three hundred tabulated eyes.

EXAMPLE.	ROWS.										TOTAL.
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	
1	8	9	10	10	9	8	6	4	2		66
2	1	10	11	11	10	9	7	6	4	2	71
3	4	9	11	10	10	9	8	6	4	2	74
4	9	10	11	11	9	8	6	4	2		70
5	1	9	10	11	10	9	8	6	4	2	70
6	8	10	10	9	9	8	6	4	2		66
7	8	9	9	10	9	8	6	4	2		65
8	10	11	11	10	9	8	6	4	2		71
9	3	9	10	10	10	9	8	6	4	2	71
10	6	10	12	12	11	10	8	6	4	2	81

It appears from this table that whatever may be the total number of rows in any eye, in the last four rows of lenses, and generally in the fourth from the last, the number of lenses is subject to very little variation, while the number in the first two or three rows may vary greatly. This variation is partially explained by the following fact: It will be found upon examination of an average eye that the anterior edge is normally nearly vertical; the *vertical row* following this edge is composed of *four* lenses. It is impossible for any lenses to be added to the anterior extremities of the *diagonal rows* terminating at this anterior margin, for new lenses are added only from the lower and upper margins of the visual surface (see further on). In immature eyes a greater variation is noticeable in the last rows, as seen in the following examples of surfaces bearing but *eight* rows of lenses.

(1)	4.	5.	5.	5.	5.	5.	4.	2.	35
(2)	4.	4.	4.	5.	5.	5.	4.	2.	33
(3)	6.	6.	6.	6.	6.	5.	4.	2.	41
(4)	7.	9.	7.	4.	6.	5.	3.	1.	42

In these instances the eye has not attained its full growth in height, which would preclude variations in the last rows.

Conversely, as the first four or five rows of lenses terminate on the lower margin of the visual surface, and as additions to the number of lenses are made most abundantly from this area, the number in these rows is constantly varying. It may be here stated, that with the exception of the right and left eyes of the same individual, no two eyes in all the specimens enumerated have shown the same number of lenses in all corresponding rows.

A definite relation exists between the number of lenses of the eyes and the size (*i.e. age*) *of the animal.* This fact has been established by recording with each enumeration of lenses a single measurement which would serve as an index of the stage of development attained by the animal. The measurement taken is the basal width of the cephalon. *Phacops rana* is rarely found with all the parts in articulation, and still retaining the lenses with sufficient distinctness for enumeration. Detached cephala are abundant, and it serves every purpose to take the indicial dimension from this part of the animal; it is, moreover, found that the peculiar form of the cheek renders this dimension of the head less liable to variation from flattening in the shales than the longitudinal measurement. Comparison of all the specimens enumerated gives the following results:—

The average number of lenses in individuals having a cephalic width less than

10 mm. is 44
Between 5 and 15 mm. is 56.5
" 10 and 20 mm. is 69.5
" 15 and 25 mm. is 73
" 20 and 30 mm. is 71
" 25 and 35 mm. is 66

Between 30 and 40 mm. is 62.5
" 35 and 45 mm. is 62.1
From 40 mm. upwards, 58

The *calculated* average basal cephalic width in this species, deduced from measurement of 1518 cephala, is 22.8 mm. The material from which this average is derived was unselected, much of it collected without reference to quality or size, and is fairly representative. I therefore venture the statement that the *average Phacops rana* has a width across the posterior margin of the cephalon of approximately 22.8 mm.

It is, moreover, probable that 22.8 mm. is approximately the dimensional index for the *average normal adult* of this species. In all specimens of the entire animal which have passed under observation, varying in axial length from 10 mm. to 100 mm., no evidence has appeared of any developmental change in the successive stages of growth, except in the increase and diminution of the number of corneal lenses. Save in this one respect the species assumed all the features of maturity at a very early point in its history; and the data given above conclusively indicate that in this feature, also, maturity was attained with this stage of growth. The important conclusion here drawn is that *the number of lenses increases from youth to maturity* (dimensional index approximately 22.8 mm.), *and decreases from maturity to senility.*

Two questions immediately arise from this inference; (*a*) how is the number of lenses increased? and (*b*) how is it diminished? These points will be adverted to in a following section.

Structure of the Lens.

Sections across the visual surface show that the lenses are unequally bi-convex, the curvature being greatest on the proximal surface. This inferior surface is perforated by a central circular aperture. Vertical sections of the lens when favorably preserved, also show this envelope as a simple, thin, distinctly black or brown corneous film; and in natural casts of the internal surface of the visual area, the ommatidial cavities are represented by a series of shallow cups standing on short pillars, and each bearing at its centre a little ball, which is the filling of the interior of the lens. These lenses are consequently *corneal* and *hollow.* It appears, also, in sections that *in the mature lens* the cornea is discrete from the sclera, lying in juxtaposition with and held in place by it, but in nowise continuous with it. This fact is also frequently apparent in specimens from which the sclera has been removed by solution, leaving the corneal lenses standing on little pillars of the matrix, which has filled the ommatidial cavities. Other specimens just as frequently show the converse, the lenses being removed, while the sclera is retained. There is evidence which I deem worthy of consideration, that these corneal lenses, during the life of the animal, were not empty, but filled possibly with some viscid or spissate humor. This evidence is of the following character:—

The cornea itself is thin, and of even calibre throughout its extent. The casts of the corneal cavities, such as are shown in Figs. 25 and 26, as little balls lying in cups, are not of sufficient size to have occupied all the space within the cornea. A specimen of *Phacops* of a species closely allied to *rana* (*Ph. cristata* var. *pipa* Hall), from the decomposed phtanite of the Corniferous limestone, seems to demonstrate this fact. This fossil was evidently originally preserved in calcic carbonate, which not only replaced the entire crust, but filled the ommatidial cavities, and the posterior cavity of the corneæ as well. This calcic carbonate was subsequently removed from within, and its place partially taken by silica, and when exposed to more rapid decomposing agencies, the remainder of the calcic carbonate was removed, leaving the fossil so preserved that the cornea and a thin film over the entire external surface of the sclera has been taken away, the remainder of the test being replaced by silica. The external surface of each lensal cast remains convex, but on carefully removing a little of the decomposed rock from beneath the position of the cornea a vacant space appears, which corresponds to the corneal cavity as represented by the ball-in-cup casts. To elucidate this point, see Plate XXI., Fig. 5, and explanation thereof.

Again, certain well-preserved sections from the limestone show a distinct difference in the character of the matrix filling the outer and inner cavities of the cornea, that in the outer being of lighter color, and more translucent (? subcrystalline), while that in the inner is the opaque mud of the sediment. More evidence upon this point is very desirable, but enough has been seen to indicate the fact that the *cavity of the cornea* was not *simple, but compound.* (May the posterior cavity-fillings represent the position of the anterior extremities of crystalline cones ?)

MULTIPLICATION AND DIMINUTION IN THE NUMBER OF LENSES.

The lenses of the visual surface are not all of the same size in any of the stages of growth observed. The size of the fully developed lens varies according to the individual development of the animal; *i.e.*, the larger the animal, the larger the lenses; but in any given subject some lenses are to be found which are below the average of size for that eye. These small lenses are found at the extremities of the diagonal rows which terminate on the posterior portions of the upper and lower margins of the visual surface.

The inferior size of these lenses is due in part to unlike causes. Of these the principal cause is (*a*) that they are new and immature lenses added in regular order to the ends of the rows of older lenses. It has not been as yet satisfactorily determined whether the increment of new lenses may take place at either upper or lower extremity of the diagonal rows, although the small lenses occur indifferently at either end. There is no reason to doubt that this addition does take place at the lower extremities, but on account of the close juxtaposition of the palpebrum to the upper margin of the visual surface, it may be questioned if at any period of growth sufficient room is allowed in this region for additional lenses.

A secondary reason for the small size of the lenses is (*b*) the constantly increasing size of the interlensar sclera after maturity, which gradually envelops the lenses especially along the upper margin of the visual surface, where, by coming into contact with the increasingly prominent palpebrum, the lenses are often nearly concealed.

To what degree the small size of the lenses along this upper margin may be due to the overgrowth of the sclera, and how much to the possibility of their being newly developed, it has been impossible to ascertain, but that it is due to a certain degree to both causes, is shown by the following facts: (1) immature eyes, in which the sclera has attained no excessive growth, very often show these small lenses along the upper margin, and they would, therefore, appear to be developed there; (2) it has already been shown that after the average normal mature growth of the animal has been reached, the number of the lenses becomes less with advancing senility. This fact must be explained either by the gradual envelopment of the lenses of the upper margin by the sclera and palpebrum, and their entire concealment within the substance of the latter, unless it is possible that atrophy of the ommatidial nerve branches and concomitant reabsorption of the lenses takes place with advancing old age.

From the examination of eyes limited to *eight* rows of lenses, it appears that with this number of rows there may be considerable variation in the number of lenses, as seen on the plate (Fig. 9, thirty-one lenses; Fig. 10, forty lenses). These figures also indicate the fact, that with a constant diminution in the number of lenses from the upper and lower extremities of the rows, the eight diagonal rows would ultimately be reduced to a single or double longitudinal row parallel to the margins of the visual surface. Hence, without overmuch hypothesis, the primary lenses probably appeared in a single or double row, a visual line parallel to the margins of the orbital node.

DEVELOPMENT OF THE LENS.

There is sufficient evidence at hand for the statement that that portion of the ommatidial cavity which penetrates the test arises from an evagination from the internal surface of the test accompanied by a corresponding but very shallow invagination from the upper surface. Natural casts of the internal surface of the visual area not infrequently show minute lensar cavities at the ends of the rows of lenses, which appear not to have penetrated to the upper surface, and bear at their summits no impression of a corneal surface or corneal cavity, as do the other lenses in the same eye. It would be inferentially true that the cornea is developed from the attenuated integument (cuticular epithelium), and is the specialized film of the test left between the depressions from its lower and upper surfaces, eventually becoming discrete.

Structure of the Sclera.

The interlensar sclera is continuous with the test, and its structure is in all points identical with that of the test.

The vertical tubules and smaller tubulipores, with which nearly every part of the test of *Phacops rana* is densely perforated, are plainly visible in every section of the sclera, no difference in the structure of the parts being discernible, although the thickness of the sclera is somewhat less than that of the adjoining portions of the test; however, the thickness of the test is of necessity very variable in different parts of the animal. Not infrequently eyes have been observed, preserved as casts in decomposed chert, in which the tubules of the sclera are represented by delicate rods traversing the vacant space left by the removal of the integument.

Abnormalities in the arrangement of the corneal lenses are of comparatively rare occurrence. They appear to be due, in every instance observed, to the failure of a lens to develop at the proper time and place in its own row, but in no case has a lens appeared so out of place as to be intercalated between rows. Marked abnormalities, such as that represented in Figs. 11 and 12, are usually confined to one of the two eyes. It is, however, not uncommon to find the right and left eye differing in the number of lenses in the corresponding rows, either with or without affecting the total number of lenses. In the following example the total is the same, although the arrangement differs:—

Right eye. 6. 8. 9. 9. 9. 7. 6. 4. 2 = 60
Left eye. 6. 8. 10. 9. 8. 7. 6. 4. 2 = 60

In another example both the number in the corresponding rows and the sum total differ:—

Right eye. 5. 7. 8. 7. 7. 6. 4. 1. 2 = 47
Left eye. 5. 7. 9. 8. 7. 7. 6. 4. 2 = 55

These instances of irregular development may be due to pathologic or other organic conditions of the animal; perhaps, also, in part to external influences.

NOTE.—No satisfactory evidence of crystalline cones within the ommatidial cavities has been ascertained, and it is not surprising that these bodies, which undoubtedly existed, were removed with the soft parts of the visual organ. With respect to this feature the sections of the eye of *Phacops* given by Barrande (*Système Silurien du Centre de la Bohême*, Vol. I., Pl. 3, Figs. 15 and 16), and reproduced by Zittel (*Handbuch der Palæontologie*, 1885), are misleading. The fillings of the ommatidial cavities are so shaded as "to indicate prisms" (compound) "corresponding with each lens," and extending very far inward without diminution in width. Such structure finds no correspondence in the eye of the living Arthropod, and is probably to a large degree schematic and imaginary. The structure of the lens, as we have found it, is also essentially different from that represented by Barrande.

MODES OF PRESERVATION OF THE VISUAL SURFACE.

a) *The cornea and sclera are normally preserved.* (Fig. 1.) This is the usual mode of preservation in the limestones where the original substance of the test has been preserved in calcic carbonate, though leaving so considerable a portion of the organic matter as to give a black and lustrous surface. Such specimens retain the minute structure of the test most perfectly and are most satisfactory for sectioning.

b) *The cornea is removed and the sclera retained.* (Fig. 2.) This is a rare mode of occurrence noticed only in specimens from the shales.

c) *The sclera is removed and the cornea retained.* (Fig. 3.) In these examples, which occur in the shales and weathered limestones, the corneal lenses stand supported on the summits of pillars of matrix. It is not an uncommon mode of occurrence.

d) *Both cornea and sclera are removed* (Fig. 4), leaving pillars of the matrix with cup-shaped upper surfaces, each bearing a little ball at the centre. This condition is often observed in the decomposed limestones and phtanites.

e) *An external film is removed from the entire visual area, destroying the cornea* (Fig. 5). A single example has been observed in which the entire test was apparently originally preserved in calcic carbonate. Subsequently this was removed from within and gradually replaced by silica, with the exception of the thin outer film, which afterward was entirely removed, leaving the space it occupied vacant.

f) *Silica deposited as a thin film upon, or replacing a thin film of the external and internal surfaces of the test, and all the rest of the substance of the test and the matrix removed* (Figs. 6 and 7). In this condition the visual surface is a mere shell appearing as when normally preserved, but the corneal lenses are hollow, and the sclera represented by a thin wall of silica. This condition is sometimes modified by the removal of the entire upper surface of the visual area, generally by its adherence to the outer part of the matrix, leaving only vertical tubes representing the ommatidial cavities.

While the foregoing observations and the essential conclusions therefrom in regard to the structure of this phase of the trilobite eye, agree in some respects with the opinions of earlier writers upon this topic, there are many important points of difference and various features of structure which have not before been noticed. I therefore give a brief historical review of the observations upon the subject.

Quenstedt, 1837 (Wiegmann's *Archiv für Naturgeschichte*, Vol. I., p. 340), was the first to recognize two distinct types of structure in the eyes of trilobite, and divided them into

1. * Aggregated eyes having a facetted cornea.
2. Aggregated eyes having a smooth cornea.

In both groups the cornea was regarded as the direct continuation of the superficial layer of the test of the cheek. The first type of structure was represented by the eye of *Phacops latifrons*, Bronn (*i.e.*, the Phacopidæ). The second type was exemplified by *Illænus crassicauda*, Dalman (*i.e.*, holochroal eyes), in which the facets are said to be in relief upon the internal surface of the general corneal (visual) area, each facet being formed by a lens or crystalline body, behind which lies a vitreous body, penetrating deeply into the organ. In these the cornea was regarded as composed of two distinct layers, of which the outer is quite smooth, the inner very finely reticulate.

Burmeister, 1843 (*Organization der Trilobiten*, p. 19), regarded the structure of the holochroal eye as directly comparable in all respects to that of the eye in *Branchipus stagnalis*, and indorsed Quenstedt's view of the compound corneal layer, while admitting but a single type of structure. He assumes with respect to *Phacops* that the cornea must have been more destructible than in the other trilobites, and by its removal the facetted surface exposed.

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* As I have not had access to this work, I am compelled to take the summary of these observations as given by Barrande (*Syst. sil.*, p. 133).

Barrande, 1852 (*Système silurien du centre Bohême*, Vol. I., p. 185), recognizes three distinct types of structure, two of which are similar in breadth to those of Quenstedt, though differently interpreted. The third type of structure is exemplified in the genus *Harpes*, the eye of which is considered as an aggregation of *ocelli* (two or three in each eye). For the schizochroal eyes Barrande establishes the fact that the sclera (cornée opaque) of the visual surface is identical with that of the test of the head, and continuous with it. He also regards the existence of a transparent cornea covering the entire surface as suggested by Burmeister, as probable, but admits that he has been unable to assure himself upon this point. For the holochroal eyes the envelope of the visual surface is shown to be of different character than that of the test, and consists of a general cornea covering the entire visual area. His observations do not seem to have led to a decisive conclusion in regard to the simple or compound character of this cornea.

Packard, 1880 (*The Structure of the Eye of Trilobites: American Naturalist*, p. 503), quotes a resumé of the status of the discussion as given by Gerstäcker in Bronn's *Classen und Ordnungen des Thierreichs*, which is virtually a reiteration of Barrande's opinions. The "ocelli" of *Harpes* are regarded as aggregate eyes, not comparable with the simple eyes or ocelli of *Limulus* and the Merostomata. The eyes of Barrande's first and second groups are considered as true compound eyes and not aggregated eyes; no essential difference is recognized in the form and arrangement of the corneal lenses of *Phacops* and *Asaphus*, and the distinctions pointed out by Quenstedt and Barrande are considered artificial.

The sections used by Professor Packard in the comparative study of the trilobite eye appear to have been altogether of holochroal forms. A close correspondence in structure is demonstrated between the eye of *Asaphus* and that of *Limulus*. In the *Limulus* eye the lenses are covered by a continuous corneal layer, which does not make itself apparent in Professor Packard's sections of *Asaphus*, although it undoubtedly exists. It may be questioned whether the conclusion drawn from this comparative study is not too broad, viz., that the *trilobite eye* is organized on the same plan as that of *Limulus*.[1]

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[1] Professor Packard's observations upon the eye of *Asaphus* show no indication of the existence of interstitial epithelium between the lenses, an extremely important

CONCLUSION.

The study of the eye in *Phacops rana* as here presented allows the statement of the following points: —

1) The schizochroal eyes of the Trilobites are *aggregated* and not properly *compound* eyes. The visual organs of *Harpes* may prove to be of similar character.

2) The scleral portion of the visual surface is of the same structure as the test, and is a direct continuation of it.

3) No evidence appears of any continuous corneal layer covering the entire surface.

4) The corneal lenses are wholly discrete from the epidermis, but are of epidermal origin. In the addition of new lenses to the visual surface, they appear to arise from a thinning of both surfaces of the integument.

5) The corneal lenses were hollow or filled with some matter not homogeneous with the cornea itself.

6) The corneal lenses, and therefore the ommatidia, are added to the visual surface with advancing age until the mature growth of the individual is attained; thereafter they diminish in number with increasing senility.

7) The addition of corneal lenses occurs regularly at the extremities of the diagonal rows.

8) No evidence is preserved of crystalline cones in the ommatidial cavities, though they may have been removed in the decomposition of the soft parts of the eye.

In conclusion I wish to call attention to the primitive structure of the eye exhibited in a Devonian subtype which is provisionally referred to the order of the Phyllocarida. Dr. J. S. Kingsley in the final paragraph of a valuable paper on the "Development of the compound eye in Crangon" (*Journal of Morphology*, Vol. I., p. 63), has written: "The observations as yet recorded are not sufficient to throw any great light on the phyllogeny of the Arthropod eye; still one or two points may be

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feature of difference from the schizochroal eyes. My own study of the holochroal eyes has not been as careful as I hope to have the opportunity of making it, but it may be observed that sections of the eye in *Proëtus Rowi* seem to indicate a very tenuous interlensar sclera; moreover, the immature *Calymene senaria* referred to in a previous footnote shows evidence of such interlensar integument.

spoken of. The mere fact of invagination[1] must be regarded as indicating an ancestral condition, but what this condition was is uncertain. The pit or groove must have had sensory functions and either wall" (retinogen and gangliogen) "must for a time have been like its fellow, as is shown by its having similar nuclei, and by the similar development of rows of nuclei."

In the species *Mesothyra Oceani,* Hall, a member of one of the faunas of the Portage group, and one of the largest known representatives of the Phyllocarida, the eye consists of a simple deep pit at the summit of the optic node. There is no evidence that this pit contained a series of lenses, but it is highly probable that it is an otherwise embryonic character retained at maturity, and may serve as the ancestral condition of the Decapod eye suggested by Dr. Kingsley. That there is Decapod blood in the Phyllocarida has been disputed by Packard, the author of the group term, but Decapod affinities are strongly indicated by the recently described Devonian genus of Phyllocarida, *Rhinocaris,* (*Palæontology of New York,* Vol. VII., 1888).

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[1] This refers to the primary optic invagination in the embryo, for the formation of the entire visual surface, first pointed out by Locy (*Bull. Mus. Comp. Zoöl.* 1886), and verified by Kingsley (*op. cit.*). The term is not used in a sense similar to that in which it has been employed in this paper in referring to the formation of the corneal lenses.

EXPLANATION OF PLATES.

FIGS. 1–7. Schematic representations showing the different modes of preservation observed in the visual surface of *Phacops*. Each figure represents a single lens with the lensal or ommatidial cavity, and the adjoining sclera or its equivalent space.

1. *The cornea and sclera normally retained*, the lensal and corneal cavities being filled with matrix. The lens is represented with its posterior cavity having the relative size indicated by the specimens figured elsewhere on the plate, and the anterior corneal cavity is characterized by radiating lines which are intended to show the difference often apparent in the character of the matrix filling the cornea.

2. *The cornea removed and the sclera retained*, the matrix showing the position and size of the posterior corneal cavity, but retaining no indication of the anterior cavity filling, which is removed with the cornea.

3. *The cornea retained and the sclera removed*, the lens standing at the summit of a pillar of matrix which represents the ommatidial cavity.

4. *Both cornea and sclera removed*, leaving pillars of matrix with a cup-shaped summit, in the bottom of which lies a little ball. The pillar represents the ommatidial cavity; the concave summit, the lower surface of the lens, and the little ball, the posterior corneal cavity.

5. *An external film is removed from both cornea and sclera*, destroying the former and leaving the filling of the anterior corneal cavity standing out prominently with almost the full size of the lens. In the single instance observed of an eye in this condition, the posterior corneal cavity is empty in all the ommatidia that were opened. The reason for this is not well understood. The sclera has been silicified, and subsequently decomposed, so that it is indistinguishable from the matrix.

6. *The outer and inner walls of the visual area have been replaced by a film of silica, and the rest of the calcareous matter subsequently removed*, leaving both cornea and sclera preserved as a mere shell.

7. The same condition of preservation, modified by the adherence of the cornea and outer wall of the sclera to the matrix outside the eye, leaving the walls of the ommatidial cavities adhering to the internal matrix as a series of short tubes. This mode of fossilization has not been observed in *Phacops rana*, but is not uncommon in specimens of *Phacops cristata*, var. *pipa*, from the decomposed Upper Helderberg phtanite.

FIGS. 8–22. Schematic representations of the lenses of the visual surface. The curved surface is projected upon a plane, and the relative size and position of the lenses is retained. Whether the representation is from a right or left eye, the lower posterior margin is at the right of the figure, the diagonal rows being enumerated from this side, obliquely downward from right to left. All the figures are drawn to the same scale.

8. The visual surface of an extremely young individual measuring 6 mm. across the base of the cephalon; composed of 31 lenses in 8 rows, nearly all the terminal lenses being immature. The older lenses show a tendency to arrangement along a single or double transverse row, parallel to the margins of the visual surface.

9. An older eye, bearing 35 lenses in 8 rows, belonging to a young *Phacops*, having a cephalic width of 7 mm. At the upper extremities of the rows the lenses are all full-grown, and all immature at the lower extremities.

10. An eye composed of 40 lenses in 8 rows, and belonging to a young individual with a cephalic width of 9 mm.

11. An eye with 42 lenses in 8 rows, belonging to a large individual, having a width across the cephalon of 34 mm. The lenses are nearly all mature, but are abnormal in their arrangement, showing a failure to develop properly at the upper extremities of the rows after the third.

12. An eye of *Phacops cristata*, var. *pipa*, composed of 50 lenses, and showing an abnormal arrangement, a single mature lens in the last row being situated high up in the base of the palpebrum. Had it developed in the vacant space in the last row but one, the arrangement of the lenses would have been normal for this variety.

13. An eye of the same variety bearing 52 lenses in 8 rows. Eight appears to be the normal number of rows in the mature eye of this form, the anterior vertical row, and the last diagonal row, consisting of three lenses. In the other diagonal rows there is apparently much greater variation than in the eye of *Phacops rana.*

14. An eye of *Phacops rana* composed of 57 lenses in 9 rows, the head having a basal width of 52 mm. This is the eye of a senile individual, and all the lenses are of mature size with the exception of those on the palpebral margin. The number of lenses in the anterior vertical row is three instead of four, as in the normal adult.

15. Another senile eye, with 60 lenses in 9 rows, belonging to a very large specimen, with a cephalic width of 70 mm. Here again the lenses are all of full size with the exception of those on the upper margin of the visual surface; the lenses of the anterior vertical row are also three in number.

16. An eye composed of 60 lenses in 9 rows belonging to an individual slightly above normal adult size, having a cephalic width of 28 mm. In the first row one interval has been skipped in the addition of the last lens.

17. An eye of normal size and development, bearing 70 lenses in 10 rows, the cephalon having a width of 24 mm. The first row consists of a single full-grown lens at a considerable distance from the posterior extremity.

18. An eye from an individual of the same size, having 70 lenses in 9 rows.

19. An eye composed of 71 lenses in 10 rows, the cephalon to which it belongs having a width of 27 mm. It essentially differs from the preceding only in the presence of the single lens constituting the first row.

20. An eye with 75 lenses in 10 rows, from an individual having a cephalon 28 mm. in width.

21. An eye composed of 88 lenses in 11 rows, from an individual measuring 17 mm. in cephalic width. This is the greatest number of lenses and rows of lenses noticed in this species.

22. An average eye of *Dalmanites Boothi*, var. *Calliteles*, Green, consisting of 206 lenses in 29 rows.

FIG. 23. A left eye of *Phacops rana*, enlarged to 3 diameters, showing the arrangement of the lenses, the smaller size of several of the terminal lenses, and the tubercles on the integument of the palpebrum and orbital ridge. The lensar cavities are represented as much too sharply hexagonal; they should be more rounded and excavate. The figure is copied from the *Palæontology of New York*, Vol. VII., Pl. 8, Fig. 6.

FIG. 24. A portion of the visual surface of a very old eye, taken from an individual measuring 70 mm. across the base of the cephalon; showing the thick and deeply excavate sclera, the full-grown lenses along the lower margin, and the small lenses at the upper margin of the area. Enlarged to 3 diameters.

FIG. 25. A natural cast of the internal surface of a portion of the visual area in *Phacops cristata*, var. *pipa*, enlarged to 6 diameters. The specimen shows very beautifully the cup-shaped casts of the ommatidial cavities, each with a little ball at its centre representing the posterior corneal cavity. At the upper extremities of the last

two vertical rows at the left, are two casts of immature lenses, in one of which the filling of the corneal cavity is just discernible; in the other the ommatidial cavity appears not to have penetrated to the upper surface. Several features of similar character are to be seen on parts of the specimen not represented in the figure. The portion of the eye represented is the posterior one-third of the right eye.

FIG. 26. Two cavity-fillings from the same specimen enlarged to 15 diameters, showing the small size of the balls compared with the probable size of the entire cavity of the cornea.

FIG. 27. A section through the eye and adjoining parts of *Phacops rana*, showing the lenses and the interlensar sclera. Enlarged to 3 diameters.

FIG. 28. The same enlarged to 6 diameters, showing the continuity of the poriferous integument of the head with the interlensar sclera, the double convexity of the lenses, and the depth of the ommatidial cavities in the sclera. At the right of the first lens in the series is an internal depression on the integument which appears to indicate the position of a newly developing ommatidium. No evidence of a lens was visible at this point before the section was made.

FIG. 29. Three lenses with their interstitial integument, from the same specimen, enlarged to 10 diameters. There is a slight difference in the character of the matrix filling the cavity of the cornea, it being possible to distinguish the line between the anterior and posterior divisions of the space. The dark color of the lower portion of the sclera is due to an increase of pigment.

FIG. 30. A portion of the eye of *Phacops rana*, from which the sclera has been removed by natural causes, leaving the corneæ standing on pillars of matrix. Enlarged to 12 diameters.

FIG. 31. A natural section of the eye of *Phacops cristata*, var. *pipa*, enlarged to 8 diameters. The sclera has been removed, and the doubly convex surface of the lenses is well shown.

FIG. 32. The eye of *Mesothyra Oceani*, Hall, enlarged to 3 diameters, showing the strong optic node with a simple, deep pit at its summit. The figure is taken from the *Palæontology of New York*, Vol. VII., Pl. 32, Fig. 2.

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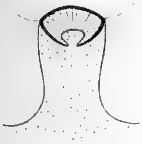

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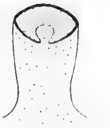

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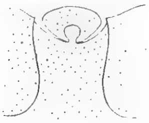

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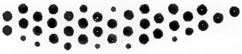

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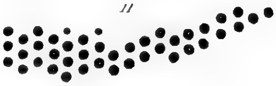

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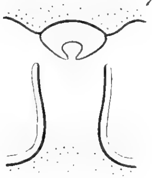

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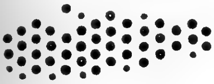

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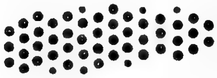

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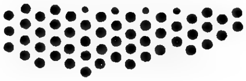

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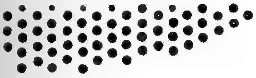

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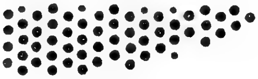

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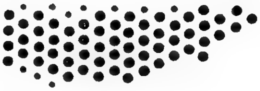

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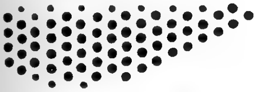

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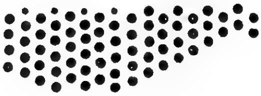

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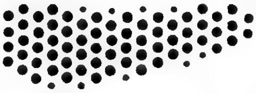

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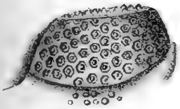

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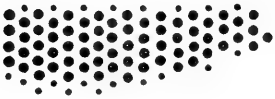

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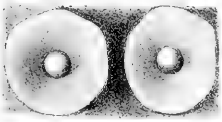

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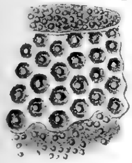

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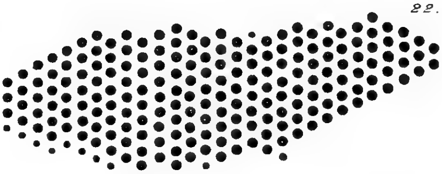

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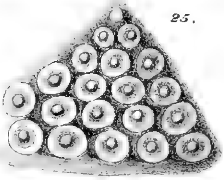

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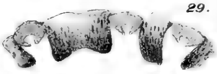

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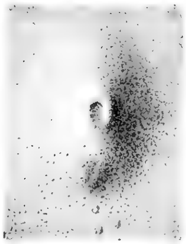

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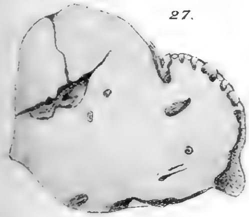

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FURTHER STUDIES ON *GRAMMICOLEPIS BRACHIUSCULUS*, POEY.

BY R. W. SHUFELDT, M.D., C.M.Z.S.

DURING the spring of 1872, Professor Poey of Havana, Cuba, came into possession of a very remarkable form of fish, which presumably was taken in Cuban waters.

Fortunate it was for science that it fell into such excellent hands, as that eminent ichthyologist promptly presented us (*Anal. de la Soc. Esp. de Hist. Nat.*, Tom. 11, 1873) with a very excellent account of this more than rare type, the duplicate of which, so far as I am aware, has yet to be found by naturalists.

This account of Professor Poey's, as will be seen, was published in the Spanish language, and it has given me much pleasure to make a translation of it, and present it here as an introduction to some subsequent examinations which I had the rare opportunity of undertaking upon the skeleton of the specimen in question. The osteology of this fish is very interesting, not only from the fact that it is the only specimen in the hands of science, but from its extraordinary peculiarities, and from the fact that it may some day be found upon our own coasts.

My translation of the original description just referred to reads as follows: —

"GRAMMICOLEPIS BRACHIUSCULUS.

TYPE OF A NEW FAMILY IN THE CLASS PICES.

BY DON FELIPE POEY,

PROFESSOR IN THE UNIVERSITY OF HAVANA, AND CORRESPONDING MEMBER OF THE ACADEMY OF EXACT, PHYSICAL, AND NATURAL SCIENCES OF MADRID.

The length of this extraordinary fish is 470 millimetres. The head enters five times into the total length of the body, and two and two-thirds times into its greatest depth. The body is much compressed, and quite deep. The very large eye is contained two and a third times in the length of the head, and lacks the membrana adiposa.

The branchial apertures are deeply cleft, but I fail to find more than four branchiostegal rays, without being able to assert that there may be a greater number of them. The snout is short. The prefrontal, the turbinal, and the anterior suborbital, are extremely hard, and covered with spiny rugosities. The preoperculum and interoperculum have rugose borders, while the remaining opercular bones are entirely so. The mouth is small, subvertically cleft; the premaxillary process is large, and is lodged in a fossa of the cranium. The maxillary is complicated. The teeth are simply a narrow row of minute prickles; they do not occur upon the vomer, nor the palatines.

D. 6–34; A. 2–33; V. 1, 6; P. 15; C. 1–13–1. The leading spine of the first dorsal series is rugose, as is the first ventral, the two post-anals, and the external ones of the tail, which latter show the condition equally well in either one.

The rays of the pectoral, second dorsal, and the anal fins are compressed, and do not ramify at their extremities. The pectorals are very short and rounded. On the other hand, the vertical fins, the dorsal, and anal are well developed.

The tail was injured, and apparently cut; the membrane which unites its rays had disappeared; the peduncle which supports it is large, and capable of communicating a powerful impulse to the act of progression. The thoracic pectorals unquestionably possess a rugose spine and six flexible ones that are branched.

Aside from the frontal bones and the suborbitals where the skin abruptly terminates, and the nasal portion of the snout, all the trunk and the head is covered with scales, including the inferior mandible.

These scales in no way resemble those found among the acanthopterygean fishes. Their length greatly exceeds their width; they have the appearance of parchment, — transparent, brittle when dry, — overlap each other, and are strengthened longitudinally by a raised lineal ridge.

Their contact with each other is so extremely intimate that it lends to the skin of either side a very smooth appearance — so much so, that the rough borders of the scales would not be suspected without the aid of the fingers.

Thanks to the length of these scales, four, five, or six of them are sufficient to span the height of the trunk, one of such a series being crossed by the lateral line, where its presence is denoted by a raised ridge.

The leading scales on the body, above as well as below, are shorter, and where carried on to the head, are doubly as firm as those found at the base of the fin rays.

Without having done more than counted the scales in a longitudinal line, I calculate that the number is considerably above two hundred; those of the head, although shorter, have the same form as those of the trunk. There are no scales upon the fins.

The caudal peduncle develops neither a cartilaginous nor an osseous plate at its sides. Posterior to the arms the ventral keel is rough.

The cranium is more cartilaginous in structure than it is osseous, except the frontals, which are rugose in lines in the supraorbital region, and bristly in front, as are the turbinals and suborbitals; these latter are four in number, the last three being very slender. There are two supratemporals.

The inferior mandible is characterized by several rows of minute spines upon the dentary and articular elements. The vertebræ number 10 + 36.

The anterior neural spine is not excavated, being lofty and smooth; the five that follow are short and inclined backwards. The remaining ones are slender, which applies also to their hæmapophyses. The last vertebra is without lateral spines.

The pleurapophyses are inconspicuous, feebly developed, and have much the same size and shape as the epipleurals. I discover but one pseudo-interneural spine in front of the one that supports the first dorsal fin ray.

The specimen I described, when received by me was without gills and without abdominal viscera. Preserved as it was three days upon ice, its general color appeared to be white; but we have reason to suspect that in the fresh condition this fish can easily assume a violet tint. The hard parts of the head were of an intense violet shade. The ascending border of the preoperculum, violet. The fins were white, changing to violet in certain lights; the caudal fin rays were of a reddish tint. Eye inclining to white.

FAMILY: The characters which are presented us in this fish are of such an extraordinary nature that they will not permit us to place their possessor in any of the recognized families of fishes. Its nearest affinities are with the *Berycidæ* and with the *Carangidæ*, two families widely separated from each other; I am inclined to believe that its better place is along-side of the last-named one. Its resemblance to the *Berycidæ* is seen in the large eye; the asperity of the cranium; the rugosities upon the fin rays; the ventrals composed of more than five soft rays, over and above the spiny one; its resemblance to the *Carangidæ* is seen in the two free spines which precede the anal fin, and especially to *Seriolas* for lacking the bony plate of the lateral line; but in the number of its vertebræ it approaches the *Scombridæ*, as the shape of its ventral fins are in pattern analogous to those of the *Acanthuridæ*, and its unramified fin rays agree with the *Balistidæ*.

The character of the scale, to which ichthyologists have attached so much importance, separates it from all other forms known to me.

My examination, then, authorizes me in establishing the family *Grammicolepidæ*, based upon the following characters: Lateral line unarmed with bony plates; ventral fins composed of more than five soft rays; two free postanal spines; caudal vertebræ numerous; scales very long and narrow, without fan-like expansions or denticulations.

GENUS: The genus *Grammicolepis* has for its etymology *γραμμιχός*, line; λέπις, scale.

The characters, in addition to those I have already pointed out for the family, are: Body deep, compressed; eye large; mouth small; head, in part, rugose, which also applies to the interoperculum and the preoperculum; to all appearances a limited number of branchiostegal rays; teeth mere asperities, the palatine arch without them; two dorsals, the first short, the second very extensive, its height insensibly increasing; pectoral short and rounded; the dorsal, anal, and pectoral fin rays do not ramify at their extremities.

HISTORY: I saw this fish for the first time in Havana, on the 5th of April, 1872, and I have not observed it since; neither fishermen nor students of the class have been able to give me its name, because neither one nor the other have seen it to know it. It is, then, one of the rarest forms in existence. The skeleton I have sent to the eminent Professor Gill, who has it in his possession, though I do not know but that he has preferred placing it in the collection of the Smithsonian Institution in Washington."

This account is completed by a plate and its accompanying description, showing the fish one-third the size of nature, and various illustrations of its scales and other parts.

Now about a year ago, Professor Gill did me the great honor to place in my hands, for a little more extended illustration, not only the skeleton of this rare type, but a life-size outline drawing of the fish made by Professor Poey himself. In addition to these treasures, this eminent zoölogist also placed at my disposal several crania of fishes, representing the genus *Caranx* and others, to be used in the present connection. Situated as I now am, at an outpost in New Mexico, notwithstanding the great value of these crania for comparison, I can only regret that the material at my hand is not still more extensive, as it might be, were I more favorably situated to undertake this kind of a paper. Especially would I like to examine specimens of *Brama Raii*,[1] which, if I have recalled the proper form, possesses vertical linear scales something like those in *Grammicolepis*, though, I believe, very much smaller.

In order to give an idea of the external appearance of the subject of this article, I brought to my aid the two drawings of

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[1] Since writing the above, a very valuable work upon ichthyology has appeared, viz.: *The Fisheries and Fishery Industries of the United States.* By G. Brown Goode, Asst. Direc. U. S. Nat. Mus. and a staff of Associates. Washington, 1884. On page 335 of the text of this book, we read of the BRAMIDÆ that "The only member of this family of interest to us is the *Brama Raii*, called "Pomfret" in Bermuda, where a few individuals were observed by the writer in 1876. In 1880, an individual was obtained on the Grand Bank of Newfoundland, and more recently the species has been found to be somewhat abundant on the coast of Washington Territory and Vancouver's Island. This species was described from the coast of South America, under the name *Brama Chilensis*." In the second volume of this work, we find an excellent figure of *Brama Raii*, Plate 112, which shows the fish possesses vertical linear scales, although they are much shorter than they are in the subject of this article.

The Pomfret also has its tail more deeply forked, and the dorsal fin is seen to be continuous. The eye is very much smaller, though otherwise there are some general external resemblances between the two forms. (R. W. S., 7 Aug., '86.)

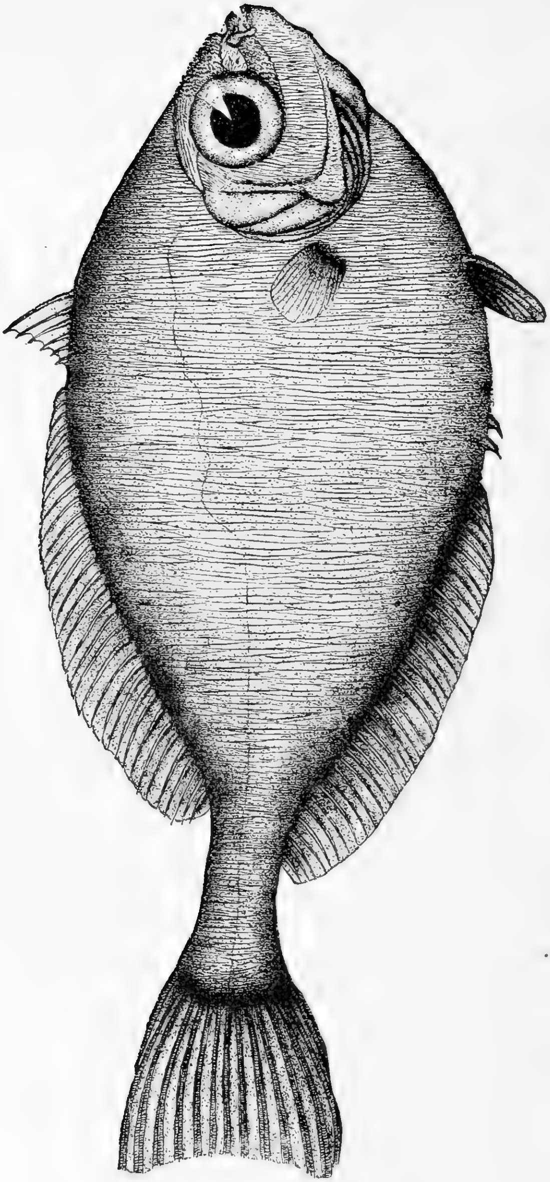

Figure 1. — Right lateral view of *Grammicolepis brachiusculus.* One-third size of nature. By the author, assisted by Poey's outline drawings, and existing material.

Professor Poey, neither of which profess to be anything more than the merest outline of *Grammicolepis*, and the scales, fins, and other parts that accompanied the skeleton. These, taken in connection with the lucid description of the fish, and all carefully compared, have resulted in my drawing presented in Fig. 1 of this memoir.

Owing to the fact that many parts of the skeleton, from long keeping and their delicate structure, have warped considerably out of shape, I propose to devote myself on the present occasion only to such as seem most important of them, and chief among these stands the cranium.

As I say, so far as I know, the specimen of the *cranium* of *Grammicolepis* before me is the only one in the hands of science, and a most extraordinary object it is. Three features strike us most forcibly when we first came to examine it: the enormous orbits, the truncate appearance of its anterior part, and the semi-transparency of its gelatinous-looking bones.

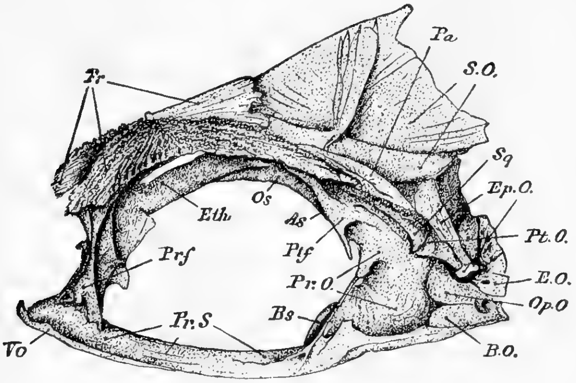

Figure 2. — Left lateral aspect of the cranium of *Grammicolepis brachiusculus;* life size, drawn by the author from the specimen. *Fr*, frontal; *Pa*, palatine; *S.O.*, supraoccipital; *Sq*, squamosal; *Ep.O.*, epiotic; *Pt.O.*, pterotic; *E.O.*, exoccipital; *Op.O.*, opisthotic; *B.O.*, basioccipital; *Bs*, basisphenoid; *Pr.O.*, proötic; *Ptf*, postfrontal; *As*, alisphenoid; *Os*, orbitosphenoid; *Eth*, ethmoid; *Prf*, prefrontal; *Pr.S.*, parasphenoid; *Vo*, vomer.

The peculiar rugose condition of a *frontal bone*, referred to by Professor Poey, is well shown in Figs. 2 and 3, *Fr.* It will be seen that these rugosities of the frontal radiate from a common centre on its superior aspect, this centre being found at about the middle of the bone, or what would be the middle of its oblong figure were its anterior internal notch completed, and we do not regard its postero-lateral prolongation. This latter part of the bone forms the superior periphery of the orbit, and is produced backwards as far as the squamosal (*Sq*). To the inner side of this process, the posterior border of the frontal shows at least one conspicuous notch, while its free margin overlaps the supraoccipital, and is in turn overlapped by the parietal (*Pa*) more externally (Fig. 2). Mesially, its surface turns upwards, more particularly behind, where with the fellow of the opposite side it grasps in the middle line the anterior portion of the supraoccipital crest. Below this point the two frontals have their straight, free, mesial edges roughly in contact with each other, and slope gradually downwards to the margin of that concavity which is found in front (Figs. 2 and 3).

This extraordinary fossa on the anterior aspect of the cranium of *Grammicolepis* is entirely open above; its rugose and subcircular margin being formed by the frontals; while below it becomes conical with its apex in the middle line, and in the ethmoid. Above, where it is most capacious, it has its posterior wall formed by descending plates developed on the part of the frontals, the left one considerably overlapping the right. Below this, in the middle line, there is an opening of some size, which leads into a commodious chamber lying between the frontals above and the mesethmoid below.

A frontal is truncate in front, where it overhangs the corresponding prefrontal, and internally articulates with the curiously shaped ethmoid. Behind this, and on its under side, it forms the major share of the roof of the orbit. Then occurs a longitudinal keel, which separates this from that other part of its under surface which forms the roof of the mid-chamber described in the last paragraph. Viewed together from above (Fig. 3), it will be observed that the rugosities of the frontals are limited behind by a subparabolic curve with its arc anteriorly directed.

In this dried cranium a *parietal* (*Pa*) is represented by a thin, flake-like, semi-transparent piece of bone, of a form shown in Fig. 3. To the outer side of its mid-longitudinal line it develops for its entire length quite a prominent, though thin, crest, which is rugose all along its superior margin.

The anterior three-fifths of the under surface of this element simply rests upon the frontal and supraoccipital, while the remaining portion behind is more firmly attached, and really holds the bone in its position. Its outer free margin articulates principally with the inner border of the posterior prolongation of the corresponding frontal, though still more posteriorly it meets to some extent the squamosal (*Sq*). With the epiotic (*Ep.O.*) it is connected simply by a feeble and thin band of bone. The parietals, then, seem to play the part here of binders, rather than their presence is at all essential to covering over any sizable vacuity in the cranial vault, that might exist were either of them removed.

The *supraoccipital* is a very extensive ossification, and is characterized by a fairly prominent crest.

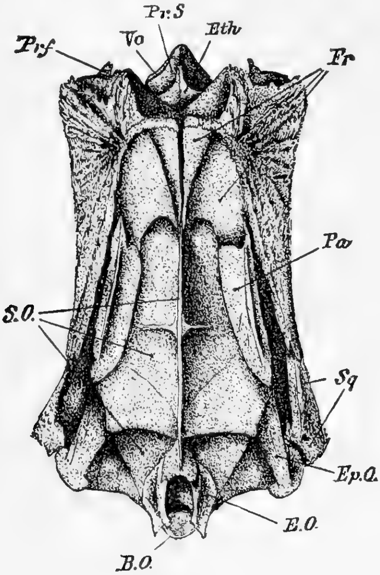

Figure 3. — Cranium of *Grammicolepis brachiusculus*, seen from above; life size, by the author. Lettering as before.

This crest is triangular in outline, with its apex above, and its base attached in the middle line, to the horizontal portion of the bone. From the middle point of this base, a narrow, fan-shaped development springs upon either side, which is incorporated with the crest, to strengthen it, being carried nearly as high as its apex (Fig. 2).

The broad and spreading horizontal portion of the bone forms the roof of the brain-case, while posteriorly, just before the termination of the crest, it is bent abruptly down to meet the exoccipitals. The flexure, being sharply defined by a transverse line, the outer end of which, either way, terminates in the apex of a pyramid, the lateral and upper sides of each being also formed by the supraoccipital. The lateral aspect of this pyramid is overlapped by the epiotic (*Ep.O.*), while outwardly its free margin articulates with the squamosal (Fig. 3).

Regarding one of these *epiotics*, we find that its fan-like portion is finished off behind by a semicircular piece, which is thickened below, where it becomes firmly attached to the neighboring bones. The blade portion is longitudinally fluted, but no rugosities are found upon it. This does not apply to the element at its outer side, the *squamosal* (*Sq*), which element develops very conspicuous rugosities upon its upper aspect in direct continuation with the longitudinal ones on the long, backward-extending process of the corresponding frontal (Fig. 3).

At the distal extremity of the squamosal I detect a small, flake-like piece of bone, thoroughly attached, though individualized by sutural traces, which I take to be the representatives of the *pterotic* (*Pt.O.*). Beneath and beyond, the squamosal seems to make the usual ichthyic articulations with the postfrontal (*Ptf*) and the proötic (*Pr.O.*). At its under side we find a small hyomandibular facet (Fig. 4, *hf*).

A *postfrontal* of considerable size (*Ptf*) develops at its outer side, a sharp, descending, spicula-form process of bone, which is transversely pierced at its base by a small foramen. The inferior articular sutural trace of the postfrontal, as I make it out, is subcircular in outline, and closely meets corresponding marginal concavities offered by the proötic and alisphenoid.

Each *alisphenoid* is necessarily a very extensive ossification, forming, as they conjointly do, the major part of the bony wall of the posterior aspect of the immense orbit (*As*).

In front they articulate with far smaller *orbitosphenoids*, which in their turn meet in the median line anteriorly (*Os*). Now above the basisphenoid (*Bs*), the alisphenoids and orbitosphenoids are separated from each other, mesially, by a vertical vacuity, broadest below, gradually tapering to a blunt apex above, which constitutes a great fenestra for the anterior wall of the cranial casket (Fig. 4).

As already stated, the hinder portion of the *ethmoid* (*Eth*) forms the mid-roof of the orbital space. This division of the bone is of an oblong outline, being encroached upon by the common, circular, anterior margin of the obitosphenoids behind, the two elements being completely united. Below, it is convex from side to side, correspondingly concave above, where it forms the floor of the interfronto-ethmoidal chamber, already alluded to above. I have previously described how now the ethmoid is deflexed, and becomes concaved in front to form the lower limits of that excavation on the anterior aspect of the cranium.

This, as we have already seen, terminates in a conical point, and even beyond this the bone is carried forwards as a median triangular process, the apex of which rests upon the parasphenoid (Fig. 3, *Eth. Pr.S.*).

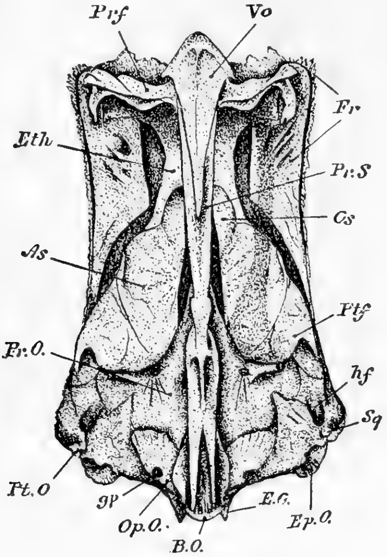

Figure 4.—Under side of the cranium of *Grammicolepis brachiusculus;* life size; reference letters the same as in former figures, with *hf*, hyomandibular facet, and *gp*, foramen for the exit of the glossopharyngeal nerve in the opisthotic (*Op.O.*).

Upon either side of the ethmoid, the flat anterior aspect of this cranium is completed by a broad prefrontal (*Prf*). The form assumed by one of these elements can best be appreciated by referring to Fig. 5, which represents the cranium of *Grammicolepis* seen from behind, while the anterior face is in the horizontal plane. In this position the posterior aspects of the prefrontals come into view.

Each one essentially consists of a thicker and vertical outer column of bone, antero-posteriorly compressed, and an expanded inner portion, which latter is reënforced by radiating projections that converge to meet at a point at the lower part of the inner margin of the columnar portion. It is hardly necessary to state that these prefrontals form the externo-lateral parts of the anterior orbital wall, the ethmoid completing it mesially.

Coming now to the *vomer* (*Vo*), we find it to be a thin scale-like bone, of a form best shown in Fig. 4. It rests in the longitudinal excavation of the anterior and lower side of the parasphenoid, while its firmest attachment to that bone seems to be by the periphery of its anterior margin.

The parasphenoid (*Pr.S.*) is gently arched as it spans the orbital space below, having its convex arc downwards. The lower side of this part of the bone, as I have already intimated, is longitudinally scooped out, while the upper side presents lateral surfaces, which are inclined so as to meet in a median line. Posteriorly, the parasphenoid makes the usual teleostean connections with the basioccipital, basisphenoid, and proötic, being deeply cleft as it passes to cover the under side of the first-named element (Fig. 4).

Occupying its usual position, the *basisphenoid* (*Bs*) not only develops the median process (Fig. 2) seen in so many true teleosts, but furnishes a firm horizontal roof for the three-sided pyramidal eye-muscle canal, the lateral walls of which are completed by the proötic and parasphenoid.

As in the majority of osseous fishes, the *proötic* is a well-defined and important element at the lateral aspect of the brain-case (*Pr.O.*). Its anterior margin is pierced by the foramen for the trigeminal nerve, from which point faint lines in the tissue of the bone are seen to radiate.

The basioccipital (*Bs*) has its thickened and longitudinal portion underlying the brain-case, as in most fishes, being completed behind the facet for the leading vertebra of the spinal column. This facet is comparatively rather small, with its conical depression very deep.

At either of its sides the basioccipital develops an upturned and semicircular plate of bone, similar in structure to the other flat bones of the lateral cranial walls, which articulates with the lower margin of the opisthotic and the posterior margin of the proötic (Fig. 2).

The *opisthotic* (*Op.O.*) is large and occupies its usual position, as generally found, in the cranium of the teleosts. Its posterior margin is pierced by a conspicuous foramen for the exit of the glossopharyngeal nerve from the brain-case. The intersutural traces defining its borders are easily made out in the specimen, and this element contributes not a little to the lateral wall of the cranial cavity, — a large vacuity existing after its disarticulation.

Each *exoccipital* (*E.O.*) develops at the outer sides of the vertically oval foramen magnum, a fan-shaped, bony thickening (Fig. 5), which nearly meets at the middle point above.

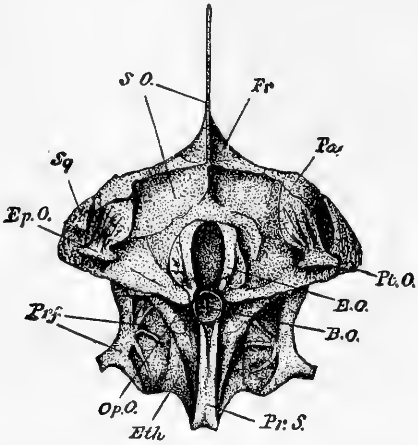

Figure 5.—Posterior aspect of the cranium of *Grammicolepis brachiusculus;* life size. Letters have the same significance as in former figures. The cranium is represented as resting upon its anterior face on the horizontal plane, the line of sight being perpendicular to the latter, and passing through the imaginary centre of the foramen magnum.

Further, these bones spread out so as to complete the hinder cranial wall, where the supraoccipital and osseous elements at the lateral angles have failed to do so.

Now a number of the bones required to complete the skull of this fish have been lost, and, as I said before, the others in my possession are too much out of shape, from their fragile nature, for me to decide, with any degree of certainty, as to their several proper positions. This is much to be regretted, as I expect a complete skull of *Grammicolepis* would prove a very interesting and instructive object.

To return to the cranium for the purpose of taking a general glance at it: we are to note especially the almost entire absence of those parial and lateral crests, developed on the part of the parietals and squamosals, so manifest in some fishes, as for instance the genus *Caranx;* we are to note, also, the very peculiar texture of the bone that composes this cranium, being more like the material that is found in ordinary fish scales rather than bone; particularly are we to observe the relation between the anterior portion of the supraoccipital crest, and the upturned portions of the frontals.

There are but few striking features within the cranial case of this strange form of fish. For the most part, surfaces, convexities, and concavities on the outside give rise to similar surfaces on the inside, the last two being, of course, reversed. The fossæ for the *otoliths* are ample and well defined, but the elements themselves have been lost.

I have already expressed my regrets at not having at hand more extensive material wherewith I might compare this extraordinary fish; they only increased as my investigations proceeded, while the remaining consolation left me, is, that I feel I have added at least my mite to the labors of Professor Poey; so should another specimen of *Grammicolepis* fall into the hands of naturalists, we can, at least, meet it with drawings of its cranium and other skeletal parts, as well as with similar drawings of some of the forms to which it is supposed to be related.

Through the courtesy of the Smithsonian Institution, and the kindness of Dr. Gill for selection, I find before me the cranium of a specimen of *Caranx hippos*, with the spinal column of the same fish (No. 13,561 S. I. Coll.). There is also the cranium (No. 11,385) of another and still larger *Caranx*, the species being unknown. This last specimen presents some points of peculiar interest not so well shown in the first. I have also the cranium of a specimen of *Teuthis cœruleus*, which will be introduced to show certain points; and finally, the cranium of *Pomacanthus paru* (No. 12,770 S. I. Coll.) brought forward to illustrate still other points.

Professor Poey's investigations evidently led him to believe that *Grammicolepis* was more nearly related to the *Carangidæ* than any other family of fishes known to him. And in this opinion, so far as I can see or am able to judge, I must concur.

The cranium of the *Caranx* No. 11,385, which bears a very close resemblance to *C. hippos*, shown in Fig. 6, although, be it known, it possesses marked differences, is composed of a bone tissue much more like that seen in the cranium of *Grammicolepis* than any of the other specimens before me. As much as it is unlike it, it evidently approaches the semi-transparent and brittle condition found in our subject. The next thing that our attention is directed to, is the strikingly large orbit of this *Caranx*, and the evident, though distant, similarity of the elements that go to form its walls. The chief difference we meet with here is the absence in the *Caranx* of the backward-extending plate of the ethmoid seen in *Grammicolepis*, while there is much to support a probable relationship of the forms, in the parasphenoid, the basisphenoid, and less so in the prefrontals, of the two.

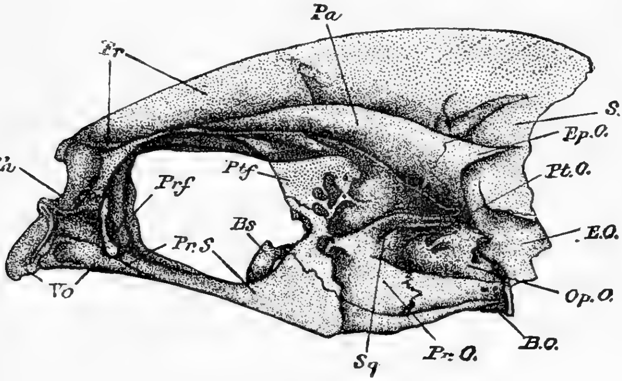

Figure 6. — Left lateral view of cranium of *Caranx hippos*. Spec. No. 13,561, Collection of the Smithsonian Institution; life size, by the author. Letters signify the same as in the other figures.

Again, in the *Caranx*, the ethmoidal mass, and parts, which of a consequence associate with it, are produced forwards, and we fail to find anything upon this aspect that in any way reminds us of the curiously truncate appearance of the front part of the cranium in *Grammicolepis*.

Another marked difference is seen in the vomerine element; this bone, as we have observed, is in our subject merely a kite-shaped scale, in no way incorporated with the parasphenoid, being merely attached around its anterior rim. Now our specimen of *Caranx*, No. 11,385, foreshadows in its vomer what eventually comes to pass, between this condition in *Grammicolepis* and what we find in *C. hippos.* In this latter fish, as will be observed by referring to the figures Fig. 6, *et seq.*, the vomer is quite a solid bone, and is moulded upon the anterior end of the parasphenoid, forming a more or less massive termination of this end of the cranium.

In our unspecified specimen of *Caranx*, this general appearance is likewise maintained; but upon a lateral view, we are enabled to look in between the vomer and parasphenoid, and the less solid formation of either can at once be appreciated as well as their less intimate relation to each other. It is a shame that this species is not known, nor was ever diagnosed when this specimen of cranium was taken, as this condition is very interesting in the present connection, as are several others, as we shall presently see.

As representatives of the *Carangidæ*, neither of these specimens develop a spine-like process descending from the postfrontal, which is a very marked feature of that bone in *Grammicolepis*. It is, however, present in other teleosteans, as seen in one crania of *Pomacanthus* and *Teuthis*, Figs. 10 and 11.

Before leaving this region of the cranium, I would like to invite attention to the anterior aspect of it, in this very specimen of *Pomacanthus* (Fig. 10). It approaches to some degree the truncate appearance, so often alluded to in *Grammicolepis;* a closer resemblance, however, is vitiated by the extraordinary forward and upward projection of the vomer in *Pomacanthus.* Posterior to this bone, in the individual in question, an extraordinary concavity is seen, the sides of which are formed by the prefrontals and parasphenoid, being perforated on either side by a group of foramina. Its bottom is completed entirely by the latter bone.

Teuthis cœruleus offers us in its ethmoid and vomer just the very reverse of this condition, as may seen by a reference to Fig. 11.

It may be as well to note in passing that in *Pomacanthus paru* the parasphenoid is very deep in the vertical direction, being longitudinally excavated above and continuous with the capacious eye-muscle canal, while anteriorly and below it is sharply carinated. Posterior to this carination the bone develops a rounded and descending prominence, which is bifid, the two lamina being directed backwards and outwards. The behavior of the anterior end of the parasphenoid of *Pomacanthus* has already been described above.

This bone is also wonderfully developed in our cranium of *Teuthis* (Fig. 11). Here the carination in front is exceedingly deep, while behind it, a distinct descending process is also seen.

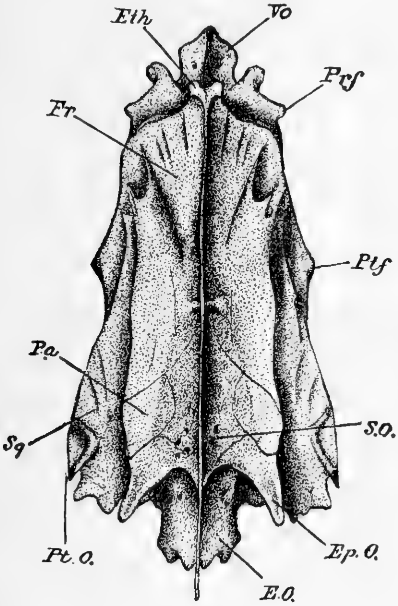

Figure 7. — Superior view of the cranium of *Caranx hippos*, same specimen as in Fig. 6; life size.

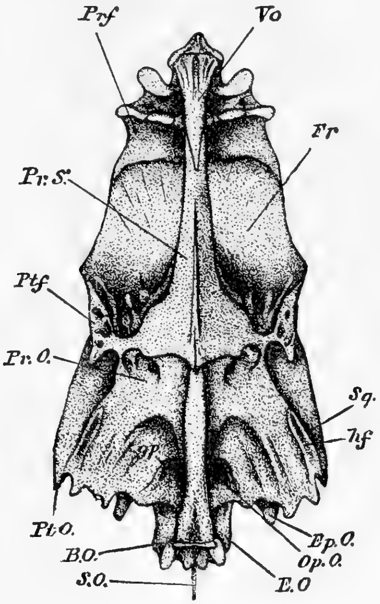

Figure 8. — The same seen from below. Letters as in the former figures.

Further, this elegantly developed element makes another curious departure from all the specimens thus far examined. It is this: where it forks over the basioccipital behind, a large foramen is found between the diverging limbs; this opening is in reality the apex of the eye-muscle canal in this fish, and consequently leads through that fossa to its continuation, which again is the longitudinal excavation on the upper side of the parasphenoid or the floor common to the orbits.

But to return to our cranium of the *Caranx* No. 11,385: we find that the anterior and horizontal portions of the frontal bone are quite transparent at their centres, while raised flutings radiate from their hinder points, forwards and outwards. The transparent areas are found to be even perforated in my specimen of *Caranx hippos*, so thin do they become. Now it will be remembered that in *Grammicolepis*, from the horizontal portion of either frontal, was developed an upturned, scroll-like projection, the free edges of the two bones meeting in the median line. There was thus formed sort of a conical prominence, the lower part and base of which was anterior, being terminated by the transverse rugosity in front, while the apex, or highest part, seized the free front margin of the supraoccipital crest. In *Caranx hippos* these vertical portions of the frontal bones are in close approximation, so that they appear to be the continuation forwards of the supraoccipital crest; the sutural traces, however, have entirely disappeared; while in the cranium of our other *Caranx*, the method of formation is very evident from the fact that the vertical frontal plates are not thus coössified, but plainly show their individual origin as well as their relation and connection with the anterior free margin of the supraoccipital crest, which is wedged in between them. (Compare Figs. 2 and 6, as well as 7 and 3.)

Pomacanthus paru has very extensive rugosities upon its frontal bones, but these latter elements are exceedingly dense and thick, as is the anterior border of the supraoccipital crest in this fish, which measures at its widest part nearly five millimetres across.

Such forms as *Pomacanthus paru* do not develop conspicuous parietal and squamosal crests; they are still less manifest in *Teuthis*. On the other hand, in the *Carangidæ* these crests constitute the most striking feature of the cranium. As already stated above, they are but feebly produced in *Grammicolepis*, though they are plainly indicated.

All the lateral parts of the cranium, made up of the hinder portion of the parasphenoid, the proötic, opisthotic, exoccipital, basioccipital, and below the squamosal line, are very much alike in *Caranx* and our unique subject, more particularly in our undiagnosed specimen of a *Caranx*. But in the latter the basioccipital enters far more extensively into the formation of the eye-muscle canal than it does in *Grammicolepis*, as in the *Caranx* we find a condition existing, as regards the opening between the hinder forks of the parasphenoid, very much the same as described for *Teuthis cœruleus*.

Upon comparing the posterior views of the crania of *Caranx hippos* and *Grammicolepis* (Figs. 5 and 9), we find, indeed, but few points of resemblance between them. The occipital crest in the former comes almost down, as it does in *Pomacanthus*, to the supero-median point of the foramen magnum. It is far above it in the latter fish. There the absence of the spreading lateral crests, seen in the *Caranx*, constitute a marked difference. Professor Poey's fish also has bony pillars developed by the exoccipitals, one being on either side of the foramen magnum. These are absent in the *Carangidæ*.

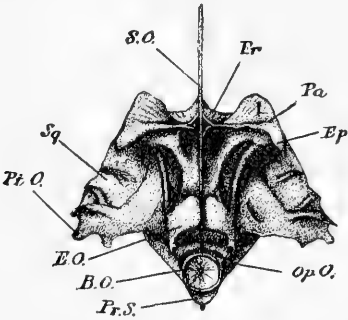

Figure 9.—Posterior view of the cranium of *Caranx hippos*, Spec. 13,561, Smithsonian Institution Collection. Life size, by the author from the specimen. Letters as before.

In *C. hippos* the facets on the exoccipitals for the first vertebra of the column meet in the middle line; these parts, however, in *G. brachiusculus* have been injured, probably during the first dissection, so that I am unable to say positively upon this point in regard to them. In *P. paru* the first vertebra of the column coössifies with the basioccipital, but this condition does not obtain in *Teuthis*. In this latter form the supraoccipital crest also fails to reach the upper periphery of the foramen magnum at its middle point.

We find that both *P. paru* and *Teuthis* have the squamosal curled downwards and forwards in the most extraordinary manner, best marked in the latter type. This is well shown in lateral view in Fig. 11, though I am not sure but that the piece there indicated by *sq* may not be a separate ossification, in which case it would be a pterotic. I would have to dissect a young fish to decide this point. These processes are very conspicuous upon posterior view, and of course *Grammicolepis* can show nothing like them.

Pomacanthus paru has another condition present, not seen in any of the other forms alluded to above. Just posterior to the proötic, and above the basioccipital and parasphenoid in the cranium of this fish, on either side, we find a subelliptical foramen, with its major axis placed longitudinally, of no inconsiderable size, through which we can easily observe the movable *otolith* (Fig. 10, *otl*).

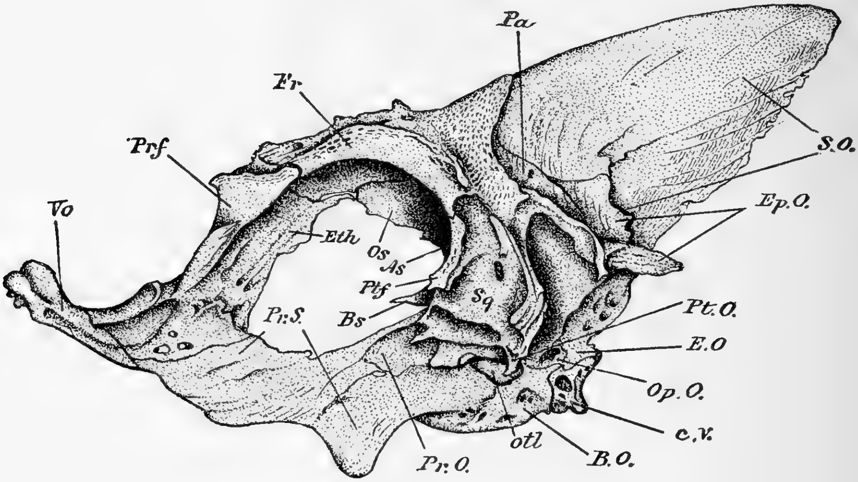

Figure 10. — Left lateral view of the cranium of *Pomacanthus paru;* life size, by the author, from specimen 12,770 of the Smithsonian Institute. Lettering as before, with *otl*, *otolith*, and *c.v.*, first vertebra of the spinal column, which is here coössified with the basioccipital.

Before concluding our comparison of these crania, we must note another point in the cranium of *Pomacanthus*, and this is, the ossified orbitosphenoids and the ethmoid meet in the middle and interorbital line, immediately beneath the frontals.

We have already fully described above, the relation of these several elements in the subject of this paper, and how any such condition is entirely absent in *Caranx*. This latter form, however, may have the ethmoid extended backwards in cartilage, which material may be missing in these dried preparations.

Now my material on this occasion will not admit of such a thing as an analysis of characters for comparison. In my opinion, without a thorough examination of the entire organization of not only the forms at my command at the present writing, but several others, such a tabulated synopsis, made up at the best from such fragmentary material, would be of but little service to us. The structure of *Seriola* taken in the present connection would come handsomely into play. *Naucrates ductor* would be another good form to examine.

From a comparison of the crania alone, I should say that the relation between *Grammicolepis* and such a fish as *Pomacanthus paru* was very distant, while its affinity with *Teuthis cœruleus* is still more remote. I should have liked, however, to have examined some of the *Salistidæ*, and perhaps glanced at one or two more of the *Chætodonts.*

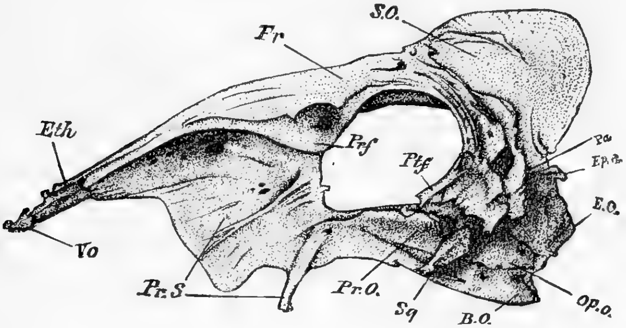

Figure 11. — Left lateral view of the cranium of a specimen of *Teuthis cœruleus;* life size. Kindly loaned the author by Professor Gill. Letters have the same significance as in the foregoing figures.

Its relationship with the *Carangidæ*, as Professor Poey predicted, is far more evident, though this, too, is extremely indirect, and many forms still unknown to us are required to demonstrate the connection.

These forms must especially show an increased density in the cranial bones; a decrease in the size of the eye and orbits; a gradual disappearance of the rugose condition of some of the flat bones of the cranium, particularly the frontals; a gradual protrusion of the snout; and finally the development of the parial cranial crests.

Of the shoulder girdle. — Although a number of the bones are lost, I am enabled at least to present a very good idea of the shoulder girdle in this fish. This is shown in Fig. 12, illustrating this paper, and if the reader happen to have at hand a copy of my osteology of *Amia calva*, published in the Annual Report of the Commissioner of Fish and Fisheries for 1883, it will be well to compare it with the figure I there gave of the shoulder girdle of *Micropterus salmoides* (Pl. 14, Fig. 35). It represents these parts as they appear in a typical teleostean fish. A glance is sufficient to satisfy us that the general form of the proscapula (*Ps*) of *Grammicolepis* is very much like that element in the Bass, differing principally in being slenderer and more sloping, and in its relations with some of the other bones. I am very sorry that I have not at hand the shoulder girdle of a *Caranx*, as it would be interesting to compare it in the present connection.

As is most usual in teleosteans, the hypercoracoid and hypocoracoid (Fig. 12, *Hyp.c.* and *Hyo.c.*) are fused together, and in the present instance, to the proscapula also. The hypercoracoid (*Hyp.c.*) is pierced by the usual foramen seen in this element among typical teleosts. The anterior projection of the hypocoracoid (*Hyo.c.*) is long and slender, almost reaching to the extremity of the proscapula (*Ps*).

It will be noted in Fig. 12 that each of these elements develop a backward, extending process, and the letters *Hyp.c.* stand between them. This recess harbors the *actinosts* of the pectoral fin, when these parts are *in situ*. These pectoral fins have been carefully wrapped up by Professor Poey in a separate little package, and I find three of these actinosts attached to each fin. It does not appear as though any of them had been lost, and I am led to expect that that is the correct number in life. They are composed of rather elementary bone, as is so much of the rest of the skeleton in this curious fish. Now the bone marked *T* in Fig. 12 I take to be the *teleotemporal*, and designated by the same letter in my drawing of the shoulder girdle of the Black Bass. On this latter form, however, as it is also in *Amia*, the teleotemporal is very loosely attached to the rest of the girdle by ligament, while here in *Grammicolepis*, it is represented (*T*) by an exceedingly long and slender bone, which has its superior extremity moulded upon the side of the proscapula *s*, and firmly attached thereto. I fail to find in any of the little packages put up by Professor Poey anything that might answer for a *lower teleotemporal*, *T*, of my Bass figure. We would, however, hardly expect to find such an addition, where the superior element proves to be so very much elongated.

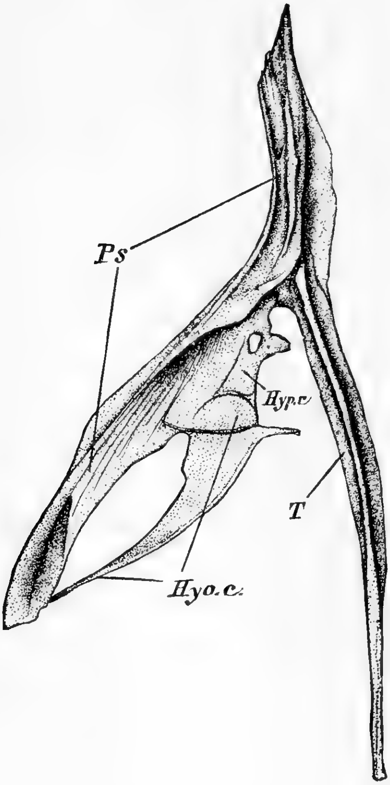

Figure 12. — Outer view of the principal elements of the left side of the shoulder girdle of *Grammicolepis brachiusculus;* life size, from the specimen. *Ps*, proscapula; *Hyp.c.* hypercoracoid; *Hyo.c.* hypocoracoid; *T*, teleotemporal. The *actinosts* are attached to the vertical border of the recess in which the letters *Hyp.c.* are contained.

Whatever we may see in the cranium of *Grammicolepis* to remind us of like parts in any of the *Carangidæ*, such resemblances are certainly not borne out when we come to compare the vertebral column of our subject with the column of a specimen of *Caranx hippos*. Figs. 13 and 14 are presented to show the extraordinary departures that take place in this part of the skeleton.

Of all the bizarre structures that pertain to the organization of fishes which it has been my pleasure to examine, I cannot recall at this moment one that presents quite so supremely a fantastic arrangement as the eleven or twelve leading vertebræ in the column of *Grammicolepis*. These are represented in Fig. 13, but I have omitted to include the first vertebra, or that one which is found between the basioccipital and the one shown in the figure with the enormous neural spine. In it the neural spine is not developed, and its connections with the skull are very intimate.

Taken in connection with Professor Poey's account of these parts, this figure obviates the necessity of my presenting a verbal description of any great length, as all the details can be plainly studied without any such additional assistance.

I am inclined to think that the bony pillars, which I described in a previous paragraph, found on either side of the foramen magnum, and completely fused with the exoccipitals, are the halves of the neural spines of this first vertebra of the spinal column. To support this view, we find by placing this vertebra in position, that their pedicles spring from the centrum as in other vertebræ, and that, moreover, the sculpturing on the external surfaces of these pillars is precisely like that upon the sides of the neural spine of the second segment of the column.

This last process is very strong, and quite firmly attached to its centrum: it curves gracefully first backwards, then upwards, in a gentle curve, as shown in Fig. 13.

The succeeding four neurapophyses are inclined well backwards, each one, as we advance in that direction, becoming shorter, more slender, and with a gradual disposition to assume the vertical attitude. This is nearly accomplished by the neural spine of the next segment following, or the seventh vertebra. Fig. 13 shows, also, the eighth, ninth, tenth, and eleventh vertebræ, and, as will be seen, the neurapophyses of these segments actually lean *forwards*. The one on the twelfth, not here shown, is nearly vertical again, while after that, they gradually incline backwards. The broken spines on the last two vertebræ of the figure I have restored by dotted lines.

Now a glance at Fig. 14 is enough to convey to us that the arrangement of these neurapophyses are entirely different in *Caranx hippos*. In this latter drawing the first vertebra is shown, and it has a vertical neural spine movably articulated with its centrum. The succeeding spines, firmly fused with their centra, gradually become slenderer, longer, and more inclined backwards, to again become nearly vertical in the mid-series of the column, to incline once more as we approach the caudal end.

In *Grammicolepis* the ventral parial apophyses at first support the freely articulated ribs with their attached epipleural appendages, but in the seventh vertebra the capitulum of the rib completely fuses with the apophysis, and as the latter lengthens, the two become indistinguishably blended. The first and second vertebræ do not support ribs, and in the third pair only, they articulate high up on the sides of the centrum, at the base of the neural arch.

Fig. 13.

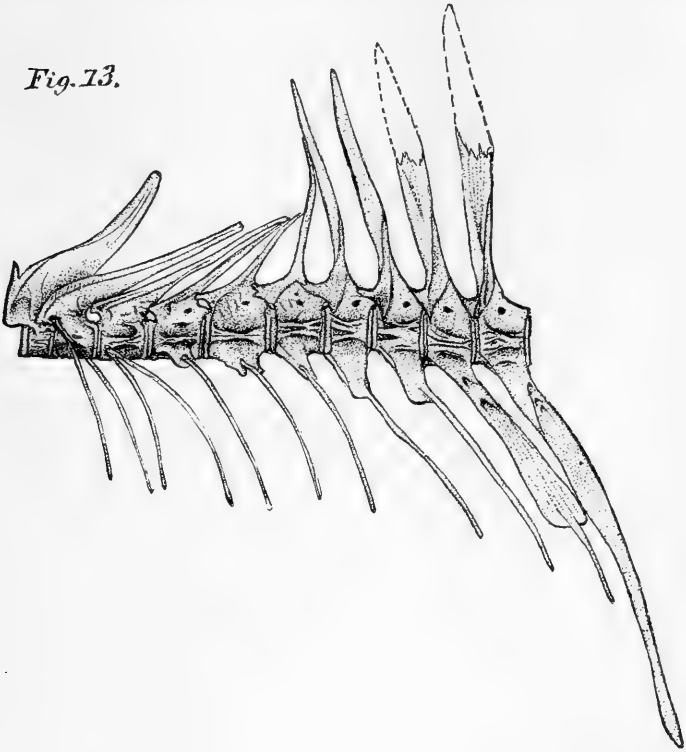

Figure 13. — Left lateral view of the anterior end of the vertebral column of *Grammicolepis brachiusculus*, the first vertebra removed; life size from the specimen.

The appendages have been lost in my specimen of *Caranx hippos*, so I am unable to say anything about them.

When we come to compare the existing differences in the latter halves of the spinal columns of these two fish, we find that they are quite as great as those shown in Figs. 13 and 14. Indeed, I can see there nothing to indicate that the forms in question have any relationship whatever and were they in the class *Aves*, I should feel justified in placing one at one end of the system and one at the other.

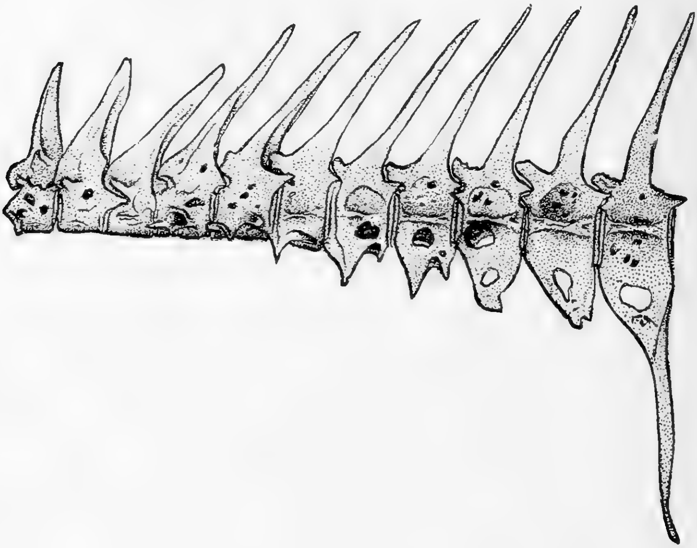

Figure 14. — Left lateral view of the first eleven vertebræ of the spinal column of *Caranx hippos;* specimen 13,561, of the Smithsonian Institution collection; life size, from the specimen.

The absence of the *hypural spine* in *Grammicolepis* has already been commented upon by Professor Poey in his memoir at the head of this article; this apophysis is quite manifest in the genus *Caranx*, as in most true teleosteans.

ON THE RELATIONS OF THE HYOID AND OTIC ELEMENTS OF THE SKELETON IN THE BATRACHIA.[1]

E. D. COPE.

THE characters of the hyoid bones of many Batrachia have been described by Dr. Parker[2] and Professor Wiedersheim,[3] and their otic elements have received much attention from the same authors. In both fields, however, much remained to be done. The otic elements of the Salientia have been extensively described by Parker, but no especial attention has been devoted to those of the Urodela by either author, except incidentally to other objects. In the present paper I desire to call attention to these elements in the Urodela, and to contribute thereby to the general theory of the morphology of the inferior arches of the skull. Whether light be thrown on the vexed question of the homologies of the suspensors of the inferior arches of the skull or not, it is desirable to see what this intermediate group of vertebrata contributes to its solution. I go over the types seriatim, commencing with the lowest.

GANOCEPHALA.

In the genus Trimerorhachis (Cope) there appears to be a distinct opisthotic bone in addition to the intercalare, as in the fishes. In form it is much like the proötic, but in reversed position; its anterior thin edge forming a suture with the posterior thin edge of the latter. The two together form on their inferior surface a spout-like groove, which extends outwards,

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[1] Read before the United States National Academy of Sciences, April, 1888. Abstract published in *American Naturalist*, 1888, p. 464.

[2] *On the Structure and Development of the Skull of the Common Frog*, Transactions of the Royal Society, London, 1870, p. 137; *On the Structure and Development of the Skull in the Batrachia*, loc. cit., 1875, p. 601; *On the Structure and Development of the Skull in the Urodelous Amphibia*, loc. cit., 1876, p. 529.

[3] *Das Kopfskelet der Urodelen; Morphologisches Jahrbuch*, 1877, pp. 352, 459.

terminating at the narrow truncate extremity of the two bones. At the base of the opisthotic, and between it and the parasphenoid, is situated the fenestra ovale. This is closed by the extremity of a columella auris, whose proximal part at least may be homologized with the stapes, since no other element corresponding with the latter is visible. The columella is then directed outwards, backwards, and upwards to the notch which is formed between the adjacent borders of the intercalars and suspensorium, where it terminates without having displayed any segmentation. This notch, which is present in all the Permian Batrachia known to me except Acheloma, may have been occupied by a membranum tympani, and that the Ganocephala had, like the Salientia, distinct external organs of hearing, thus differing from the Proteida and Urodela.

RHACHITOMI.

The only genus in which I have observed ossicula auditus is Zatrachys (Cope). Here the parts resemble nearly those described in Trimerorhachis. The columella[1] is curved outwards and backwards, and terminates at the notch external to the *os intercalare*, which was, I suspect, covered by a membranum tympani as in the Salientia.

PROTEIDA.

In Necturus (Pl. XXII., Fig. 1) the stapes is osseous and has its columella directed abruptly forwards. It articulates with a corresponding process of the squamosal bone, which extends posteriorly to meet it from the posterior bone of the latter. The quadrate part of the suspensorium of the mandible is extensively osseous. The distal extremity of the ceratohyal is not articulated with anything, but is connected with the quadrate by the hyosuspensorial ligament, and with the angle of the mandible by the mandibulo-hyoid ligament, as has been pointed out by Huxley.[2]

In Proteus the relation of the stapes to the squamosal is similar in general to that in Necturus, but the connection

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[1] *Transactions American Philosophical Society*, 1886, p. 290.

[2] *Proceedings Zoölogical Society*, London, 1874, p. 192, Pl. XXIX. Professor Huxley does not describe or figure the relation of the stapes to the squamosal bone.

between the anterior process of the former and the posterior process of the latter is accomplished by an intervening bit of ligament. The quadrate cartilage is little or not ossified in Proteus. The ceratohyal is not articulated at its distal end, but the latter is attached to the squamosal by two ligaments, the superior and inferior hyosuspensorials (Pl. I., Fig. 2). The attachment is higher up than in Necturus, as the ceratohyal is longer.

URODELA.

Trematodera.

In Cryptobranchus the columella of the stapes is directed forwards, and terminates in a cartilaginous stem. This is articulated with the suspensorium of the mandible at its proximal part, at the line of junction between the squamosal bone and the quadrate cartilage. The latter is not ossified. The distal end of the ceratohyal is not prolonged, and it is connected with the distal half of the posterior border of the quadrate cartilage by a wide hyosuspensorial ligament. This ligament is interrupted by a subtriangular cartilage, the hyosuspensorial cartilage.

I have not examined the genus Megalobatrachus.

Amphiumoidea.

In Amphiuma the stapes is lateral in position, and its short columella is directed outwards. It is continued as a cartilage to the truncate posterior apex of the osseous quadrate bone, with which it articulates by a suture. The quadrate is extensively osseous. The distal extremity of the ceratohyal is long and free, and is connected with the middle of the posterior border of the quadrate by an elongate hyosuspensorial ligament.

Apoda.

Merrem *Pseudophidia* De Blainville. *Gymnophiona* Müll.

In Typhlonectes (compressicaudus) the stapes is osseous, and is lateral in position. Its columella is short, and is directed forwards, and is connected by ligament with the posterior border of the quadrate. The distal end of the ceratohyal is entirely free from the manibular suspensorium.

In Dermophis (mexicanus) the stapes is lateral in position, and is osseous. Its columella is robust and osseous, and extends forwards, abutting against the posterior border of the quadrate, with which it forms a close movable articulation. The quadrate is completely osseous, and is freely articulated proximally with the cranium. The ceratohyal is free, and not connected with the suspensorium.

Pseudosauria.

De Blainville; *Myctodera*, J. Müller.

This extensive group is most conveniently considered by families.

In the Amblystomidæ the columella of the stapes is replaced by the stapedius muscle. This is directed posteriorly, and away from the suspensorium. The ceratohyal is short distally, and its extremity is articulated to the distal part of the posterior border of the quadrate cartilage. The quadrate cartilage is ossified distally, but not proximally.

In the Plethodontidæ the stapes has the same character as in the Amblystomidæ, except that in some specimens a slender cartilaginous process is seen to be directed towards the quadrate cartilage in *Plethodon glutinosus* and *Spelerpes ruber.* This is probably the persistence of the larval condition of both this family and of the Amblystomidæ. In the larva (Pl. I., Figs. 7, 9) the columella of the stapes is directed forwards, and is connected with the proximal part of the quadrate cartilage by a short cartilaginous rod. In the larva of *Chondrotus tenebrosus* the connection is completed for a short distance by ligament. Thus the larvæ of these two families present the character of the mature members of the suborders Trematodera, Amphiumoidea, and Pseudophidia. The quadrate in the Plethodontidæ is ossified in its proximal part only. The ceratohyal has its distal extremity curved forwards, and articulated by distinct suture with the quadrate cartilage or bone; in *Plethodon glutinosus* it is inserted in a fossa (Pl. I., Fig. 14).

In Desmognathidæ the characters are as in Plethodontidæ.

In Salamandridæ the position of the stapes is as in the previous families, but the relations of the extremity of the ceratohyal are as in the larvæ of those animals, or as in the

Amphiumoidea. The extremity is connected with the quadrate bone by a hyosuspensorial ligament. In Salamandra the ceratohyal and the ligament are of moderate length.

In the Pleurodelidæ the arrangement is as in the Salamandridæ. In some of the species the ceratohyal is greatly elongate. In the *Diemyctylus torosus* the free extremity of the ceratohyal extends to the inferior line of the occipital condyle, carrying with it the hyosuspensorial ligament. This ligament is elongate, and arises from the proximal part of the posterior border of the quadrate cartilage (Pl. II., Fig. 3). In the *D. viridescens* this peculiarity is carried still further. The ceratohyal extends to the lateral crest of the exoccipital, and is received into a fossa of its inferior surface, as has been pointed out to me by my friend Dr. E. E. Galt. The hyosuspensorial ligament extends from the proximal part of the quadrate cartilage beneath the ridge mentioned to the apex of the ceratohyal (Plate II., Fig. 4).

TRACHYSTOMATA.

In Siren the stapes is osseous. Its columella is replaced by the stapedius muscle, which extends posteriorly. It has no connection with the suspensorium. The quadrate is cartilaginous. The ceratohyal is large and is much produced distally. It is connected with the posterior part of the quadrate, the exoccipital, and the stapes by a wide hyosuspensorial ligament. It is inserted on the anterior side of the ceratohyal opposite the quadrate, and is interrupted by a hyosuspensorial cartilage, as in Cryptobranchus.

SALIENTIA.

Laurenti. *Anura* Duméril.

The stapes in this order resembles that of the Urodela. It is an oval disc without distinct process, and gives insertion to a stapedius muscle near its centre. But this order differs totally from the other existing orders, in the presence of a chain of *ossicula auditus*, which extends from the border of the stapes to the dermal membranum tympani. There are three of these, which have been named the interstapedial, the mesostapedial, and the epistapedial. The interstapedial is a bony style with a cartilaginous basis which originates alongside of the anterior border of the stapes, in a shallow cup-like expansion which abuts against the cranial wall. The shaft is cylindric. The mesostapedial is a cartilage which is attached to the narrow extremity of the interstapedial much as an anther of a flower is attached to its filament. The proximal part of this element is shorter than the distal, and is connected with the superior part of the quadrate by a ligament, the mesostapedial. The distal part is deflected at a strong angle to the interstapedial, and is frequently somewhat spatulate by reason of an expansion distally. Its external face is flat and is applied to the internal face of the epistapedial. The latter is a cartilaginous disk which closes the tympanic chamber externally. It fits like a lid on the cartilaginous annulus tympanicus, which extends beyond it all round. The annulus tympanicus is a thin and wide cartilaginous ring with a thickened margin, which is not continuous, but is interrupted at its superior outline. This interruption is occupied by the distal end of the interstapedial, and the proximal part of the mesostapedial. The distal part of the latter extend vertically across the median foramen. These structures have been described and figured by Parker (l.c.), who has found them to be generally similar in all the families of the order. I have examined all the principal types, and give figures of them in the genera Xenopus, Discoglossus, Stereocyclops, Scaphiopus, Bufo, Hyla, and Rana (Pl. II., Figs. 7–12; Pl. III., Fig. 1).

The ceratohyal is slender at the point of connection with the skull. This is just in front of and external to the cartilaginous base of the interstapedial. It is continuous with the cranial wall in some species. It is involved, just distal to its origin, in the annular *ligamentum tympani*, which forms the posterior wall of the tympanic chamber; but it has no structural connection with it.

The development of the Saliential skull has been studied by various authors, especially by Dugés, Huxley, and Parker. I have examined series of *Rana virescens*, *R. clamata*, and *R. catesbriana* for the purpose of determining the homologies of the auricular bones of this order, by a study of their development. It has been shown that the ceratohyal cartilage is, for the greater part of the life of the tadpole, articulated with the quadrate cartilage, first on its inferior, and then later on its posterior face. Professor Parker believes that it is a dismemberment of the distal half of the third ventral arch of the skull, and that the superior half of the same becomes fused later with the second arch, thus forming the quadrate cartilage as it exists in adult Salientia. On approaching maturity, the ceratohyal leaves this connection, and is attached to the base of the skull as above described. My observations coincide with those of Parker in that the ossicula auditus do not appear until a later period of larval life in the genus Rana. But they appear before the ceratohyal has abandoned its articulation with the quadrate cartilage. They then arise as follows: the epistapedial occupies from the first its normal position as a disk of cartilage at the flexure of the quadrate cartilage. The interstapedial, on the other hand, arises as a bud from the normal position of its base, and gradually extends itself anteriorly. It early appears as cartilage with a short, free membranous extremity. The latter becomes the mesostapedial cartilage. These elements gradually elongate until they reach the epistapedial. For a time they reach no farther than the quadrate cartilage, and they rest on it, as in the Proteida and larvæ of Urodela.

CONCLUSIONS.

From what has preceded, the following conclusions may be derived: —

First. The relations of the stapes to the quadrate cartilage or bone are of two types in the Urodela. The one is possessed by the Proteida, Trematodera, Amphuimoidea, and Pseudophidia; the other by the Pseudosauria and Trachystomata. The larval structure in the Pseudosauria, and inferentially in the Trachystomata, is identical with the structure characterizing the adults of the other division. This is confirmatory of the opinion which I have expressed[1] as to the origin of the genus Siren. This is to the effect that Siren is an animal which is descended from a land salamander, and that its immediate ancestor became aquatic again at a comparatively late period of geological time. My opinion was at first suggested by the condition of the branchiæ in very young animals, where they are functionally abortive, and do not become respiratory organs until later in life, the largest animals having the best developed gills. The characters

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[1] *American Naturalist,* 1885, p. 1226.

of the stapes confirm this view, since they are those of land salamanders, as distinguished from those of aquatic habitat.

Second. There are also three types of relation between the ceratohyal arch and the skull. In the one there is no connection between the two, as in the Pseudophidia. Secondly, the connection is by ligament. This is seen in Proteida, Trachystomata, and all Pseudosauria except the Amblystomidæ and Plethodontidæ. The last two families embrace the third type, in which the ceratohyal is articulated by suture with the quadrate. This last type is the most specialized, since the larvæ of those families display the connection between the ceratohyal and the skull similar to that seen in the types first and second. Thus the Salamandridæ, which are superior to the Plethodontidæ in their osseous carpus and tarsus, and opisthocœlous vertebræ, have the hyoid connected with the skull, as in the larvæ of the latter.

Third. At a stage in the history of the development of the Salientia, the relations of the stapes and of the ceratohyal to the skull are the same as in a transitional stage of the Urodele family of Plethodontidæ; or, taken separately, the relations of the stapes are those of Proteida, Trematodera, and larval Pseudosauria, while the relation of the ceratohyal is as in adult Plethodontidæ and Amblystomidæ. This is when the interstapedial cartilage connects the stapes with the posterior face of the quadrate cartilage, and where the ceratohyal articulates with the posterior face of the quadrate at its distal part.

Fourth. It is not probable that the epistapedial forms an integral part of a single primitive element, which includes the other *ossicula auditus*, as it originates independently of the interstapedial and mesostapedial.

Fifth. The interstapedial and mesostapedial do not, at any time in the history of the development of the genus Rana, form any part of the ceratohyal or meckelian ventral arches. As the incus and malleus of the Mammalian *ossicula auditus* are segmented from the proximal parts of these arches, embryology indicates that they are not homologous with the ossicula of the Salientia. From this point of view, the latter form a special line of development, distinct from that displayed by the Mammalia, unless the developmental record has been greatly falsified by cænogeny. From the embryological standpoint, it follows that the *ossicula auditus* of the Batrachia Salientia must be excluded from the discussion of the homologies of the Mammalian ossicula.

Sixth. But the characters of the Ganocephala and Rhachitomi permit the following reflections, since the latter order is the one from which the Salientia derive their descent. The existence of a well-developed columella auris, which is unsegmented, in the former orders, apparently like that of the Lacertilia, suggests that the segmentation seen in the Salentia is a specialization of later origin. This columella has also the position of the proximal part of the ceratohyal in the adult frog and the larval salamander. As the position of this element in all but the youngest tadpoles is a result of cœnogeny, it may be inferred that the *ossicula auditus* of both the Rhachitomi and the Salientia represent the separated proximal end of that arch, and hence be truly homologous with the incus of the Mammal. The probability that this is the case is increased by the character of this element in the Pelycosaurian genus Clepsydrops,[1] — where the columella extends to the cranial wall, leaving the stapes to one side. This is exactly comparable to the relation between the interstapedial and the stapes seen in the Salientia, except that the two elements are not actually connected, as in Clepsydrops. Palæontology then modifies the evidence from embryology, and renders it probable that the columella auris of the Permian genera, the interstapedial, and the incus are homologous elements, and originated by segmentation from the proximal end of a ventral cranial arch, probably the ceratohyal.

Seventh. It follows from what has preceded, that the condition of the representatives of the *ossicula auditus* in the Urodela is one of degeneration.

Eighth. It becomes probable, but not certain, from the position of the tympanic disk in the Rhachitomi, at the proximal base of the quadrate bone, that the epistapedial cartilage has originated as a segmentation from the proximal extremity of the quadrate cartilage, and is therefore truly homologous with the Mammalian malleus. This is, however, nothing more than a probability. For a considerable part of the material described in the preceding pages I am indebted to the United States National Museum.

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[1] See *Proceedings American Philosophical Society,* 1884, p. 41, Pl. I., Fig. 2.

EXPLANATION OF PLATE XXII.

The relations of the quadrate, stapedial, and hyoid apparatus. In Figs. 1, 3, 9, 14, 15, and 76, the squamosal bone has been removed.

Figures twice natural size, excepting 1, 3, 4, 7, and 8, which are natural size, and 10, 11, and 12, which are three times natural size.

FIG. 1. *Necturus maculatus;* squamosal removed.

FIG. 2. *Proteus anguinus.*

FIG. 3. *Cryptobranchus allegheniensis;* the middle of the squamosal removed, the extremities remaining.

FIG. 4. *Amphiuma means; a,* from behind.

FIG. 5. *Typhlonectes compressicaudus;* from the Belize.

FIG. 6. *Dermophis mexicanus;* with the quadrate bone turned up, exposing its inferior face, and that of the quadrato jugal; 4*a*, the same with the quadrate in normal position. From Mexico.

FIG. 7. *Chondrotus tenebrosus;* larva 250 mm.

FIG. 8. *Chondrotus tenebrosus;* adult.

FIG. 9. *Amblystoma tigrinum;* larva; squamosal removed.

FIG. 10. *Amblystoma punctatum;* adult.

FIG. 11. *Hemidactylium scutatum.*

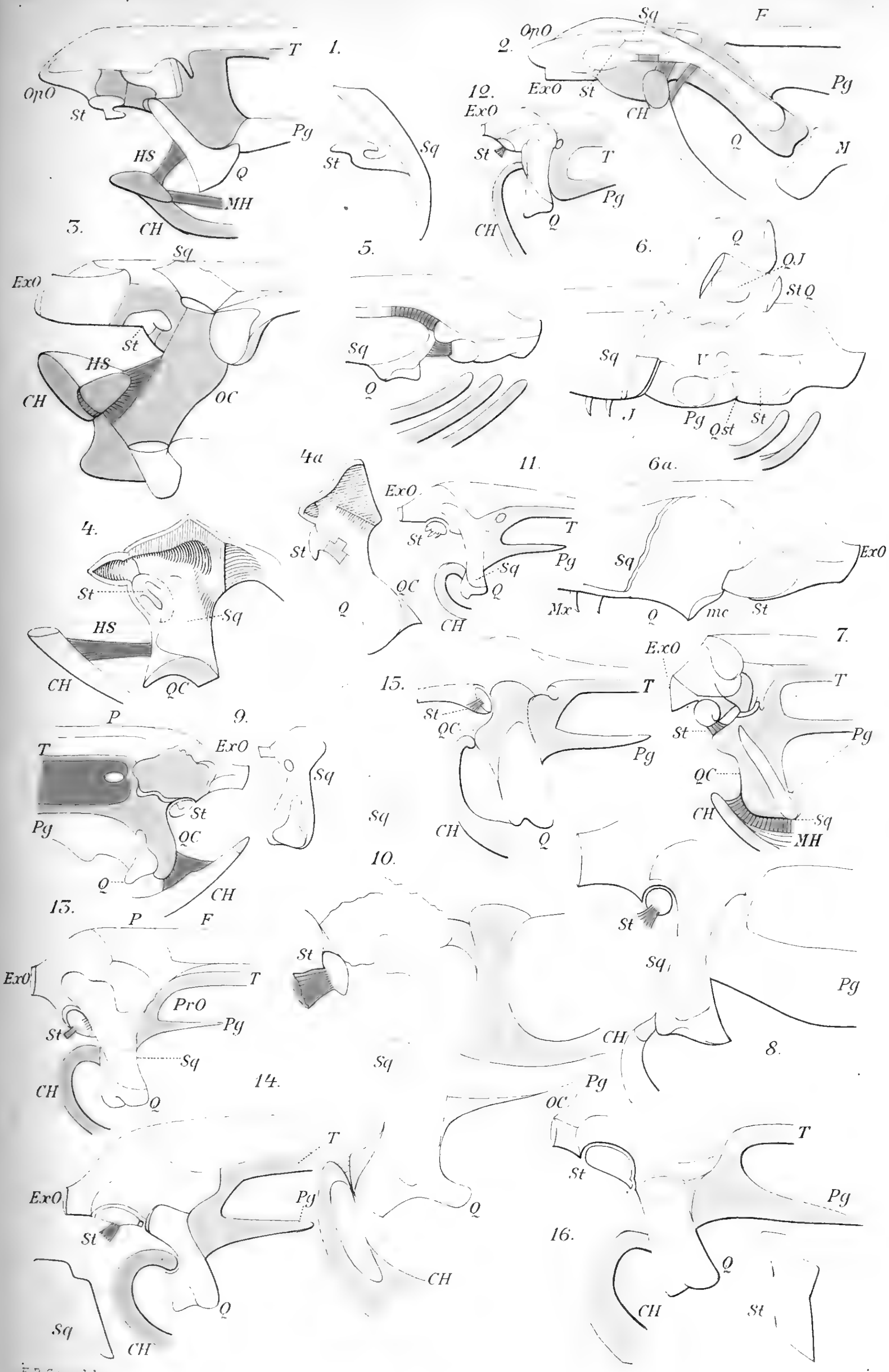
FIG. 12. *Batrachoseps attenuatus.*

FIG. 13. *Gyrinophilus porphyriticus.*

FIG. 14. *Plethodon glutinosus;* squamosal removed.

FIG. 15. *Autodax lugubris;* squamosal removed.

FIG. 16. *Spelerpes ruber;* squamosal removed.



E. D. Cope del.

Lith Anst. v Werner & Winter, Frankfurt a/M

EXPLANATION OF PLATE XXIII.

The relations of the quadrate, stapedial, and hyoid apparatus in Urodela and Salientia. Figures twice natural size, with separate details larger.

FIG. 1. *Desmognathus nigra; a,* stapes separate and enlarged, the squamosal in place.

FIG. 2. *Salamandra maculata* $\frac{2}{1}$; the squamosal separated.

FIG. 3. *Diemyctylus torosus,* squamosal removed; *a,* separate squamosal.

FIG. 4. *Diemyctylus viridescens,* three times natural size; the squamosal removed. 2*a,* the squamosal, external side; *b,* apex of ceratohyal, with hyoquadrate ligament.

FIG. 5. *Siren lacertina* $\frac{1}{1}$; squamosal in place.

FIG. 6. *Discoglossus pictus,* partly posterior view; *a,* ear bones, and origin of ceratohyal, enlarged.

FIG. 7. *Bufo lentiginosus americanus,* the squamosal removed; *a,* the squamosal separate.

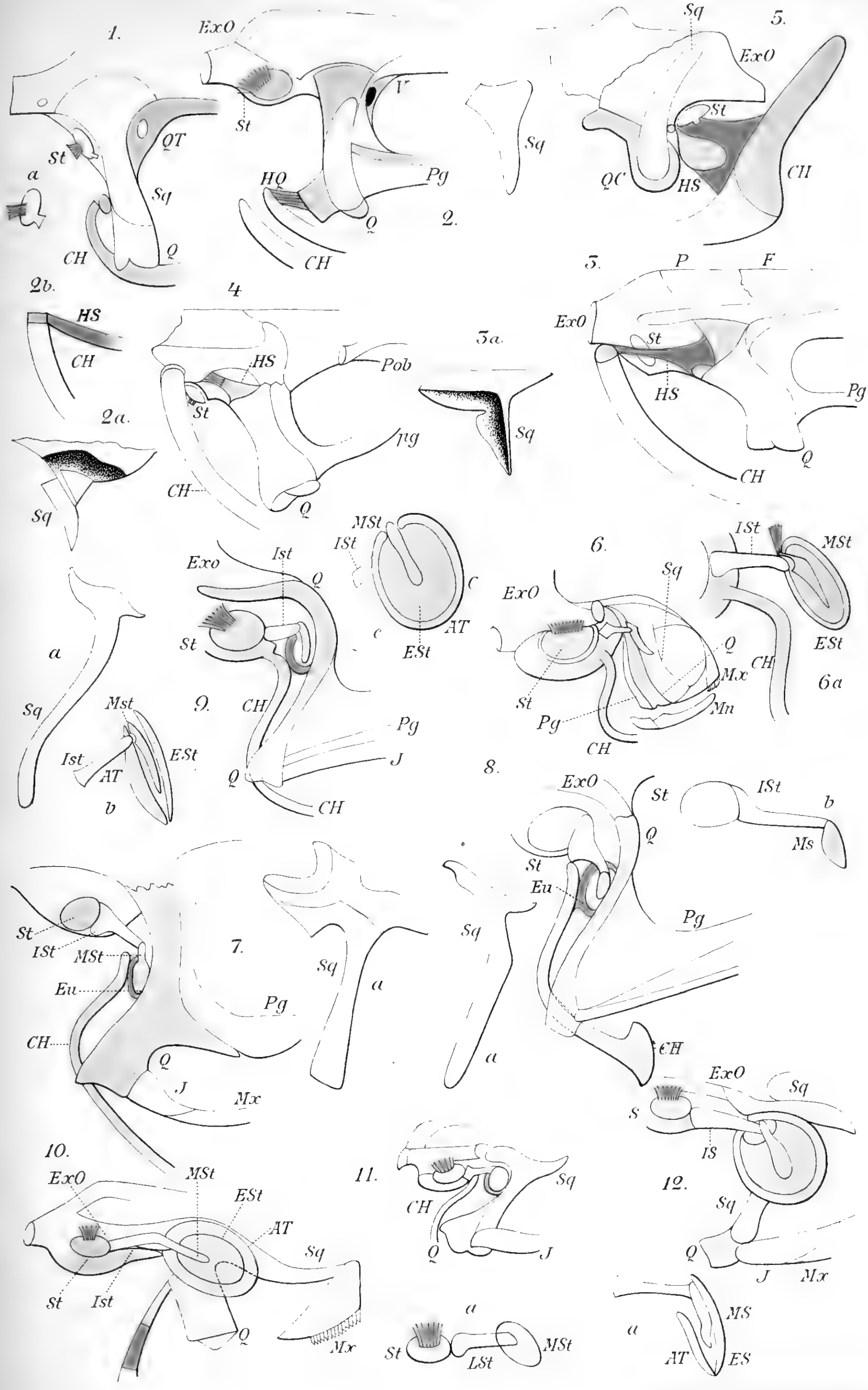
FIG. 8. *Scaphiopus hammondii,* the squamosal removed; *a,* the squamosal; *b,* the ear bones.

FIG. 9. *Hyla gratiosa,* the squamosal removed; *a,* the squamosal; *b,* the ear bones and cartilages in profile, the cartilages of the tympanum divided by vertical section; *c,* the ear bones and cartilages undivided, external view.

FIG. 10. *Xenopus calcaratus,* partly from behind, with squamosal in place.

FIG. 11. *Stereocyclops incrassatus,* squamosal in place; *a,* stapes and ear bones and cartilages.

FIG. 12. *Rana pretiosa,* squamosal in place; *a,* ear bones and vertically divided cartilages.



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Lith. Anst. v. Werner & Winter, Frankfurt a/M.

EXPLANATION OF PLATE XXIV.

FIG. 1. *Rana virescens*, adult, × 2; *a*, squamosal bone; *b*, ear bones without epistapedial.

FIG. 2. *Rana virescens*, larva with hind legs, and developed fore legs concealed, the skull × 2; *a*, the hyoid apparatus from below, × 4.

FIG. 3. *Rana catesbeyana*, larva further advanced than that represented in Fig. 2; showing the first appearance of the auditory cartilages at *ST* and *AT*.

FIG. 4. *Trimerorhachis insignis* of the Permian bed of Texas; part of skull from below, showing columella at *st.*; natural size.

FIG. 5. *Trimerorhachis insignis* basicranial axis from below, without stapes; natural size.

FIG. 6. *Zatrachys serratus*, upper posterior part of skull from above; natural size.

FIG. 7. *Zatrachys serratus*, inferior view of external part of posterior part of skull of individual represented in Fig. 6; showing columella.

EXPLANATION OF LETTERING.

A.T., Annulus tympanicus; *B.O.*, basioccipital; *C.Br.*, Ceratobranchial; *C.H.*, Ceratohyal; *C.Tr.*, Cornu trabeculi; *E.S.*, Epistapedial; *Eth.*, Ethmoid; *Ex.O.*, Exoccipital; *F.P.*, Frontoparietal; *Hm.*, Hyomandibular; *H.Q.*, Hyosuspensorial ligament; *Int.*, Intercalare; *I.St.*, Interstapedial; *J.* Jugal; *Ll.*, Lower labial cartilage; *Mk.*, Meckel's cartilage; *Mx.*, Maxillary; *Mn.*, Mandible; *M.S.*, Mesostapedial; *O.C.*, Occipital condyle; *P.*, Parietal; *Par.*, Parasphenoid; *Pg.*, Pterygoid; *Pm.*, Premaxillary; *Pob.*, Postorbital arch; *Q.*, Quadrate; *Q.C.*, Quadrate cartilage; *S.*, *St.*, Stapes; *Sq.*, Squamosal; *Sl.*, Superior labial cartilage; *T.*, Trabeculum; *Ty.*, Position of Membranum tympani.

Cartilage, blue; ligament and membrane, yellow; bone, white.

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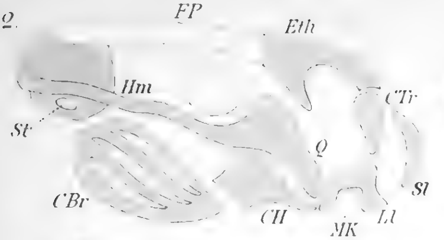

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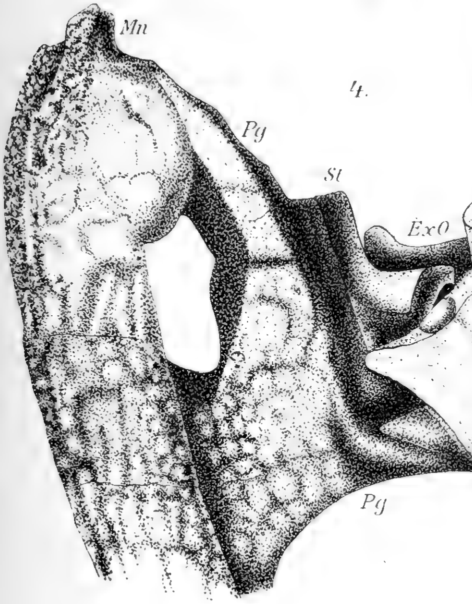

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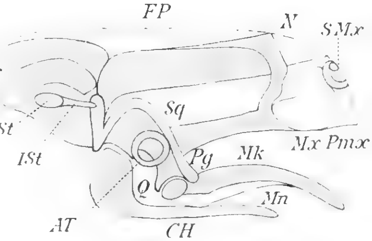

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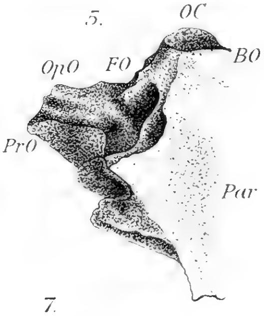

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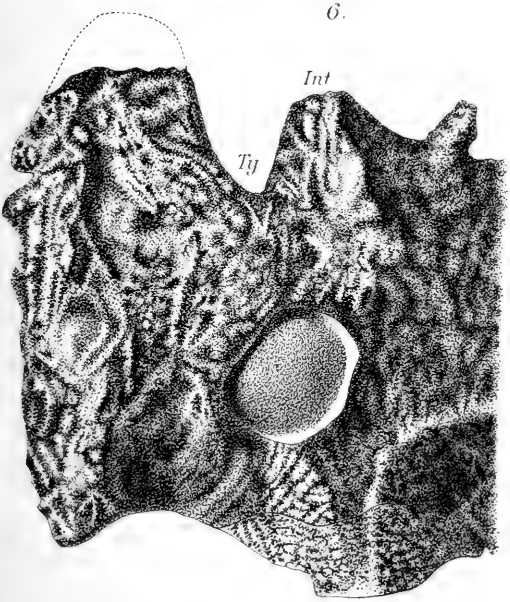

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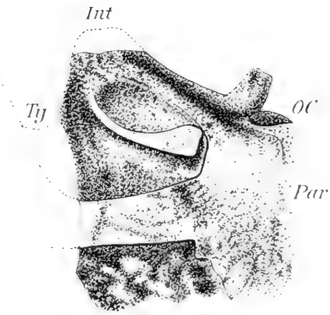

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ON THE AFFINITIES OF *APHRIZA VIRGATA.*

[*Based upon a comparative study of its skeleton.*]

R. W SHUFELDT, M.D., C.M.Z.S.

DURING the latter part of November, 1885, Surgeon Thomas H. Streets of the United States Navy, then naturalist of the United States Exploring Steamer "Patterson," kindly sent me a skeleton of the Surf-bird, the subject of the present memoir; and again in August, 1886, the same distinguished officer forwarded me a fine pair of skeletons of this species, representing both sexes, adult. All of this material was collected by Dr. Streets in Alaska, and I am indebted to him also for skeletons of *Charadrius squatarola* and *Arenaria melanocephala*, the former taken in San Francisco Bay, the latter at Port Townsend, Washington Territory, and placed at my disposal for comparison with the skeletons of *Aphriza.*

As additional material for the osteological comparisons the writer here proposes to make, I find I have at my command two skeletons of adult specimens of *Hæmatopus bachmani* (Nos. 13,636 and 13,637), belonging to the Smithsonian Institution of Washington; and finally, in my own cabinet several skeletal preparations of the *Charadriidæ* and *Tringeæ*, all of which will be of assistance in the work now in hand.

Aphriza virgata constitutes but another one of those forms around which centres so much that is of interest to the systematic ornithologist, owing to the fact that even after more than a mere superficial examination we discover not a little in its anatomy that is inclined to puzzle one, when called upon to pronounce as to its kinship with more or less nearly related groups or types.

Of the first skin that he ever examined, Audubon wrote: "The remarkable bird here represented, which in form and size bears a considerable resemblance to the Knot [*Tringa canutus*], was procured by Mr. Townsend on the shore of Cape

Disappointment, and proved to be a female."[1] And Dr. Coues remarks, in defining the genus, — "General character of plumage, in its pattern of coloration and seasonal changes, as in *Tringeæ.* One species, a remarkable, isolated form, perhaps a plover, and connecting this family with the next by close relationships with *Strepsilas,* but with hind toe as well developed as usual in Sandpipers, and general appearance rather sandpiper-like than plover-like. *Aphrizinæ* might go under *Hæmatopodidæ* next to *Strepsilas;* or, perhaps better, *Aphriza* and *Strepsilas* might together constitute a family Aphrizidæ, next to, but apart from, *Hæmatopodidæ.*"[2]

Two years after the publication of the doubts here candidly expressed by this eminent authority, the American Ornithological Union issued its official Check-List, wherein the arrangement proposed was adopted; and we find the *Aphrizidæ* with its one species, *A. virgata,* including the sub-family *Arenariinæ,* the Turnstones, standing between the Plovers on the one hand, and the Oyster-catchers on the other,[3] an arrangement which probably meets with the views of the majority of avian taxonomists of the present time.

Believing that under these circumstances a full account of the skeleton of *Aphriza* will prove an acceptable contribution to the literature of the family, as well as a useful work to the better understanding of the osteology of the *Limicolæ* generally, it was in view of this that I undertook the task. So far as my material at hand will admit of it, the study will be made thoroughly comparative, and in the end it may go to show that, for osteological considerations at least, the position selected in the system by ornithologists may be the most natural one to create for our Surf-bird, or a somewhat different light may be cast upon the problem; in any event we are satisfied that more light in such matters is a thing most to be desired, and this alone morphology has the power of affording.

The Skull. — When we come to submit the skulls of adult specimens of certain true *Tringeæ* to moderately prolonged maceration in water, we invariably find that the premaxillary bone detaches itself, as does the dentary of the mandible, leaving in

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[1] *Birds of America,* Vol. V., pl. 228.

[2] Coues, E, *Key to North American Birds,* 2d. ed., p. 605. 1884.

[3] *Check-List of North American Birds,* pp. 160–166. New York, 1886.

the first case the long, thread-like extremities of the palatines and median processes of the nasals freely projecting forwards, and in the latter instance, a similar condition of the mid-ramal elements of the lower jaw. *Tringa*, *Actitis*, and others have their skulls behave in this manner, under similar circumstances, and it is quite characteristic of them; whereas, on the other hand, macerate the skulls as long as we may, no such detachment ever takes place in the Surf-bird, nor in Turnstones and Oyster-catchers, nor in such forms as *Gallinago* and *Philohela*. Indeed, this peculiar feature seems to be restricted to the more typical Sandpipers, and it is worthy of our notice that in *Aphriza* it never happens, and I may add that one never observes it to be the case in any of the Plovers.

Aside from this fact, the general *facies* of the form of the superior osseous mandible in *Aphriza*, carried back as far as the rhinal chamber and frontal region, is more as we find it in such a species as *Actitis*, for example, or some of the genus *Tringa*, than it has any semblance to either *Arenaria*, or much less *Hæmatopus*. Even when we come to compare the individual parts, this assertion holds true, including in the observation the extensive outline of the triangular aperture, on either side, of the external nares; and the superior ends of the fronto-maxillary processes of the nasals not overlapping, mesiad, the outer and juxtaposed margins of their premaxillary processes; which latter condition obtains both in the Turnstones and in Oyster-catchers. Again, in *Aphriza* we note that the extremity of the superior mandible in the skull is somewhat tumefied, and marked over with minute pits, as we find it to be in *Gallinago*. This character is absent in such a form as *Actitis* and other Sandpipers, nor do we find it to be present in *Charadrius*, *Arenaria*, and *Hæmatopus*.

In Bachman's Oyster-catcher (*H. bachmani*) the superior osseous mandible is about seven centimetres long, the remainder of the cranium being something over 3.5 cm. long, measured along the median line. Taking these same distances in the Black Turnstone, we find the first to be 2.5 cm., and the latter 2.3 cm.; but barring this difference in proportion between beak and cranium in these two species, the superior osseous mandible in the Turnstone is almost the perfect miniature of that part of the skull in an Oyster-catcher. We are to note, however, one other difference, and that is, in *Hæmatopus* the anterior extremities of the palatines fuse across the median interspace much further back than they do in the Turnstone, but essentially, as I say, the plan of these parts in the two birds in question is the same, and quite different from the corresponding structure in *Aphriza.* Plovers in this particular seem to stand between the Surf-bird and *Arenaria.*

Taking next these several skulls upon their superior aspects, and comparing them with the same view in *A. virgata* (Fig. 1), we find that the latter bird again agrees with such a Sandpiper as *Actitis macularia,* or with such a species as *T. minutilla.* The cranium being very narrow in the frontal region between the superior orbital margins, while the vault of the brain-case is externally rounded, smooth, and ample, being occasionally marked in some of the Sandpipers by a median, longitudinal furrow.

In both, the lacrymals jut out about in the same proportion, and much in the same manner, as they do in a Turnstone. *Aphriza* and *Actitis* show scarcely any tilting upwards of the superior orbital peripheries, a feature so very conspicuous in *Charadrius squatarola ;* less so in *Hæmatopus,* and again quite absent in *Arenaria.*

Oyster-catchers exhibit their strong larine affinities in their prominent out-jutting lacrymal bones, and still more in their deep and sharply defined glandular fossæ over the orbital roofs. These latter depressions are but fairly well marked in Turnstones, while in *A. virgata,* again agreeing in this respect with most, if not all true *Tringeæ,* they are entirely absent.

Passing to the basi-posterior aspect of the cranium, the Surf-bird is seen to possess, in common with all North American *Limicolæ,* a well-marked supraoccipital prominence, which shows one on either side, the supraoccipital vacuities being larger in this species than they chance to be in any Sandpiper at my hand. Plovers have them next largest, they being very minute in *Arenaria,* and not present in any of the skulls of the genus *Hæmatopus* before me, although these latter have large supraoccipital prominences.

In this last-named genus, too, the "occipital area" is sharply defined by a very strong and raised crest, of a subcircular outline. This crest is very much mellowed down in *Charadrius ;*

more manifest again in the Turnstones, in which genus the occipital area is proportionately much smaller; and finally, in Sandpipers and *Aphriza* the crest is present only as a raised line, which in them also bounds an occipital area of a subcircular outline, the extremities of the boundary line terminating, on either side, at the apex of a paroccipital process.

Most limicoline types have the plane of the foramen magnum nearly coincident with the horizontal plane; and so it is in all the skulls of the species now before me. But the outline of this great foramen of the occiput differs considerably in the several genera, being perfectly cordate in the Surf-bird, with the prominent posterior apex standing well in between the pair of vacuities of the supraoccipital prominence, which condition is enjoyed by most *Tringeæ*; while in *Arenaria* and the Plovers there is a slight tendency for this aperture to become rounder, its circularity becoming quite evident in *Hæmatopus.* In all these species, the condyle of the occiput is proportionately very small in each and every species, it being of a hemispherical form, and unnotched.

So in general pattern, taken as a whole, the basi-posterior aspect of the cranium is more nearly alike in *Aphriza* and any true tringine form; while in Turnstones the approach is towards the Oyster-catchers. And Plovers in this particular seem to maintain sort of a mid-position between the two latter groups. *Hæmatopus* is notorious for the restricted confines of its basi-temporal area at the base of the cranium,[1] and this space is never very wide and deep in any of the *Limicolæ.*

Figure 3 of my drawings in the plate shows the skull of *A. virgata* upon direct lateral view, and here we have a number of points to examine. First, it will be observed that the *pars plana* is of a quadrilateral outline, thoroughly ossified, and with its superior and inferior borders not in contact with either the orbital roof above or the maxillary bar below. The out-jutting *lacrymal* sends down a spicula of bone, which diminutive process turns backwards to have its lower end anchylose with the *pars*

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[1] Had not the writer already fully figured the skeleton of the Black Oyster-catcher (which figure and its description has been accepted for publication by the *Journal of Anatomy* of London), I should have taken pleasure in presenting drawings of it in the present connection, as it constitutes a wonderfully interesting form for comparison in this way with species now under consideration.

plana, on its anterior aspect at a point below, and to the inner side of its externo-superior angle. I am thus particular in describing in detail the point of attachment of this extremity of the descending process of the lacrymal, for the reason that in some Sandpipers it is found to be attached to the very angle above referred to, while just before arriving there it sends forwards another small, pointed spine, the extremity of which latter is free, and directed somewhat inwards towards the rhinal chamber. No little variety, however, is to be met with in this particular among the *Tringeæ*, and in such a form as the solitary Sandpiper (*R. solitarius*) the free end of the lacrymal is attached at a point corresponding to the site of its attachment in *Aphriza*. With the true Plovers the case is still different, for in them the *pars plana* is quite small and with rounded angles, while the lacrymal has a long, slender, descending process terminating in a free point below, and likewise has the anterior-projecting spine coming off from a mid-point of its continuity.[1]

Arenaria has a large square *pars plana*, and in this form the lacrymal soon fuses at its lower end with the supero-external angle of the osseous lamina in question; while in *Hæmatopus* the *pars plana* is again found to be small, and the lacrymals very large, with their descending processes thick and strong, being fully anchylosed with the outer border of the *pars plana*, and projecting a short distance below that plate, though not arriving at the maxillary bar.

From all this I should say, then, that in *Aphriza, Arenaria*, and most true Sandpipers the *pars plana* and the lacrymal bones were more or less alike, having much the same relation to each other; but in Plovers and Oyster-catchers these structures are essentially very different; not only do they differ with each other, but with the aforesaid mentioned types, and in a manner set forth in the last paragraph.

Limicoline birds are notorious for the large vacuities that occur in their interorbital septa, rendering that osseous partition in the vast majority, if in not all the species, a very deficient bulwark between the orbits. *Hæmatopus* has it most entire, while in *Aphriza*, the Turnstones, Sandpipers, and Plovers, it commonly

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[1] For an excellent figure of this arrangement of the lacrymal, see Huxley's figure of the enlarged skull of *C. pluvialis* in his paper, "On the Classification of Birds." *P.Z.S.*, 1867, p. 427, Fig. 7, L.

presents two large deficiencies, or often one imperfectly divided by a backward-extending remnant of the septum springing from the mesethmoid (Fig. 3).

In the Sandpipers (*Actitis*) the entire anterior wall of the brain-case is, mesiad, wonderfully lacking in bony support; on the other hand, in the black Oyster-catcher the foramina for the first pair, as well as for the optic nerves, are entire and completely encircled by bone. All the species that we have thus far mentioned in this memoir possess a straight and slender *infraorbito maxillary bar* of nearly uniform calibre throughout.

Figure 1 of the plate will show the peculiar orbital processes of the *quadrates* in the Surf-bird, and indeed they are nothing less than unusually enlarged, thin, and compressed lamina of bone, which in no small degree contribute to the floor of the orbit on either side. We also find the two remaining apophyses of a quadrate to be more than commonly large and stout, and each of these bones has a double mastoidal facet; two mandibular facets, the inner one being as good as two in *Aphriza*, though less markedly divided in Turnstones, Oyster-catchers, or Sandpipers; and finally, a proportionately large pterygoidal facet situated upon the internal aspect of the bone, just above mandibular articulation. Few departures are to be detected from this almost common pattern of the quadrate among the *Limicolæ;* where, too, I may add, this bone is always found to be perfectly pneumatic, as is the greater share of the skull itself among these shore-birds. Still confining ourselves to the lateral aspect of the skull, we are to note the long, spicula-form, sphenotic process possessed by *Aphriza*, and the less conspicuous and bifurcated squamosal apophysis; both of which features are far better marked in this species than they are in any of its allies now before me. Turnstones show quite deeply marked *temporal fossæ* that lack something less than a centimetre of meeting posteriorly over the supraoccipital prominence. *Hæmatopus* also show these, but here they are strictly confined on either side to the squamosal region, and do not encroach in the slightest degree upon the posterior aspect of the cranium. *Charadrius* likewise faintly displays the same feature, a feature which is so prominently seen in any of the skulls of the *Laridæ* and their kin.

Careful search through my material fails to detect the presence of such fossæ, either in the Surf-bird or among the Sandpipers. *Actitus* has a skull as free from any such depressions in its temporal region as the veriest Thrush that ever lived, and the same remark fully applies to our least Sandpiper and others of its genus. Another interesting point to notice in the cranium of *A. virgata* is the marvellous degree to which a tympanic cavity is exposed, as well as the external opening of the Eustachian tube within it. These parts seem to depend upon the large quadrate anteriorly, and the somewhat arching paroccipital process behind, for their protection, in so far as any osseous surrounding defence is concerned.

This condition obtains in varying degree in the allied forms we have under consideration; it being notably the case in Turnstones and in *Hæmatopus,* though Plovers and *Tringeæ* are but little better off in this respect, perhaps the former of these last being the better provided of them all.

And now, finally, turning to the nether aspect of the skull in *Aphriza,* we are at first struck with the diminutive size of its pair of *pterygoid* bones. These are short, compressed from above downwards, sharpened all along their anterior margins; while behind they are characterized by strong basipterygoid processes, which articulate in the usual fashion with the facettes designed for them at the base of the sphenoidal rostrum.

In the black Oyster-catcher, a pterygoid is no longer than the mandibular aspect of the corresponding quadrate is wide, and this statement holds true for the other skulls we have been examining in connection with *Aphriza.*

For the Plovers the pterygoids are well shown in Professor Huxley's figure of *Charadrius pluvialis,*[1] although they are comparatively much smaller in such a species, for instance, as *C. squatarola,* or others of our North American *Charadriidæ.*

Upon comparing the *palatines* of *A. virgata* with those bones in the allied forms before us, we meet with several excellent distinctive characters, especially when we include in this comparison the maxillo-palatines. In Plovers, Sandpipers, Turnstones, and Oyster-catchers, the postero-internal angles or heads of the

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[1] *Ibid. P. Z. S.,* 1867, p. 427, Fig. 6. These bones are also represented in my figure of the base of the skull in the Mountain Plover (*Æ. montana*); *Jour. of Anat. and Phys.* London, October, 1883, Pl. V., Fig. 3, *pg.,* where their relatively small size can at once be appreciated.

palatines, each turns outward as it articulates with the anterior end of the corresponding pterygoid; nor do these palatine heads meet each other in the medium plane. With this common feature, *Aphriza* agrees; but when we come to examine the postero-external angles of these bones, we find them obliquely truncated in our subject, or at least the hinder ends of the palatines themselves thus obliquely truncated, forming obtuse postero-external angles, which angles are rounded off in *Actitus*, *Charadrius*, and in *Arenaria*, while in *Hæmatopus* a moderate, backward-extending and rounded process is found at their site. In this latter species, too, the internal and external laminæ of a palatine bone are very conspicuous, as they are, though less so, in the Surf-bird, Spotted Sandpiper, and the Black Turnstone. Plovers have this character much subdued. Mesiad, the superior and at the same time, internal borders of the palatines, beyond the "pterygoidal processes," along the rostrum, come in contact with each other in all of the enumerated species; and in all completely fuse anteriorly with the hinder limbs of the vomerine bifurcation. Coalescence, again, is most thorough in all these forms among the anterior ends of the palatines and those parts of the maxillaries and premaxillaries with which they come in contact, upon either side (Fig. 2). From this description, then, of the palatines, it is clear that *A. virgata* possesses them in a form essentially its own, and further that the pattern varies in all the allied groups or species.

Not so, however, is this altogether the case with the *maxillo-palatines*. One of these in *Aphriza virgata* is seen to be a shell-like process; extending backwards, concave externally; the reverse being the case upon its mesial aspect; perforated by a few foramina; and finally, *not united along its inferior border with the palatine of the same side* which extends beneath it. *Charadrius* also possesses a maxillo-palatine almost identical with this, and in the last-named feature, the true Sandpipers also agree, but in these latter birds the bone is much narrower and more curved.

Passing to the Oyster-catchers and Turnstones, a very different state of affairs is to be met with; for in *Hæmatopus*, for instance, we find a maxillo-palatine to be quite a thick, laterally compressed and unperforated lamina of bone, which completely fuses with the corresponding palatine for the *entire length of its inferior* *margin*, appearing in the adult to be a part of the palatine itself. A similar arrangement is to be found in *Arenaria*, — so that in this character, Turnstones and Oyster-catchers agree, while the Surf-bird, Plovers, and *Tringeæ* are fundamentally alike; in the first, the maxillo-palatines have, in the adult individual, coalesced with the palatines, each on its own side; while in the three last-mentioned families the maxillo-palatines are independent and freely projecting processes.

Aphriza agrees with all the allied types before us, in having a long, slender *vomer*, its posterior limbs anchylosing with the palatines behind, and a median carination extending for its entire length along its nether aspect. With the exception of *Hæmatopus*, the bone in all is pointed anteriorly, and in the excepted genus it is at that end distinctly bifurcated.[1]

In the form of its *mandible*, *A. virgata* substantially agrees with the Plovers and Sandpipers. The upturned, slender process at the angle is well developed, and the inturned ends of the articular cups are quite prominent, showing the usual single pneumatic foramen at each extremity. Two vacuities occur in either ramus, a small surangular one, and a long, semi-closed, splenial one, the sides of the jaw in this region being vertical and rather deep. The symphysis is rounded beneath, concaved above, and equals in length about one-fifth the length of a ramus. In the Black Oyster-catcher the symphysis equals more than a third of the ramus, and is scarcely at all excavated above, while it is decidedly wedge-shaped below. *Arenaria* also has a deep symphysis to its mandible, but here again it is concaved above and rounded beneath, and the larger of the two ramal vacuities is represented by a very open, subelliptical foramen.

Among the more ordinary types of existing birds, the *hyoidean apparatus*, as we know, presents but few differences when we come to compare it for the various families. Our subject forms no exception to this statement, and little need be said here in reference to this part of the skeleton in *Aphriza*. We find the arches alluded to to be very delicately constructed, and have the basibranchials in two separate pieces, the second one being very short and finished off behind in cartilage. The cerato-

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[1] Here we have a departure from the rule laid down by Huxley, who has said that in *Schizognathous* birds, "the vomer, sometimes large and sometimes very small, always tapers to a point anteriorly." *P. Z. S.*, 1867, p. 426.

hyals largely coalesce, but the ossification proceeds but a limited distance into the glosso-hyal, which latter element in the adult is found to be in cartilage only. Thyro-hyals are notably slender and of considerable length; they, too, being posteriorly tipped with cartilage throughout the life of the individual. Most Sandpipers possess a hyoidean apparatus similar to the one I have just described for *Aphriza;* and, indeed, no material difference can be detected for the allied species from other groups.[1]

Upon carefully examining the special ossifications of the ear in a skull of *A. virgata,* I fail to detect anything worthy of detailed record; the form of the *stapedial plate* and the coössified shaft of the *columella* have much the same pattern as we find these parts in the Fowl, and so clearly drawn for us by Parker.[2] Dr. Streets, in preparing my skeletons of *Aphriza* for me, threw away the eye-balls, so I am unable to make any observations here upon the sclerotal plates in this species; they have also been lost from my skeletons of *Hæmatopus,* the Turnstones, and Plovers.

This completes what I have to say here in reference to the comparative osteology of the skull and its associate parts of the skeleton in *Aphriza virgata,* and such deductions as may be drawn from the study the writer proposes to defer making until the closing paragraphs of the memoir are arrived at, when the skeleton as a whole, in this species, will be passed in review, and the proper comparisons made with the others we have been considering.

Remainder of the Axial Skeleton. — Since the days that anatomists first took to counting the total number of vertebræ in the spinal column of any of our existing *Carinatæ,* there have been difficulties and differences upon that point; and as to the differences, these have been but multiplied by the many attempts that have been made to state exactly the num-

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[1] Unfortunately the hyoid arches of both my specimens of *Hæmatopus bachmani* have been lost, and I am unable to add, by way of comparison, anything about them here. I am inclined to believe, however, that if any essential difference is to be hereafter detected in these arches for adult specimens of various representations of the *Limicolæ,* it may be that some form will show a fusion of the first and second basibranchials; but I look for nothing more than some such a difference as this, and even it may never be found to exist.

[2] Parker, W. K., *Morphology of the Skull,* p. 258, Fig. 74, *m.st.* and *st.*

ber of cervical vertebræ, and the number of true dorsals, in any particular species. In the case of the total count for the vertebræ in any adult bird of the kind alluded to, the trouble is with the pelvic sacrum, and the skeleton of the tail. In nearly every example it is almost impossible to decide with certainty as to the number of vertebræ that have been incorporated in its fusion; while in the case of the tail, the pygostyle is the stumbling-block, for sometimes in representatives of the same species this bone in one individual will thoroughly appropriate to itself a terminal caudal vertebra, that will perhaps remain free in the other, thus making an additional segment for a bird of the same species. Then, again, it is pretty well agreed that when we come to define the line between cervical and dorsal divisions of the column, we look chiefly to the ribs for assistance; yet these are by no means to be always relied upon; as sometimes, in the same species, an additional pair may remain free at the further end of the cervical region, or an additional pair (always at the anterior part of the dorsal division) may connect with the sternum by a pair of hæmapophyses. So that one observer might state that the first pair of free ribs in a certain species of bird were to be found upon the 13th cervical vertebræ, while another observer, equally careful, finds an individual of the same species wherein it is the 14th cervical that has the leading pair of free ribs. Thus it is that confusion and doubt creeps into the work.

After having paid no little attention to the osteology of birds for more than ten years, now, I am fairly convinced that there is but one safe or very nearly safe method of arriving at the total number of vertebræ in the spinal column of any particular species of the class, and to do it we should have the prepared skeletons of the young of the species, two, or, better, three, of them, made just at the time when fusion is about to take place among the vertebræ, which eventually go to form the pygostyle in the adult, and when the vertebræ composing the pelvic sacrum are all still individualized. Then the count can be made with certainty, and we should not fail to have by us at the time several skeletons of the adult of the same species for comparison. Finally, our remaining difficulty, it is evident, cannot be settled in any such manner, and the only course left to pursue here, is to state, if possible, *the general rule* and *the noted* *exceptions.* For instance, we may say in a certain species, it has been found as a general rule that free ribs occur upon the 13th and 14th vertebræ, and that upon the 15th, the ribs connect with the sternum by costal ribs, but examples have been found in the same species where free ribs were found upon the 12th, 13th, and 14th vertebræ; or again, a specimen of the same species showed free ribs on the 12th and 13th vertebræ, while the ribs on the 14th connected with the sternum. This is by no means a fanciful description, as I have studied cases quite like it, and it only goes to show the utter hopelessness of laying down hard and fast lines in describing the cervical and dorsal divisions of the vertebral column in existing birds. On the other hand, I am inclined to believe that if the *total number* of vertebræ be counted in the skeleton of the chick of any particular species, the number will be found to be quite constant. Now I believe, after carefully re-counting the vertebræ in the skeleton of the tail in the Mountain Plover (*Æ. montanus*), there should be a quære placed after the number I have given in my memoir upon the osteology of that species,[1] as I believe it should be seven, *not* counting the pygostyle; further, I am inclined to think I made another miscount, for some reason, in my specimen of *Hæmatopus*, and too many vertebræ have been mentioned as forming the skeleton of its tail in another paper of mine.[2]

At the present writing I have not at hand the immature skeletons of any of the species we have here under consideration, and consequently am unable to carry out the suggestions made in the foregoing paragraphs, so I can candidly admit that the number of vertebræ given below as found in the sacra of the birds there enumerated must be taken *cum grano salis;* although I will add that I counted them to the best of my ability: the process can often be assisted by holding the pelvis up to a strong light, with the *dorsal* aspect towards you.

In my female specimen of *A. virgata*, the "epipleural appendages" are present upon the pair of free ribs on the 15th vertebra, the reverse being the case in the skeleton of two males

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[1] *Ibid.*, p. 97.

[2] Shufeldt, R. W., "Osteology of *Numenius longirostris*, with notes upon the Skeletons of other American *Limicolæ.*" *Journ. of Anat. and Phys.* London. Vol. XIX., October, 1884, pp. 71, 72.

of the same species. *Charadrius squatarola* seems to have the usual cervical vertebræ (6th to 9th inclusive) modified beneath for the carotid canal; while in a Killdeer before me, the series so modified includes the fifth cervical. Only the *free* caudal vertebræ have been counted in the subjoined "Table," omitting in every case to include the pygostyle; a bone that may include several more, and *perhaps vary for the species* here given.

TABLE.

SPECIES.	Number of cervical vertebræ without free ribs.	The first cervical vertebra that has free ribs.	The second cervical vertebra that has free ribs.	The third cervical vertebra that has free ribs.	The first vertebra that has ribs which reach the sternum by costal ribs.	Number of vertebræ that possess ribs which reach the sternum by costal ribs.	Pairs of sacral ribs (they do not reach sternum).	Number of vertebræ in pelvic sacrum.	Number of free caudal vertebræ.	Total number of free prepelvic vertebræ.	Total number of vertebræ in column exclusive of pygostyle.	Carotid canal in following cervical vertebræ (inclusive).
Aphriza virgata	13	14	15	. .	16	6	1	13	8	21	42	6th to 9th
Charadrius squatarola .	13	14	15	. .	16	6	1	12	7	21	40	6th to 9th
Actitis macularia	13	14	15	. .	16	6	1	12	7	21	40	6th to 9th
Hæmatopus bachmani .	12	13	14	15	16	6	1	14	7	21	42	6th to 9th
Arenaria melanocephala	13	14	15	. .	16	6	1	13	8	21	42	6th to 9th
Rhyacophilus solitarius	13	14	15	. .	16	6	1	12	7	21	40	6th to 9th

We find nothing especially noteworthy in the vertebræ of *Aphriza virgata*, as they in a general way are fashioned upon the usual ornithic pattern of those bones among ordinary birds. The *axis*, and the three cervical vertebræ that follow it, are especially conspicuous for their prominent neural and hæmal spines, and their postzygapophyses, which latter extend upwards, outwards, and backwards, as strong processes in the second and third cervicals. This last feature is not so manifest in *Aphriza* but becomes more so in *Arenaria*, and in *Hæmatopus* arrives at its maximum development, for in this species the postzygapophyses of the axis and the vertebra next behind it are nearly as lofty as the great neural spines upon these vertebræ, giving them the appearance of being tricornuted upon their dorsal aspects. Oyster-catchers have comparatively short parapophyses in the cervicals, while in both the Surf-bird and in Turnstones these are quite long and spicula-form in the fourth, fifth, sixth, and seventh vertebræ; and these last species differ with *Hæmatopus,* in that in this bird the vertebræ of the entire column are unusually large in proportion to the size of their owner. Free ribs in all the species before us possess both capitula and tubercula; the leading pair being of diminutive size, and gradually increasing as they near the ribs of the dorsal region. The last pair usually do not develop unciform appendages, though they may do so, as in the skeleton of my female Surf-bird, and an Oyster-catcher before me. In the dorsal region only the first two, or at the most, three, leading vertebræ possess hæmapophyses, while ossified metapophyses link their transverse processes together above. *Aphriza* has the neural spines of its dorsals very low, they being more lofty in the Turnstone, and still more so in *Hæmatopus.* Plovers and *Tringeæ* have them of a medium height. We find few or no especial distinctive differences in the true dorsal ribs of the several species before us, to render any aid as pointing to near or remote kinship in the case of any two species compared. Agreeing with the majority of limicoline birds, these parts are for the most slender, curved as usual, and rather long, with uncinate processes that do not completely anchylose with the several ribs to which they belong.

Elsewhere, as I have already said above, I have presented figures of the *pelvis* of the Black Oyster-catcher, and it can be said here now that this bone in *Hæmatopus* very markedly differs from the pelvis either of *Aphriza* or of *Arenaria.* Indeed, in some respects, the pelvis of an Oyster-catcher reminds us not a little of the pelvis in *Gallus bankiva;* it lacks, however, the propubic spine, and the antero-median borders of the ilia do not fuse with the sacral crista. Further, it is noted for having a certain solidity and thickness of the several bones that compose it, quite in keeping with the other parts of the skeleton of this powerfully built bird. It differs with the general plan of the pelvis in *Aphriza* (Fig. 21), and in the Turnstones, in that in *Hæmatopus* the ilium forms a ledge, overhanging to some extent the ischium and the ischiadic foramen; the postpubis is far separated from the lower ischiadic margin, and is truncated almost immediately after passing the ischium behind; finally, anchylosis is very strong between all the several bones making up the pelvis in the Oyster-catcher, so that prolonged maceration does not tend to separate them.

One skeleton of *Hæmatopus* at my hand shows a curious dilatation of the latter third, or less, of the postpubis of the *left* side, not present in any other specimen, nor upon the opposite side of the same individual. All these points and characters are very different in the pelvis of the Surf-bird, wherein this bone is remarkable for its breadth, and for being, as it were, flattened out in the vertical direction, — shallowed; its sides narrow, and ilia more or less spread. As among Plovers, and most or all Sandpipers, it shows a double row of interapophysial foramina down the sacrum (Fig. 21); and the anterior ends of the ilia are subtruncated and embellished with a delicately raised rim, nearly always to be seen in limicoline birds. Between the hinder ends of ilium and ischium, a rounded notch occupies the entire margin of the bone, which notch in *Hæmatopus* is angulated. Postpubis is in contact, more or less, for its entire length with the lower border of the ischium above it; and is carried beyond for some little distance to a pointed extremity, much the same being the case in the Turnstones.

The ischiadic foramen is of considerable size, and of a subelliptical outline; this vacuity being unusually large in an Oyster-catcher, and such a species as the Killdeer Plover.

Without, then, further entering upon a fuller discussion of minor details, although they have all been carefully noted and weighed by the writer, I would state that in so far as the *Hæmatopodidæ* are concerned, the pattern of the pelvis in that group, as represented by the bone from the skeleton of *H. bachmani*, is of quite a different style from the pelvis of either *Aphriza* or *Arenaria.* That when we come to study the pelvis of *A. virgata*, and compare it with the bone in allied types, we discover that notwithstanding the fact that it exhibits many characters held in common by the limicoline forms generally, still it is impressed with a character of its own, being proportionately broader and shallower than the generality of either charadrine or tringine pelves. It is most nearly approached by the pelvis of a Turnstone, while this latter bird shows in its pelvis a marked shading towards the style of the bone in the Plovers.

Again, *Actitis* and *Ægialitis vocifera* possess pelves almost identically alike in their general form; and in both these species the postpubis is separated by more or less of an interval from the lower margin of the ischium of the same side, along the middle of its continuity.

Figure 20 of the Plate shows the form upon lateral view of the pygostyle in *A. virgata,* and that is not far departed from by the representatives of nearly affined *Limicolæ.* In Oyster-catchers it varies, because in them the ultimate caudal vertebra usually is coalesced with the bone, giving it the different shape. The Surf-bird and its allies show the diapophyses of the caudal vertebræ to be spreading in the first few leading ones; then in mid-course they become shorter and bend downwards; then long and more flaring again, to terminate by an aborted one just before coming to the pygostyle. The ultimate two or three may develop bifid hæmapophyses, which anteriorly stand between the joints of the centra as chevron bones; this feature is well marked in *H. bachmani.*

Oyster-catchers have the neural spines of the caudal vertebræ notched in front, while *Aphriza, Charadrius,* and the majority of the *Tringeæ* possess these apophyses as plain points.

That time-honored standby of avian skeletologists, the *sternum,* presents among the birds we have been noticing in this memoir but few insignificant departures from a common pattern, except in the cases of *R. solitarius* and *Actitis.*

Aphriza has the bone (Figs 12 and 15) doubly notched on each side posteriorly, the outer notches being fully twice the dimensions of the inner ones, — the outer pair of xiphoidal processes thus formed having a tendency to flare outwards; otherwise, the outline of the sternal body is quadrilateral, being much concaved above and correspondingly convexed upon its pectoral aspect. Either costal border shows six hæmapophysical facettes for the costal ribs, while extensive "costal processes" of a triangular outline rear above these in front.

The manubrium is small and sessile, being sharp beneath and blunt above, and directly between coracoidal grooves, thus preventing the coracoids in the articulated skeleton from infringing upon each other; the reverse being the case in Oyster-catchers and *Arenaria,* wherein these bones are in contact posterior to the manubrium, when the former are *in situ.* Returning to the sternum of *Aphriza,* we are to note its ample carina, which extends the entire length of the sternal body, being thickened for the upper two-thirds of its anterior border, sharpened below, and concaved throughout. Along its lower margin a thickened rim defines its edge, which is outlined by a long, gentle convexity from carinal angle in front to mid-xiphoidal process behind (Fig. 12).

Viewing the bone upon its pectoral aspect, a muscular line — the *interpectoral muscular line* we will call it here — extends, on either side, from the boundary of the costal fossa beneath, to the inner of the pair of xiphoidal notches behind, to the mesial edge of the same. This line occurs sharply defined in both Plovers and Oyster-catchers, where it is similarly drawn, as it is likewise in a Turnstone.

Arenaria has a sternum, which, excepting the fact of its being a size smaller, is the perfect counterpart of the bone in *A. virgata*, though in the latter species the sternal keel seems to be comparatively a trifle deeper in proportion.

When I published my *Osteology of Numenius longirostris*, I therein stated that the sternum to a skeleton of the Spotted Sandpiper (*A. macularia*) possessed two notches upon either side, a large outer pair and a very small inner pair. Those skeletons were prepared and the species diagnosed by a very incompetent man, and at the present writing I am not prepared to vouch for the correctness of the statement. I have had to regret many times since, the confidence I placed in the identification of the skeletons which went to make up the collection of the vertebrate series in the Museum and Library of the Surgeon General's Office of the Army at Washington; they were the cause of a number of oversights creeping into my avian osteology in early days, which now are being corrected in my more recent papers. So I am inclined to believe that the *four-notched sternum of Actitis* may be a specimen from the same category; it was "on file" in the same institution. At any rate, we have before us now an excellent skeleton of *Actitis* of my own collecting, and it possesses but a *pair of notches* in its sternum, otherwise the bone has the general pattern of the *Limicolæ* at large.

In a few days *The Auk* for July (1888) will be issued, and in there, in a letter to its distinguished editors, I point out the fact that the Solitary Sandpiper is another species which has but a pair of notches in its sternum, and suggest that its old genus, *Ryacophilus*, be restored for it (at the present writing it is a subgenus of *Totanus*). But the majority of *Tringeæ*, as for example, all the true representatives of the genus *Tringa*, have the "four-notched" sternum, and the fact that *Actitis* and *Ryacophilus* have each only a pair of notches, may be of more significance in so far as the true *affinity* of those two species is concerned, than some of their external characters (that are so very subject to change from minor causes), but which have alone been relied upon thus far by the systematist, to classify them.

Finally, then, the fact may be broadly stated, that with respect to the sterna of *Aphriza* and *Arenaria*, they are to all intents and purposes the miniatures of that bone as we find it in *Hæmatopus bachmani;* and although this is very interesting, the circumstance goes to prove, in the light of other skeletal characters of these species, we would utterly fail were we to rely upon this bone alone as any indication of family, or much less, generic, affinities.

All the sterna that the writer has examined from the skeletons of North American *Limicolæ* were non-pneumatic bones, and if it is ever found to be otherwise, we must believe that it is the exception. In a specimen of *Tringa minutilla* in my collection, the bone is so thin that a large perforation occurs on either side of the keel in the sternal body, and one through the keel itself, high up in front.

Speaking of the pneumaticity of the skeletons of the several species we are here considering, I am strongly inclined to believe that the skull is the only part in any of them where air gains access to the interior of the bones, and as a rule to no very great extent, comparatively, there.

Turning our attention next to the *shoulder girdle* (Figs. 11, 16, and 17) in *Aphriza virgata*, we meet with a *scapula* having much the form that that bone assumes among the Shore Birds, generally, being shaped a good deal like the blade of a miniature cimeter, and when *in situ* in the articulated skeleton bearing the usual relations to the clavicle and coracoid of its own side. A *coracoid* is conspicuous for its short, sub-cylindrical shaft; its head being tuberous and much crooked over towards the median plane, while the sternal extremity of the bone is not only thickened from before, backwards, but much expanded lateral-wise, showing at its outer angle a prominent lamelliform process, compressed in the antero-posterior direction, and curved somewhat upwards. *Os furcula* typifies the U-shape form of the bone, and has in all *Limicolæ*, that the writer has ever studied, the merest apology for a hypocleidium, below. Its limbs are of nearly uniform calibre throughout, being slightly heavier above than below, and moderately compressed transversely for their entire lengths. Their heads, that is, the free ends of the clavicular limbs, are much elongated, and when articulated *in situ*, reach far back to the heads of the scapulæ. Viewed upon direct lateral aspect, it will be noticed that the *os furcula* is very considerably, though gracefully, curved in the antero-posterior direction, the convexity of the curvature being to the front.

In *Hæmatopus* the shaft of a coracoid is pierced by a small oval foramen, from before, backwards, and just below the scapular process, that does not occur in either the Surf-bird or among Turnstones.

Now, aside from the exceptions of this foramen, and differences as to the method of articulation of the coracoids with the sternum, already alluded to, and finally, the mere matter of size, — the description of the shoulder girdle here rendered for *Aphriza*, will apply almost equally well to the shoulder girdles of the *Tringeæ*, the Turnstones, and the Plovers, and no doubt to many other Shore Birds. Were we to depend for characters, upon which to base distinctive differences, on the shoulder girdle alone in *Aphriza*, *Arenaria*, and a true Plover of a corresponding size, we should surely be disappointed, for the bones of this arch do not offer them in the genera enumerated.

Of the Appendicular Skeleton.

The Pectoral Limb. — The majority of the bones of this part of the skeleton in *Aphriza* are shown by my drawings in the Plate, as already stated above. The corresponding parts for *Hæmatopus* and Plovers have been given in other connections.

It will be seen that in the *humerus* of our Surf-bird, both "radial crest" and "ulnar tuberosity" are strikingly well developed, while the articular humeral head between them is rather small (Figs. 18 and 19). The pneumatic fossa is an extensive excavation, although the bone itself is not pneumatic. As to the shaft, it shows but little curvature, is smooth, and subcylindrical in form. At the distal extremity of the bone, a conspicuous "ectocondyloid process" is to be observed; and at the extreme end, the oblique and radial tubercles, or condyles, stand out with more than their usual boldness, a condition which is enhanced by the fact that just above them there exists a fossa of some considerable depth. When the bones of this limb are articulated, and the arm tightly closed, the head of the radius accommodates itself to this latter depression at the distal end of humerus. Upon the anconal aspect of this extremity of the bone, we also find strong and powerfully impressed grooves for the passage of the tendons of muscles inserted upon it, and at the shoulder joint, during the life of the individual.

Neither *radius* nor *ulna* exhibit any very great degree of curvature, and as a consequence the interosseous space in the articulated arm is not very wide. The latter bone develops down its shaft a row of some eight or nine papillæ, for the quill butts of the secondaries of the wing, a feature common to so many of our Shore Birds. Comparatively speaking, the distal extremities of these bones of the antibrachium in *Aphriza*, as in all *Limicolæ* which the writer has examined, are small, though to this fact the Oyster-catcher seems to offer an exception.

The carpal segments are two in number, as usual, and present nothing, either in their size, form, or method of articulation, in any way different from what we usually find.

In the pinion (Figs. 13 and 14), the *carpo-metacarpal* bone is long, large-headed, and with its coalesced shafts straight, and more than commonly close together. As a negative character, we miss the overlapping process at the proximal end of the mid-metacarpal, — an apophysis which characterizes this bone in all true *Gallinæ*. Prominent and upturned, the pollex metacarpal supports a phalangeal joint that is clawless; the same being the case with the distal phalanx of the digit of the succeeding finger.

Regarding the expanded and proximal phalanx of this last digit, it is to be noted that its somewhat narrow blade, although more or less scooped out upon either aspect, is never perforated as we find it in some of the *Laridæ*. At its further end a little process protrudes, against which, in life, the head of its following phalanx plays; this latter joint being very long and slender, as in some Plovers and Sandpipers. The little phalangeal joint of the remaining digit is crooked so as to accommodate itself to the outline of the posterior border of the blade of the proximal joint of index finger.

Equal correspondence of characters in the pectoral limbs of Plovers, Sandpipers, and Turnstones, as compared with the bones of the skeleton of the arm, in *Aphriza* seem to prevail, as they were found to prevail among the shoulder girdles and sterna of the same species. Practically, the description I have just given for the arm bones of the Surf-bird will answer all purposes of exactness for the representatives of the genera *Tringa*, *Arenaria*, and most, if not all, true pluvialine types. This, of course, does not apply to the mere question of the difference of size, but to the salient features only. Our engaging little *T. minutilla* has a pectoral limb, the skeleton of which corresponds, in so far as its available taxonomic points are concerned, with the same parts in the Surf-bird, to a degree of nearness most exasperating to the comparative anatomist, and discouraging to one eagerly searching for strong diagnostic distinctions in the structure of such types. Turning to the skeleton of the black Oyster-catcher we find but one sure point of difference that can be relied upon, apart from its size, as distinguishing the fundamental plan of the structure of the skeleton of its arm from the above species. In this bird we find *a claw* upon the end of the pollex phalanx, which, by the way, is also found in some Curlews.

Aside from this character, then, we might, were it possible, reduce the arm bones of this Oyster-catcher until they equalled in size those of a Surf-bird, and it would puzzle the best of us to correctly decide to which species either belonged, after such a hypothetical reduction.

These limicoline birds all seem to lack the *os humero scapulare* at the shoulder joint, and I have yet to find in any of them the sesmoidal ossicles at the elbow, such as we do find, for instance, in some of the Puffins.

Of the Skeleton of the Pelvic Limb. — In *Aphriza virgata* the *femur* possesses only a moderately sized, semi-globular head, with barely any depression on the top of it for the insertion of the teres ligament. The trochanter is lofty and thick, reaching conspicuously above the articular summit of the bone, which latter is broad and smooth. Little or no curvature is met with as we descend the shaft, and this is quite cylindrical for its middle third. As to the condyles, we find nothing worthy of special note, as they are fashioned much as we generally find them in ordinary birds; the external one being the larger and lower, while it shows behind the usual vertical groove for the head of the fibula.

In the leg the *fibula* is free, not anchylosing with the tibiotarsus, being but a trifle longer than the half of this latter bone. Its lower two-thirds are almost hair-like in proportion, and as for that matter it would seem that this delicate osseous filament can add next to nothing to the skeletal support for the structures of the limb (Fig. 8).

Tibio-tarsus also has very nearly a straight shaft, but commonly shows, as in *Hæmatopus*, a curvature in the transverse plane, being gently bowed outwards towards the fibular side. Its procnemial process is much the larger of the two laminar crests in front of the head of the bone, and it is pointed almost directly forwards, while the ectocnemial process is turned outwards, and curves downwards, as a pointed hook.

They both rear slightly above the articular summit of the proximal end of the shaft. Occupying the middle part of the upper third, the fibular ridge stands out quite boldly at the outer aspect, as in all birds. Proceeding to the distal extremity of the shaft we find a marked difference in the form of the two condyles, the outer one being decidedly uniform in outline, and the inner one more elongated and showing compression in the vertical direction. Between, and at the same time above them, in front, we detect the usual little osseous bar for tendinal confinement. A *patella* is absent in the Surf-bird, the case, I believe, in all *Limicolæ*—at least the writer is not aware of any exception to the rule.

Having a length just equal to that of the femur, the *tarso-metatarsus* exhibits at its usual site at the upper end and back part of its shaft a stumpy hypotarsus, that appears to be both pierced and grooved, for the guidance of tendons. Two minute foramina in this locality also perforate the bone in the antero-posterior direction, which is also the case in an Oyster-catcher. A mid-section of the shaft of tarso-metatarsus would show a quadrilateral outline, but the calibre increases, and this form changes as we pass to its distal extremity, where we find three large and prominent trochleæ, the middle one of which is the biggest and placed the lowest on the bone. The ones upon either side of it are directed to the rear. At its usual site, above the innermost one, is faintly to be discerned the facette for the articulation of the *os metatarsale accessorius*, of hallux phalanx. Already the ornithologist has placed at our command the fact that the arrangement of the joints of pes in this species, as in *Arenaria* and many *Tringeæ*, is upon the most common plan of 2, 3, 4, and 5 bones from hind toe to outermost digit, respectively, and a study of these in the skeleton reveals nothing peculiar in them.

The Black Turnstone being a somewhat smaller bird than *Aphriza*, it has a correspondingly smaller pelvic limb and skeleton ; aside from this fact, however, the several bones of that extremity are fashioned quite as they are in our Surf-bird, and present no decided differences in any particular. This statement applies with equal truth to various Sandpipers, and would to *Charadrius* were it not that in the latter genus a disproportion, and a disproportion merely, exists in the hallux, — that toe being much smaller in the Plover, though all the other bones of the limb are remarkably similar in all their essential features, bone for bone, as we have described and figured them for *Aphriza virgata*. Hallux is also missing in *Hæmatopus*, where we sometimes find a process of bone anchylosed to the shaft of tarso-metatarsus, at a point where the accessory metatarsal is commonly attached by ligament. In a specimen of *H. bachmani* before me, such a process is to be found upon the shaft of the tarso-metatarsus of the right pelvic limb, but is missing from the corresponding bone in the opposite limb of the same individual. Strange to say, this is precisely the state of affairs in the skeleton of a second specimen at my hand, — the process is present in the right, absent in the left. It may prove of interest to look further into this point with additional specimens. Returning to our comparison between the pelvic limb of this Oyster-catcher, then, with the same part of the skeleton in *Aphriza*, we may say in brief that beyond the few exceptions mentioned the limb in the former is simply an amplification of the limb in the latter species, — its bone for bone, character for character, — the same thing over again, only the mould happened to be several sizes larger wherein the skeleton of these parts in our Oyster-catcher were cast.

Having now briefly passed over the more salient characters to be found in the skeletons of *Aphriza*, *Arenaria*, *Hæmatopus*, and several representative Plovers and Sandpipers, we are, I think, in a position to offer our conclusions upon the affinities of the Surf-bird, in so far as they seem to be indicated through this study of its osteology.

CONCLUSIONS.

Taking the skull as the part of the skeleton, I would invite attention to the peculiar form of the superior osseous mandible in *Hæmatopus;* and in the cranium of the same bird to the deeply sculpt, supra-orbital, glandular depressions; to its bold, outstanding lacrymal bones, and their mode of meeting the *pars plana* on either side; to its vomer, which is forked at its anterior extremity; to the absence of the supra-occipital foramina; to the complete coalescence of the maxillo-palatine, with the palatine of the same side; to its cranial foramina in front for exit of the first and second pair, they being completely surrounded by bone; and, finally, to the subelliptical outline of its foramen magnum. All these points, and many minor ones in its skull, are totally different in *Aphriza*, and alone are sufficient to warrant us in at least drawing strong lines of family distinction between these two types. Equally clear is the difference between the skull in *Hæmatopus* and *Charadrius*, but when we come to compare it in the former with the skull of *Arenaria*, a faint indication of affinity may be made out, which indication is principally seen in the Turnstone, having similarly formed nasals; feebly developed supra-orbital glandular depressions; a somewhat similar superior osseous mandible; and, lastly, in that its maxillo-palatines unite along their entire lower margins with the corresponding palatine on either side below them.

The differences presented to us, however, in the skulls of *Hæmatopus* and *Arenaria*, amount at least to family distinction. So, too, when we come to compare the skulls of *Arenaria* and *Charadrius*, they are very different, and undoubtedly belong to representatives of distinct families.

Comparing next the skull of a Turnstone with that of the Surf-bird, we are at first struck with the radical differences exhibited in the superior osseous mandibles of the two species. Then in the former the maxillo-palatine fuses, in a manner already described, with the palatine, and finally, the "crotophyte fossæ" are pretty well defined in *Arenaria*, whereas in *Aphriza* not a vestige of them is to be seen. The posterior external angles of the palatines are obliquely truncated in *A. virgata*, rounded in the Turnstone; and finally, the mandibles of these two types are essentially very different, both as to form and structure, as in the Turnstone a large vacuity persists between the forks of the dentary, which is nearly absent in the Surf-bird.

Taking it all and all, the skull, mandible, and associated parts of the skeleton of the head in *Aphriza* agree more nearly with the corresponding structures in the skeleton of the head of some of the larger *Tringeæ* than with any other class of limicoline birds. I have arrived at this point by carefully comparing this part of the skeleton in the numerous species at my hand, and I am fully convinced of the truth of the assertion.

Passing next to the remainder of the axial skeleton, and without enumerating the differences that have been dwelt upon quite at length when under review, it is evident from the arrangement and number of the ribs that *Hæmatopus* differs essentially from the several types we have been examining, and agrees only with *Arenaria* in the number of its free caudal vertebræ. If we were to be guided in this matter by the *total* number of vertebræ, as shown by these several species of birds, providing our count is correct, it would seem that in this respect *Hæmatopus*, *Arenaria*, and *Aphriza* fall together, while some Plovers and some Sandpipers are thus associated. *Hæmatopus* has a very different style of pelvis from the other species we have enumerated, while the pattern of this bone is not a little different when compared in *Aphriza* and *Arenaria*. Were we allowed the expression, it might be said that in so far as the pelvis goes in the genera *Aphriza*, *Charadrius*, *Actitis*, *Arenaria*, and some few others, the pluvialine design seems to be impressed with more or less strength upon them all. This statement will not apply to the pelvis in an Oyster-catcher.

The sternum and shoulder girdle do not materially assist us in this matter; we found it with but *two* notches in such species as *Actitis macularia* and *R. solitarius*, and in the other forms it is of a markedly pluvialine stripe throughout.

As to the appendicular skeleton, a marvellous sameness of style — barring the question of mere difference in size — seems to pertain to the skeleton of the limbs in Surf-birds, Turnstones, Sandpipers, Plovers, and others. *Hæmatopus*, as we saw, possesses a claw upon its pollex phalanx, while some of the species possess but three toes, as in the last-named genus and in *Himantopus* and others.

To sum up, then: my comparative studies of the osteology of *Aphriza virgata* lead me to believe that in the first place its affinity with *Hæmatopus* is by no means a close one, the Oyster-catchers forming a very well-marked and distinct family of limicoline birds by themselves, showing by the structure of certain parts of their skeletons strong larine derivation.

Secondly, the skull in *Arenaria* is in some respects more upon the plan of the skull in *Hæmatopus* than it in any way approaches the structure of that part of the skeleton in *Aphriza;* indeed, so far as the skulls are concerned, the skulls in *Charadrius*, *Arenaria*, and *Aphriza* might be represented as each occupying the angle of an equilateral triangle, each sharing certain characters in common and each removed from the other, equally distant by an equal set of others, not possessed by either of the other species. Were the skulls of *Hæmatopus* and an average *Tringa* introduced into this hypothetical figure, the skull of the Oyster-catcher would be, as far as the characters they hold in common are concerned and for no other reason, on the line joining the skulls of the Turnstone and Surf-bird, and considerably nearer the first species than the last. The Sandpiper's skull would be on the line joining the skulls of *Aphriza* and the pluvialine type, and considerably nearer the former species than the latter. Aside from the skull, the remainder of the skeleton of *Arenaria* would answer fully for the skeleton of an equal-sized Plover, but hardly so for *A. virgata.*

To conclude: the sum total of the skeletal characters of *Aphriza virgata* place this species nearer the *Tringeæ* — say some typical large-sized *Tringa*, with a four-notched sternum — than it does to the Plovers; less so to *Arenaria*, and far less so to *Hæmatopus*. Some pluvialine forms, however, are not so distantly removed from *Aphriza*, if we may be allowed to judge from osteological premises.

There is not the slightest doubt in my mind that had such a form as *Charadrius squatarola* been the sole representative of the *Charadriidæ* in the entire world's avifauna, and been found taking the place, the habitat, of *Aphriza*, modern systematists of the class would surely have grouped it with the Turnstones as forming a family Aphrizidæ. We must believe that the fashion is far too prevalent, that when an isolated form like *Aphriza* is met with, to lay about and endeavor to hit upon a family, a corner, where best to stow it away, without creating, as in the majority of cases should be done, a separate family for it.

Now *Aphriza* is no more nearly related to *Arenaria* than is *Charadrius* related to *Arenaria*, and as at present classified by American Ornithologists, by no means indicates its true position in the system. I would propose then, in view of the anatomical facts brought out in the present memoir, that the family Aphrizidæ be made to contain the sole representative of it, *Aphriza virgata;* and that another family, the Arenaridæ, be created to contain the Turnstones.

It would seem that *Aphriza* in some way connects the Plovers with such *Tringeæ* as may possess the hallax and a four-notched sternum; while *Arenaria* links the Plovers with *Hæmatopus*, albeit that the Turnstone is much nearer the Plover than the far more remotely affined Oyster-catcher would in any way appear to be.

EXPLANATION OF PLATE XXV.

NOTE. — The figures in this Plate were all drawn by the author from the skeleton of a single individual, an adult male, and are all of natural size.

FIG. 1. The skull of *A. virgata*, seen directly from above; mandible removed.

FIG. 2. The skull of *A. virgata*, seen upon basal aspect; mandible removed.

FIG. 3. The skull of *A. virgata*, seen upon direct lateral view; right side, including the mandible.

FIG. 4. The mandible of *A. virgata*, direct superior view.

FIG. 5. The right tarso-metatarsus of *A. virgata*, anterior view.

FIG. 6. The right radius of *A. virgata*, palmar aspect.

FIG. 7. The right ulna of *A. virgata*, palmar aspect.

FIG. 8. The right fibula of *A. virgata*, inner side.

FIG. 9. The right tibio-tarsus of *A. virgata*, mesial aspect.

FIG. 10. The right femur of *A. virgata*, anterior surface.

FIG. 11. The os furcula of *A. virgata*, seen obliquely from the right side.

FIG. 12. The sternum of *A. virgata*, seen upon right lateral aspect.

FIG. 13. The right carpo-metacarpus of *A. virgata*, anconal surface; pollex phalanx *in situ*.

FIG. 14. The right proximal phalanx of the index digit of *A. virgata*, anconal side.

FIG. 15. The sternum of *A. virgata*, seen upon direct anterior view.

FIG. 16. The left coracoid and scapula of *A. virgata*, outer aspect, and articulated *in situ*.

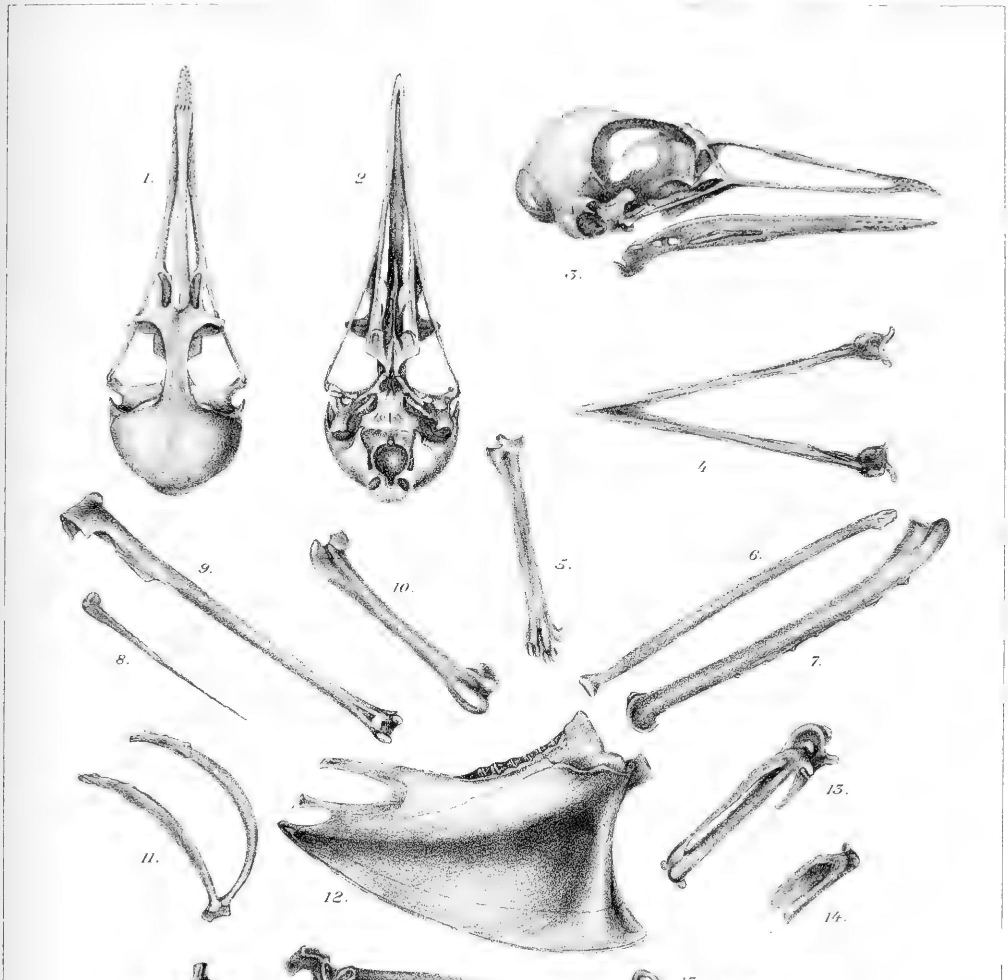
FIG. 17. The right coracoid of *A. virgata*, seen upon direct anterior view.

FIG. 18. The left humerus of *A. virgata*, palmar aspect.

FIG. 19. The left humerus of *A. virgata*, anconal aspect.

FIG. 20. The four last vertebræ of the skeleton of the tail of *A. virgata*, and the pygostyle, seen upon the right lateral aspect.

FIG. 21. The pelvis of *A. virgata*, dorsal view.



R. W. Shufeldt, ad nat. del.

B. Meisel, lith Boston.

Aphriza virgata, ad. ♂, × 1.

Volume II. *April, 1889.* *Number 3.*

JOURNAL

OF

MORPHOLOGY.

UTERUS AND EMBRYO:—I. RABBIT; II. MAN.

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I. Rabbit.

II. Man.

This paper arose not as the result of a special investigation, but as the outcome of general studies undertaken in connection with the preparation of a *Treatise on Human Embryology.* For such a work, knowledge of the fœtal envelopes seemed especially important. I was thus led to examine them, and found in so doing that the structure of the parts differed in many respects from what had been assumed. The rabbit's uterus was examined in the hope of obtaining light as to some of the changes in the human uterus, but the differences are so great that little help was gotten; but on the other hand I was brought to a conception of the changes in the rabbit's uterus so fundamentally different from the views of previous writers that I was induced to carry my observations far enough to make sure of the essential alterations. The following communication is therefore in no sense monographic, but only supplementary to the work of others. My own work has been accomplished by the aid of a grant from the American Association for the Advancement of Science, without which it could not have been carried out. The recipient of such aid naturally wishes to publish what he has accomplished, since such a publication is the most fitting acknowledgment of the assistance enjoyed. I feel my obligations to the Association the more deeply because the grant is the first made from its Research Fund. May I express the hope that that fund will be largely increased, and the Association enabled to make numerous grants to other workers, for in so doing it will do more for the promotion of science than, I believe, by any other means whatsoever.

I. RABBIT.

The observations here recorded were made upon pregnant uteri of the rabbit at various intervals from the sixth to the fifteenth day of gestation, both inclusive. The uteri were cut out carefully, stretched very slightly, and the ends of each uterus tied to an iron rod; the specimens were then hardened in Kleinenberg's picrosulphuric acid, according to the directions given in Foster and Balfour's Embryology, 2d ed. pp. 425, 426. Although this reagent worked fairly well, and preserved the histological elements of the uterus and of the older embryos satisfactorily, it failed to preserve the blastodermic vesicles in uteri of six and seven days; and in the older specimens, after hardening, the extra-embryonic fœtal membranes were somewhat rumpled. Owing to the great difficulty of obtaining doe-rabbits in Boston, and their consequent high price, I have been unable to experiment with other methods of hardening. The specimens after hardening were for the most part stained *in toto* with alum cochineal and eosine, imbedded in paraffine and cut into serial sections with an automatic microtome, made by Herr G. Baltzar of Leipzig.

§ 1. **Uterus at six days and three hours.** — The position of the ova is recognizable externally, being marked by a very slight protuberance on the free side of the tubular uterus. Transverse sections show that there is a considerable dilatation of the uterine cavity, corresponding to the swelling; the walls are considerably thinned out by stretching. The glands are much altered, otherwise there is no striking change in the uterine structure. The shape of the glands varies, but everywhere their cavities are very much expanded, and the epithelial linings of adjacent glands are separated only by very thin connective tissue partitions; on the side of the mesentery the glands are distinctly tubular, and grouped on folds of the mucosa; the relations of these folds are described in the next section. On the opposite side of the uterus, that is, away from the mesentery, the glands are short, with wide cavities, constituting a series of irregular ampullæ with wide mouths. The epithelium is thickened everywhere; it stains deeply, and has enlarged nuclei; it has many intercellular vertical fissures, and therefore a good many of the cells are separated from their neighbors; adjacent cells project unequally, rendering the surface of the epithelium irregular. The change in the epithelium is greatest opposite and least near the mesentery, but is everywhere similar in kind, though varying in degree.

I am unfortunately unable to state anything in regard to the relations of the ovum, owing to the failure of its attempted preservation in my specimens.

§ 2. **Uterus of seven days and three hours.** — The placental swellings are well marked as smooth, rounded bulbs only a little larger in diameter than the unaltered uterus between the swellings, and not projecting at all on the mesenterial side of the uterus. Transverse sections show at once the changes which have taken place. As is well known, the rabbit's uterus has six longitudinal folds, symmetrically disposed; the line of insertion of the mesentery (mesometrium or broad ligament) corresponds to the space between two folds, which alone participate in the formation of the placenta; accordingly we may designate them as the *placental folds.* In the region of the swellings the placental folds are already hypertrophied, and form a marked contrast to the opposite side, where the folds have completely disappeared, and their glands have become shorter and somewhat contorted; the two lateral folds are intermediate in appearance. In the placental folds there is a great increase in the connective tissue, which consists solely of anastomosing cells, forming a loose meshwork of very granular protoplasm, of which only a small amount is accumulated around each nucleus. Described in other words, the cells are small, granular, with long processes continuous with those of adjacent cells. The glands extend only a short and nearly uniform distance down from the surface of the folds; the glands themselves are somewhat dilated; their epithelium stains deeply; its free surface is quite irregular; the nuclei are greatly increased in number, and lie crowded throughout the whole thickness of the layer; the nuclei are round or oval in outline, with a well-marked reticulum densest superficially. In many places the nuclei are grouped, three, four, or five together, and sometimes one can distinguish a distinct outline around the group. These appearances I interpret as evidence that the nucleus of each cell proliferates, rendering the cell multinucleate. The blood-vessels are likewise hypertrophied in the placental folds, and to a less extent in the adjacent folds, but not at all in the folds opposite the placenta. In the placental folds there are larger blood-vessels running for the most part longitudinally, and all situated in the zone next the muscularis; between this zone and the glandular layer, the blood-vessels are, on the contrary, all of small calibre, most of them taking a more or less radial course, and lying approximately in the plane of the transverse sections. All the blood-vessels of the mucosa have, so far as I have observed, the character of capillaries, for they consist of merely an endothelium without adventitial or muscular envelope, although some of them are many times the diameter of ordinary capillaries. The blood-vessels of the placenta of the Guinea pig are stated by Creighton, **77a**, p. 544, to have the same character. There is a single layer of connective tissue cells condensed around the vessels, and representing the commencement of the perivascular decidual cells, though the cells themselves scarcely differ yet from the ordinary connective tissue cells between the vessels.

We find at this stage all the regions of the placental swellings, to be found in later stages, already definitely marked out.

These regions are as follows: —

1, PLACENTAL: subdivided into
    A, glandular zone.
    B, sub-glandular vascular zone with (*a*), sub-glandular zone with small vessels (*b*), outer zone with large vessels.
2, PERI-PLACENTAL.
3, OB-PLACENTAL.

Each of these regions comprises two folds of the mucosa, viz.: the *placental,* the two folds next the mesentery;[1] the *periplacental,* the two lateral folds; and the *ob-placental* region, the two folds opposite the mesentery. The three zones of the placental area persist and become much more marked in later stages, owing to the great divergence of the processes of histological differentiation in each zone. Of the two vascular zones, the *sub-glandular* is characterized later by its very large multinucleate cells, while the *outer zone* is characterized by its crowded uninucleate decidual cells. All the regions and their subdivisions will be perhaps better understood by the descriptions and figures of the nine days' uterus. (See below.)

In my specimens, although the uterus seemed to be very well preserved, the blastodermic vesicles were completely shrivelled up; hence I could make no observations as to the relations of the embryo to the uterine wall.

§ 3. **Uterus of eight days and three hours.** — It is unnecessary to describe the appearances at this age in detail, as they have been described already with admirable clearness and exactitude by Masquelin and Swaen, **114,** 25–30. I have therefore only to confirm their account and refer to certain points on which my observations extend or differ from theirs; it is also necessary to describe the extra-placental structures, which are left out of consideration by Masquelin and Swaen.

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[1] Although this use of the term mesentery is etymologically indefensible, it seems permissible, and not likely to lead to misunderstanding any more than the etymologically indefensible terms cell, endothelium, terminology, etc., etc.

The connective tissue is but little altered from the condition at seven days; it has the same adenoid character; the cells are elongated in directions more or less parallel to one another, and the appearance of the protoplasmic reticulum therefore varies according as the section passes at right angles or parallel with the long axes of the cells; in the former case the meshes are smaller, in the latter larger and longer. The perivascular cells have grown; Masquelin and Swaen trace their origin to a metamorphosis of the connective tissue cells, in doing which I entirely agree with them; these authors likewise describe fibrillæ in the connective tissue, but in my preparation I can find none, nor from what we know of the structure of the mammalian uterus is it probable that any are present; in regard to this point I think that Masquelin and Swaen's account needs rectification.

The placental blood-vessels have increased in size, and, I think, in number; their epithelium, particularly in the larger vessels, is decidedly thickened.

The uterine epithelium has entered upon its complex degenerative metamorphosis — most of the changes have been seen and correctly described by Masquelin and Swaen for the placental area. They conclude that the changes lead to a new formation of blood corpuscles out of the substance of the epithelium. My own observations oblige me to regard the changes as phases of a hyaline degeneration with hyperplasia of the degenerating elements, and having nothing to do, therefore, with blood formation. In all parts of the uterine dilatations the epithelium is considerably thickened (Plate XXVI., Fig. 1). The thickening is due to the enlargement and fusion of the epithelial cells, and this enlargement of the cells is due to the proliferation of the nuclei and to the growth of the protoplasm, which begins later and continues longer (as later stages show) than the multiplication of the nuclei. That the nuclei multiply within each cell can be distinctly seen in my specimens of this age; the same fact has been observed by Masquelin and Swaen. The growth of the protoplasm is more properly described as an enlargement, due to degenerative metamorphosis. As to the nature of this metamorphosis I am unable to speak with much precision. The substance presents a very granular appearance, and possesses a slightly greater affinity for coloring-matters than the unaltered protoplasm. Examination with an apochromatic oil immersion shows in some parts of the degenerated epithelium a distinct network, the threads of which are rather coarse and hyaline in appearance. In default of chemical and further microscopic examination we may accept the hypothesis that the degeneration consists in direct change of the protoplasmic reticulum into hyaline substance, accompanied by thickening of the reticular threads. The degeneration of the epithelium has progressed much further over the non-placental area than elsewhere, and much less over the placental area: the peri-placental regions are in an intermediate stage.

It is also important to note that the deep portions of the glands are nowhere degenerated. The glandular layer may be divided accordingly into an upper degenerated zone and a lower not degenerated zone.

In the placental area there is no stretching of the tissues, and accordingly the glands retain their tubular character. The nuclei fill up most of the epithelial layer; there are three, four, or even five, in each cell in the upper part of the gland; the cells of the fundi are but slightly altered from their usual appearance. The embryo is attached to the maternal placental surface only by the ectoderm, without any participation of the other germ layers, direct or indirect, so far as I can observe. That portion of the ectoderm which is soldered to the uterus is very much thickened, in marked contrast to all other parts of the layer. As shown in Fig. I., Pl. XXVI., the placental ectoderm runs over the surface only of the placenta, and stretches straight across the mouths of the glands, shutting them completely; it does not dip down into the glands at all, and possesses no villi whatsoever. On the surface, between the glandular orifices, the uterine epithelium, already degenerated, is clearly distinguishable.

In the other regions the stretching of the walls stretches the glands also, and of course proportionately to the extent of the strain; hence, in the non-placental area the glands become slits running parallel to the surface, and in the peri-placental part become wide cavities. The upper zone of the peri-placental glandular layer has its epithelium changed into a very thick layer, and beginning to undergo resorption, as evidenced by the presence of cavities. As we follow round towards the non-placental area, the evidences of resorption are greater, and over the area itself a large part of the upper glandular zone has disappeared altogether. Similar relations are found in the uterus of nine days, from which the drawings have been taken. For the sake of greater clearness, and to avoid repetition, we pass at once to the next stage. The fact that I have found the uterus at eight days so much nearer in its stage of development to that of nine than to that of seven days, may be attributed to accidental variations.

§ 4. **Uterus at nine days and three hours.** — Fig. 2, Pl. XXVI., represents a transverse section through a swelling. The attenuation of the walls everywhere, except in the placenta, is very marked, and affects both the outer and inner muscular layers, *lm*, *cm*, and the mucosa, *muc.* In the placental region, *Pl*, on the contrary, the walls are thickened; the placenta itself is formed chiefly by the hypertrophy of the connective tissue of the two longitudinal folds nearest the mesentery, *mes:* the superficial glandular layer, *gl*, owing to its deeper staining, is readily distinguished even by the naked eye; each lobe of the placenta is imperfectly subdivided into two lobules; the embryo, in the specimen figured, appears in transverse section over the right-hand lobe, directly above the furrow separating its lobules; the actual disposition is shown in Cut 1; in Fig. 2 the embryonic structures are purposely omitted on account of the small scale; to the consideration of the fœtal membranes the next section (§ 5) is devoted.

The connective tissue of the placenta is already far advanced in its metamorphosis, which progresses as described by Masquelin and Swaen. It consists of a rich cellular network, Fig. 3, *conn*, of which the cell bodies are much larger than in previous stages; these bodies are for the most part elongated, with very irregular surfaces, and are, therefore, perhaps best characterized as roughly spindle-shaped; their long axes are more or less parallel with the blood-vessels; the nuclei are round, oval, or elliptical, granular, but with a clearer cortical layer, as is usually the case in young connective tissue cells: compare Rollett's Figs. 4 and 5 in Stricker's *Handbuch der Lehre von den Geweben*, I., pp. 63 and 65. The processes of the cells are numerous and very fine, forming a meshwork, between the cells, of such delicacy that it can be followed out only with high powers

(400–500 diams.). The observation of the threads of this network has led certain investigators to assume the presence of connective tissue fibrillæ. Scattered about in the connective tissue are a not inconsiderable number of leucocytes, *l, l, l*, easily recognized by their size and shape, their granular appearance, deep staining and characteristic nuclei. Around the blood-vessels is the perivascular layer of decidual cells, *per v*, which have already been amply described by Masquelin and Swaen, Ercolani, Godet, Creighton, and others. Ercolani's descriptions, of which the most important to us is that of the rabbit at fifteen days,[1] **89**, p. 278, is far from sufficient. Godet's paper I know only from an unsatisfactory abstract. Creighton's account of the perivascular layer in the Guinea pig, **77a,** 544, is also good, and he agrees with the Belgian authors in tracing the origin of the cells to the metamorphosis of the connective tissue. Ercolani opposed this view and maintained that the uterine mucosa is completely destroyed, leaving the whole placental tissue of the mother to arise as a new formation. My preparations render it impossible to agree with Ercolani, since they show all the phases of the metamorphosis. It is only necessary to follow, in Fig. 3, the three series of cells numbered 1, 2, 3, 4, each, and to find in all parts of the placenta the same appearances; to see the perivascular layer at six and seven days, before it is much differentiated; and finally to see the perivascular accretions at later stages, to render inevitable the conviction that the perivascular layer is modified connective tissue. Neither at this stage nor at any earlier or later one have I been able to detect any evidence whatsoever of the resorption of the connective tissue affirmed by Ercolani, **89.** Masquelin and Swaen describe multinucleate cells, but I fail to find them until later stages.

The blood-vessels have their endothelial lining considerably thickened, each cell for itself, and to its individual degree, Fig. 3, *Endo;* they are stained by alum-cochineal and eosine more deeply than the adjacent decidual cells, from which they are sharply distinguished. I am unable to recognize any cells which might be interpreted as intermediate stages between the endothelial and decidual cells, as we should anticipate, were Erco-

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[1] The specimen described by Ercolani I consider to have been probably really only about thirteen days.

lani's suggestion correct that the decidual cells arise from the blood-vessels. The contents of the blood-vessels are blood corpuscles and coagulum; the blood corpuscles resemble the ordinary red globules of the rabbit, a point deserving notice in view of the change occurring later. There are occasional leucocytes, but they are nowhere numerous.

The two layers of the vascular zone are now distinguishable not only by the size of the vessels (not well illustrated in the section drawn as Fig. 2), but also by the much greater development of the perivascular cells in the outer zone; in the subglandular zone the cells are now not far from their maximum development, forming a coat one or two cells thick around the vessels; on the outer zone, on the contrary, the number of layers of cells has still to increase very much; consequently as development progresses, the difference between the subglandular and outer zone becomes more conspicuous.

The epithelium and glands repay careful study at this stage. The degenerative processes are similar in certain essential respects in all parts of the uterine swelling. The likeness concerns five chief points: 1°, the deep portions of the glands show little change in the epithelium; 2°, the upper portions are very far degenerated; 3°, the protoplasm of the degenerated epithelial cells is fused into a continuous thick hyaline mass, the growth of which ultimately obliterates the cavity of the glands; 4°, the nuclei of the degenerated epithelium multiply enormously; 5°, the degenerated tissue is absorbed by progressive vacuolization.

But although these resemblances are dominant, each of the three principal regions, the placental, peri-placental, and ob-placental, presents now a very distinctive appearance, and has its distinctive further history.

In the peri-placental region, with which we begin, because the relations are more obvious there than elsewhere, we find the appearances shown in Fig. 4. The line of demarcation from the placenta, though not definite or sharp, can be approximately determined, but the passage into the ob-placental region is very gradual. The most striking feature of the section is the degenerated and enormously thickened epithelium, *h.ep*, deeply tinctured by the eosine, and remarkable for the crowded band of nuclei. Within the area of the degeneration the former gland cavities are closed; the diameter of the glands has enormously increased, and in some places two adjacent glands have swollen until they have come in contact and fused, the glands then forming a network; in the placental region the conversion of the glands into a network goes very far. The distribution of the nuclei as at *a* and *b* preserves in some parts the original grouping in opposite walls of the gland tube; at other points they lie in irregular patches. Secondary cavities, *vac*, appear at various points; they are irregular in size, shape, and position, and arise by the resorption of the degenerated tissue. There is probably a certain amount of resorption carried on upon the surface against the connective tissue, for that surface becomes jagged and irregular, presenting a corroded appearance, as can be seen at various parts of Fig. 4. The vacuolization is, however, the principal factor of destruction. As to the manner in which the spaces are produced in the heart of the very compact layer, my observations give no satisfactory information. There are no accumulations of leucocytes either in the epithelial layer nor even in the connective tissue (see Fig. 4), in which all the cells are copied with approximately entire accuracy from the preparation. The only material I have ever noticed in the vacuoles is broken-down fragments of the surrounding hyaline tissue (epithelium) itself. The hypothesis may be suggested that the resorption vacuoles are produced by liquefaction, but the suggestion calls for no further discussion since there are no direct observations to test the validity of the hypothesis.

The deep portions of the peri-placental glands, Fig. 4, *gl*, are dilated transversely to an extent which has converted them from tubes into wide vesicles. Towards the ob-placental region the transverse stretching gradually increases. The epithelium differs but little from that of the resting utricular glands; it is composed of cylinder cells with basally placed oval nuclei.

In the ob-placental region the mucosa is much thinner than elsewhere. As we proceed from the edge of the peri-placental region towards the pole furthest from the placenta we find that the layer thins out and is more advanced in its degeneration. Near the peri-placental thickening there is a wide superficial layer of degenerated epithelium with the characteristic central band of nuclei, but the prolongations corresponding to the degenerated gland ducts are short; the deep portions of the glands are oval slits parallel with the muscularis, Fig. 5, *gl.* A little further along, the resorptive vacuolization begins, producing a curious irregular layer, Fig. 5. The degeneration and vacuolization is found still further along to have involved the inner adjacent wall of the gland vesicles, thus producing the appearances shown in the left-hand part of Fig. 5, where there are shallow cups, *gl*, of epithelium, each entirely separate from its fellows, and all overlaid by the hyaline stratum, *h.ep.* There is usually a dome-like hollow in the degenerated stratum above each cup. Since the processes described vary in rapidity, there is not a uniform, but only a general, progression of stages towards the centre of the ob-placental region. Moreover, the variability is great, and the images from different sections and different parts of the same section are correspondingly multifarious, but the general succession of changes is everywhere the same; hence it would be profitless to expand the descriptions.

The *placental* glands have preserved their tubular character; they are less degenerated than the uterine glands of the non-placental parts; their walls are less thickened and in most parts the glandular cavity is still present. The deep portion of the glands are tubes lined by columnar epithelium. For the rest, I may refer to the satisfactory description of Masquelin and Swaen, **114**, 30–31, except as to one point. As shown in Cut 1, p. 355, the ectoderm of the embryo is firmly soldered to the placental surface over certain areas. The nature of this connection and the accompanying structural changes in the uterus are illustrated in Fig. 7, which has been copied with great care from one of the sections. For the sake of clearness, only the nuclei of the connective tissue have been drawn in; the perivascular cells are represented by their nuclei and outlines, and the nuclei and cells of the fœtal ectoderm are given in outline; but there is nothing diagrammatic in the drawing; of course in the figure the distinction between the fœtal and maternal tissues is more marked, though not more real than in the section; in fact there is scarcely a cell even on the line of junction of the ectoderm with the uterus about the assignment of which one could have any doubt, so distinct is the texture and the staining of the fœtal and maternal tissues. This is a matter of importance, as it renders it possible to ascertain beyond question that there are no villi; nevertheless their presence has been assumed not infrequently. To pass on:

where the ectoderm, Fig. 7, *Ecto*, touches the placenta, the active resorption of the degenerated glands is going on (see the part of Fig. 7, above bracket C); whereas in other parts the glands present the appearance shown in Fig. 7, *A*, *gz*, and described by Masquelin and Swaen. There is also an intermediate zone shown in Fig. 7, above bracket B, where the transition phases between the two states are found; the zone of transition lies immediately underneath the point where the ectoderm, *Ecto*, joins the uterine epithelium, *h.ep*; here the glands are thickened and hypertrophied; the lumen is obliterated, but the cylindrical shape is irregularly preserved; where the distal end of the ectoderm leaves the placenta, there is again a similar transition: in other words, the resorption is less advanced around the periphery than in the centre of the area of ectodermal attachment. The resorptive process is essentially the same as outside the placenta, — superficial corrosion and internal vacuolization, — but the vacuoles formed are relatively small and consequently more numerous: moreover, the space left by the disappearing epithelium is at once occupied by connective tissue cells, so that there are no cavities. The resorption goes on principally in the superficial layers of the placenta, where it results, as later stages show, in the complete disappearance of the glands immediately underneath the ectoderm; deeper down the glands at the present age are hypertrophied and without lumina, but even in the region of bracket C of Fig. 7 (Pl. XXVII.) most of the glands show very few or no vacuoles.

§ 5. **Embryo at nine days and three hours.** — It is not proposed to consider here anything but a few points bearing on the relations of the embryo to the uterine walls.

First, as to the *position of the embryo:* the dorsal surface of the embryo is turned towards the placenta; the embryo may be situated over one or the other lobe of the placenta or across both; its long axis may be either parallel or oblique or at right angles, to the long axis of the uterus. In the specimen represented in Cut 1, both the uterus and embryo appear in transverse section. Similar variability appears in my specimens of uteri of eight days, and of nine days and seventeen hours. The statements of Van Beneden and Julin, **44**, and other authors,[1]

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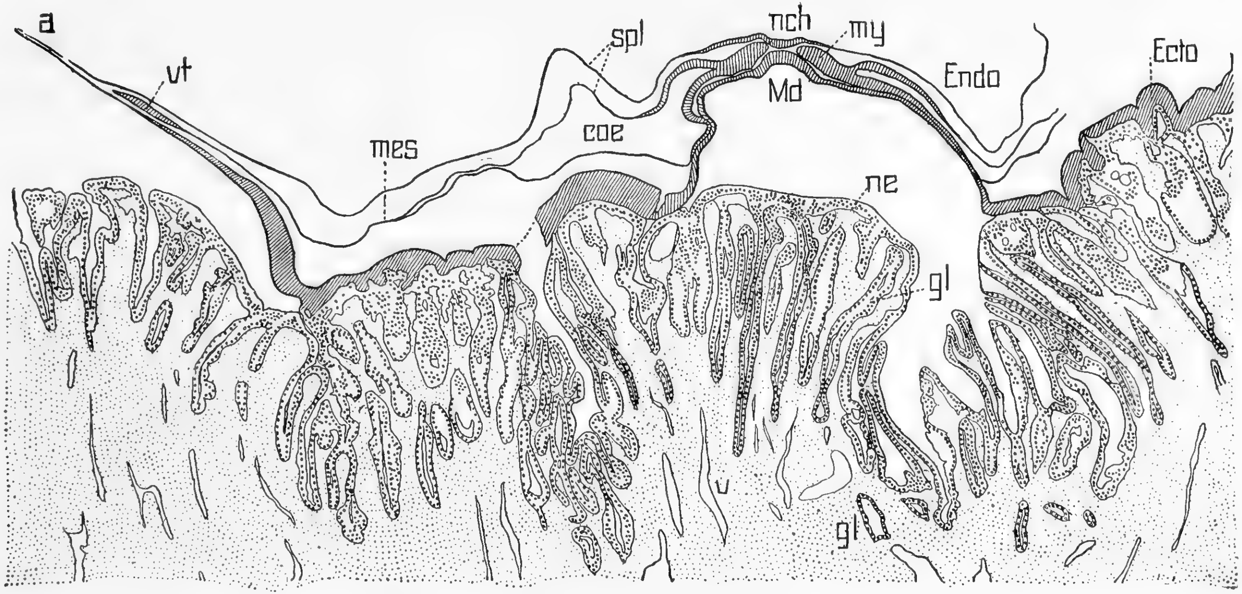
[1] Compare Bischoff, *Entwickelungsgesch. d. Kaninchens*, p. 138, and von Baer, *Entwickelungsgesch.* II., 232.

lead rather to the supposition that the embryo normally lies across the uterus; but this is true in my experience only of the later stages after the embryo is suspended more freely.

Next as to the extra-embryonic portions of the germ layers: my observations compel me to differ as to the composition of the walls of the blastodermic vesicle or yolk sack. Sections through the middle region of the embryo, Cut 1, show an open medullary groove, *Md*, the thickened notochordal band, *nch*, of the entoderm; the mesoderm of the *Stammzone* is undivided; that of the *parietal zone* is split to form the cœlom, *Coe*, which may be followed a considerable distance from the axis of the embryo, when the two leaves of the mesoderm again unite into a single distal plate, *mes*, in which the two layers can be distinguished for a certain distance; the distal edge of the mesoderm is sharply marked; the mesoderm is thickened around its margin. Beyond the margin the ectoderm and entoderm come into contact, *a*; the former is the thicker layer, being composed of cubical cells, while the entoderm consists of very thin broad cells; the two layers continue outwards until, having passed over the peri-placental thickening, they reach the region of transition from the peri-placental to the ob-placental area, where the ectoderm changing to a thin flat-celled membrane is intimately conjoined to the degenerated epithelium of the uterus. Where the concrescence takes place, the union of the two layers becomes very intimate, so that it is difficult to satisfy one's self how much farther the ectoderm extends, but apparently it goes completely around, forming a closed vesicle, as is generally stated and as is found later. Apparently the ectoderm is not involved in the resorption of the uterine epithelium, which disappears — but further investigation is required. The entoderm of the other hand is readily followed, and although somewhat crumpled and torn in the ob-placental region of my specimens, there is to my mind very little doubt that it forms a closed sack, corresponding to the entodermic lining of the yolk sack of other mammals. From the observations above recorded it is evident that two germ layers are readily traced for some distance from the embryo, but that beyond a certain line only one layer, the entoderm, is readily followed. Now this fact is carefully represented in van Beneden's and Julin's diagram, **44**, Pl. XXIV., but the membrane which stops is there given as entoderm, which, as seen in my



Cut 1. — Transverse section of a rabbit embryo, *in situ*, of nine days and three hours. *d*, wall of yolk-sack composed of ectoderm and endoderm only; *vt*, vena terminalis; *mes*, mesoderm; *spl*, splanchnopleure; *coe*, cœlom; *nch*, notochord; *Md*, medullary groove; *my*, myotome; *Endo*, endoderm; *Ecto*, ectoderm; *gl*, glands; *v*, blood-vessel; *he*, hyaline uterine epithelium.

specimens, is continued around. It is probable that when embryos of nine days are removed, that a portion of the ectoderm remains attached to the uterine wall, and consequently the inferior portion of the vesicle is without any ectoderm. Being unaware of such a possibility, van Beneden and Julin have perhaps represented the single layer left as ectoderm on account of the theoretical necessity of an ectodermal covering on the external or apparently external surface of the ovum. The question, therefore, is to be posed: Have not observers found two layers up to a certain limit beyond the *vena terminalis*, and only one layer over the remaining inferior portion of the embryonic vesicle, and *assumed* the single layer to be ectoderm, whereas it is entoderm, and the true ectoderm is left upon the uterus, to which it is indissolubly attached? The view I advocate brings the further question whether a portion of the embryonic ectoderm disappears by being involved in the resorption of the ob-placental uterine epithelium. This I think is not the case. The intimate adherence of the extra-embryonic portions of the germ layers to the uterine walls has been carefully recorded by Bischoff, *Entwickelungs gesch. Kaninchens*, p. 131, "Vom dem Umkreise der Vena terminalis an ist das Ei [of ten days] in die in dieser Lage, etc. . . . und von hier an sind auch alle Eihäute so innig unter einander und durch den Uterus vereinigt, dass es nicht gelingt sie zu lösen."

The attachment of the embryo takes place as described by van Beneden and Julin, p. 402, 403, by an area of thickened ectoderm; the general arrangement is well shown in Cut 1, while the fitting together of the fœtal and maternal surface is better illustrated by Fig. 7, Pl. XXVII. The fœtal mesoderm does not participate even indirectly in this attachment, but runs along free from the outer germ layer. The ectoderm, as it nears its attachment (see Fig. 7), gradually thickens. Just where it joins the uterine surface there are several large cells with very large nuclei; appearances which are probably connected with the growth of the layer, for beyond the line of the large cells the ectoderm is very much thicker. Extremely distended nuclei also occur very strikingly in the developing supra-renal capsules, and are also there connected presumably with cell proliferation. If these suppositions are correct, there is a modified form of cell division characterized by dilatation of the nuclei and which deserves special study. Over the area of attachment the uterine epithelium, Fig. 7, *h.ep*, is degenerated as before described, its surface is extremely irregular, but the ectoderm, *Ecto*, is perfectly fitted to every irregularity, but the free surface (towards the mesoderm) is comparatively smooth; the layer consists of two, three, or four strata of cells. Beyond the area of attachment the ectoderm again thins out.

As to how the tissues are held together, my observations afford no explanation. It seems to me possible that the two tissues actually grow together as a grafting unites with a bough; but for aught we know it may be by some other process, perhaps simple agglutination. The thickening of the ectoderm I am inclined to regard as degenerative, and therefore somewhat comparable to the degenerative thickening of the uterine epithelium. I am brought to this view by no conclusive observations, but chiefly by two facts: 1°, that in later stages the ectoderm seems to have disappeared over the greater part of the placenta (see § 7. Uterus of eleven days); 2°, hyperplasia is often the commencement of degeneration, as is familiarly known to pathologists. To this evidence may be added the appearance of the ectoderm at nine days and seventeen hours, which I interpret as indicative of degeneration.

§ 6. **Uterus of nine days and seventeen hours.** — In my specimen there are not many changes from the previous stage last described, but of these changes the following deserve special mention: 1°, the commencing formation of perivascular decidual cells in the peri-placenta; 2°, the reconstitution of the ob-placental epithelium; 3°, the formation of the true chorion; 4°, changes in the extra-embryonic ectoderm; 5°, the contents of the placental blood-vessels.

1°. The peri-placenta is still only a small bolster at the side of the placenta; its glands are still recognizable and its blood-vessels are more conspicuous; the connective tissue cells are enlarged and have begun to form more or less distinct coats around the blood-vessels. I feel assured that the decidual cells arise here in the same way as those of the outer zone of the placenta; the cells in the two parts appear to me identical in character as soon as they attain their full development, and to differ only in the period during which their development takes place; later on, Fig. 8, Pl. XXVIII., the peri-placenta forms, together with the outer zone of the placenta, a continuous layer of uninucleate decidual cells, extending over half the uterus.

2°. In the ob-placental region the degenerated portion of the uterine epithelium is almost completely resorbed around the pole opposite the placenta, (compare Figs. 4, 5, and 6). Fig. 6, taken from an older stage, in which the phase existing at nine days and seventeen hours at the pole is found near the peri-placenta, illustrates the manner in which the patches of unaltered epithelium, *gl*, of Fig. 5, grew together by the union of their edges into a continuous sheet of epithelium, Fig. 6, *gl*, forming a series of shallow cups, widely open.

3°. The chorion of mammals, as I have defined it elsewhere, is "the whole of that portion of the extra-embryonic *somatopleure* which is not concerned in the formation of the amnion."[1] The term is not applicable until the mesoderm has united with the ectoderm in the region outside the embryo to form a single membrane: such a union has now taken place; the thickened placental ectoderm is coated by a thin layer of flat cells, epithelial in character and with bulging nuclei. These cells represent the lining of the body cavity, or, as this lining is conveniently called, mesothelium. The mesothelium, and consequently the cœlom, extend a slight distance beyond the edge of the placenta; the mesothelium then bends over onto the yolk sack, of which it becomes the vascular coat, and then runs *towards* the embryo; the vascular coat has a large vessel, *sinus terminalis*, near the end of the cœlomatic space, and the mesoderm stretches a short distance beyond away from the embryo. The ectoderm, on the contrary, extends beyond the end of the mesoderm *away* from the embryo over the rest of the yolk sack. Thus the yolk sack, as is well known, comprises two parts, one near the embryo with walls composed of entoderm covered by mesoderm, and away from or opposite the embryo, with walls composed of entoderm covered by ectoderm; compare the clearly expressed summary of the relations in the rabbit given by Balfour in his *Comparative Embryology*, II., 199, 200.

4°. The ectoderm of the embryo presents the same general arrangement as at nine days. The area of thickened entoderm, however, which is attached to the placenta has changed in appearance; at nine days and three hours each cell outline was

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[1] Wood's *Reference Handbook of the Medical Sciences*, II., 143; article, *Chorion*.

distinct, and the protoplasm around each nucleus dense and finely granular; now the cell outlines are hard to follow and the picture is confused by broader lines of hyaline matter, which is colored by the eosine; the nuclei are enlarged, the protoplasm is more coarsely and more irregularly granular, and somewhat vacuolated. The characteristics enumerated concord with the idea that degeneration is going on, — an idea suggested, also, as before stated, by the failure to find this part of the ectoderm in later stages.

5°. The blood-vessels show increased hypertrophy of their epithelium, and the perivascular cells form two or three layers around them; they are especially remarkable for containing a very large number of multinucleate leucocytes and comparatively few red corpuscles. The excessive abundance of white globules continues up to the oldest stage I have examined (sixteenth day). The predominance of nucleated corpuscles causes the contents of the maternal vessels to resemble fœtal blood when examined with a low power; with high magnifications the difference is evident. To the fœtal blood in the placenta we shall have to recur.

§ 7. **Uterus at eleven days and three hours.** — Very great changes have taken place — so great that they cannot be understood completely until some of the intermediate phases are studied. Want of suitable material has hitherto prevented my doing this. At the present stage — the beginning of the twelfth day — the placenta is distinctly pedunculate, and there is consequently a circular cleft between its sides and the closely adjacent peri-placenta; in the middle of the placenta a deep fissure corresponds, of course, to the space between the two folds of the uterus, out of which the placenta is developed, and therefore runs lengthwise of the uterus. The allantois has acquired considerable size and is attached to the surface of the placenta, from which the ectoderm has disappeared. The glands of the placenta are very far degenerated and altered; in the sub-glandular zone the multinucleate cells have appeared, and in the outer zone the perivascular cells have increased so as to occupy nearly all the space between the vessels. In the peri-placental and ob-placental regions, the modifications are equally noteworthy. Such, in brief, are the more striking changes. Let us consider them with greater detail.

The diagram on Pl. XXIX. will enable the reader to follow the ensuing descriptions. The general explanation of the diagram is given in the next section.

The placenta is shaped somewhat like a mushroom: it has a very thick stalk, with a somewhat broader top. The top is bilobate, there being a deep fissure between the two lobes; this fissure persists at thirteen days (Fig. 8, *f*); its fundus is the sub-placenta (Ercolani's cotyledonary organ). The sides of the fissure are, of course, part of the surface of the placenta, morphologically speaking, and bear glands. The three zones of the placenta are well marked. In the outer zone the blood-vessels are very wide, with thickened degenerated epithelium; the perivascular cells occupy the entire space between the vessels in all that part of the zone towards the muscularis and most of the space in the part towards the glands. Next to the sub-glandular zone, therefore, we see the vessels surrounded, each by its separate thick perivascular coat, while the intervening tissue still consists of anastomosing cells, like those which in earlier stages occupied more of the space and which formed the only packing between the vessels at six days. The blood-vessels convert the layer, by their enlargement, into a spongy tissue, which has been described not only in the rabbit, but in other rodents; the vessels themselves have been generally described as glands, but the study of their development renders doubt as to their true character impossible. The vessels are partially empty in my preparations, but they contain very numerous leucocytes, nearly all of which have several nuclei apiece, which are conspicuous from their dark staining: there are a few red globules and here and there a little coagulum. As the corpuscles of the embryo are large nucleated bodies, there is no difficulty in distinguishing the fœtal from the maternal blood, even in the upper part of the placenta, where the two circulations are juxtaposed. The middle or sub-glandular zone has undergone greater changes still. In it, as likewise in the glandular zone, the perivascular cells have almost entirely disappeared,[1] but they are, as it were, replaced

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[1] This statement is perhaps not correct. There are certain spaces surrounded by epithelial or epithelioid cells to be seen in the upper part of the sub-glandular and in the lower part of the glandular zone; these spaces I have interpreted as parts of the glandular system, but they are perhaps maternal vessels with perivascular cells. The uncertainty as to their character could be probably removed by the examination of the ten days' placenta, which presumably offers the intermediate stages.

by multinucleate cells (compare Fig. 14, Pl. XXVIII., of these cells from an older placenta); their origin appears to be due to the development of clusters of connective tissue cells, which lie scattered about between the blood-vessels; each cluster consists of from three to six cells lying together and connected on the one hand by short processes with one another, and on the other by longer processes with the cells of adjacent clusters. The larger clusters are separated by membranes from one another, and thus every cluster becomes enclosed in a membrane and appears as a multinucleate cell. The development of these cells would doubtless repay more accurate investigation. The multinucleate cells do not yet form a continuous bed under the placenta, but are divided into parts by masses of very loose connective tissue. At the base of the fissure between the two lobes of the placenta the glands have almost entirely disappeared, but we still find a few unresorbed fragments of their degenerated epithelium; these fragments are conspicuous by their very deep staining, both of the hyaline substance and of the nuclei: the neighboring tissues are less colored. The fissure itself is like an inverted ⊥; that is, it is transversely expanded at the base; the floor of the expansion is thrown up into folds and covered by a cylinder epithelium, which I feel some hesitation in designating as the regenerated uterine epithelium, although it resembles the epithelium on the peri-placenta, where the glands are resorbed and the epithelium reconstituted from its degenerated self. On the other hand, as shown in the next section, there is some proof that the fœtal ectoderm penetrates, by villous growths, far into the placenta. It seems possible that the fissure is filled by villous excrescence of fœtal origin and that the epithelium of the sub-placenta belongs to the villus. This view does not commend itself to me. Neither upon the upper wall of the expansion nor on the sides of the fissure have I recognized any epithelium. The upper part of the fissure is closed by an ingrowth of connective tissue. Hence the lower part is changed into a shut cavity in the centre of the placenta, and into this cavity the folds covered with epithelium project.

So far as I am informed, this curious structure has not been described hitherto, but what appears to be clearly its homologue has been observed by Ercolani, **89**, pp. 290, 291, Tav. IV., Fig. I., O, and specially studied by Creighton, **77b**. Both of these authors examined late stages when the fissure is completely filled by connective tissue, so that there is no space — a condition found in the rabbit at thirteen days. It will be convenient to designate the structure as the *sub-placenta.* Its occurrence is confined to rodents so far as at present known. Finally, we have to note that at the edge of the placenta, toward the peri-placenta, the sub-glandular layer, which we are now considering, is characterized by the presence of deeply stained fragments of glandular epithelium irregularly scattered through the other tissues and similar in appearance to the remnants of the glands about the sub-placenta. These fragments appear to have been seen by Ercolani, Creighton, Masquelin, Swaen, and others, and variously interpreted, their true nature not being recognized. The disappearance of the glands at the centre and at the periphery of the placenta virtually increases the domain of the sub-glandular layer. The greatest changes have occurred in the glandular layer. Scarcely a trace of the perivascular cells can be found; the space they formerly occupied is taken up by a very loose embryonic tissue; the glands are completely altered; they have lost their special affinity for eosine and cochineal, neither the hyaline substance of which they are composed nor the nuclei they contain being more stained than other tissues (compare Fig. 8); they are irregularly cylindrical in shape, very much contorted, and united with one another at irregular intervals, so as to constitute an actual network: they are very much vacuolated; their deep portions (fundi) are somewhat wider than the upper parts; here and there one sees a remnant of the original central lumen. The contorted masses, which I consider glands, are apparently the same as have been seen by Mauthner in the placenta at term, **115**, p. 121. He describes these cords as consisting of the fused epithelium of adjacent fœtal villi, and the spaces I have designated as vacuoles he describes as maternal blood-channels; he states explicitly that he has injected them from the maternal vessels, and in other cases found them gorged with maternal blood. These statements are irreconcilable with my own views, detailed in the present article. The uterine epithelium has entirely disappeared both from the top and the sides of the placenta. The top surface is covered by a very thin layer of flat epithelium, Fig. 8, *msth*, which is found, when followed out, to be continuous with the lining of the body cavity of the embryo; it is therefore mesothelium. Underneath this covering, and above the glands, there is a layer of varying thickness containing some large and a few small blood-vessels with embryonic blood in them, and consisting otherwise only of scattered anastomosing connective tissue cells,[1] which can be followed without the slightest break on the one part until they pass directly into the mesoderm of the superjacent embryo; on the other part, down between the glands, Fig. 8, *mes;* compare, also, later stages, Figs. 10 and 11. Between the glands, also, are blood-vessels containing embryonic blood. On the top surface of the placenta I can find nothing recognizable as even a trace of the fœtal ectoderm, which formed a thick and conspicuous covering in the latest previous stage examined (nine days and seventeen hours). At the edge of the top of the placenta, Fig. 8, the relations change: the mesothelium, *msth*, bends up and leaves the placenta, and together with a few subjacent mesodermic cells joins a sheet of cylinder epithelium, *Ecto*, which is shown by its connections to be fœtal ectoderm. The ectoderm from the point where the mesothelium, *msth*, bends on to the top of the placenta continues downward, *Ecto*, to clothe the side of the placenta which faces the peri-placenta. Between the placenta and peri-placenta, as shown in Fig. 9, there is a fissure; the ectoderm can be followed to the bottom of this, and from there extends,—not on to the peri-placenta,—but turns abruptly back on to the side of the placenta, up which it stretches a minute distance and thereupon ends abruptly. The disappearance of the ectoderm is discussed in the next section.

The peri-placenta is now characterized by the enormous increase of the perivascular decidual cells and the accompanying expansion of the blood-vessels; by the disappearance of its glands and by the reconstitution, in part, of its superficial epithelium. The peri-placenta appears like the continuation of the outer zone of the placenta, for it directly adjoins it, is of about the same thickness, and is histologically similar. The blood-vessels are wide with hypertrophied endothelium; the perivascular cells are disposed as in the sub-glandular zone of the placenta; that is, in the half towards the uterine muscularis they completely fill the intervascular room, but in the half towards

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[1] A layer closely similar to this, and presumably homologous with it, exists in the Guinea pig (Creighton, 77a, p. 558), in the rat (Ercolani), and other rodents.

the interior of the uterus they form a discrete envelope around each vessel, the spaces between the perivascular coats being occupied by simple connective tissue cells. The glands which at nine days, Fig. 4, were so bulky and conspicuous, have almost completely disappeared, being now represented only by remnants of multinucleate hyaline matter scattered superficially, and easily recognized by their distinctive and conspicuous coloration: some of these remnants are still united with the surface. The epithelium is in two forms: on the half of the peri-placental surface towards the placenta it is entirely in the phase of degeneration, while over the other half it is already reconstituted as irregular cylinder epithelium, the cells of which are more or less separated from one another, and somewhat variable in height; this epithelium stops abruptly near the middle of the peri-placenta and is replaced towards the placenta by a hyaline nucleated layer occasionally thickened into a lump, where the nuclei are clustered; the cylinder epithelium is deeply stained by the cochineal; the hyaline epithelium has a marked color from the eosine, and its nuclei are dark with cochineal. The glands are further resorbed under the cylinder epithelium than nearer the placenta.

The ob-placenta is now characterized by the disappearance of its degenerated epithelium, by the fusion of the epithelium of the deep portions of its glands into a new continuous layer, and by the development of peculiar monster cells in its central area facing the placenta. The resorption of the epithelium by vaculization has already been described in the account of the nine days' uterus, § 3. The epithelium, Fig. 6, *gl*, is everywhere re-formed as a continuous layer; portions, Fig. 6, *h.ep*, of the degenerated layer remain especially near the peri-placenta, but for the most part the new epithelium is entirely uncovered, and in the central region it has grown, so that the glands are already deepened. But the most remarkable feature is the accumulation, opposite the placenta, where the mucosa is much thickened, of the curious bodies, to which I apply the term *monster cells*. They are round or oval masses many times the size of any other histological element of the uterus or embryo, and possess huge nuclei. They are shown in Fig. 17, which represents them at a later stage, when they are further enlarged. I regard these bodies as detached epithelial cells, undergoing degenerative hypertrophy. In spite of long searching for the phases representing their early history, I have failed to ascertain positively their origin. In the next section the question is recurred to. The monster cells vary in size: the smallest ones lie near the epithelium; the larger ones, for the most part, deeper down and even among the muscular fibres, but a few large cells lie next the surface. The body of the cell is evenly and coarsely granular and resembles the hyaline degenerated protoplasm of the epithelium; its external outline is distinct, well-rounded, and without processes; the nucleus, which often has a slight space around it, as if it had shrunk a little, has a clear regular outline, being apparently provided with a membrane; it is well colored by cochineal, and contains an indistinct network with imbedded granules of various sizes; in the smaller cells the nuclei have one or two granules much larger than the rest, and which may be spoken of as nucleoli; the size of the nucleus increases with that of the cell, and at the same time the granulation becomes coarser.

The description of the placenta at ten and eleven days given by Masquelin and Swaen I have not been able to follow in all respects. Owing to their conclusion that the epithelium of the uterus gives rise to blood, they apply the term *cavités hæmatoblastiques* to apparently all the cavities of the placenta except those of the maternal blood-vessels. I have compared their description very carefully with my own preparations: so far as this enables me to judge, their "cavités hæmatoblastiques" include the fœtal blood-vessels, the vacuoles in the degenerated glands, the spaces included within the epithelial U's described in the next section, and which are supposed to be the tips of fœtal villi, the multinucleate cells and perhaps also the sub-placenta. Why the multinucleate cells are included among the blood-forming organs the authors do not render clear. Their failure to recognize the variety of constituents in the glandular layer of the placenta must be ascribed to the want of the perfected methods at present at our disposal. With the means now at command there is no difficulty in obtaining preparations which show indisputably that the glands though degenerated persist intact, and do not give rise to blood cavities nor blood corpuscles as Masquelin and Swaen have erroneously believed.

§ 8. **Embryo at eleven to thirteen days.** — As known already, the embryo is completely separated from the yolk sack, and the allantois has grown forth and attached itself to the placenta. The relations of the extra-embryonic structures have been represented by Bischoff in the diagrams of Pl. XVI. of his classical memoir on the development of the rabbit. These diagrams have since been reproduced again and again, sometimes with modifications as notably by Kölliker in his manual, and by Van Beneden and Julin. Guided by these and by my own preparations I venture to construct a new diagram, Pl. XXIX., which I hope will approximate more nearly to the actual relations of the parts, with which we are now concerned.

In the first place it is to be noted that most of the section is occupied by uterine tissue: — compare Fig. 9, Pl. XXVIII. The largest space is occupied by the placenta, on the surface of which is situated the embryo, lying upon its side. Opposite (above in the figure) the embryo is the ob-placenta, *ob-pl*, with its central area, containing the monster cells, *mo cl*; the inferior wall of the yolk sack is fitted upon, but not attached to, the ob-placental surface. The peri-placenta, *PP*, appears as the continuation of the outer zone, *oz*, of the placenta; it has no glands: its blood-vessels are enlarged, and all the space between them is filled with uninucleate decidual cells. This description of the peri-placental structure applies also to the outer zone, *oz*, of the placenta. A narrow space separates the surface of the peri-placenta from the side of the glandular zone, *gl*, of the placenta: the letters *a* and *b* lie in this space. The placenta consists of three zones: 1°, the upper glandular zone, *gl*, divided by a fissure, *f.*, into two lobes. This fissure is partly filled with an ingrowth of embryonic mesoderm, *mes*; the transversely expanded bottom of the fissure forms the sub-placenta, *sb.pl*; the glandular zone as a whole constitutes a protuberant mass with top and sides clearly distinguishable. Below the sub-placenta is the sub-glandular zone, *s.-glz*, with dilated blood-vessels and multinucleate decidual cells.

The embryo lies upon the surface of the placenta. From its ventral side spring the allantois, *all*, and the stalk of the yolk sack; for the sake of clearness the amnion and pro-amnion are entirely omitted, since they have no direct relation to the uterus.[1] The allantois expands upon the placenta; the yolk

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[1] For diagrams of the pro-amnion, etc., see Van Beneden et Julin. Copies of their figures are given in Buck's *Reference Handbook of the Medical Science*, VI., 32.

sack expands over the ob-placenta. The cavity of the allantois, *all*, is of course lined by entoderm; it is, however, quite small, and in my preparations by no means the spacious vesicle commonly represented, for instance, by Kölliker in his *Grundriss* (2te Aufl., Fig. 88), or by Balfour (*Comparative Embryology*, II., Fig. 148). The allantoic mesoderm, *mes*; on the other hand, spreads out, over the surface of the placenta, down its sides, down into the fissure, *f*, between the two lobes, and penetrates between the glands, *gl*, of the placenta; wherever it goes, the mesoderm carries fœtal blood-vessels. The free, *i.e.*, inner or cœlomatic, surface of the mesoderm bears the mesothelium, *msth*; as the extra-embryonic cœlom does not extend beyond the top of the placenta, there is, of course, no mesothelium upon the sides of the glandular zone (between *a* and *b*), but at the edge of the top of the placenta the mesothelium is reflected back, and after a short course joins the wall of the yolk sack near the *sinus terminalis*, *v.t.*

The yolk sack, as has been long known, consists of two parts:[1] 1st, the *area vasculosa* bounded approximately by the *sinus terminalis*, *vt*; within this area the entoderm is united with the mesoderm, which passes only a very short distance further out; 2d, the remaining portion without mesoderm, excepting always the pro-amnion, which is included in the *area vasculosa*; over this second region the entoderm, *en*, rests directly upon the outer germ-layer, *ecto*.

If we follow the ectoderm around, we find that it leaves the yolk sack, just before the *sinus terminalis*, *vt*, is reached, and being joined by the mesodermic lining of the cœlom passes down *b* on to the lateral surface between the peri-placenta, *P*, and the glandular placenta, *gl*, where, as already described, it bends inwards, and turning back runs a minute distance upwards; according to my hypothesis it continued earlier over the surface of the placenta, as indicated by the broad dotted line, *d*. The layer of embryonic epithelium upon the side wall of the rodent placenta has been seen by other observers, among whom may be mentioned Ercolani and Creighton; the latter, **77b**, 560, directs especial attention to it, in the Guinea pig, but refers it to the entoderm. I consider it probable that it is really ectodermal in the Guinea pig, as in the rabbit. Underneath the

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[1] Leaving the pro-amnion out of consideration.

ectoderm, *b*, to be seen at eleven to thirteen days at the sides on the placenta, is a layer of mesoderm without any cœlom. Now, if my suppositions are correct, then the ectoderm forms at first an independent fold, *ba*, beyond the terminal vein, *vt*; the mesoderm, but not the mesothelium, extends into this fold, which covers the sides of the placenta. The disappearance of the fœtal ectoderm from the surface of the placenta, and the penetration of the fœtal blood-vessels between the glands, are changes which take place during the eleventh day. How those changes occur, observations on the development at that age must decide. Meanwhile let us make shift with two hypotheses. The first is: The whole of the ectoderm attached to the placenta degenerates and is resorbed. Since the uterine epithelium, as observation indicates, has likewise disappeared from the placenta, the mesoderm, *mes*, of the allantois, *all*, is brought into direct and free contact with the connective tissue and degenerated glands of the placenta, and is thus enabled to carry by its own ingrowth the fœtal blood-vessels into the very substance of the placenta. The second hypothesis is that the ectoderm and mesoderm have produced villi, which have grown into the placenta. In favor of this latter hypothesis there is certain evidence which I have not yet alluded to. In the deep portions of the glandular layer of the placentas of both eleven and thirteen one finds narrow loops of epithelium like a tuning-fork in shape; the open ends of the U-loops are towards the top of the placenta; the epithelium composing them is a cylinder epithelium, which gradually thins out towards the upper end of the legs of the U; it differs altogether in appearance from the degenerate gland epithelium, the interiors of the U's contain vessels with fœtal blood; so far, then, these structures might be longitudinal sections of the ends of fœtal villi. Towards the surface of the placenta the epithelium of the loops thins out, and I have not been able to follow them. If we have to do with villi, we must assume that the ectoderm has become exceedingly thin over their basal portions, but is preserved as a thicker layer over their tips, and my failure to trace the villi would be attributable to the imperfection of my preparations and observations. Balancing the *pros* and *cons* leads me to favor the second hypothesis. Let me add that the mesoderm of the embryo is continuous without a break with the interglandular connective tissue;

this statement is correct beyond any doubt, for I have several sections, in each of which the direct passage is observable under the microscope without even displacing the slide. By hypothesis this mesoderm is, however, really separated by a very thin covering of fœtal ectoderm from the uterine tissue, and the whole constitutes a system of villi which have grown down like roots into the placental soil.

That there is no communication between the fœtal and maternal circulations must be deduced from the fact that the two bloods are never mingled in one vessel, although found side by side in adjacent vessels. The separation of the fœtal and maternal blood has already been insisted upon. The full elucidation of the double placental circulation must be left for injections to bring.

In brief: The rabbit embryo is attached to the placenta by the ectoderm, which disappears from the surface of the placenta during the eleventh day; the vascular connective tissue of the allantois grows probably by forming true villi into the placenta, and so comes close to the maternal circulation.

In other rodents the placenta contains fœtal vessels; its surface is covered after a certain stage by a thin epithelium like the mesothelial layer of the rabbit, and by a layer of vascular connective tissue. Hence it seems probable that the structure in the rabbit is typical of the class — compare § 12.

§ 9. **Uterus at thirteen days and three hours.** — The placenta and embryo are considerably bigger than at eleven days, but the structure of the parts is comparatively little changed.

A complete section is drawn in Fig. 9. The longitudinal muscles, *l.m.*, and the circular muscles *c.m.*, form the external covering. They differ in microscopical appearance from the muscles of the resting uterus, but I have not investigated the change in them.

The placenta is very bulky. Its two lobes have begun to form separate protuberances, so that the top of the placenta is no longer a nearly plane surface. The placental surface is covered by the mesothelium, which is a little thicker than in the previous stage, the cells having a greater vertical diameter. Between the mesothelium and the glandular layer, *gl,* is the vascular mesoderm, several of the large vessels of which are shown in Fig. 9. The central fissure, *f,* of the placenta is very deep; it is completely filled with the ingrowth of mesoderm and its accompanying large vessels. At the bottom of the fissure next the outer placental zone, *o.z*, is situated the sub-placenta, *sb.-pl.* The section drawn in Fig. 9 does not show the connection between the fissure and sub-placenta, which appears in sections 208–214 of the same series. The thickness of the mesodermic covering of the placenta has increased very considerably, and the larger vessels are now provided with well-marked muscular as well as endothelial walls. Many of the fœtal vessels run in spaces which stretch down nearly vertically from the placental surface; in some cases the vascular columns can be followed until they enter a cap of epithelium which forms a sort of U. These relations suggest the presence of a series of fœtal villi covered in part by a very thin epithelium, and covered at their tips by a relatively thick epithelium. This interpretation has been discussed in the previous section. Beside the normal-looking epithelium, we find the degenerated glands not much changed from eleven days. The sub-glandular zone, *sgl.z*, shows further enlargement of the blood-vessels, so that they are now larger than those of the outer zone, *o.z*, thus reversing the earlier relative proportions; the multinucleate cells have increased in number and size, and contain more nuclei than at eleven days; they occupy all, or nearly all, the room between the vessels. Towards the outer zone the vessels are surrounded by the uninucleate perivascular cells, but the intervening tissue consists of multinucleate cells, so that there is a boundary region which cannot be assigned strictly either to the subglandular or to the outer zone. The outer zone, *o.z*, is solidly packed with perivascular cells.

The sub-placenta, *sb.pl*, lies still deeper than before, being now close to the outer zone. Its epithelium is undergoing hyaline degeneration, and accordingly is irregularly thickened, and its nuclei are multiplied: the substance of the layer stains deeply with eosine.

The peri-placenta, *P*, differs from that at eleven days, principally in having the perivascular cells as a solid packing throughout the whole of its extent, except just where it adjoins the glandular layer of the placenta. As at eleven days, its covering epithelium is reconstituted on the part towards the sub-placenta, and is in the phase of degeneration towards the placenta.

The ob-placenta, *ob.pl,* shows everywhere a marked growth of its glands; as illustrated by Fig. 10, the glands are follicular; their cavities wide. The glands are not branched or pouched, as the appearances in the sections suggest; they are broad tubes closely packed, and are necessarily cut obliquely in most cases. The rather ragged-looking epithelium is composed of long cylinder cells (Fig. 10), with the nuclei at various heights, and the protoplasm a good deal colored by the cochineal. The connective tissue of the mucosa has also grown, and forms both thin inter-glandular dissepiments and a thickened sub-glandular stratum. In the centre of the ob-placenta the mucosa is still further thickened to make room for the monster cells, which lie for the most part below the glands, but are found also between the glands and in the superficial portion of the muscularis. At one point the ob-placenta is interrupted by a protuberant mass, *x*, resembling the peri-placenta in structure; it consists of crowded perivascular cells with dilated blood-vessels, and is covered by epithelium. As I have seen nothing analogous to this mass in any other specimen of any age, it must be regarded as a singular sporadic variation from the normal processes of development.

The origin of the monster cells I am inclined to seek in the uterine epithelium, as stated in § 7. The appearance of their cell bodies, and of their nuclei at once suggest this origin on account of the similarity with the appearance of the degenerated epithelium elsewhere. We find, also, the smallest monster cells near the epithelium. In Fig. 11 portions of the epithelium of the peri-placenta are represented. The cells are all multinucleate, as seen both in vertical section, *A*, and surface views, *B*; occasionally, but very rarely, there is a cell with the nuclei gathered together in a central mass, with an indistinct line enclosing the bunch, Fig. 11, *c*. These cells are larger than the rest, and their protoplasm is somewhat degenerated. If such a cell were to detach itself, and hypertrophy and the bunch of nuclei to break down, it would resemble a monster cell. Yet I can find no evidence that such a metamorphosis actually takes place in the ob-placenta. In the ob-placenta itself there appear a few epithelial cells with a single nucleus which are slightly enlarged, and are possibly the initial stages of monster cells, but between them and the youngest monster cells observed I have failed to discover any intermediate stages. The difficulty of finding the first stages of the monster cells indicates that their development must be extremely rapid, almost sudden.

§ 10. **Uterus and embryo at fifteen days and four hours.** — The swelling of the uterus has considerably increased; the placenta is larger; the cavity containing the embryo is very much larger; the peri-placenta has grown but little. We notice now that of the six folds of the uterus, the two placental have expanded both in width and thickness to a far greater extent than the remaining four folds, except that the lateral expansion of the two ob-placental folds, by attenuation of their walls, has enabled the ob-placenta to occupy an extent of the circumference of the uterus which is about equal to that taken up by the placenta proper; only about one-sixth of the whole circumference is allotted to the peri-placenta. With the naked eye one can see that the fissure of the placenta has opened so that the surfaces of the two lobes of the placenta now face each other like the sides of a V; the surface of each lobe, though somewhat irregular, is as a whole arched. The glandular zone is perhaps slightly thicker than at thirteen days, but the diameter of the sub-glandular zone is markedly lessened, owing apparently to the opening of the interlobal fissure and the consequent flattening of the surfaces of the lobes. With a hand-lens one easily recognizes that the blood-vessels of the vascular zone of the placenta are of much greater diameter than at thirteen days, while the dissepiments between the vessels are not only relatively but absolutely thinner than before: this observation does not necessarily involve the conclusion that there has been an actual loss of tissue, for the placenta as a whole has increase in bulk. Let us turn now to the microscopical examination.

The placenta differs but little, except in the respects above mentioned, from the stage last described. The mesodermic covering of the placenta is well marked, Fig. 12, *mes*, and the fœtal mesothelium, *msth*, is perfectly distinct; it leaves the placenta at its edge to curl over on to the yolk sack, just as at an earlier stage, Fig. 8, *msth*. The side of the lobe next the periplacenta is clothed by ectoderm essentially as described at eleven days and partially shown in Fig. 8, *ecto*; but the ectoderm is now more irregular than at earlier periods and is thrown into small folds near the point where it is reflected back on the placenta; similar appearances are clearly indicated in Ercolani's memoir, **89**, Tav. IV, Fig. 1, *i*, *i*, for the Guinea pig. It is quite possible that the folds are more developed in the rabbit later. The placental glands are very much contorted, Fig. 12, *gl*, *gl*; very coarsely grandular, with numerous irregular vacuoles and with the nuclei lying for the most part against or near the outer surface of the gland, Fig. 13, *gl*: the nuclei no longer stain deeply as they do during the first stage of the gland degeneration, Fig. 7. In the upper part of the placenta the glands are much narrower and more widely separated than in the deep part of the layer, as can be seen in Fig. 12, which takes in about half of the glandular layer from the surface down; towards the surface the glands often form wide loops, Fig. 12, and join one another, making a network with closed meshes. As regards the supposed fœtal villi, I find the columns of the fœtal mesoderm running down more distinctly than at thirteen days, but as before, the only epithelium which I clearly distinguished, is that in the deepest part of the glandular layer disposed as if covering the tips of the villi. The blood-vessels are very numerous, and some of those above the glands in the fœtal mesoderm are very large, Fig. 12, *v*. It will be remembered that these vessels belong to the fœtal system and that the plexus of vessels, which is so conspicuous upon the surface of a freshly excised placenta, pertains therefore to the embryo. At certain points there rise thin membranes from the surface of the placenta, which carry good-sized vessels: whether these are accidental or constant, I am unable to say. Examined with a still higher power, Fig. 12, the glandular layer shows the peculiarities of its structure still more clearly; the mesothelium, *msth*, upon the surface, though composed of flat cells, has considerable thickness; the mesodermic cells, *mes*, are for the most part spindle-shaped and their processes anastomose; the fœtal blood-vessels, *v*, *v*, come close against the glands, *gl*; if, therefore, there is a layer of fœtal ectoderm separating the fœtal mesoderm from the uterine tissues, it must be very inconspicuous from extreme thinness.

As to the relations of the sub-placenta, my preparations are unsatisfactory.

The sub-glandular layer shows the vascular endothelium advanced in degeneration, the cells projecting far from the surface.

Many parts of the vessels are filled with coagulum, suggesting thrombi formed during life, as has been asserted to occur normally in the human placenta. For the most part, the vessels contain normal blood, save that there is an excess of leucocytes; in some vessels, however, there are large clear refringent bodies which look like vesicles. What these bodies are I am unable to say — possibly they come from breaking down of the endothelium. The multinucleate cells, Fig. 14, are large and very much crowded; they contain each a dozen nuclei, more or less. I have nothing of importance to add to the previous descriptions.

In the outer zone we notice at once that the expansion of the blood-vessels is far less active near the muscularis than further in; indeed, we might subdivide the zone into an outer compact and an inner cavernous layer. The vascular epithelium is far degenerated, Fig. 16; A is a surface view; B and C vertical sections; each cell forms a more or less independent projection; the cells vary extremely in size; the nuclei are either single or multiple; in the former case they may be small and comparatively regular, or large and very irregular in shape; in the latter case they are of unequal sizes. The perivascular cells are innumerable; their appearance is indicated by Fig. 15; but where the blood-vessels are wider, or, in other words, towards the glandular zone, they exhibit signs of breaking down; the signs in question are indistinctness of outline, granular appearance of the protoplasm, and the difficulty of staining the nuclei. As the changes are slight, they are perhaps accidental. It must be left for future examination of later stages to show whether they do break down or not. I also think that there is a tendency for the multinucleate cells to invade the territory of their uninucleate neighbors.

The peri-placenta agrees with the outer zone of the placenta in its parenchymal structure, except as to two points: 1°, it is now invaded to a slight extent by the multinucleate cells, at the spot nearest the placental glands; I have no reason to suppose that these cells actually migrate into the peri-placenta, but presume that they arise *in situ;* 2°, near the ob-placenta there are in some parts young monster cells lying close under the epithelium; the evidence is better here than anywhere else I have observed that the monster cells arise from the epithelium.

The ob-placenta now has monster cells throughout almost its entire extent, but the greatest accumulation is where they first are developed, directly opposite the placenta. In this region (Fig. 17) they occupy not only the connective tissue of the mucosa, *a*, *b*, but also the territory of the circular muscular coat, where they lie, *c*, between the bundles, *musc*, of muscular fibres, which they have forced apart to make room for themselves. The smallest monster cells, *a*, are found nearest the lining epithelium, *ep*; those at the base of the mucosa, *b*, are bigger, but the biggest of all are those which lie in the outer part of the muscularis, *c*; if, therefore, the cells arise from the epithelium and migrate outwards, they must grow while they move. My preparations show in the nuclei of the monster cells certain large, deeply stained fragments which are perhaps chromatine, Fig. 18. Owing to the stretching of the uterine walls, the regenerated glands of the ob-placenta are no longer follicular as at thirteen days (Fig. 10), but are again stretched out, so as to approximate a second time to the form of shallow, open cups, which they had at eleven days (Fig. 6); but where the monster cells have accumulated most (Fig. 17), the only distinct trace of the glands is the irregularity of the free surface covered by epithelium, *ep*.

The embryo and its appendages do not show much alteration in the parts concerning us in the present article. We may, however, note especially two changes in the outer germ layer. 1°. On the strip of ectoderm between the *vena terminalis* of the yolk sack and the points where the ectoderm joins the placenta, there are a number of thickenings, which form small papillæ upon the outer surface of the layer. These outgrowths are solid ectoderm, and like the buds of the villi of the human chorion contain no mesoderm. Whether these structures do become actual villi in later stages, I am unable to say. 2°. Over the yolk sack the ectoderm has become a cylinder epithelium, of which the outer surface is irregular, each cell projecting a little more or less than its neighbors. A similar modification occurs in the opossum according to H. F. Osborn, **61 A**, 378–379, Pl. XVII., Fig. 4, and Selenka (*Entwickelungsges. d. Thiere*, Taf. XXVIII., Fig. 5). It is probable that the ectoderm assumes this modification in other mammals, where it remains attached to the yolk sack owing to failure to form a complete chorion.

§ 11. **Summary.**[1] — In the resting uterus of the rabbit there are six longitudinal folds. The ovum attaches itself on or between the two folds nearest the mesentery, and the placenta is there developed; the two adjacent lateral folds form a cushion (the peri-placenta) about the placenta, but the two folds opposite the mesentery are flattened out by the stretching of the walls to form the swelling to contain the embryo; they constitute the ob-placenta. In the region of the placenta the mucosa undergoes an enormous hypertrophy: there is likewise an enlargement, but much slighter, of the peri-placenta.

The entire epithelium lining the uterine swelling degenerates; its nuclei proliferate, and its protoplasm hypertrophies, becoming at the same time hyaline and granular. The degeneration affects the glands also. The degenerated epithelium becomes vacuolated and in large part resorbed. The process goes on with distinctive features in each of the three primary divisions of the swellings.

The connective tissue increases by hyperplasia in the peri-placenta and to a still greater degree in the placenta, and is transformed for the most part into uninucleate perivascular decidual cells, but also in part, — namely, immediately below the glandular layer of the placenta, — into large multinucleate cells. In the placenta, and to a less extent in the peri-placenta, there is a new formation of blood-vessels, which subsequently enlarge to great size, although their only walls are an endothelium which undergoes rapid hypertrophic degeneration.

In the placental region the uterine epithelium degenerates and disappears, but the glands are preserved as irregular anastomosing rows of coarse granular matter, with numerous vacuoles and scattered nuclei, but without central lumina. Below the glands is a zone containing wide vessels and large multinucleate cells. The outer layer has wide blood-vessels, with numerous uninucleate decidual cells, which arise from the connective tissue cells and arrange themselves in successive coats around the blood-vessels until they occupy the entire room between the vessels.

The embryo is attached at first to the surface of the placenta

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[1] It will be remembered that the observations cover the period of from six to fifteen days *only*, and do not include the eleventh day, when several important developments occur.

only by the ectoderm, to which the mesoderm soon joins itself. As soon as the cœlomatic fissure appears, we can speak of a fœtal chorion adhering to the placenta. When the allantois grows out, it forms the stalk of connection between the embryo and the placental chorion. After the development of the chorion, the free surface of the placenta is, of course, covered by mesothelium (the epithelium of the cœlom). Outgrowths of the chorion penetrate the glandular layer of the placenta; whether these outgrowths are in the form of villi in the sense that they preserve a covering of fœtal ectoderm was not ascertained, although the tips of the outgrowths appear to have such a covering, and there is no mingling of the fœtal with the maternal circulation. The cœlom of the embryo does not extend to the edge of the placenta next the peri-placenta, but the mesoderm does, and is covered by ectoderm.

In the peri-placenta, the glands degenerate and disappear completely, but the covering epithelium is reconstituted except on the part near the placenta. The blood-vessels and connective tissue change as in the outer zone of the placenta, though later. At the fifteenth day a few young monster cells were found near the surface.

In the ob-placenta the degeneration and resorption affect only the surface epithelium and the upper part of the glands; the deep portions remain as a series of shallow cups, having been stretched transversely by the expansion of the ob-placenta; the epithelium of the cups unites into a new continuous layer; the glands grow up into follicles and are again stretched out by the expansion of the walls. Meanwhile there appear monster cells, which probably arise by the hypertrophy and migration of single cells of the epithelium; they are characterized by the granular hyaline appearance of their bodies, by the coarse granulation and large scattered fragments of chromatine of their nuclei, and by their hugeness. The monster cells continue to enlarge and subsequently invade the whole thickness of the annular muscularis. They appear first and are always most numerous directly opposite the placenta, but they are ultimately present throughout the ob-placenta.

The relations of the embryo having been outlined in § 8, with the aid of Plate XXIX., it is not necessary to recapitulate them again.

§ 12. **Comparison with other rodents.** — The history of the rabbit's placenta elucidates also that of the Guinea pig, of which we possess descriptions by Bischoff, Ercolani, **89**, Creighton, **77a**, **77b**, Tafani, **134**, and others. These authors being unaware of the nature of the metamorphoses of the uterine glands, and not knowing the disappearance of the fœtal ectoderm over the placenta, but, on the contrary, seeking for fœtal placental villi, lacked the necessary basis for a correct interpretation. Ercolani was further misled by his erroneous belief that the placental tissues of the mother arise as new formations, not as metamorphosed constituents of the uterine mucosa, but coming after the assumed but non-occurrent complete destruction of the mucosa. Tafani's work betrays gross inaccuracy, for he based his figures and descriptions upon schematic notions, based in their turn upon very superficial, and often entirely false, observations. To justify a judgment so severely unfavorable, it is necessary only to direct examination to some of Tafani's plates. His drawings of the human placenta, for instance, *l.c.* Tav. VII., leave a great deal to be desired; in Fig. 1 the sections of the villi are altogether too large and too few; the separate triangle of tissue at the edge of the placenta does not exist; the decidua is represented without any compact layer, and its gland cavities are made into blood-vessels. The section of the rabbit's placenta (Fig. 2, Tav. IV.) is even more open to criticism, since it is impossible to determine the foundation of observation. Ercolani, on the other hand, was an observer of considerable ability, and his numerous memoirs on the placenta are valuable, although his hypothesis of *neoformazione* led him to adopt an unfortunate terminology which makes it difficult to follow him. Creighton observed with more impartial objectivity. That Bischoff was a first-class observer every one knows; he never leaves any confusion between what he saw and what he inferred; for us he has the disadvantage of having written before the developments of recent histology. On the whole, we probably do best to turn to Ercolani, who figures **89**, Tav. IV., Fig. I., a section of a placenta of a Guinea pig near full term. Let us compare it with the rabbit's placenta.

It is discoidal, pedunculate, and bilobed. The upper surface is covered by a thin epithelium beneath which is a layer of vascular connective tissue, *Z*, extending over the sides of the placenta, *g*, *f*, *f*, and down between the lobes, *q*: the epithelium therefore corresponds entirely with the placental mesothelium of the rabbit. The upper portion of the placenta, *p*, corresponds to the meshwork of degenerated glands in the rabbit's placenta. The layer of epithelium, *i*, *i*, *m*, covering the side of the placenta, corresponds to the fœtal ectoderm in a similar position in the rabbit; at an earlier stage it resembles very closely in appearance what I find in the rabbit (Creighton, **77a**, p. 560, Pl. XIX., Fig. *b*, *c*, *c*, *c*,). Deep down under the space between the lobes of the placenta comes the sub-placenta, Ercolani's cotyledonary organ, *O*, which was compared above with the sub-placenta of the rabbit; the thick pedicle of the placenta, *e*, *n*, *n*, corresponds to the sub-glandular layers of multinucleate decidual cells, which has encroached upon and apparently replaced the outer zone of uninucleate decidual cells, which is present earlier, as it is in the rabbit. At the side of the placenta is the peri-placental thickening, *g.d*, and springing from it the so-called reflexa, *c*, which is probably only the peri-placenta hypertrophied. The reflexa is entirely absent in the rabbit. In regard to what I suppose to be the glands, *P*, neither the descriptions nor the figures of Ercolani suffice to indicate their character.

The interpretation offered differs in nearly every respect from Ercolani's own; and yet though I have no preparations of the Guinea pig's placenta, and am acquainted with the organ only through the publications of others, I think the homologies drawn may be accepted with considerable security; but let me add that I am well aware that their actual justification can come only from the specimens.

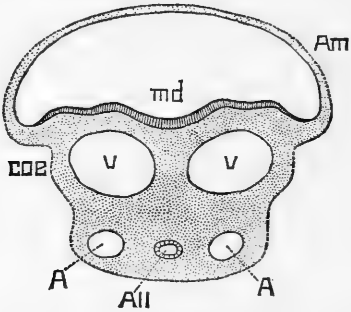
Sections of the rat's placenta near full term show that the structure in that species is strictly comparable to what exists in the rabbit. The surface is covered by a thin epithelium overlaying a vascular connective tissue layer; the vacuolated tubular glands, very much degenerated, occupy the greater part of the placenta, leaving only a thin vascular zone from which the outer zone is lost, and which is therefore occupied solely by the much altered sub-glandular zone of multinucleate cells. There are many differences in details of structure from the rabbit, but the fundamental likeness is self-evident.

As the similarity of the placentæ of various rodents has been noted by previous authors, it is probable that the type of placental organization is the same throughout the class.

II. MAN.

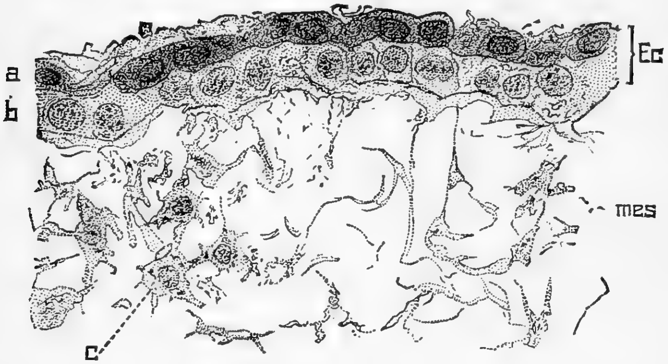
The following observations are of a fragmentary character, but may serve to round out our information in certain respects. Some of the facts have already been recorded in the series of numerous embryological articles contributed to Dr. Buck's *Reference Handbook of the Medical Sciences;* but as that work is for consultation rather than the publication of original observations, it will hardly seem a mistaken repetition if I include here some things already published there.

§ 13. **Allantois and umbilical cord.** — Prof. W. His has shown that the entodermal cavity of the allantois is the terminal stretch of the entodermal canal; the posterior end of the body is prolonged into a mass to which he gives the name of "Bauchstiel" (*Anatomie menschlicher Embryonen,* III., 222–226), and which develops in the same general manner as the body proper, having a rudimentary medullary groove, a somatopleure and splanchnopleure, Cut 2. It is morphologically the hind portion of the body. After its closure and separation from the amnion it appears as the umbilical cord. Its development requires that the umbilical cord should be covered, not by the amnion, as it is almost universally stated, but by an extension of the fœtal epidermis. Histological examination shows that this is the case. The amnion is characterized by the ectoderm remaining a single layer of cuboidal or low cylinder cells, and by the matrix of mesoderm being distinct, owing to its high refran-



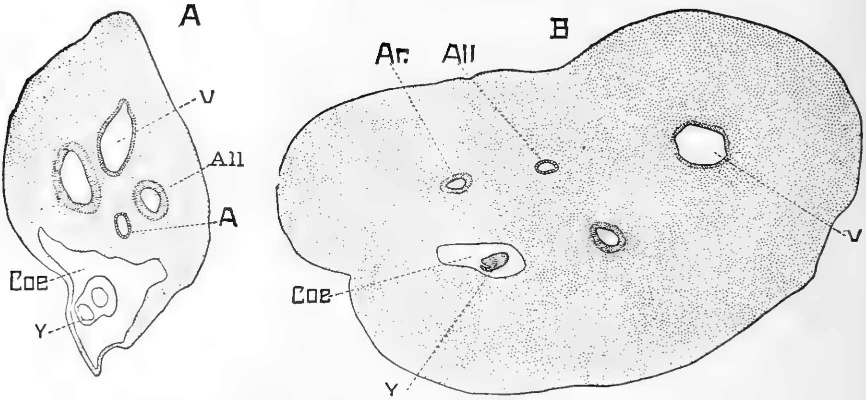
Cut 2. — Diagrammatic section of the Bauchstiel of a human embryo, modified from W. His. *Am,* amnion; *md,* medullary groove; *v, v,* veins; *A, A,* umbilical arteries; *All,* allantois; *coe,* cœlom.

gibility. The fœtal skin is characterized by the ectoderm becoming many layered, while the cutis remains for a long time undifferentiated from the mesoderm below, and the matrix is of low refrangibility. In comparing the ectoderm of the umbilical cord with the skin, therefore, we do not expect to find any differentiated cutis. The epithelium of the cord is at first, of course, single layered, the condition which is permanent over the amnion. In the cord of a three-months embryo, Cut 3, I find the two-layer stage. The outer layer is granular, and in some parts each cell protrudes like a dome. Dome cells also appear on the young epidermis, and as I learn from Dr. J. T. Bowen, who has been investigating the subject in my laboratory, are probably the precursors of the epitrichium. The cells of the inner layer are larger and clearer than those outside. By the fifth month the epithelium is distinctly stratified, and the superficial layers consist of flattened cells similar to those of the horny layer of the skin at an early stage. The ectoderm of the cord agrees therefore entirely with that of the embryo proper in its general development, but the differentiation proceeds more slowly, so that at any given age the ectoderm of the cord is at a less advanced stage than that of the embryo.



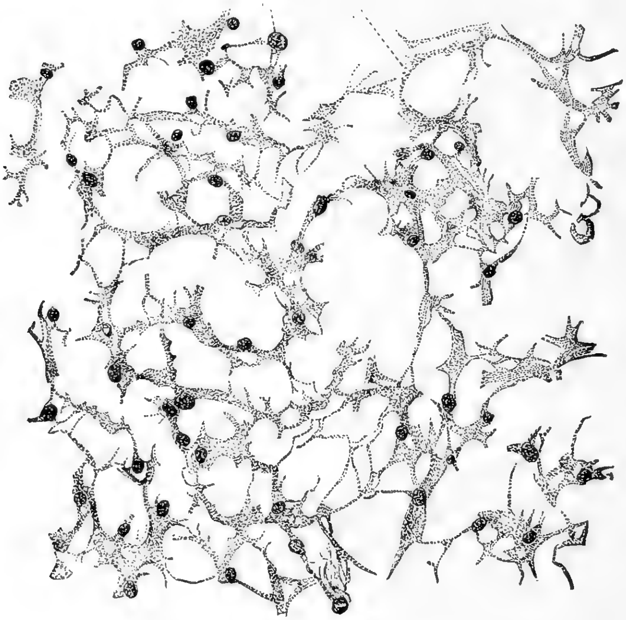
Cut 3. — Epithelial covering of the umbilical cord of an embryo of three months. × 545 diams.

The appearance of the cord in cross-sections is instructive. Cut 4, *A*, is a section through a cord of sixty days; the right umbilical vein is already aborted; the cœlom, *coe*, is a large cavity, and contains the yolk stalk, *Y.S*, with its two vessels,



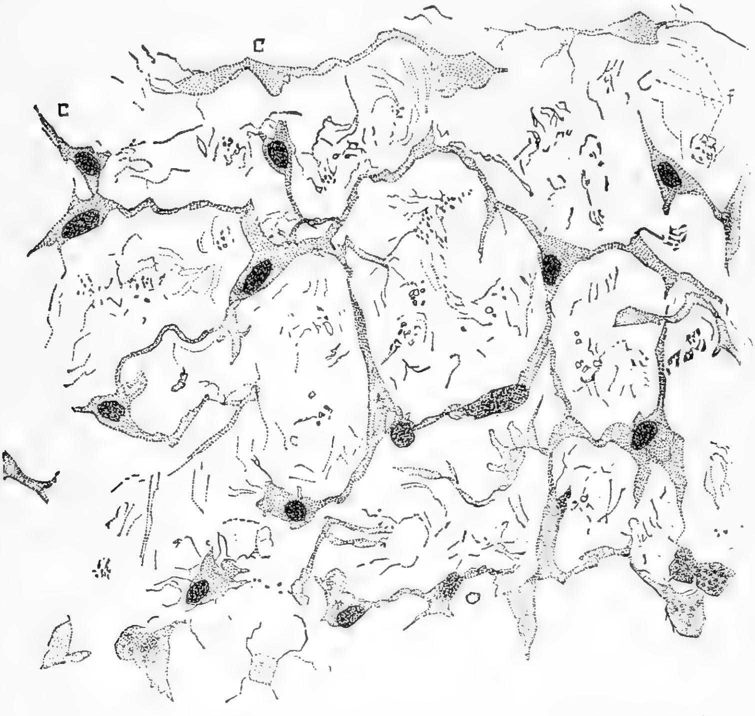
Cut 4.—Two sections of umbilical cord. A, at sixty days; B, at three months; *V*, vein; *Ar*, artery; *All*, allantois cavity; *Coe*, cœlom; *Y*, yolk sack; × 22 diams.

and its entodermic cavity entirely obliterated. Near the embryo the cœlom may become much enlarged, and is often found during the second month and even later to contain a few coils of the intestine, as has been long known. Above the body cav-



Cut 5.—Connective tissue of the umbilical cord of an embryo of 21mm; × 540 diams., stained with alum-cochineal, and eosine.

ity is the duct of the allantois, *All,* lined by entodermal epithelium; and in this region are situated the two arteries and single vein; the section is bounded by ectoderm.[1] The further development of the cord depends upon three factors: 1°, the growth of the connective tissue and blood-vessels; 2°, the abortion of the cœlom, yolk stalk, and allantoic duct in the order named; 3°, differentiation of the connective tissue and of the ectoderm.



Cut 6. — Connective tissue of the umbilical cord of a human embryo of about three months, × 511 diams. Stained with alum-cochineal, and eosine.

The growth and differentiation of the mesoderm proceeds rapidly, encroaching upon the cœlom, which is obliterated (early in the fourth month). At first the connective tissue, Cut 5, is composed merely of numerous cells embedded in a clear substance; the cells form a complex network, of which the filaments and meshes are extremely variable in size; the nuclei are oval, granular, and do not have always accumulations of protoplasm about

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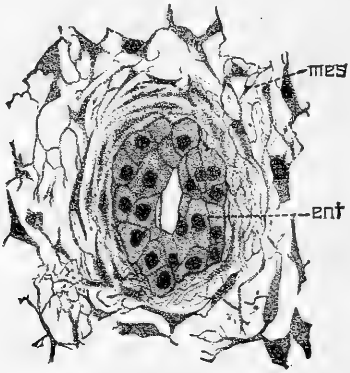
[1] The ectoderm is often wanting, owing to its frequent destruction *post mortem.*

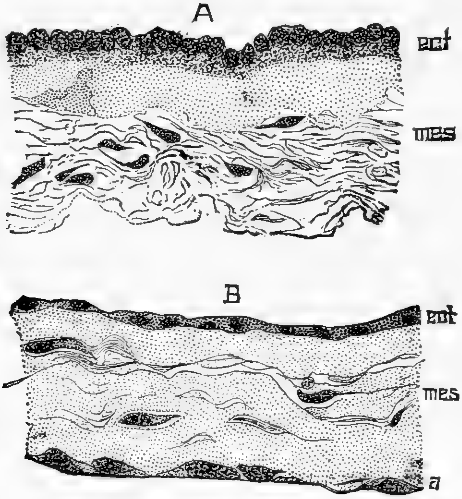
them, forming main cell bodies. I notice, also, a few cells which I suppose to be leucocytes, but see no other structures. By the end of the third month the cells have assumed nearly their definite form; the protoplasm has increased in amount, and forms a large cell body around each nucleus, Cut 6. The network has become simpler and coarser, the meshes bigger, and the filaments fewer and thicker; in the matrix are numerous connective tissue fibrils, not yet disposed in bundles, except here and there; as they curl in all directions many of them are cut transversely, and therefore appear as dots. In older cords there is an obvious increase in the number of fibrils, and they form many bundles. In the cord at term the matrix contains mucin, and may be stained by alum hæmatoxylin; at what period this reaction is first developed I have not ascertained. I have observed nothing to indicate the presence of special lymph channels in the cord at any period, but I have not investigated the point. Tait's lymph channels are merely the intercellular spaces.



Cut 7.—Section of the allantois from the umbilical cord of an embryo of three months; *ent*, entoderm; *mes*, mesoderm. × 340 diams.

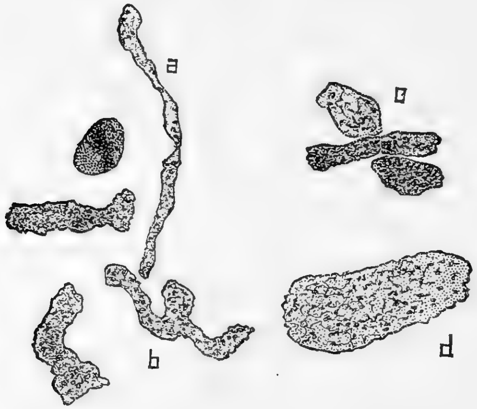
The tube of allantoic entoderm increases very little in diameter after the second month; compare A and B, Cut 4. It is very persistent, appearing usually even in the cord at full term, at least in the proximal end, according to Kölliker (*Entwicklungsges.* 2te Aufl., p. 34). After the second month it is a small group of epithelioid cells, with distinct walls, irregularly granular contents, and round nuclei; around the cells, *ent*, which may or may not show a remnant of the central cavity, there is a slight condensation, *mes*, of the connective tissue to form, as it were, an envelope. This structure has been regarded by Ahlfeld and others as the persistent yolk sack. I think the correct interpretation was first suggested by Kölliker.

§ 14. **Amnion.** — The tissues of the amnion do not progress beyond an early embryonic stage; the ectoderm remaining at the one-layered stage, the mesoderm preserving much of the primitive matrix. Emery (*Arch. Ital. Biol.*, III., 37) has directed attention to the primitive homogeneous matrix of the vertebrate mesoderm, and especially to the separate sub-epidermal layer of the embryo, which contains no cells at first. In the human amnion there is a non-cellular layer under the epithelium, as is well shown in Cut 8, A and B. Sometimes this layer is invaded to a certain extent by connective tissue cells, B; in other cases the portion of the matrix towards the chorion acquires a fibrillar character, A, as if partially resorbed, but in no case have I seen the matrix entirely altered from its primitive character. The cells of the mesoderm lie in lacunæ; they are flattened in the plane parallel to the surface, and hence in vertical sections, Cut 8, appear more or less fusiform. They present no special features, so far as I have observed, to distinguish them



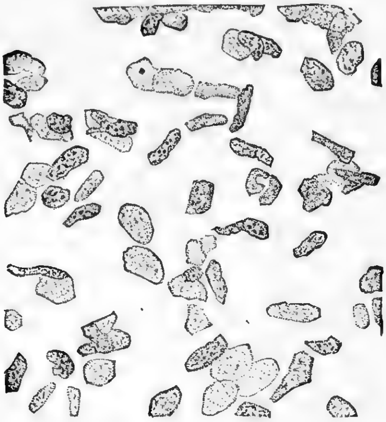
Cut 8. — Two sections of the placental amnion: A, from an embryo of the eighth month; B, at term; *ect*, ectoderm; *mes*, mesoderm; *a*, layer of mesodermic cells. × 340.

from other embryonic connective tissue cells. Their bodies have little affinity for coloring-matters, hence it is difficult to follow the processes by which the cells are united. Their nuclei are at first round or oval. After the third month they often show a great variety of alterations in shape and size, Cuts 9, 10; some of the nuclei are then very large, with a distinct net-work, *d;* others are smaller and differ but slightly from the normal; some are very irregular, *b*, and others again strangely elongated, *a;* many other forms beside those represented in Cut 9 are to be found. The changes indicated I consider of a degenerative character, and in fact many of the nuclei are breaking down, for one finds in some specimens every stage between a nucleus and scattered granules, — nuclei, nuclei with indistinct membranes, nuclei without membranes, masses of granular matter, clusters of granules crowded together, and finally other clusters more or less scattered. This degenerative process may be compared with that described by Phisalix (*Arch. Zool. Expt.*, Sér. II., T. III., 382) as occurring in the blood cells of the spleen of teleosts. Compare also the chromatine degeneration observed by Flemming to occur in ova of the vertebrate ovary (*His and Braune's Archiv.* 1885, 221–244). In the human amnion the nuclear degeneration described is not always to be recognized so clearly, although the nuclei in all amnia older than three months, which I have observed, are more or less



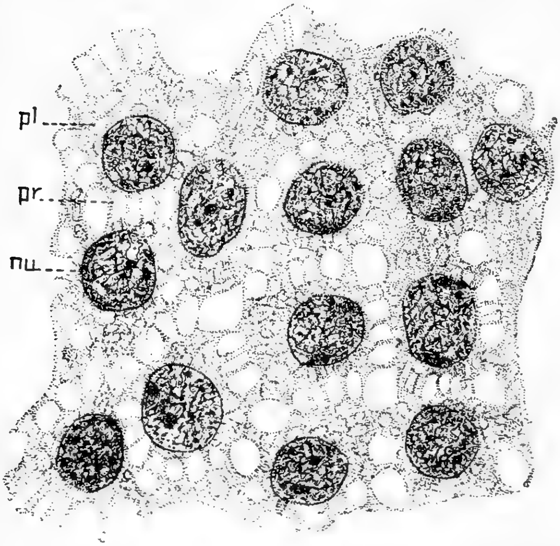
Cut 9. — A natural group of nuclei from the mesoderm of the amnion of a fœtus of the fifth month. × 1225 diams.

irregular and distorted. Finally it is to be added that not infrequently the cells form a distinct epithelioid layer upon the surface of the amnion next the chorion, as represented in Cut 8, B, *a*.



Cut 10. — Mesodermic nuclei of the amnion of an embryo of about four months. × 713 diam.

The epithelium of the amnion varies in appearance, as seen in transverse sections. Usually the cells are cuboidal or low cyl-



Cut 11. — Surface view of the amniotic epithelium of an embryo of 144 days; stained with alum — hæmatoxyline, and eosine. *pl*, protoplasm; *pr*, intercellular processes; *nu*, nucleus. × 1225 diams.

inders, Cut 8, A, each one with a rounded top, in which is situated the more or less nearly spherical nucleus; sometimes, however, the nuclei lie deeper down. Less frequently the epithelium is thin, Cut 8, B, and its nuclei, which are transversely elongated, lie further apart. It is probable that these differences are not structural, but conditional upon the greater or less degree to which the amnion is stretched. I have observed no constant differences between the placental and the remaining amnion. The most interesting peculiarity of the epithelium is best seen in surface views; namely, the intercellular bridges. They display themselves with a clearness which I have never seen in other epithelia; see Cut 11.

The nuclei, *nu*, are relatively large, rounded with distinct outlines; they have a more or less well marked intra-nuclear network, with thickened nodes, and a small number of deeply stained granules, which are probably chromatine. Each nucleus is surrounded by a cell body, *pl*; and the adjacent cell bodies are separated from one another by clear spaces. With high powers, as represented in the cut, one sees that these spaces are separated from one another by threads of material, *pr*, stretching across as bridges, connecting neighboring cells. Examined attentively, the protoplasm of the cells exhibits a vacuolated appearance. One is thus led to view the epithelium as a sponge work of protoplasm somewhat condensed around each nucleus; according to this interpretation the intercellular spaces are large meshes of the sponge work, and the intercellular bridges are protoplasmic. A recent paper[1] by M. Manille Ide, which I owe to the kindness of the author, brings a series of interesting observations to show that the intercellular bridges of the Rete Malpighi of the mammalian epidermis are not protoplasmic, but processes of the cell membranes. This paper has led me to reexamine my preparations of the amniotic epithelium, but I have been unable to find in them any indications of membranes around the cells or reasons for considering the intercellular bridges as other than protoplasmatic in constitution. Whether this result is due to the imperfection of my preparations, or is in accordance with the truth, must be decided by further investigation.

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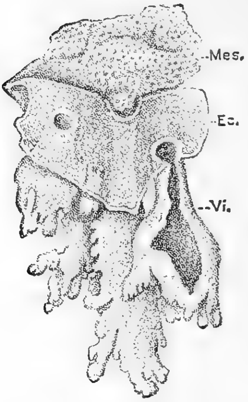
[1] Manille Ide, La membrane des cellules du corps muqueux de Malpighi. *La Cellule*, IV., 2me fasc., 1888.

Meola, **59**, ascribes a much more complex structure to the amnion than his predecessors, in which he is followed by Viti, **21**. Both of these authors subdivide the mesodermic stratum into three layers: a *lamina connetivale*, next the ectoderm, a *sostanza intermedia*, and a *membrana limitante*. As to the histological details, Viti differs somewhat from Meola, but agrees with him in finding a histological distinction between the three layers enumerated. The extent to which I can distinguish three layers is indicated by the description of the mesoderm given above: I have been unable to find the marked structural differences affirmed by Viti. Viti's paper is to be commended for its excellent historical reviews, particularly for his summary of the various theories as to the origin of the amniotic fluid.

§ 15. **Chorion.** — The human chorion has been the object of greater misconception than perhaps any other organ of the body. Even at the present time there prevail numerous false conceptions concerning it, nor do I know of any text-book which gives a satisfactory or even tolerably correct account of its structure. This singular confusion is not due to deficiency of observations, for from the vast literature of the subject (by trusting the accurate observers, such as Coste, Farre, Kölliker, Turner, Langhans, Waldeyer, etc.), we may cull a fairly complete and exact history of the development of the chorion. But the literature of the chorion consists chiefly of papers of little value, and often remarkable for the gross crudeness of the observations they record, and for the proofs they are of their author's ignorance of other and better investigations. It appears that the anatomists and physiologists, by a species of tacit understanding much to be regretted, have regarded the uterus and placenta outside of their province, and have left the investigation of the anatomy and functions of these organs to gynæcologists and others, whose capacities have lain rather in the direction of medical practice than of original research, although among them are some notable exceptions. The majority of the practitioners who have written on the uterus and fœtal appendages have done at least as much harm as good. It would be a sheer waste of time to subject this mass of literature to a critical revision in order to extract from it what little there may be of value. I have, however, read a large number of the articles, and studied those which seemed worthy of it. Upon this course of reading and a study of my own extensive material I have based the following history of the chorion, which passes briefly over what is known, and dwells upon what is founded on my own observations.

The human chorion as I have defined it[1] is "the whole of that portion of the extra-embryonic somatopleure, which is not concerned in the formation of the amnion." The human chorion is remarkable for its very early complete separation from the yolk sack, and for its precocious development of villi. Both of these developments had already taken place in His' youngest embryo, and in Reichert's ovum, which is supposed to be normal and the youngest known, there were chorionic villi, though no embryo was distinguished. Reichert's description is not satisfactory, his long memoir[2] being principally concerned with speculations.

The villi of the chorion, as shown long ago by the observations of Coste, are formed at first only by the ectoderm. I reproduce here Fig. 6, of Pl. II., referring to the human species from Coste's great work. The hollowness of the villi and their clumsy shape are to be especially noted. The mesoderm grows into the villi subsequently. The branches of the villi grow out in a similar manner, the process being led, as it were, by the ectoderm. Orth, in a special paper, **118**, has used these facts to argue against Boll's *Princip des Wachsthums*. Kollman's observations[3] on the growth of villi during the fourth week are particularly instructive. The outgrowth of the branches is very rapid and occurs with every degree of participation of the connective tissue. The two extremes are: 1°, a bud consisting wholly of epithelium, which may become a process with a long, thin pedicle, and a thickened free end remaining entirely with-



Cut 12. — Portions of the chorion of an embryo supposed to be about eighteen days; *mes*, mesoderm; *ec*, ectoderm; *vi*, hollow villi. After Coste.

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[1] Buck's *Reference Handbook, Medical Sciences,* — Art. Chorion.

[2] Reichert, *Berlin Akad. Abhandlungen*, 1873.

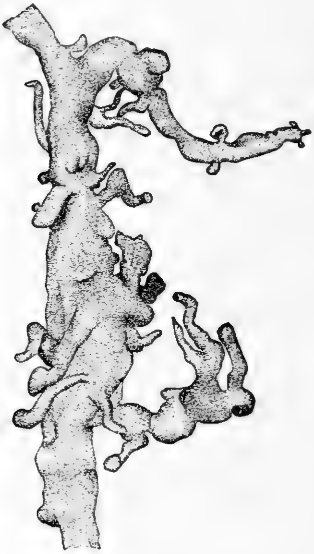
[3] Kollman, *Arch. Anat. Physiol. Anat. Abth.*, 1879, 297.

out mesoderm; 2°, a thick bud with a well-developed core of connective tissue, and having a nearly cylindrical form. Between these extremes every intermediate state can be found. Other observers have noted this peculiar manner of growth, which I have found still going on in the placental chorion during the fourth month. Robin, **125**, appears also to have crudely observed both the young hollow villi, and the solid epithelial buds. The blood-vessels he traces to the division of the cavity of the villi into an artery and a vein; from the nature of things he offers no observations in support of this assertion.

Only the tips of the villi touch the surface of the decidua, either at first or subsequently, except of course, over the chorion læve during the abortion of the villi. The tips of the villi are attached to the uterine surface; they penetrate the decidua for a short distance, but even in the placental area at the close of gestation, the penetration is slight, and the villi make their way only into the surface stratum of the decidua serotina. There is no evidence of any sort that the villi penetrate the glands at any period. The relation of the villi to the decidua has now been so accurately ascertained, that there can be, I think, no longer any question whatsoever on this point. The best discussion is by Langhans, **110**, p. 231 ff.

Cut 13.—Isolated terminal branch of a villus from the chorion of an embryo of twelve weeks.

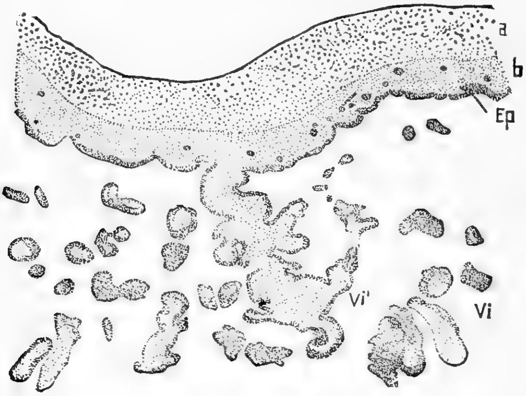
The shape of the villi varies according to the part of the chorion and the age of the embryo. They gradually abort over the chorion læve, and gradually grow over the chorion frondosum. Let us begin with the placental villi: At first they are short, thick-set bodies of irregular shape, as shown in Cut 12; at twelve weeks their form is extremely characteristic, Cut 13; the main stem gives off numerous branches at more or less acute angles, and these again, other branches, until at last the terminal twigs are reached; the whole of the space between the chorion and decidua is occupied by these ramifications; the branches and twigs, as the illustration shows, are extremely irregular and variable, although in general they may be described as club-shaped, being more or less constricted at their bases. The branches may be bigger than the trunk which bears them, or of any less size; some of the smallest are merely slender outgrowths of the epithelial covering of the villus, such as have already been alluded to. Gradually there is a change. During the fifth month we find the irregularity, though still very marked, decidedly less exaggerated, Cut 14; the branches tend to go off at more nearly right angles; one finds very numerous free ends, as of course only a small proportion of the branches touch the decidual surface; the branches, too, are less out of proportion to the stems, less constricted at their bases, or, in other words, less remote from the cylindrical form; the awkward cucumber shapes of the twelfth week are no longer found except here and there. The change continues in the same direction; that is, is towards



Cut 14.—Villous stem from a placenta of the fifth month. × 9 diams.

Cut 15.—Terminal villi of a placenta at full term. The little spots represent the proliferation islands of the covering epithelium.

greater regularity of configuration. It is hardly necessary to describe the intermediate phases that have been examined, but it will suffice to describe the form at full term, Cut 15, when the branches are long, slender, and less closely set, as well as less subdivided, than at earlier stages; they have nodular projections, like branches arrested at the beginning of their development; there are numerous spots upon the surfaces of the villi; microscopical examination shows that these spots are *proliferation islands*, as we may call them, or little thickenings of the ectoderm with crowded nuclei. It appears that not all the villi change to the slender form; for some villi, having still the earlier, thicker form, are found even in the mature placenta, a fact already noticed by Jassinsky, **105**, 346. These thick villi usually show also a distinct "cellular layer" in their ectoderm, a peculiarity to be considered below again. Seiler, **131a**, has given figures of the villi at various ages, but fails to show the characteristic forms. Langhans has observed the alteration in the villi, **110**, 199, and even justly remarks that many of the villi in so-called "moulds" are not pathological, as they have been frequently considered, but normal young villi. The differences in the villi, according to age, are very conspicuous in sections. The sections should of course be made so that the fragments of the villi will remain *in situ;* imbedding in celloidine is convenient for this purpose; if this end be attained, one

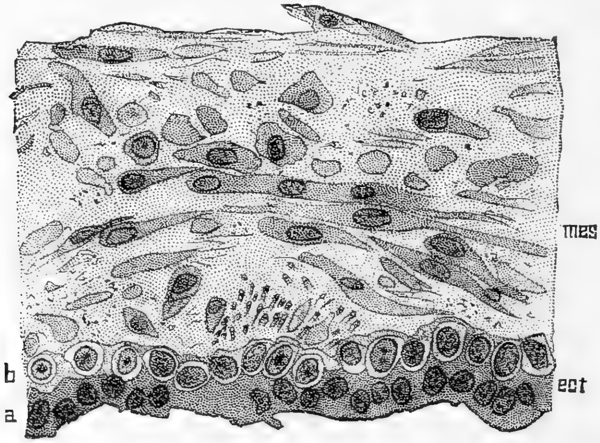


Cut 16. — Section of the chorion at three weeks. *a*, layer of coagulum; *b*, mesoderm of chorion; *Ep*, epithelium, also extending over the villi; *Vi* and *Vi'*; the mesoderm, *b*, contains a number of blood-vessels, nearly all in transverse section. × 65.

finds below the chorionic membrane numerous sections of villi; if the specimen be a young chorion, — first to third month, — the villi are large, with a good deal of room between them; their outlines are very irregular, and there are relatively few small branches (Cut 16). The older the specimen, the larger the proportion of small branches. In an old chorion — seventh to ninth month — the number of small villi of nearly uniform size is very striking (see the figure of a section through a placenta *in situ*, given in Cut 35).

Cut 17. — Aborting villus from a chorion of the second month.

The abortion of the villi of the chorion læve takes place by an arrest of development and a subsequent slow degeneration of the tissues, which lose all recognizable organization in the protoplasm, and to a large extent of the nuclei; at the same time they alter their shape (Cut 17), becoming more and more filamentous; by the fourth month only a few tapering threads, with very few branches, remain. The villi disappear almost completely from the læve, except near the edge of the placenta, where they are to be found, even in the after-birth, imbedded in



Cut 18. — Section of the chorionic membrane of an embryo of three weeks; stained with osmic acid; *mes*, mesoderm; *ect*, ectoderm; *a*, outer, *b*, inner layer of ectoderm. From a section prepared by Prof. Theodor Langhans. × 445 diams.

the degenerated epithelium of the chorion and the upper layers of the decidua, as shown in Cut 25, *vi*, the epithelium and decidua being so fused at this point that it is impossible to determine any line of demarcation between them.

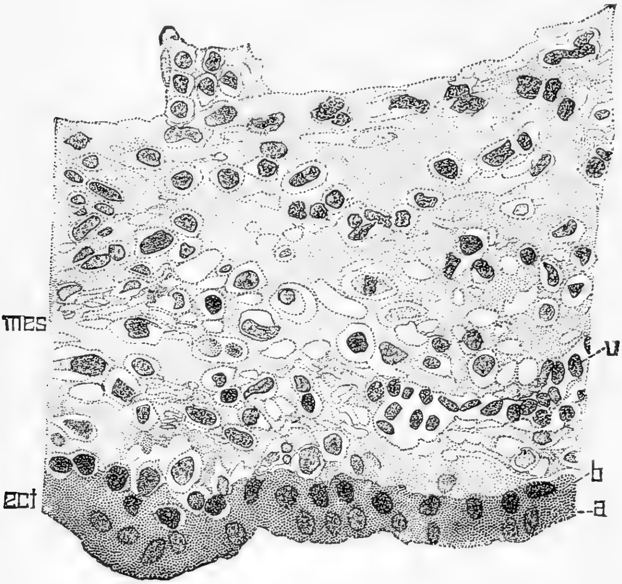
The chorion, being a portion of the somatopleure, consists, of course, of two primary layers, the mesoderm and ectoderm. During the second half of the first month, the earliest period concerning which we have any accurate knowledge, the mesoderm is already a vascular layer of considerable thickness (Cuts 16 and 18, *mes*), and the epithelium (ectoderm) has two layers of cells (Cut 18, *a* and *b*) ; of which the outer is the darker in specimens stained with osmic acid, carmine, cochineal, or hæmatoxyline, and has also smaller and more granular nuclei. The same distinction exists in the two-layered stage of the ectoderm of the umbilical cord (Cut 3), and of the fœtal skin. Hitherto most authors have entirely overlooked the inner layer at early stages. It was first clearly recognized by Langhans, who directed attention to it in a special memoir, **111**, he having already described its later history, **110**. In some earlier writers are allusions to the layer. Kastschenko, in his paper on the chorionic epithelium, has also described it, although he has not followed its history very far. The interpretation to be offered seems to me clearly to be, that the chorionic epithelium advances in its differentiation to a stage equivalent to the two-layered stage of the epidermis and there stops ; whatever further change occurs is degenerative.

The two primitive layers of the chorionic epithelium have been more or less clearly observed at later stages by several anatomists, and have been variously interpreted. Ercolani and Turner regard them as absolutely distinct, assigning the deep layer to the chorion as its true and only epithelium, and the outer layer to the uterus, thus enabling themselves to conceive the villi as covered by a maternal as well as a fœtal epithelium, so that maternal blood found between the villi is still within the maternal tissue. After accepting the outer layer as maternal, the question as to its origin still remained. Some authors affirmed it to be the uterine epithelium, others to be the lining of expanded uterine blood sinuses. So far as I am aware, no one has made observations to show by the developmental history of the layer, that one or the other of the last mentioned hypotheses is correct. When we consider the precision and exactitude of Kastschenko's observations, which actual specimens enable one to verify, there is in my judgment no reason left for differing from the conclusion that both layers are parts of the fœtal ectoderm.

Governed by the difficulty of accounting for the presence of maternal blood in the intervillous spaces, and therefore apparently outside the maternal tissues, several investigators have been led to seek for at least an endothelium outside the chorionic epithelium. Some authors, as for instance Winkler, have asserted the existence of such an endothelium, but after a prolonged and careful search, I fail to find anything of the kind, and in this result it seems to me the best observers are agreed.

The conclusion, I think, may now be safely formulated that the chorion is covered externally by the fœtal ectoderm, and has no other covering in any part except, of course, where the chorion læve rests upon the surface of the decidua, and where the tips of the villi touch the serotina; but the morphological distinction holds, and the decidua is no more the covering of the chorion, than are clothes morphologically the covering of the body. I believe further, on grounds stated below, that the conclusion just formulated holds true of the chorion at all periods.

The further history of the chorionic mesoderm is so fully given by Langhans in his invaluable memoir, **110**, and Kastschenko, **107**, that there is little to be added. In the earliest stage I have been able to examine, an ovum of the third week, the matrix of the chorionic connective tissue, in a preparation stained with cochineal or hæmatoxyline, and imbedded in paraffine for cutting, appeared hyaline and glistening, owing to its refrangibility (Cut 19); it has lacunæ in which the cells lie; the cell bodies are either shrunken or colorless, so that lacunæ, except for the staining of their contained nuclei, are clear and light. This appearance I find again in specimens a little older. The image is entirely distinct from that of the same layer later, for then the cells are stained darker than the matrix, which at the same time has lost its homogeneous character, and acquired a fibrillated look. Very different from my own sections are several which I owe to the kindness of Professor Langhans of Bern, and which that distinguished investigator informs me are from a three-weeks ovum, which had been preserved in osmic acid (see *ante*, Cut 18). In Professor Langhans' preparations the cells are all stained much deeper than the matrix; they have an elongated form, and run in various directions more or less parallel to the epithelium *ecto;* hence many of them are cut transversely or obliquely. Whether the differences noted are due to the methods of preparation must be decided by preserving the same chorion in part with osmic acid, in part with Müller's fluid or picrosulphuric acid, the latter being the reagents I have used. In specimens of the tenth week, the matrix of the chorionic mesoderm has quite altered in character, being no longer homogeneous, and at the same time it has increased in thickness. For the most part the matrix stains lightly, and where it is lighter it contains fibrils of extreme fineness, and running curly courses; there are also streaks of lightly stained matrix, giving the impression of fibres resulting from portions of the primitive colorable matrix being left. In other parts of the layer the primitive matrix is still present, and we find a homogeneous well-colored basal substance, the cell lacunæ of which appear light by contrast, as in Cut 19. One can distinguish also the



Cut 19. — Section of the chorionic membrane of an ovum supposed to belong to the third week; *ect*, ectoderm; *mes*, mesoderm; *a*, outer, *b*, inner layer of ectoderm; stained with alum-cochineal. × 445 diams.

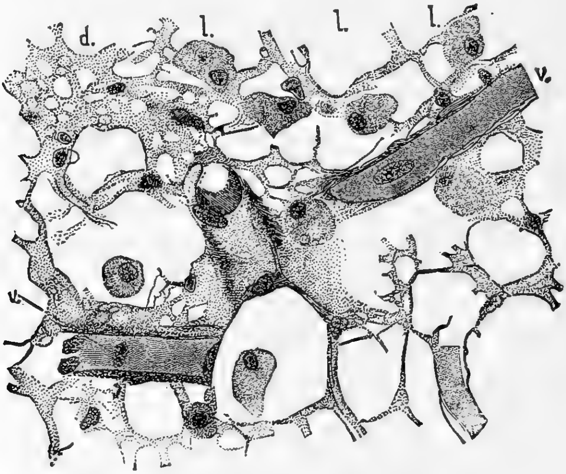
commencement of the perivascular coats, at least of the larger vessels, the matrix being quite dense around them, and the cells elongated almost into fibres, and possessing a slightly increased affinity for coloring-matters. The larger blood-vessels and unmetamorphosed part of the layer occupy a middle portion between the two surfaces, but the smaller blood-vessels lie near the ectoderm (compare Cut 19, *v*), thus presaging the formation of Langhans' vascular layer (*Gefässschicht*). The development of the mesoderm of the *chorion læve* stops at about this stage, or at the stage when the matrix has completely changed from its first state; in the region of the frondosum, however, development proceeds much further by the production of fibres throug out the whole of the layer; usually, but not invariably, the fibres become much more numerous near the ectoderm than in the inner part of the mesoderm, thus differentiating a well-marked sub-epithelial fibrillar layer, Cut 20, *fib*, from the deeper and wider stroma, *Str.* The fibrillar layer is that commonly spoken of as the connective tissue layer of the chorion: for details of its structure, including the "*Gefässschicht*," see Langhans and

Cut 20.—Section of the amnion and placental chorion of the fifth month. *Ep*, amniotic epithelium; *Am*, amnion; *Str*, stroma; *Fib*, fibrillæ layer; *fbr*, fibrine layer; *c*, cellular layer; *Vi*, villi. (From a section cut in celloidine, and stained with Weigert's Hæmatoxyline. The drawing is only approximately correct as to details. × 71 diams.).

Kastschenko. The inner layer, *Str*, is called the *Gallertschicht* by many German writers, and seems to be what Kölliker (*Entwickelungsgeschichte*, 2te Aufl., p. 322) designates as "Gallertgewebe zwischen Chorion und Amnion"; it usually contains a considerable number of large granular wandering cells. Jungbluth, **106a**, describes a network of capillaries, which exist during the first half of pregnancy, apparently in the upper part of the stroma, — *i.e.* next the amnion — but I fail to find any. Where the amnion comes into contact with the chorion the adjacent parts of the two membranes are more or less loosened, forming a network of strands by which the membranes are united: most of the uniting strands appear to belong rather to the chorion than to the amnion. This loose tissue is perhaps that which Kölliker designates as a *Gallertgewebe* distinct from the chorion.

Although the chorion bounds the cœlom, I have observed no mesothelium upon its mesodermic surface; but I have not made search for it by any special methods. In the rabbit, it will be remembered, the mesothelium is very evident over the placenta, but the rabbit differs from man by the absence of union between the amnion and chorion. Nor have I been able to find any basement membrane, properly so called, under the chorionic ectoderm. As to the appearance which suggests it, I accept Kastschenko's explanation, **107**, 455.

The mesoderm in the villi is differentiated otherwise than that of the membrane of the chorion. In the youngest stage I have examined there is some of the primitive matrix present in the villi; and I presume that earlier the whole mesoderm has the same character. In my specimen (three weeks) the change is progressing. I have not succeeded in satisfying myself as to the process of change which takes place, but I think it probably essentially as follows: The cells gradually develop large bodies and acquire a more decided affinity for coloring-matters; meanwhile vacuoles appear in the matrix, presumably by its modification into a new substance; the vacuoles increase in size and number, transforming the matrix into a network and ultimately causing its total disappearance, leaving the intercellular spaces filled entirely with the new substance, which has come from a metamorphosis of the original matrix; probably this new substance is more or less fluid, since wandering cells are scattered freely through it. Leaving this half-hypothetical history, let us pass on to direct observations. In the placental villi of embryos of four months and older, the mesoderm exists in two principal forms, — adenoid tissue and fibre-cell tissue around the blood-vessels. The adenoid tissue, Cut 21, is that of which the supposed development has just been sketched; it may be considered as the proper tissue of the villus. It consists of a network of protoplasmic threads, which start from nucleated masses (cells). There are many large meshes, which are partly occupied by the coarsely granular wandering cells, *l*, *l*, which are scattered about, and are usually present in large numbers. About the capillaries the network is much more finely spun. Kastschenko, **107**, 454, found the wandering cells most abundant near the epithelium, but I have noticed no such peculiarity, except that they do not often enter the dense perivascular tissue; and as the blood-vessels are centrally situated, the adenoid tissue and the wandering cells in it are of course more peripheral. It seems to me that the leucocytes are distributed more or less evenly throughout the adenoid tissue. I fail to recognize any intercellular substance. The abundance of nuclei deserves special mention. Around all the non-capillary vessels the mesoderm is very different, for it exhibits distinct intercellular substance, with a ten-



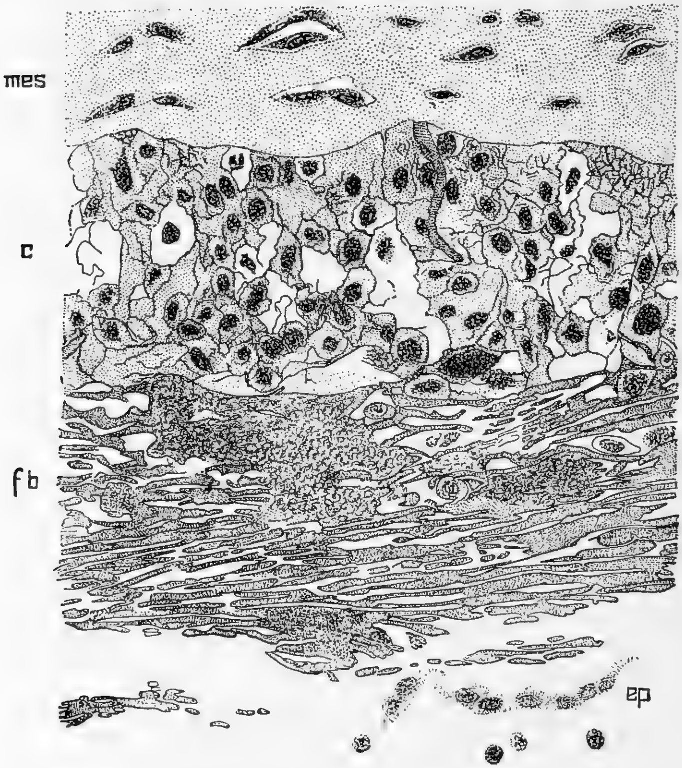
Cut 21. — Adenoid tissue of a villus from a placenta of four months. *l*, *l*, *l*, wandering cells; *v*, *v*, capillary blood-vessels; *d*, finer meshwork from near a capillary. × 352 diams.

dency to fibrillar differentiation in quite a wide zone around the blood-vessels; in this zone the cells become elongated and irregularly fusiform; around the larger vessels the cells are grouped in lamina, making the structure similar to that already described in the walls of the vessels of the umbilical cord; after the perivascular coats acquire a certain thickness, the cells of the inner layers are more elongated, more regularly fusiform, and more closely packed than those of the outer layer; the transition from the denser to the looser tissue is gradual. We are perhaps entitled to recognize in the denser inner layer the *media*, in the outer looser layer the *adventitia*, although neither of the layers has by any means the full histological differentiation characteristic of the like-named layers of the blood-vessels of the adult.

The epithelium of the chorion becomes differentiated in three different ways: 1°, upon the chorion frondosum; 2°, upon the chorion læve; 3°, upon the villi. For a correct knowledge of the remarkable changes which the epithelium undergoes, particularly in the placenta, we are indebted to the remarkably exact investigations of Langhans, **110** and **111**. This author left two points of importance unsettled; namely, the origin of his "*Zellschicht*," and of the "*canalisirtes Fibrin*." Kastschenko has traced the cellular layer (*Zellschicht*) to the epithelium, as already stated: compare pp. 463-469 of his memoir, **107**. My own observations show, I think conclusively, that the canalized fibrine arises through a degenerative metamorphosis of the epithelium, which begins in the outer layer and may invade the inner layer (Langhans' *Zellschicht*). Let us consider separately the three series of modifications of the chorionic ectoderm.

In the region of the chorion frondosum the inner layer of the ectoderm (the cellular layer of Langhans) becomes irregularly thickened in patches, which present every possible degree of variation as to number and as to their breadth and thickness. Although at first the cellular layer is more or less continuous and composed of uniform cells, this is not the case in later stages. We must assume that with the growth of the membrane the epithelium increases in area, but remains in many places single layered, developing no "*Zellschicht*." The patches of cells have been well described by Langhans, **110**, and Kastschenko, **107**, 466, and are represented with lower power in

Cut 20, *c*, and with a higher power in Cut 22, *c*. They vary much in appearance: the cells are more distinct in the small patches, but are less individual in the large patches, owing to the spread of the process of degeneration into the layer, Cut 22, *c*. The cell bodies are lightly stained, and the granular nuclei are not very sharply defined and vary in size and shape. The cellular layer is always sharply defined against the stroma, although there is no true basement membrane, but towards the outer layer of the ectoderm its boundary is sometimes distinct, sometimes lost in a gradual transition.



Cut 22. — Placental chorion of an embryo of seven months; vertical section through the ectoderm and portion of the adjacent stroma. *mes*, mesodermic stroma; *c*, cell layer; *fb*, fibrine layer; *ep*, remnant of epithelium. × 445 diams.

The outer layer of the ectoderm of the frondosum is even more variable. As stated by Kastschenko, it is primitively a dense protoplasmic reticulum, with nuclei in a single layer and without any cell boundaries. In the chorion frondosum at four months and after I find spots where this structure still prevails, either with or without an underlying cellular layer; in other spots the layer is thickened and contains an increased number of nuclei, which are sometimes crowded in a bunch; elsewhere the layer is thinned out and has no nuclei; in still other spots the thickening has gone on much further, and usually, but not always, where the outer layer is much thickened the cellular layer under it is also thickened; wherever it is thickened, and occasionally where it is thin, the outer layer of the ectoderm shows a marked tendency to degenerate into canalized fibrine, Cut 20, *fbr*, and Cut 22, *fb*. It is not difficult to assure one's self that the fibrine arises by direct metamorphosis of the ectoderm. I now think that its formation begins in the outer layer and thence spreads into the cellular layer; for, in fact, when both layers are distinguishable, as in Cut 22, the fibrine layer, *fb*, is always external, and the external layer of nucleated protoplasm has either totally disappeared or is represented by mere remnants, as in Cut 22, *ep*. The fibrine layer consists of a hyaline, very refringent substance permeated by numerous channels, Cut 22, *fb*; the substance has a violent affinity for carmine and hæmatoxyline, and is always the most deeply colored part of a stained section; the channels tend to run more or less parallel to the surface of the chorion and are connected by numerous cross-channels; some of the channels contain cells or nuclei. This complex system of canals is by no means of uniform appearance in all parts of the placenta, both the spaces and dissepiments varying in size and shape. The fibrine often sends, as shown in Cut 22, long outshoots into the cellular layers upon which it seems to encroach. The frequency of these images in my preparations led me to the opinion[1] that the fibrine arises from the cellular layer only, and I concluded that the ectoderm was first transformed into the so-called cellular layer, which was then transformed into fibrine. It still appears to me that much of the degeneration goes by these stages; but, on the other hand, it seems clear that the degeneration begins, as above stated, in the outer layer. Another appearance is presented by the ectoderm where it is thickened and wholly transformed into the cellular layer. In brief: the ecto-

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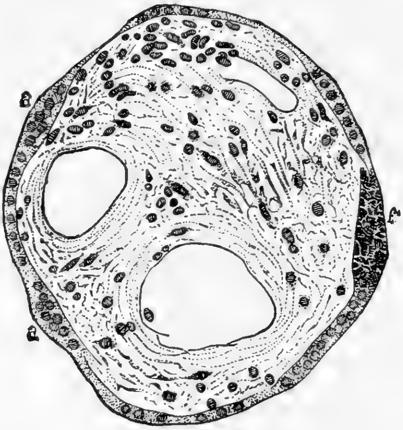
[1] *Anatom. Anzeiger*, ii. 23.

derm of the placental chorionic mesoderm undergoes patchwise manifold changes; it exists in three chief forms: 1°, the nucleated protoplasm; 2°, the cellular layer; 3°, canalized fibrine. A patch of the ectoderm may consist of any one of these modifications, of any two or of all three, but they have fixed relative positions, for when the nucleated protoplasm is present, it always covers the free surface of the chorion; when the cellular layer is present, it always lies next the mesoderm; and when all three forms are present over the same part, the fibrine is always the middle stratum. In general terms it may be said that the amount of canalized fibrine increases with the age of the placenta, but it is very variable in its degree of development. The peculiar layer into which the ectoderm is transformed has long puzzled anatomists. E. H. Weber recognized the fibrine layer and described its appearance correctly; it has probably been often seen, but generally regarded as either pathological or a blood coagulum. Robin, for instance, may be cited, **125**, 70-71, as one who saw, without observing correctly and understandingly, the tissue in question. An important gain was made when Winkler recognized the modified ectoderm as a constant layer, and in 1872 directed especial attention to it under the name of "*Schlussplatte*," **152**. Kölliker (*Entwickelungsgeschichte*, 2te Aufl., 337) added essentially to our knowledge of its structure, but it is to Langhans that we owe the first clear light. Meanwhile, other writers, following the lead of Ercolani and Turner, **146**, 551–553, have been influenced chiefly by the presence of the cellular layer, in the large size of the elements of which they found a resemblance to the decidual cells, which has guided them to the conclusion that the cellular layer is derived from the wall of the uterus. This error has been definitely corrected by Kastschenko, as already stated. In further support of the conclusion that the chorionic cellular layer is not decidual, may be brought forward the fact that there is a certain immigration of decidual cells into the placenta at its margin; but they remain entirely distinct from the cells of the cellular layer. This is readily seen in radial sections through the margin of a placenta from a normal after-birth — compare below, the account of the ectoderm of the chorion læve. The origin of the canalized fibrine from blood, which Langhans left in his first paper as an open possibility, and which even so recent a writer as Ruge, **129a**, 123 and 130, has advocated, cannot be maintained. Of course, there may be a deposit of blood fibrine (coagulum), but it would be pathological, and therefore to be distinguished from the normal fibrine of ectodermal origin. Moreover, the microscopic appearance of a blood clot or thrombus is so extremely characteristic that one can readily distinguish it from the placental canalized fibrine.

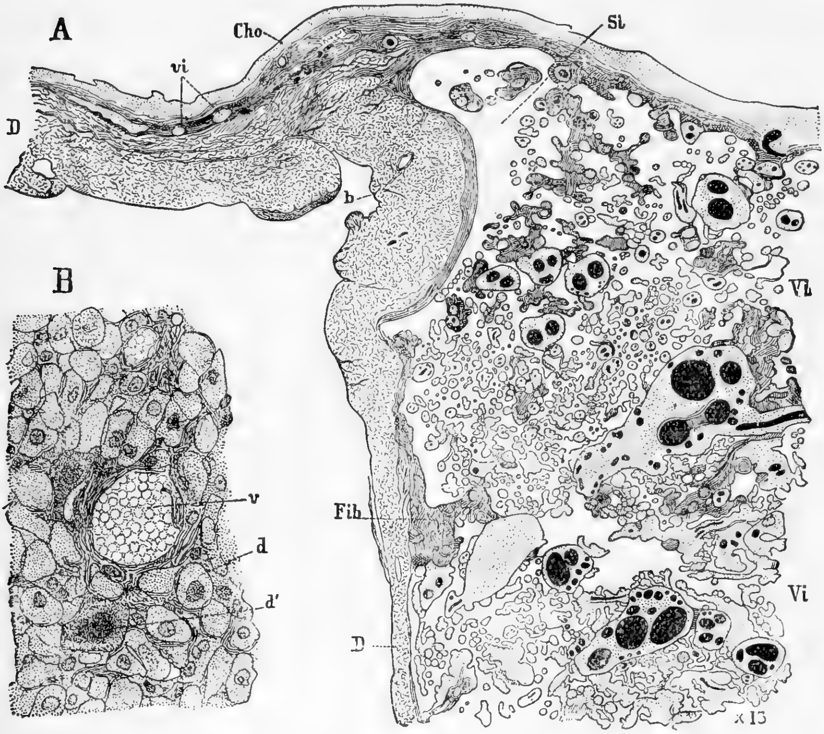
The ectoderm of the villi of the placenta differs from that of the chorionic membrane in several respects: 1°, the cellular layer after the first month becomes less and less conspicuous, and after the fourth month is present only in a few isolated patches, known as the *Zellknoten*, and carefully described by Langhans and Kastschenko; both of these authors were impressed by the resemblance of the cells to those of the decidua serotina; Langhans concludes that the *Zellknoten* arise from the serotina, but Kastschenko, having traced their development from the chorionic epithelium, denies his predecessor's conclusion, but still clinging to the idea of a genetic connection between the *Zellknoten* and the decidua, reverses the reasoning, and concludes that the decidual cells arise in part at least from the *Knoten*. Neither of these authors have found the intermediate forms between the two types of cells, and when we examine their descriptions critically we find that they have really no evidence except the likeness of the cells to offer in favor of their genetic relationship, and accordingly Langhans expresses himself with characteristic caution. To me the resemblance appears altogether superficial; hence my conclusion that the *Zellknoten* are remnants of the cellular layer. 2°, For the most part the villi remain covered by the nucleated protoplasm, which in many places is thickened. In the later stages these thicken-



Cut 23. — Cross-section of a villus from a placenta of seven months; three blood-vessels are shown; *a*, *a*, thickenings of the ectoderm; *f*, a thickening transformed into canalized fibrine. × 222 diams.

ings are small and numerous, constituting the so-called "*Proliferations-inseln*": compare Cut 15. Many of the little thickenings appear in sections of the villi, Cut 23, *a*, *a*, and here and there are converted into fibrine, *f*. I have interpreted them (Wood's *Reference Handbook of the Medical Sciences*, V., 695) as commencing buds, and consider that in earlier stages they grow into branches, but in later stages are in part at least arrested in their development. 3°, The proliferation islands are converted into canalized fibrine, and at the same time grow and fuse, forming larger patches, particularly on the larger stems: in this manner are produced the large areas and columns of fibrine found in the placenta at four months and after; they have been well described by Langhans, and form a striking feature in sections of placentæ. Some of the columns, as stated by Langhans, stretch along the villi from the chorionic membrane to the surface of the serotina as if to act as supports. Ercolani appears, if I understand his account, to have seen the fibrine columns, without, however, ascertaining either their structure or their origin. 4°, Over the tips of the villi, which are bent considerably where they are imbedded in the decidua serotina, the relations are not clear; the epithelium is certainly not present in its original form over the imbedded ends of the villi, which are, however, surrounded by a hyaline tissue of the character of the canalized fibrine, except that the canals are often indistinct or even wanting; the hyaline tissue forms an almost continuous coat over the decidual surface; in earlier stages the ectoderm of the terminal villi is often considerably expanded. The natural interpretation of these facts is that the ectoderm of the villi expands over the decidua serotina and degenerates. In this manner we account for both the absence of any cellular ectoderm over the ends of the villi and the presence of canalized fibrine upon the serotinal surface — but the hypothesis must await the final test by observation.

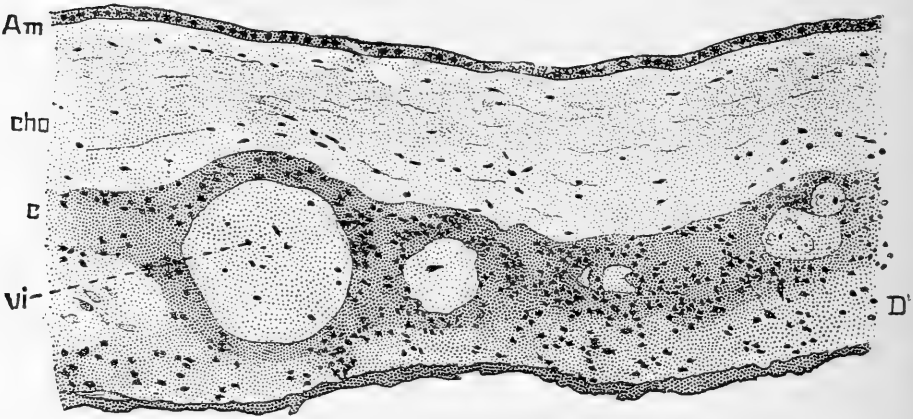
The ectoderm of the chorion læve loses by the seventh month all traces of the protoplasmic layer, and is without any canalized fibrine, except near the placenta; *cf. infra.* It is transformed into a *Zellschicht.* In a section of the læve *in situ* at seven months, Cut 33, the chorionic ectoderm, *c*, rests directly upon the decidua, which has no epithelium of its own. The ectodermal cells lie two or three deep; they are described by Kölliker and Langhans, the former designating them as the chorionic epithelium, while the latter doubtfully traces their origin to the uterus. That Kölliker (*Entwickelungsgeschichte*, 2te Aufl., p. 322) is right, I am confident. It is easy to follow the layer of cells in question at the edge of the placenta, and see that it is directly continuous with the cellular layer of the frondosum, which it resembles in character. On the other hand, the ectodermal cells of the læve are distinct in character from the decidual cells next to them, Cut 34, having smaller and more darkly stained nuclei, and much more coarsely granular protoplasm; the ectodermal cells are much smaller than the decidual. The ectoderm is sharply marked off from the decidua, but its surface



Cut 24. — Placenta at full term. A, vertical radial section through the margin; D, decidua; *vi*, aborted villi outside the placenta; *Cho*, chorion; *Si*, circular sinus; *Vi*, placental villi; *Fib*, canalized fibrine. B, portion of A more magnified to show the decidual tissue near *b*; *v*, blood-vessel; *d.d'*, decidual cells; *d*, with one, *d'*, with several nuclei.

is often corrugated, and then the line of separation between the tissues is irregular, and in sections it may even appear that there is a true interpenetration and mingling of the decidual and ectodermal cells; but it is only apparent, and the demarcation is always preserved.

At the edge of the placenta, as shown by examination of after-births, the relations of the layers are somewhat different. I reproduce with a few additions the descriptions given in my article on the *Placenta*[1] of a radial section through the margin of a normal placenta discharged at full term, Cut 24, A, from which the amnion had been removed. The chorion, *Cho*, and decidua, *D*, are in immediate contact at the left of the figure; that is, outside of the placenta, though remnants of the aborted villi, *vi*, are still plainly recognizable; but, as stated previously, they occur only in the immediate neighborhood of the placenta. These villi are surrounded by hyaline matter which resembles and can be followed into continuity with the canalized fibrine layer, *Fib*, covering the surface of the decidua serotina and the fibrine layer of the chorion frondosum. Below the aborted villi, *vi*, of the chorion læve, the fibrine layer is broken down and penetrated by the decidual tissue, so that the demar-



Cut 25. — After-birth at full term; vertical section of the amnion, chorion, and decidua in their natural relations near the placenta. *am*, amnion; *cho*, chorion; *c*, cellular layer or ectoderm; *f*, fibrine and decidual tissue, degenerated; *D'*, decidual tissue. × 125 diams.

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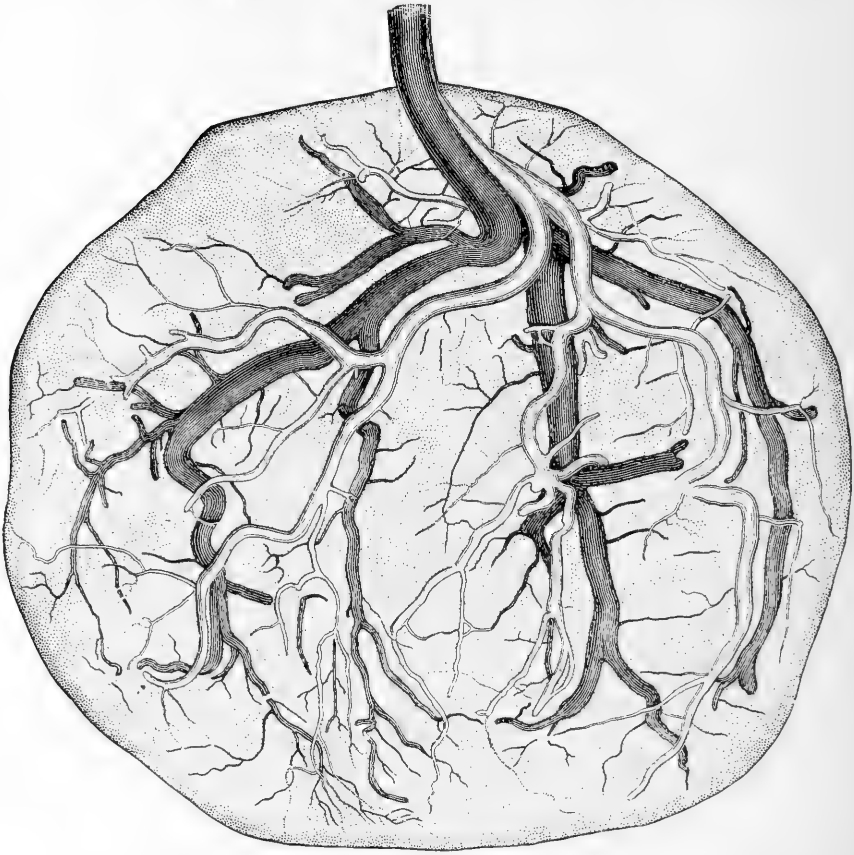
[1] Wood's *Reference Handbook Medical Science*, V., 694, 695.

cation between the fœtal and maternal tissues is here lost, and in fact, at the edge of the placenta the decidual cells make their way into the chorionic tissue, and for a certain distance towards the centre of the placenta they are found lying chiefly in the ectoderm. In other placentæ the fibrine layer and the decidual tissue around the margin of the placenta have not only intergrown, but also undergone a common degeneration, Cut 25, in consequence of which all distinct structure is obliterated, and we find the villi, *vi*, imbedded in a stratum, *f*, of more or less colored substance, without definite organization except irregularly scattered nuclei. Attentive examination shows that this layer, *f*, has unmistakable remains, *c*, of the cellular layer next the mesoderm of the chorion, and that it passes into an outer layer, *D'*, in which the traces of decidual structure are unmistakable; the dark line at the lower edge of the decidua, *D'*, is merely detritus and coagulum, as is often found on after-births. If we follow the layers in this, or a similar specimen, in the direction away from the placenta, the layers gradually alter, losing their degenerated character, until we reach a point where the chorionic ectoderm and the uterine decidua both exhibit their normal features. Returning now to the placenta we were previously considering, Cut 24: The placental chorion begins to exhibit its characteristic stratification a short distance within the margin. I have found, however, that the distinctness of that stratification varies considerably, not only in different placentæ, but also in different parts of the same placenta. The decidua, *D*, outside the placenta is very thick, but at the edge of the placenta it begins to thin out, and as it passes over the under side of the placenta, rapidly becomes so much reduced as to be even less in thickness than the chorion, *cho*. The decidua is everywhere crowded with an immense number of decidual cells, but in some other specimens they are less crowded. The surface of the decidua serotina is covered by a layer of fibrine, easily recognized by its deep staining; this coat of degenerated material has not yet received the attention it deserves, as a feature of the human placenta, which is quite constant, so far as my observations go; as stated previously, I consider its origin to be the epithelium of the ends of the villi imbedded in mucosa. Up to the edge of the placenta the chorion læve and decidua are united; at the edge they separate, to make room for the villi, *Vi*, *Vi*, of the frondosum. In the angle, *Si*, where the two membranes first separate there are very few villi, so that there is a comparatively clear space left, which is known as the circular sinus. It is not, as some of the older writers have believed, a distinct vessel, nor does it extend as a clear space completely around the placenta; but, on the contrary, it is interrupted here and there by an ingrowth of villi. In the cut, the spaces occupied of maternal blood are left white; the fœtal blood-vessels are drawn black.



Cut 26. — Placenta at full term, doubly injected by Dr. H. P. Quincy, to show the distribution of blood-vessels upon the surface; the arteries are drawn light; the veins dark. × 0.7 diams.

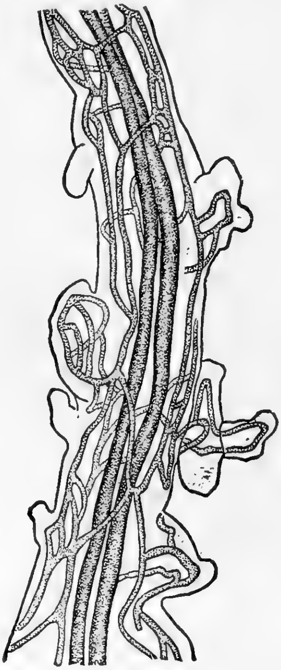
The chorionic circulation is complete in itself. The single vein and the two arteries of the umbilical cord spread out over the surface of the chorion, marking their course by projecting ridges. The insertion of the cord is always, so far as I have observed, obviously eccentric; the degree of eccentricity varies from a nearly central position to the so-called velamentous insertion, — compare B. S. Schultze, **159**; the degree of eccentricity is easily seen to be related to the distribution of the vessels, — a point not mentioned in current text-books. The arteries come down together from the cord, and are usually connected, but not invariably, by a short transverse vessel, situated about half an inch above the surface of the placenta, and which has been noted by many observers. I have never noticed any arterial or venous anastomoses on the surface of the placenta. The two kinds of vessels do not run together; the arteries lie nearer the surface, the veins deeper, Cut 26; the arteries fork separately until they are represented only by small branches and fine vessels; some of the small branches disappear by dipping down suddenly into the villi below; the veins are considerably larger than the arteries, and some of the larger branches disappear from the surface in the same abrupt manner as do the smaller arteries. There is the greatest possible variability in the vessels of the placenta; I have never seen two placentæ with the vessels alike. The more eccentric the insertion of the cord, the more do the vessels tend to distribute themselves symmetrically; the more central the position of the cord, the less can any vascular symmetry be made out.

The two following paragraphs are copied without change from my article on the placenta (Buck's *Reference Handbook of the Medical Sciences*, V., 696, 697): —

"To follow the course of the fœtal blood-vessels within the placenta, the best method is by corrosion injections. These may be made either with fusible metal, wax, or celloidine. The first is specially suited for the study of the large trunks; the latter, for that of the smaller vessels also. I have a very beautiful celloidine injection by Dr. S. J. Mixter, which, with others of wax and metals, has served as the basis of the following description: The veins leave the surface somewhat more abruptly than do the arteries, which gives off more small branches to the surface than do the veins, Cut 26. Both kinds of vessels leave the surface by curving downward for a short distance into the trunk of a villus; the vessels then divide, and their branches again take a more horizontal course; the branches then curl over downward, and, after a second short descent toward the decidua, again send out horizontal branches. The result of this arrangement is a terrace-like appearance in the course of the vessels; they approach the uterine side of the placenta in this very characteristic manner. The number of terraces is variable; usually there are two or three, but sometimes there is only one, or they may number four or even five. Arrived at the end of its terraces, the main vessel takes a more nearly perpendicular course, and rapidly subdivides. Immediately after entering the villi, the arteries and veins give off but few capillaries, but after a short course in the main stalk of the villus, the vessels give rise to many branchlets, and gradually the character of the circulation changes, until in the smallest villous twigs there are capillaries only, Cut 27. The vascular trunks have a marked tendency to dichotomous division, which is maintained within the villi to a certain extent; the arterioles and veinlets in the mature placenta go from their trunks at wide angles for the most part, and subdivide in the same manner, so that they spread out through the whole substance of the placenta. The vessels next the decidua take a more horizontal trend, like the top branches of a wind-swept tree. As the vessels run in the villi, of course the way in which the latter branch out determines the paths of the former; hence by following the distribution of the vessels we inform ourselves as to the ramifications of the villi. Thus the horizontal course of the vessels on the uterine side of the placenta corresponds to the well-known fact that the ends of the villi attached to the uterus become bent and adhere by their sides to the decidual surface."

Cut 27. — Portion of an injected villus from a placenta of about five months; magnified 210 diams.

"The capillaries of the villi are remarkable for their large size, and on this account have been described as arteries or veins by E. H. Weber, Goodsir, and other writers. Their calibre is often sufficient for from four to six blood-disks abreast. They are very variable in diameter, and also peculiar in exhibiting sudden restrictions and dilatations, Cut 27. In the short bud-like branches there is often only a single capillary loop, but as the branch becomes larger, the number of loops increases, and they form anastomoses. In branches large enough to serve as a stem, some one or two of the vessels may be enlarged, as may be seen in Cut 27; in the branches large enough to admit of it, there are two (or sometimes only one) longitudinal central vessels, an artery and vein, and a superficial network of capillaries, Cut 27*a*. Goodsir and other early writers laid great stress on the formation of the capillary loops, but this feature is a common one in the development of the fœtal vascular system, as is also the width of the capillaries. In my opinion these peculiarities are characteristic rather of the fœtus than specifically of the placenta. In some of the older writers (Goodsir, Farre, *et al.*) it is asserted that the true capillary system disappears toward the end of gestation. I am unable to confirm this, but find instead that in the slender terminal villi of the placenta at term there is often only a single, sometimes long, capillary loop; the capillary is very wide, and its width is probably the reason of its having been held formerly to be a vein or an artery."



Cut 27 a. Placenta of about five months; portion of a small villus, to show the central vessels and superficial capillaries. × 105 diams.

§ 16. **Uterus during menstruation.** — I have little to add to the descriptions of previous authors, particularly those of Leopold, **36**, and Kölliker.[1] It is, however, worth while to present the accompanying illustration, Cut 28, since there is a lack

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[1] Kölliker's *Handbuch der Gewebelehre*, 5te Aufl., p. 563.

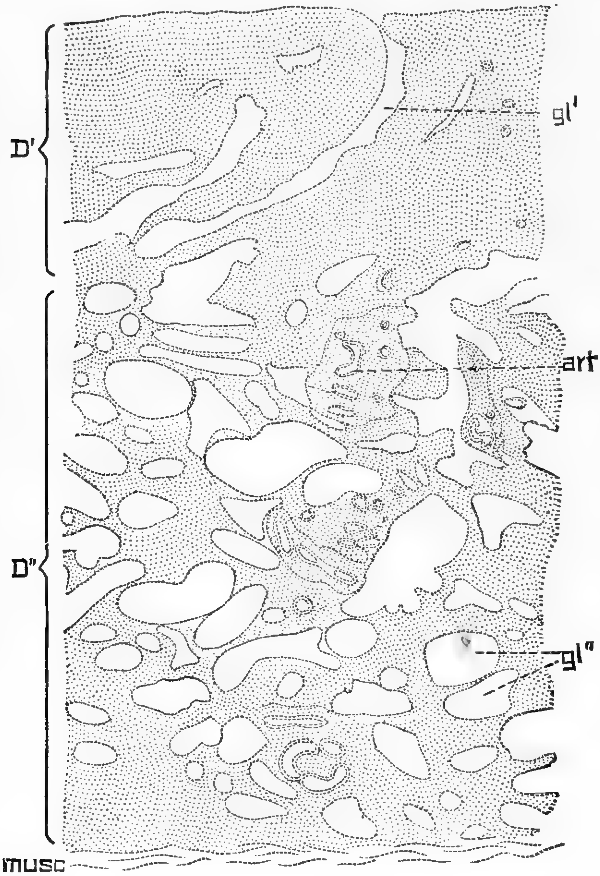
Cut 28.—Mucous membrane of a virgin uterus during the first day of menstruation. *ep*, epithelium; *d*, disintegrated layer; *v*, *v*, blood-vessels; *musc*, muscularis. × 65 diams.

of figures. The cut represents a transverse section of the *corpus uteri* of a fine specimen, for which I am indebted to Dr. W. W. Gannett. The woman died from acute miliary tuberculosis; the autopsy was made almost immediately after death, and within four hours from death the complete genitalia were placed in Müller's fluid, the uterus having been first carefully opened by a single median ventral incision. Death is said to have occurred on the day of the regular period. The hymen was intact. There was no sign of pathological change in any of the genitalia. In one ovary, the right, there was a fresh *corpus hæmorrhagicum*. These data afford a sufficient basis for the belief that the uterus was well preserved in a perfectly normal condition.

The mucous membrane is from 1.1–1.3 mm. thick; its surface is irregularly tumefied; the gland openings lie for the most part in the depressions. In the cavity of the uterus there was a small blood-clot. The mucosa is sharply limited against the muscularis, Cut 28. In transverse sections one sees that the upper fourth of the mucosa is very much broken down and disintegrated, Cut 28, *d*; the cells stain less than those of the deep portions of the membrane; as represented in the cut the tissue is divided into numerous more or less separate small masses; some of the blood-vessels appear torn through, but it is difficult to make sure observation: Overlach, **39**, considers it probable that the infiltration of blood takes place by diapedesin, not by rupture of the capillaries. The superficial epithelium, *ep*, is loosened everywhere; in places fragments of it have fallen off, and in some parts it is gone altogether; it stains readily with cochineal and its nuclei color well, the epithelium differing in this respect from the underlying connective tissue, which does not stain well; the blood-vessels in the disintegrated layer are for the most part small.

The deeper layer of the mucosa is dense with crowded well-stained cells, which lie in groups separated by clearer lines; in the cut this grouping shows less plainly than in the preparation; the lighter channels are perhaps lymph-vessels, a suggestion which occurs to me, because in so-called "moulds" one sometimes finds similar channels crowded with leucocytes. The cells appear to be the proliferated interglandular tissue; there are very few leucocytes, so far as I can distinguish; the cells have small, oval, or elongated, darkly stained nuclei, with a very small granular protoplasmatic body each; there is certainly no noticeable enlargement of the cells, but only a remarkable multiplication. The point is important; I see nothing to suggest the presence of decidual cells, nothing even like definite enlargement of any of the cells. The image of the tissue is comparable to that of the connective tissue of the rabbit's placenta at six days, except that there the cells are widely separated, here closely crowded, but in each case the cells are small, with little protoplasm, and connected by their processes. In another specimen in my possession of a normal uterus at the close of menstruation, the condition of the mucous membrane agrees with that of the specimen we have considered, except, of course, that the disintegrated superficial layer is lost, and that the superficial layers stain poorly. In this second specimen, also, the interglandular cells are small and very crowded; there are few leucocytes and no decidual cells. The two specimens further agree in having the glands distended and contorted; each gland is surrounded by a distinct basement membrane or layer of connective tissue cells closely investing the epithelium, as has been observed by Leopold, **36**. In my article on the decidua in the *Reference Handbook,* II., p. 390, is a summary of the changes occurring during menstruation, and stress is there laid upon two points emphasized by previous writers; namely, the increase in the number of leucocytes and the presence of decidual cells. Since my own observations have failed to confirm these statements, I can no longer accept them. The proliferated connective tissue cells are those, probably, which become decidual cells when the *decidua menstrualis* is changed into the *decidua graviditatis* — compare the account of the one month's uterus in the next section.

§ 17. **Uterus one month pregnant.** — The specimen to be described came from a woman who committed suicide by violence, not by poison, and I was informed that she was known to be about one month pregnant. Further information was not obtained, and I was requested not to seek it. The specimen was received in very fresh condition, but it had been opened, the reflexa was torn and pretty much gone; the embryo had been removed, and I was therefore unable to verify the age, or investigate the attachment of the villi of the chorion to the uterus. There was a beautiful *corpus luteum* in one ovary, quite similar to that figured by Dalton in his Report on the *corpus luteum* in the transactions of the American Gynæcological Society for 1877, Fig. 9. The surface of the uterus seemed uninjured. The specimen was hardened in Müller's fluid, and found subsequently to be well preserved. It may be considered, I think, perfectly normal.

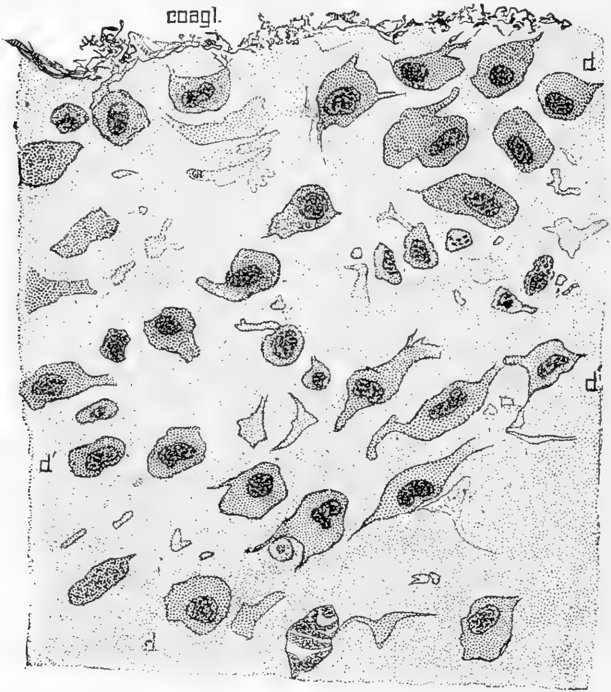


Cut 29. — Uterus one month pregnant; outlines of the glands from a vertical section: to show the division of the mucosa into an upper compact layer, *D'*, and a lower cavernous layer, *D''*; *gl'*, *gl''*, glands; *art*, spiral artery; *musc*, muscularis.

My specimen enables me to confirm in most respects Turner's accurate description of two uteri of about the same age, **146**, 546–548. The inner surface shows the hillocks (*Inseln*) described by Reichert in the uterus of two weeks, studied by him, which have been figured by Coste in slightly older specimens, and found by Turner also, **146**, 540.

The three illustrations given herewith are all from sections through what I suppose to be the placental region.

There is an upper compact layer, Cut 29, *D'*, and a lower cavernous layer, *D''*; the caverns, being gland cavities, which appear as rounded areolæ lined with epithelium, are filled with broken-down epithelial cells. The drawing, reproduced in Cut 29, was obtained by drawing the outlines very carefully, stippling the areas occupied by the connective tissue, representing the blood-vessels by double outlines, and omitting the glandular epithelium altogether. It will be noticed that about three-fourths of the diameter of the mucosa is occupied by the cavernous layer, *D''*.



Cut 30. — Uterus one month pregnant; portion of the compact layer of the decidua seen in vertical section; *coagl*, coagulum upon the surface; *d*, *d'*, decidual cells. × 445 diams.

The upper or compact layer is shown in Cut 30. The surface is without any trace of epithelium, but is covered only by a thin fibrous and granular coagulum, *coagl*; the tissue itself consists almost exclusively of young decidual cells, *d, d'*, with a clear homogeneous matrix; here and there are leucocytes, but they are nowhere numerous; the decidual cells are all quite large, with their bodies deeply stained by the eosine; the nuclei are round, oval, or slightly irregular in shape, coarsely granular, and sharp in outline; the cells themselves, though irregular and variable in shape, are all more or less rounded with processes running off in various directions; scattered between the cells are many sections of their processes; occasionally it can be seen that two cells are connected; in fact, we have in this tissue evidently a modified embryonic or so-called anastomosing connective tissue. Now, as we know through the observations of Leopold, **36**, which I have verified, the connective tissue of the uterine mucosa consists of anastomosing cells, and as stated in the previous section, the cells are found proliferated in the menstruating uterus; we have therefore only to imagine the cells enlarged with certain accompanying modifications, to obtain the tissue figured in Cut 30. There is no special formation of cells around the blood-vessels, where, according to Ercolani, the decidual tissue arises by new formation. In Turner's specimens the upper part of the compact layer was imperfectly preserved, but according to his description there appears to have been a coagulum similar to that which I have found, but thicker. In the deep part of the layer the cells are less enlarged, and when the cavernous layer is reached, there occurs a rapid transition in the character of the cells, which become smaller and more fusiform, and their nuclei more elongate, smaller, and deeper stained by alum-cochineal. The gland openings upon the surface of the uterus lead into tubes, Cut 30, *gl'*, which run slightly obliquely through the compact layer, taking a more or less nearly straight course and joining the contorted gland tubes, Cut 30, *gl''*, of the cavernous layer. The gland ducts are completely devoid of lining epithelium, which has disappeared except for a very few loose cells, occasionally found lying free in the ducts; the cells have not fallen out from the sections, but were lost before the tissue was imbedded.[1] The ducts then

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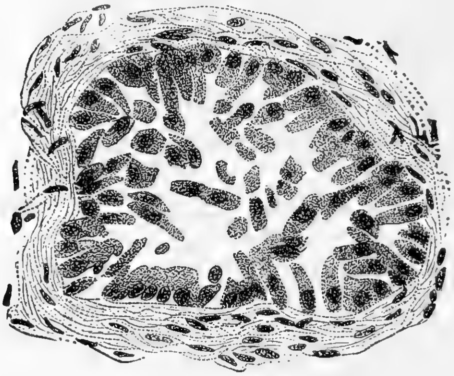
[1] The blocks to be cut were stained *in toto* with alum-cochineal and eosine, imbedded in paraffine, etc. The sections were fastened on the slide with celloidine, to keep the parts in place.

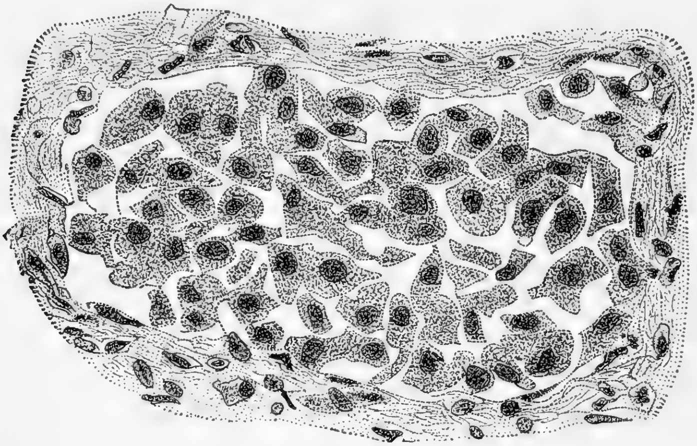
are wide tubes running nearly straight through the upper part of the decidua and bounded directly by the decidual tissue; they communicate below with a contorted cavity. Similar tubes appear in later stages and have been described as blood-vessels — see the next section.

The cavernous layer contains numerous spaces, the areolæ of Turner, **146**, 547, who was uncertain as to their character, though he ascertained that many of them belonged to the glandular system. In my specimen it is perfectly clear that all the larger areolæ belong to the glands, which must be extremely distorted and distended to give the shapes shown in Cut 29. The thin dissepiments between the areolæ are composed of connective tissue, the long dark nuclei of which, Cut 31, are strikingly different from those of the cells of the compact layer, Cut 30. The areolæ present two extreme modifications and all intermediate phases between these two. The smaller areolæ are lined by a well-preserved cylinder epithelium, or by one in which the cells are separated by small fissures; in other areolæ the cells are a little larger, Cut 31, each for the most part cleft from its fellows, and some of them loosened from the wall and lying free in the cavity. The other extreme is represented in Cut 32; the size of the areolæ is much increased, — compare Cuts 31 and 32, — both drawn on the same scale; the epithelium is entirely loosened from the wall, and the cells lie separately in the cavity which they fill; the cells are greatly enlarged, their bodies having three or four times the diameter of the cells in the small areolæ; they have not the cylinder shape, but are irregular in outline: their protoplasm is finely granular and stains rather lightly; the nuclei are large, rounded, glandular, and with sharp outlines; they are less darkly stained than the nuclei of the epithelium of Cut 31.



Cut 31. — Uterus one month pregnant; section of gland from cavernous layer, with the epithelium partly adherent to the walls. × 445 diams.

The obvious interpretation of the appearances described is, that the glandular epithelium is breaking down, that it is lost altogether from the ducts, but is still present in the deep portions of the glands; in breaking down the cells separate from one another, and then from the wall, and falling into the gland cavity, there enlarge, the cavity enlarging also. Similar appearances are also found in "moulds" of the second month; very likely they have been often observed and mistaken for pathological changes.

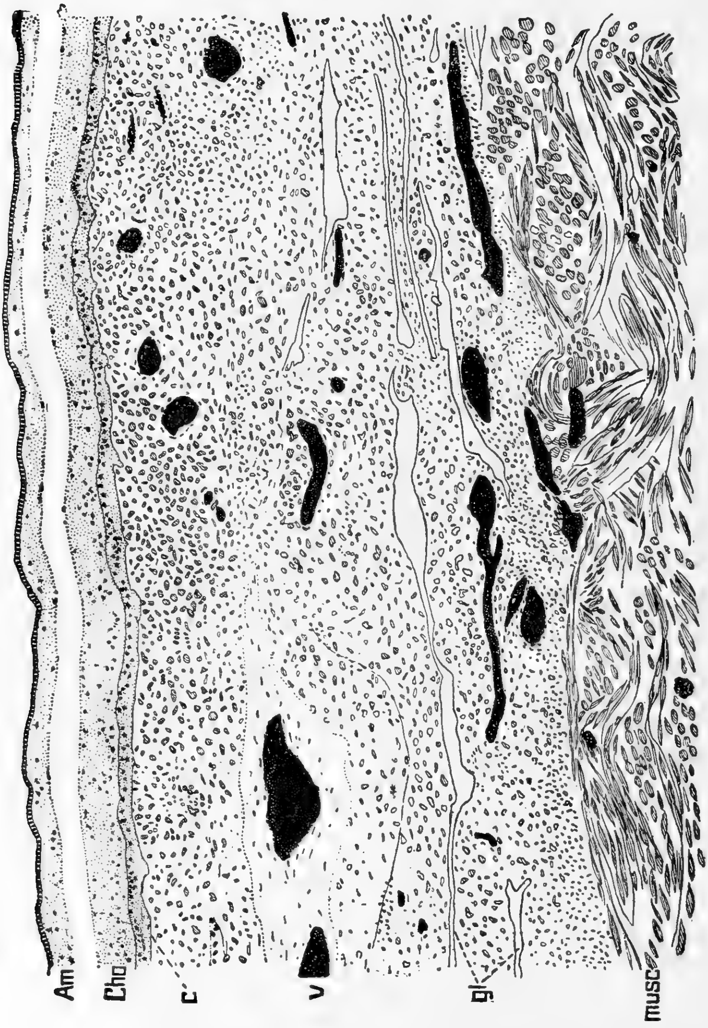


Cut 32. — Uterus one month pregnant; section of gland from cavernous layer, with the epithelium loosened from the walls; × 445 diams.

The blood-vessels of course lie in the dissepiments between the glands. I observed nothing to correspond with the "colossal capillaries dilated into small sinuses," mentioned by Turner **146**, 548. Were not these supposed capillaries gland cavities, from which the epithelium had fallen out? Occasionally the sections pass through a spiral artery, Cut 29, *art*, which is cut again and again as it twists around in its characteristic separate column of connective tissue.

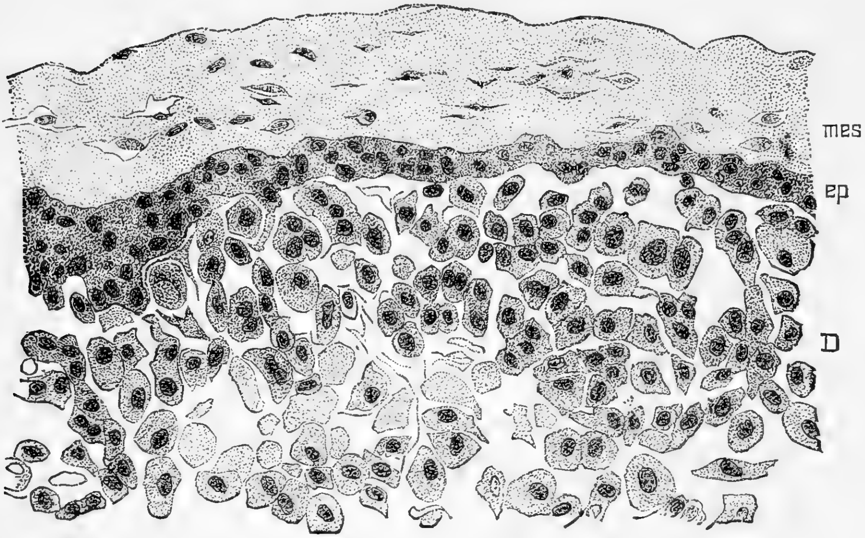
§ 18. **Uterus seven months pregnant, with the fœtal membranes in place.** — The specimen to be described was obtained for me through the kindness of Dr. W. W. Gannett. It is an apparently normal uterus, which contained a normal embryo weighing 1150 grammes and having an umbilical cord 58 centimetres long, — probably about seven months old, or a little more: there were no data as to the duration of gestation. The uterus was opened, and preserved in Müller's fluid without disturbing the membranes.

A section through the amnion, chorion læve, and uterine mucosa, stained with hæmatoxyline, and viewed with a low power, is represented in Cut 33; the dark spots are maternal blood-vessels, which have been shaded for the sake of clearness. The amnion, *am*, and chorion, *cho*, present the characteristics

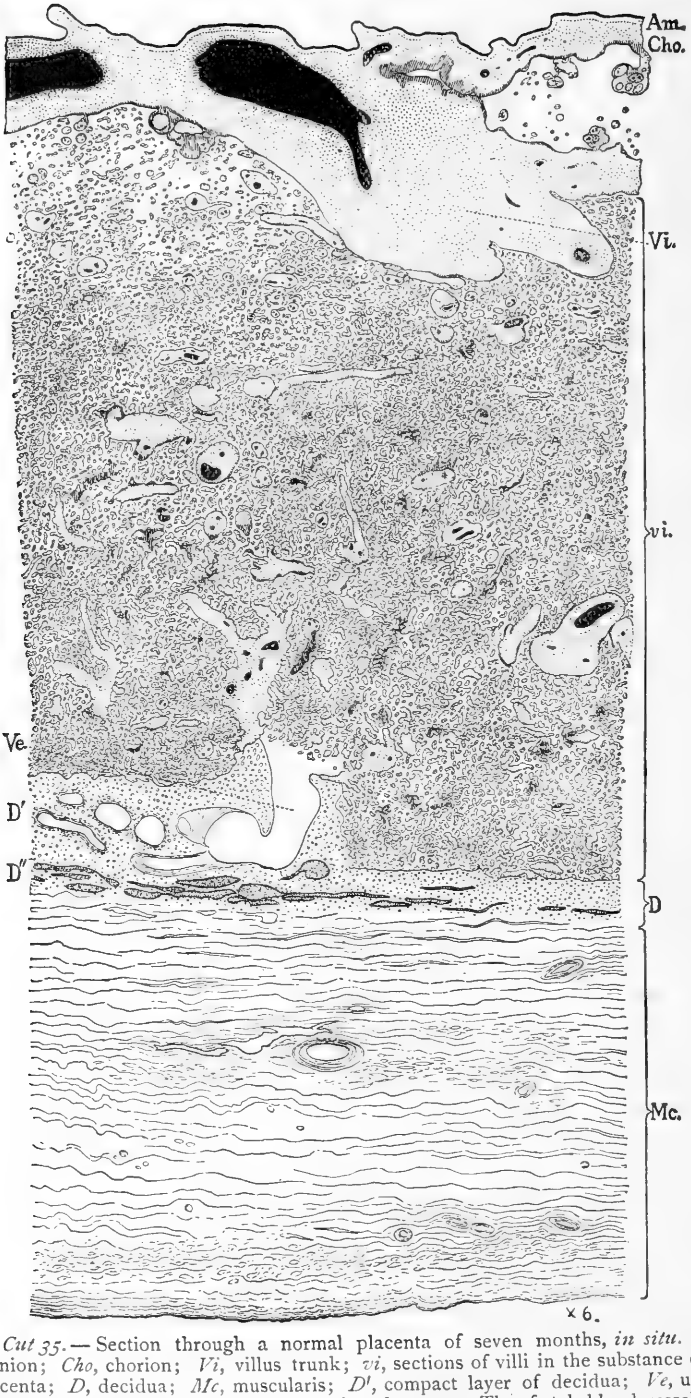


Cut 33.—Uterus about seven months pregnant; vertical section through the decidua vera, with the chorion læve and amnion *in situ*. *Am*, amnion; *Cho*, chorion; *c*, epithelium (cellular layer of chorion); *v*, blood-vessel; *gl*, spaces supposed to be gland cavities; *musc*, muscularis: the blood-vessels are represented dark. × 40 diams.

previously described, §§ 14, 15; the chorion is bounded against the decidua by an epithelium *c*, which I interpret as the chorionic ectoderm; there is no trace of a second layer of epithelium; so that the uterine epithelium must be considered lost, a conclusion agreeing with the observations of Kölliker, Turner, and myself upon earlier stages, and the statements of Ercolani. The decidua has eight or nine times the thickness of the chorion; it has an upper compact and a lower cavernous layer; the former contains numerous decidual cells, most of which are a little larger than those nearer the muscularis; the compact layer contains a few blood-vessels of moderate calibre, and occasionally a large vessel, *v*, surrounded by connective tissue containing no decidual cells. Examined with a higher power, the decidual cells — compare Cut 34, *D'* — are found to resemble quite closely those at one month, Cut 30, but they are much more numerous and closer together, and their processes are fewer; they vary also more in size; some of the larger ones are multinucleate; it is probable that the cells are multiplying by division; the matrix presents a fibrous look, but whether it contains actual fibres, I am not sure; between the decidual cells are a



Cut 34. — Uterus about seven months pregnant; upper portion of decidua vera, with the chorion læve *in situ*. *mes*, mesodermic layer of chorion; *ep*, epithelial layer of chorion; *D'*, decidua. × 340 diams.



Cut 35.—Section through a normal placenta of seven months, *in situ*. *Am*, amnion; *Cho*, chorion; *Vi*, villus trunk; *vi*, sections of villi in the substance of the placenta; *D*, decidua; *Mc*, muscularis; *D′*, compact layer of decidua; *Ve*, uterine blood-vessel (or gland?) opening into the placenta. The fœtal blood-vessels are drawn black; the maternal blood spaces are left white; the chorionic tissue is stippled, except the canalized fibrine, which is shaded by lines; the remnants of the gland cavities in *D″* are stippled dark. (Drawn from nature by J. H. Emerton.)

certain number of nuclei, some of which belong to leucocytes, others to blood capillaries, and still others, which I am uncertain about, which are few in number, and possibly belong to connective tissue corpuscles. The cavernous layer resembles now, in contrast to the first month, the upper layer of the decidua in histological constitution, but the decidual cells are smaller and at little wider intervals from one another; the cavernous layer is especially characterized by the slit-like spaces in it; some of these spaces, as indicated by the drawing, Cut 33, are undoubtedly blood-vessels or sinuses, but still others contain no blood, or at most three or four isolated corpuscles, although close to them are capillaries gorged with blood; once in a while a few epithelioid cells can be seen adhering to the walls of the spaces. These spaces can hardly be assigned to the vascular system; they have been held by Kundrat and Engelmann, **180**, and various subsequent writers, to be the gland cavities; we have not sufficient observations to establish the actual metamorphosis of the areolæ of the one month's uterus into the slits, *gl*, of Cuts 33 and 35, *D′*, but there is no ground to question the occurrence of the change, which appears to be a necessary consequence of the stretching of the decidua due to the expansion of the uterus during pregnancy.

A complete section through the placenta *in situ* and uterus is represented in Cut 35, which has already appeared in my article, "Placenta" (Buck's *Handbook*, V., 696), and been sufficiently described. The chorion is separated by a dense forest of villi from the decidua, *D*; the ends of some of the villi touch and are imbedded in the decidual tissue; these imbedded ends are without epithelium, but their connective tissue is immediately surrounded by hyaline substance. The decidua is plainly divided into two strata—*cf. infra.* The section passes through a wide tube, *Ve*, which opens directly into the interior of the placenta and contains blood; in my article, *l.c.*, this opening is referred to as that of a vein, the identification being in accordance with my understanding of the descriptions of Waldeyer,[1] **149**. Professor Langhans has since informed me, that according to his own observations the opening of the arteries are characterized by the absence of villi projecting into their openings.

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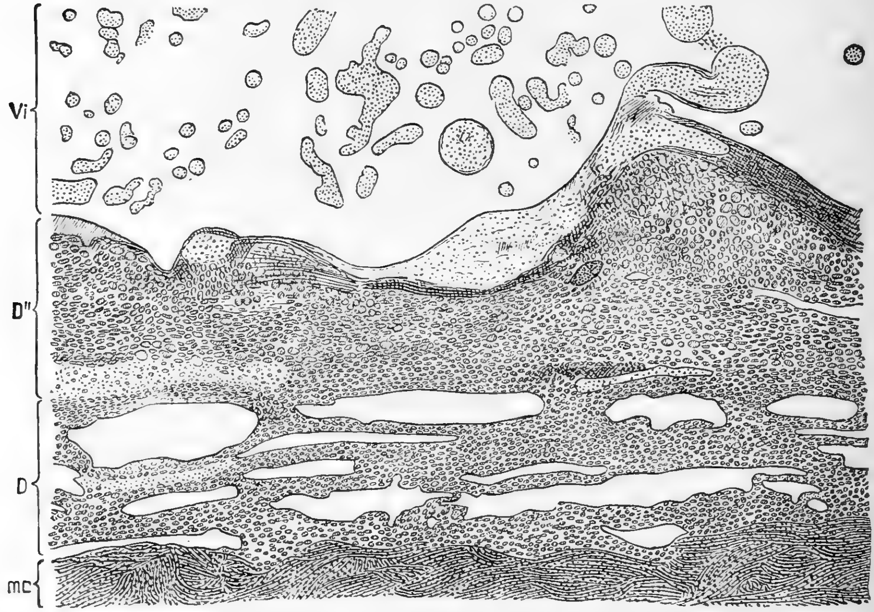
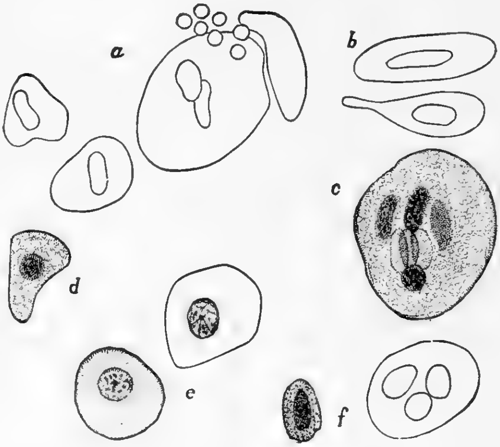
[1] I am under much obligation to Professor Waldeyer for an opportunity to examine some of the injected specimens upon which his very important researches were conducted.

His pupil, Raissa Nitabuch, has since published a dissertation, **117**, confirming this opinion, according to which the vessel shown in Cut 35, *Vc*, is not venous, but arterial. Another possibility has occurred to me, viz.: that it is a gland duct; in fact, it resembles very closely the undoubted gland ducts of the one month's decidua: there is no reason apparent why the gland ducts, which pass nearly vertically through the compact layer, should be obliterated; on the contrary, one might expect to find them widened by the stretching of the uterus; as there is blood in the intervillous spaces, it could easily make its way into the distended glands, and its presence there would not prove the glands to be blood-vessels. While, therefore, I accept Waldeyer's researches, **149**, as well as those of Langhans and Nitabuch, **117**, as verifying Farre's neglected account, **172**, *722*, of the placental circulation, I venture to express a note of caution as to the danger of mistaking glandular for vascular openings.



Cut 36. — Uterus of seven months, vertical section of the decidua serotina from near the margin of the placenta. *mc*, muscularis; D', D'', decidua serotina; D', cavernous or spongy layer; D'', compact layer; *Vi*, scattered chorionic villi. The intervillous spaces were filled with blood, which is not represented in the figure, × 50 diams.

The following additional points deserve notice: The serotina is about 1.5 mm. thick, and contains an enormous number of decidual cells, Cut 36. The cavernous, *D'*, and compact layers, *D''*, are very clearly separated; the mucosa is sharply marked off from the muscularis, *mc*, although scattered decidual cells have penetrated between the muscular fibres. The muscularis is about 10 mm. thick, and is characterized by the presence of quite large and numerous venous thrombi, especially in the part towards the decidua. The decidua contains few blood-vessels. Upon the surface of the decidua can be distinguished a special layer of mingled hyaline and decidual tissue, which in many places is interrupted by the ends of the chorionic villi, as is well shown in Cut 36. The supposed gland cavities of the spongy layer, *D'*, are long and slit-like; they are filled for the most part with fine granular matter, which colors light blue with hæmatoxyline; they also contain a little blood, sometimes a few decidual cells. I have seen in them also a few oval bodies several times larger than any of the decidual cells, and presenting a vacuolated appearance; what these bodies are, I have not ascertained. In places the glandular epithelium is distinct; its cells vary greatly in appearance, neighboring cells being often quite dissimilar; nearly all are cuboidal, but some are flattened out; of the former there are some with darkly stained nuclei, but the majority of the cells are enlarged, with greatly enlarged hyaline, very refringent nuclei.



Cut 37. — Decidual cells from the section represented in part in Cut 36. *a, b, d, f,* various forms of cells from serotina; *c,* giant cell from the margin of the placenta; *e,* clear cells from chorion; at *a,* seven blood globules have been drawn in to scale. × 545 diams.

The decidual cells are smaller and more crowded in the cavernous layer, and mostly larger in the compact layer — compare

Cut 36. The largest cells are scattered through the compact layer, but are most numerous towards the surface. The decidual cells exhibit great variety in their features, Cut 37; they are nearly all oval disks, so that their outlines vary according as they happen to lie in the tissue; they vary greatly in size; the larger they are, the more nuclei they contain; but I observe no cells with more than ten nuclei. The nuclei are usually more or less elongated; the contents of the cells granular. Some of the cells present another type; these are more nearly round, clear, and transparent, *e*; the nucleus is round, stained lightly, and contains relatively few and small granules; such cells are most numerous about the placental margin.[1]

§ 19. **Uterus twelve hours after abortion at six months.** — For this specimen, also, I am indebted to Dr. W. W. Gannett. The woman was brought into the Boston City Hospital in a comatose condition; the fœtus, estimated to be about six months, was removed by the forceps; the mother died twelve hours later; the autopsy by Dr. Gannett showed death to have been caused by tubercular meningitis. The uterus is apparently normal; I received it in a fresh state, and hardened it in Müller's fluid. It was already very much contracted; the mucosa measured about 2 mm. in thickness; its surface was ragged and more or less covered with clotted blood, presenting very much the appearance so superbly figured by Coste (*Développement des Corps organisés,* Pl. X., Éspèce humaine).

Vertical sections, Cut 38, show that the surfaces of the mucosa are very uneven; on the free surface there is a thin layer of clotted blood, *coagl*; the upper or compact layer of the decidua has entirely disappeared, leaving only the deep portion, *D*, permeated by numerous large empty spaces, which I take to be in part gland cavities, in part blood sinuses, both changed from their slit-like form by the contraction of the uterus during and since the delivery of the child. Between the spaces are the brownish and hyaline cells, and a great many blood-corpuscles, which lie throughout the tissue itself as well as in the blood-vessels. In short, the conditions found agree with those described by Leopold as present in the uterus a short time after normal delivery at full term, **36**, and accordingly, further details concerning my specimen may be omitted.

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[1] This and the preceding paragraph are taken with sundry alterations from my article on the placenta, *l.s.c.*

§ 20. **Origin of decidual cells.** — Besides the erroneous hypothesis of Ercolani, there are three views as to the origin of the decidual cells known to me, to wit: 1°, they are modified leucocytes (Hennig, Langhans, *et al*); 2°, they arise from the connective tissue cells of the mucosa (Leopold, **36**); 3°, they are produced by the epithelium (Overlach, **39**). The first view is not supported by observation, even by its advocates, and may be dismissed. Overlach's observations certainly favor the third view, but inasmuch as he has studied only *one* uterus with pseudo-menstruation from acute phosphorus poisoning, his the-

Cut 38. — Uterus twelve hours after artificial delivery at six months; *coagl*, blood-clot; *D*, decidua; *m*, muscularis. × 22 diams.

ory cannot be accepted definitely until verified by further observations on normal uteri. Overlach found in the cervix of the uterus in question, the lining epithelial cells to contain an endogenous brood of small cells, one to fifteen in each parent-cell; the daughter-cells begin as nuclei, around which there gathers a protoplasmatic body for each. The cells are like the young decidual cells just below, so that the latter may be assumed to have wandered forth from the epithelium. I may recall that in the normal menstruating uterus I find no true decidual cells, and consequently I must regard Overlach's find as pathological.

The observations of Creighton, of Masquelin and Swaen, and of myself may be fairly considered to establish the fact that in rodents, at least, the decidual cells arise from the connective tissue cells of the mucosa. That they arise from the same cells in man is rendered extremely probable by the investigations of Leopold, which have been confirmed and extended by the observations recorded in §§ 16, 17, and 18, of the present article. Accordingly I assent to the second of the views above enumerated.

Ercolani erroneously regarded the decidual tissue as a new formation, arising after the total destruction of the mucosa. He observed the degenerative processes of the uterine epithelium, and the arrangement of the decidual cells around the vessels of the placenta in rodents and other mammals; he inferred that the whole mucosa was degenerated and lost, but he never established the inference by observation; he also inferred that the perivascular cells, being different from the surrounding tissues, were a new formation, but he never traced the actual genesis of the cells. In spite, however, of the absence of the observations necessary to establish his double thesis of the total destruction of the mucosa and the new formation of the decidua, he advocated his doctrine with the greatest earnestness, even to the last — see **91**, **92**. The failure of his hypothesis to find acceptance has been due not to any unreadiness to bestow merited acknowledgment upon his researches, but to the incompatibility of the hypothesis itself with the ascertained facts of the structure and development of the placenta. While, therefore, we utilize Ercolani's numerous and valuable observations, it will be a distinct gain for science to set aside his theory of the new formation of the decidua.

§ 21. **General considerations.** — We are now in a position to compare the changes in the uterus during menstruation and gestation. In both cases the processes begin with tumefaction and hyperæmia of the mucosa; they continue with hyperplasia of the connective tissue (the decidual cells being regarded as modified connective tissue corpuscles) and with hypertrophy, accompanied by distention and contortion of the glands; they both close with casting off the superficial layers of the mucosa, after which follows the regeneration of the membrane. The essential steps, then, are the same in both cases. The difference is, that during the long life of the *decidua graviditatis*, changes supervene in the tissues which do not take place during the rapid menstrual cycle; the mucosa of gestation is distinguished by the loss of both its surface and glandular epithelium, and by the enlargement of its connective tissue cells into so-called decidual cells. We must accordingly view the changes in the uterus during gestation as a prolonged and modified menstrual cycle. The relation in time between menstruation and the commencement of pregnancy is attributable to the menstrual process rendering the uterus receptive; that is to say, capable of receiving and retaining the ovum. We must conceive that the ovum has no power of initiating the development of a *decidua*, but only of modifying the menstrual process; hence pregnancy *can* begin only at a menstrual period. The ovum, too, exercises this influence at a distance, for in all mammals, the earliest development of which is known, the ovum passes through its segmentation in the oviduct (Fallopian tube), and takes from three to eight days to reach the uterus; but during this period the change in the womb is going on. The most plausible explanation of this action of the ovum at a distance is a reflex stimulus passing from the oviduct to the central nervous system of the mother, and thence back to the uterus; the validity of this hypothesis must be tested by physiological experiment. That the nerves are able to effect morphological changes is already abundantly proven, not only by the influence of the secretory nerves upon gland cells, by the degeneration of muscular and other tissues, when their nerves are severed, but also by certain embryological observations tending to show that histological differentiation does not progress very far until the tissues are joined by the outgrowing nerves.

When the ovum reaches the uterus, it appears to exert a more direct influence, for one set of changes occurs in the placental area, where there is concrescence of fœtal and maternal parts; another in the region around the placenta (peri-placenta, decidua reflexa), and still another in the rest of the uterus (decidua vera, ob-placenta). Whether the three zones enumerated can be distinguished in the pregnant uteri of all placental mammals, and whether they have more features in common than appear from a direct comparison between man and the rabbit, are questions to be decided by increased knowledge. However, it already seems very probable that the decidua reflexa and peri-placenta are homologous at least in rodents.

Concerning the evolution of the amnion nothing definite is known, nor do the speculations of Balfour (*Comparative Embryology*, II., 256) nor of van Beneden and Julin, **44**, 425, seem satisfactory, although the view of the latter is suggestive. They say:—

> "'Dans notre opinion, la cause determinante de la formation de l'envellope amniotique réside dans la descente de l'embryon, déterminée elle même par le pois du corps. C'est par une accélération du développement que la cavité amniotique en est venu a se former quand l'embryon ne possède encore qu'un pois insignifiant.' The chief objection to this theory is that it really gives no cause for the expansion of the somatopleure and chorion; there is no proof that a mere strain of weight can cause the cells of a membrane to proliferate, and since such proliferation is the immediate cause of the growth of the amnion, van Beneden and Julin must assume for their theory that the strain of weight does cause proliferation; but this assumption lacks support. Moreover, they give no evidence to show that the embryo *in utero* is situated in the primitive amniota upon the upper side of the ovum, although it is probable such is the case."[1]

Ryder's theory, **19**, of the origin of the amnion, like that of van Beneden and Julin, to which he does not refer, is purely mechanical; but Ryder seeks the cause in a rigid *zona radiata*, forcing the embryo down into the yolk. See his summary, *l.c.*, p. 184. So far as we know, however, the embryo of the Sauropsida cannot be said to sink into the yolk, and so lead to the development of an amnion; but, on the contrary, the amniotic

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[1] Quoted from Buck's *Reference Handbook*, I., 140.

folds rise up clear above the yolk. Moreover, the formation of the amnion is really a very complex process, part arising from the pro-amnion, part by a dilation of the pericardial cavity (*Parietalhöhle*), and part as the extra-embryonic tail folds. These facts speak, in my judgment, unequivocally against the amnion having arisen by the sinking of the embryo into the yolk sack. Nor is there any justification, I think, for seeking these simple mechanical explanations, which are worthy of Herbert Spencer, since the formation of the amnion depends upon inequalities in the growth power of the germ layers, and only such explanation can be valid as explains that inequality — which Ryder's hypothesis fails to do, so far as I can see.

As regards the evolution of the placenta, we are in the dark. Contrary to prevalent opinion, it is not an organ of the allantois, nor is it an organ of the yolk sack. On the contrary, it is always, so far as we know, an organ of the chorion, and begins its development by a differentiation of that membrane. The allantois is a secondary and later structure. Its primitive rôle is apparently only that of a stalk of connection between the chorion and embryo. There is no evidence to show that the tissue of the allantois spreads out over the chorion to form the mesodermic layer thereof, but the mesoderm of the chorion is proper to it as much as to any part of the somatopleure the mesoderm thereof. When the allantois becomes a large sack, we have a subsidiary change, so that we are brought squarely to the conclusion that the fœtal placenta is chorionic. From this premise phylogenetic speculation must start. Further, we know through the discovery of fundamental importance by His that the allantois cavity is at first a small entodermal tube lying in a posterior prolongation of the body (*Bauchstiel*), and that at this time the so-called allantoic vessels run to and branch out upon the chorion; the placental differentiation of the chorion has already begun, without participation of the allantois, the enlargement of which, when it occurs at all, occurs at a later stage. To speak, therefore, of an allantoic chorion as do Balfour and Selenka (*Studien über Entwichelungsges.*, p. 135) is unjustifiable. Nor can we trace the origin of the placenta to the yolk sack, since in most mammals the mesoderm does not spread over the yolk until quite late, so that the yolk sack consists, as in the rabbit and opossum, in large part of ectoderm and entoderm only, and is without vessels, and therefore unable to form a placenta, which, however, is developing meanwhile from the chorion.

We seek nowadays, following the lead of Professor Cope, to deduce mammalia from the reptilia. Since the reptilia have a free allantois, it is a temptation for embryologists to seek to trace the placenta to a modification of the allantois; but the placenta of mammals appears in the embryo before the allantois becomes free, and the great size of the allantoic vessels is connected primitively not with the allantois, but with the already important chorionic circulation. The placenta is interpolated in the ontogeny of mammals before the specialization of the allantois, which functions as the vascular pathway between the embryo and the chorion, both primitively and permanently. The enlargement of the allantois, which takes place in certain mammals, is a supervening change, probably a survival of reptilian ontogeny. The question is, not how is the connection of the allantois with the placenta (chorion) established in mammals, for it exists from the start,[1] but what becomes of it in reptiles and birds.

Ryder's theory, **128a**, of the origin of the discoidal placenta[2] by constriction of the villous area of the zonary placenta, is difficult to accept. The placenta, being chorionic, cannot of course develop, except so far as the chorion is differentiated; that is to say, so far as the ectoderm (exochorion) is underlaid by mesoderm. Now, in mammals, the chorion, as mentioned above, does not go at first but part way over the yolk sack, even at the period when the development of the placenta has begun. Accordingly, so far as our present knowledge enables us to judge, the discoidal is probably the primitive placental type. If the chorion is completed by the further extension of the mesoderm around the yolk sack, then the placental formation also may spread, and a diffuse type arise. At present, the whole subject is very obscure, but there is certainly no sufficient evidence to prove that the diffuse placenta is the primitive type.

In conclusion, let me point out that we have no satisfactory

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[1] This is beautifully shown by Selenka's investigations on the opossum, cited in the text.

[2] The human placenta is *not* discoidal, but metadiscoidal.

knowledge of the nutrition of the embryo. We know positively scarcely more than that the maternal and fœtal circulations are brought very close together in the placenta. We infer that there must be a transfer of nutritive material from one blood to the other. As to *what* material is transferred and *how*, we have only theories, but of them an abundance. Under these circumstances, the best beginning is undoubtedly a frank acknowledgment of our ignorance.

§ 22. **Summary.** — The following paragraphs attempt to give the more important of the conclusions reached in the second part of this paper.

§ 13. The umbilical cord is not covered by the amnion, but by an extension of the fœtal epidermis. Its cœlomatic cavity is completely obliterated during the third month, and a little later the stalk of the yolk sack is resorbed. The allantoic epithelium persists as a tube or cord of cells for a long period. The blood-vessels have specialized walls derived from the surrounding mesoderm, but have no true adventitia. Connective tissue fibres begin to develop during the third month.

§ 14. The amnion is covered by a single layer of ectodermal cells, which are connected by conspicuous intercellular bridges. It has no true stomata. Its mesoderm consists of anastomosing cells, with a dense matrix; it is imperfectly divided into three strata, of which that next the ectoderm is without cells, that furthest from the ectoderm is often of a loose texture.

§ 15. The chorion consists of two layers, mesoderm and ectoderm, both of which are present over all parts of the chorion throughout the entire period of pregnancy. The mesoderm has at first a dense colorable matrix, with cells, which color very slightly. During the second month the matrix loses its coloring property, and subsequently the cells acquire a greater affinity for coloring-matters; the matrix assumes a fibrous appearance, and ultimately in the region of the chorion frondosum connective tissue fibrils appear in it, most numerously next the ectoderm, so that the mesoderm is differentiated there into an outer fibrillar layer and an inner and thicker stroma layer. The ectoderm during the first month divides into two strata, an outer dense protoplasmic layer and an inner less dense cellular layer. In the latter part of pregnancy the whole ectoderm of the chorion læve has acquired the character of the cellular layer, except close to the margin of the placenta; at the same period the cellular layer forms a number of irregular patches over the chorion læve, while the protoplasmic layer remains over the entire surface, both where the cellular is present and where it is absent; the protoplasmic layer may undergo complete or partial degeneration into canalized fibrine, which is developed in irregular patches. The cellular layer remains on the villi only in a few patches (*Zellknoten*) and over the tips of certain villi; the protoplasmic layer of the villi remains everywhere and develops numerous nodular thickenings; it changes partially into canalized fibrine. It is probable that the fibrine covering the surface of the decidua serotina is derived from the ectoderm of the ends of the villi imbedded in the decidua. The villi are at first of awkward and irregular forms, but their branching gradually becomes more regular, and the twigs acquire a slender and more uniform shape.

§ 16. The menstruating uterus is characterized by hyperæmia, by hyperplasia of the connective tissue of the mucosa, and by hypertrophy of the uterine glands; the upper fourth of the mucosa is loosened and breaks off: there are no decidual cells.

§ 17. The uterus one month pregnant has lost its epithelium from its surface, and from the ducts of its glands; owing to the dilatation and contortion of the deep parts of the glands, it is divided into a lower cavernous or spongy layer and an upper compact layer; the connective tissue of the upper layer is transformed into decidual cells; in sections the glands of the lower layer appear as crowded areolæ, which are lined by a cylinder epithelium more or less disintegrated, or else filled with isolated enlarged epithelial cells.

§ 18. The uterus seven months pregnant is without epithelium either on its surface or in the glands, except a few isolated patches in the deep parts of the latter; there is no trace of the decidua reflexa; the decidua vera is covered by the epithelium of the adherent chorion læve; the decidual serotina is covered for the most part by a layer of fibrine, which is probably derived from the degeneration of the chorionic ectoderm covering the imbedded ends of the villi; the decidua is divisible into an upper compact and a lower cavernous layer, in which latter the gland cavities are reduced to slits; the decidual cells are very numerous and crowded; the larger ones lie near the chorion;

the multinucleate decidual cells are found chiefly in the serotina; at the edge of the placenta decidual cells are found in the chorion.

§ 20. The decidual cells arise by direct enlargement of the connective tissue cells of the mucosa. All parts of the decidua and placenta arise in place by metamorphosis of the tissue; the mucosa is preserved, and there is no production of placental tissues by new formation.

§ 21. The changes of the uterus during menstruation and gestation are homologous, the menstrual cycle being prolonged and modified by pregnancy; hence it is that conception takes place only at the menstrual period, for the ovum can only modify the menstrual change, not initiate the formation of a decidua. No satisfactory explanation of the origin of the amnion has yet been offered. The placenta is an organ of the chorion; its evolution cannot be traced to modifications of either the allantois or the yolk sack; the allantois is originally the intestinal canal of the *Bauchstiel*, which serves as the means of vascular communication between the chorion and embryo; the enlargement of the allantois is secondary. We possess no positive information as to how the placenta performs its nutritive functions.

BOSTON, Aug. 3, 1888.

§ 23. Preliminary Bibliography of Works and Articles specially relating to the fœtal envelopes of mammals, exclusive of general works.

⁂ I shall be much obliged to any who will inform me of errors in and omissions from this list. I have other titles, but the following are all I have been able hitherto to verify.

ALLANTOIS.

(See also FŒTAL MEMBRANES.)

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2. Beddard, F. E.	Note on the presence of an Allantoic (Anterior Abdominal) Vein in Echidna.	Zool. Anz., VII., 653–654.	1884.
3. Budge, A.	Ueber die Harnblase bei Vogelembryonen.	Deutsche med. Wochenschrift, VII., 69–70.	1881.
4. Cadiat.	L'allantoide.	Gaz. med. Paris, 4 Sér., VI., 97–98.	1887.
5. Dastre, A.	Recherches sur l'allantoide et le chorion de quelques mammifères.	Ann. Sci. Nat., 6 Sér., III., pp. 118. Pls. VII.–X.	1876.
6. Dobrynin, P.	Ueber die erste Anlage der Allantois.	Wiener Akad. Sitzb., LXIV., 185–192. Taf. I.	1871.
7. Krause, W.	Ueber die Allantois des Menschen.	Arch. f. Anat. u. Phys., 1875, 215; 1876, 204–207.	1876.
8. " "	Ueber die Allantois des Menschen.	Zool. Anz., IV., 185.	1881.
9. " "	Ueber die Allantois des Menschen.	Z. Z., XXXVI., 175–179. Taf. IX.	1881.
10. Kuppfer, C.	Die Entstehung der Allantois und die Gastrula der Wirbelthiere.	Zool. Anz., II., 520–522; 593–597; 612–617.	1879.
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13. Preuschen, Franz von.	Die Allantois des Menschen, eine entwickelungsgeschichtliche Studie auf Grund eigner Beobachtung.	Wiesbaden, pp. 195. Taf. I.–X.	1877.
14. Strahl, H.	Ueber die Entwicklung der Allantois der Eidechse.	Marburger Sitz., 47–49.	1880.
15. " "	Die Allantois von Lacerta vividis.	Sitz. Marburger Ges., 25–27.	1883.

AMNION.

(See also Fœtal Membranes.)

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17. Hoffmann, C. K.	Ueber das Amnion des zweitblättrigen Keimes.	Arch. f. mikr. Anat., XXIII., 530–536. Taf. XXV.	1884.
18. Hotz, Anna.	Das Epithel des Amnions.	Bern (Inaug. Diss.).	1878.
19. Ryder, J. A.	The Origin of the Amnion.	Am. Nat., XX., 179–185.	1886.
20. Schenk, L.	Beiträge zur Lehre vom Amnion.	Arch. f. mikr. Anat., VII., 192–201. Taf. XVIII.	1871.
21. Viti, Arnaldo.	L' amnois umano nella sua genesi e struttura ed in rapporto all' origine del liquido amniotico.	Siena, pp. 59. Pl. I.	1886.
22. Winkler, F. N.	Die Zotten des menschlichen Amnions.	Jenaischr. Z. Med. u. Naturu., IV., 535–540.	1868.
23. " "	Textur, Structur und Zellleben in der Adnexen des menschlichen Eies.	Jena (Hermann Dabis), pp. 56. Taf. I.–II.	1870.
24. " "	Erwiderung und Berichtigung zu "Ueber die Zotten des Amnion" (Arch. f. Gynäk., VI., 358).	Arch. f. Gynäk., VII., 325–330.	1875.

DECIDUA.

(See also Placenta and Uterus.)

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32. Gervais, H. P.	Sur un uterus gravide de Pontoporia Blainvillei.	C. R. Paris, XCVII., 760–762.	1883.
33. Haussmann.	Lehre von Decidua Menstrualis.	Beitr. z. Geb. u. Gynäk., Berlin, I., 155–277.	1872.
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37. Möricke.	Die Uteruschleimhaut in den verschiedenen Alters-Perioden und zur Zeit der Menstruation.	Zeitschr. f. Geburtsk. u. Gynäk., VII., 84–137.	1882.
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FŒTAL MEMBRANES.

(See also ALLANTOIS, AMNION, and PLACENTA.)

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PLACENTA.

(See also FŒTAL MEMBRANES, AMNION, ALLANTOIS, and DECIDUA.)

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(See also ALLANTOIS.)

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UTERUS.

(See also DECIDUA and PLACENTA.)

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YOLK-SACK.

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EXPLANATION OF PLATES.

Nearly all the figures were drawn by Mr. E. Stanley Abbot under my supervision. The outlines were drawn with the camera lucida, and the details added free-hand. The drawings are all accurate representations of the preparations, and though of course not photographically exact, are not diagrammatic, except in the case of a few figures expressly specified below. I owe much to Mr. Abbot's patient skill.

Reference Letters.

all, allantois.
cm, circular muscles.
conn, connective tissue.
ecto, fœtal ectoderm.
emb, embryo.
en, entoderm.
endo, endothelium.
ep, epithelium.
f, placental fissure.
f.v, fœtal blood-vessel.
gl, gland ; glandular layer.
h.ep, hyaline epithelium.
l, leucocytes.
lm, longitudinal muscles.
mes, mesoderm.
mo.cl, monster cells.
msth, mesothelium.
muc, mucosa.
musc, muscularis.
ob.pl, ob-placenta.
o.z, outer zone of placenta.
P, periplacenta.
per.v, perivascular cells.
sp.pl, sub-placenta.
Sgl.z, subglandular zone.
V, blood-vessel.
vac, vacuole.

EXPLANATION OF PLATE XXVI.

FIG. 1. Placenta of rabbit at eight days, with dilated glands, *gl*, and superjacent fœtal ectoderm, *ecto* (× 125 diams.).

FIG. 2. Rabbit's uterus at nine days, transverse section of a swelling (× 7 diams.).

FIG. 3. Portion of the placenta of Fig. 2 (× 445 diams.), to show the connective tissue, *conn*, the perivascular cells, *per.v*, and the thickened endothelium, *endo*, of the blood capillaries.

FIG. 4. Portion of the periplacenta of Fig. 2 (× 175 diams.), to show the degeneration of the epithelium, *h.ep*.

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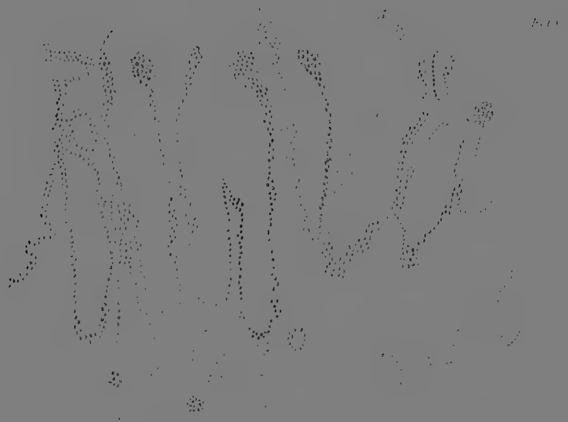

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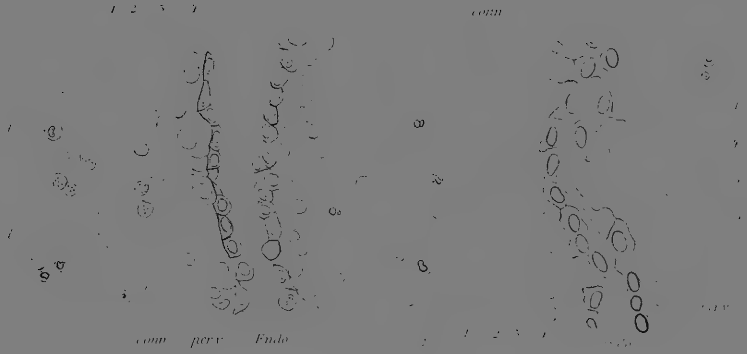

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EXPLANATION OF PLATE XXVII.

FIG. 5. Portion of the ob-placenta of Fig. 2 (× 175 diams.), to show the degenerated epithelium, *h.ep*, and the saucer-shaped glands, *gl*, *gl'*.

FIG. 6. Rabbit's uterus of eleven days; portion of the ob-placenta to show the degenerated epithelium, *h.ep*, and the regenerated glands, *gl* (× 175 diams.).

FIG. 7. Portion of the placenta of Fig. 2 (× 175 diams.), to show the degeneration of the uterine tissue and the relations of the fœtal ectoderm to the placental surface.

FIG. 10. Rabbit's uterus of thirteen days; portion of the ob-placenta (× 175 diams.), to show the regenerated glands.

FIG. 11. Portions of the epithelium of the periplacenta at thirteen days. A, vertical section (× 175 diams.). B, surface view (× 175 diams.). C, single cell (× 445 diams.).

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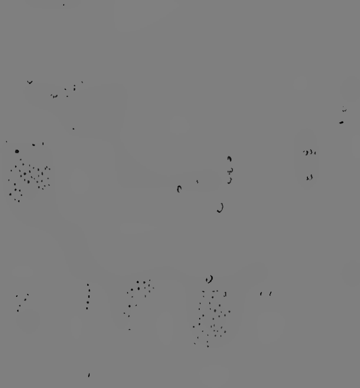

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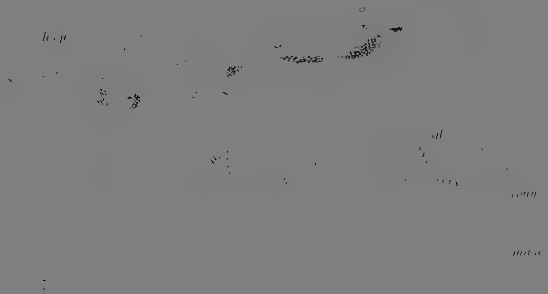


EXPLANATION OF PLATE XXVIII.

FIG. 8. Portion of a vertical section of the placenta at eleven days of a rabbit, to show the relations of the mesothelium, *msth*, to the top, and of the ectoderm, *ecto*, to the side of the placenta (× 175 diams.).

FIG. 9. Complete transverse section of a rabbit's uterus at thirteen days, with the embryo, *emb*, in place (× 7 diams.); the details are only approximately accurate; *x*, mass of perivascular decidual cells, developed in the region of the ob-placenta.

FIG. 12. Rabbit's uterus at fifteen days; portion of a section through the placenta (× 90 diams.), to show the degenerated glands, *gl*, and the mesoderm, *mes*, and mesothelium, *msth*, covering the surface of the placenta; the blood-vessels are drawn dark.

FIG. 13. Portion of upper part of a rabbit's placenta at fifteen days (× 340 diams.), to show the histological structure of the glandular layer of the placenta.

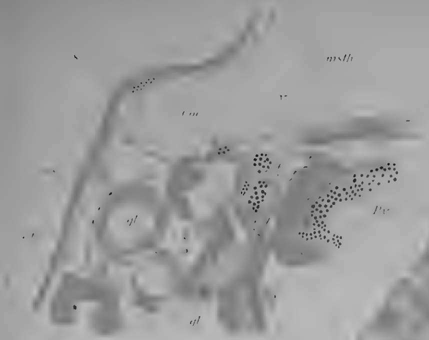
FIG. 14. Multinucleate decidual cells from the subglandular zone of a rabbit's placenta at fifteen days (× 540 diams.).

FIG. 15. Uninucleate perivascular decidual cells from the outer zone of a rabbit's placenta at fifteen days (× 540 diams.).

FIG. 16. Endothelium from the blood-vessels of the periplacenta of a rabbit at fifteen days (× 240 diams.). A, surface view; B, C, in section.

FIG. 17. Ob-placenta of a rabbit at fifteen days (× 125 diams.), to show the monster cells, *a*, *b*, *c*, and the uterine epithelium, *ep*.

FIG. 18. Nucleus of a monster cell from the ob-placenta of a rabbit at fifteen days (× 445 diams.).



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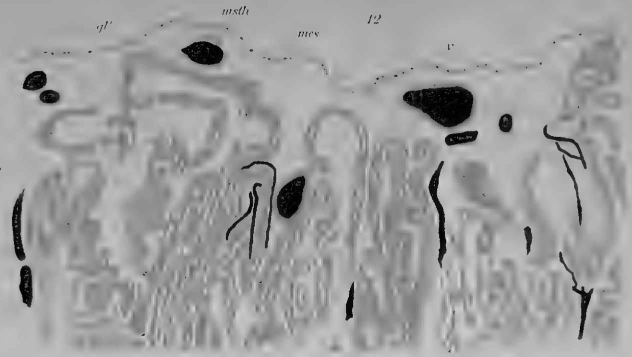

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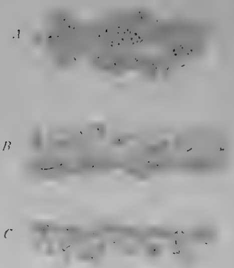

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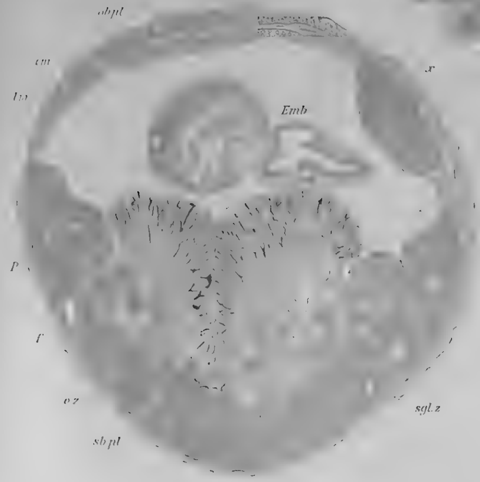

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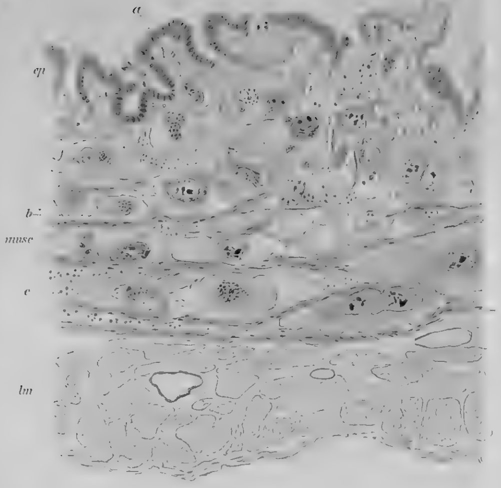

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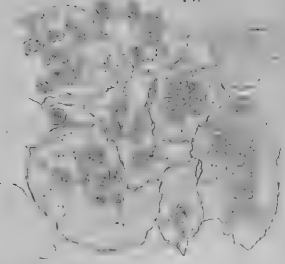

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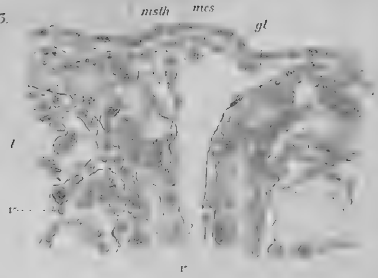

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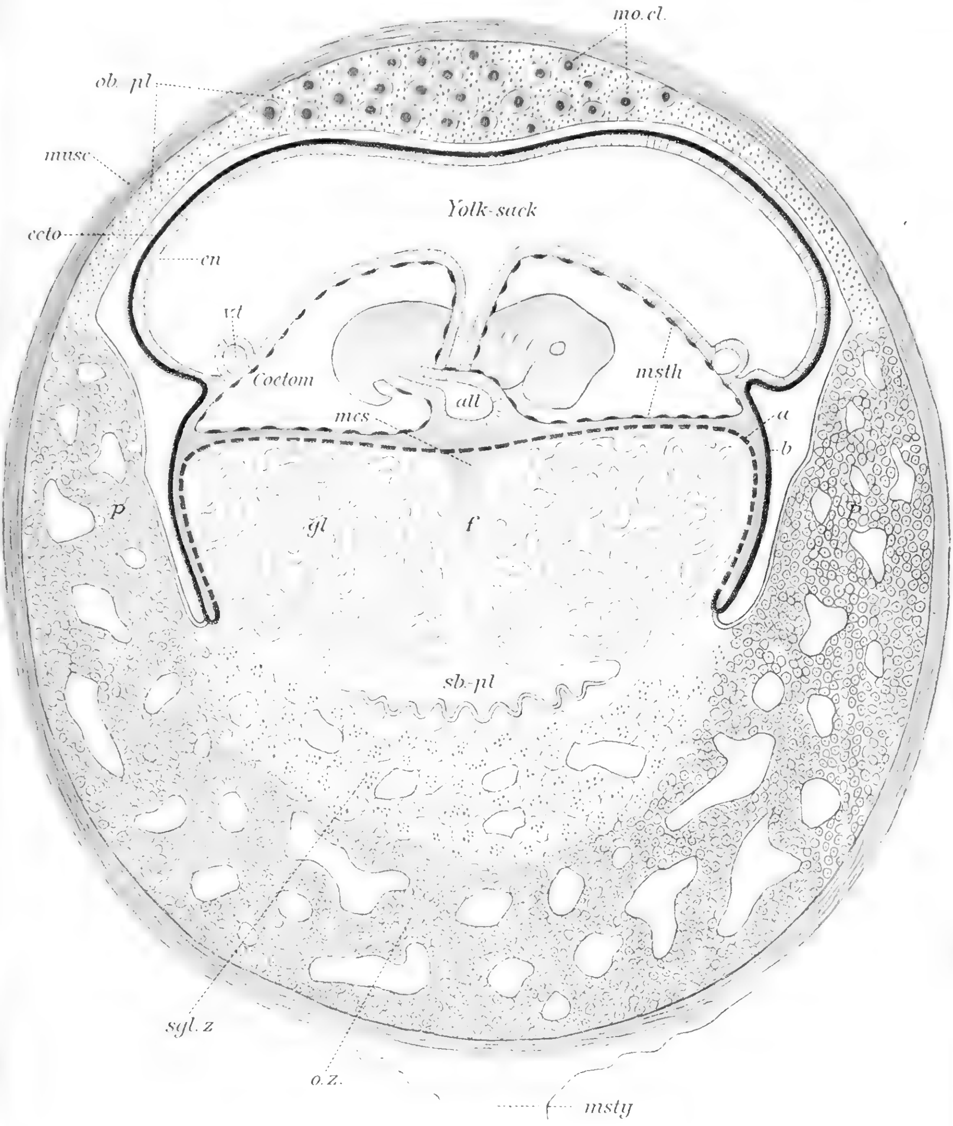
EXPLANATION OF PLATE XXIX.

Diagram to show the relations of the embryo and uterus in the rabbit from the eleventh to the thirteenth day of gestation.



a	*ectoderm, lost part*	*musc.*	*muscularis*
all	*allantois*	*msth.*	*mesothelium*
b	*ectoderm at side of placenta*	*msty*	*mesentery*
ecto	*ectoderm of yolk-sack*	*ob.pl*	*ob placenta*
en	*entoderm of yolk-sack*	*o.z*	*outer zone of placenta*
f	*fissure between lobes*	*P.*	*periplacenta*
gl.	*glands.*	*sb.pl*	*sub-placenta*
mes	*mesoderm*	*sgl.z*	*sub-glandular zone*
mo.cl.	*monster cells*	*v.t.*	*vena terminalis.*

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THE ANATOMY AND DEVELOPMENT OF THE LATERAL LINE SYSTEM IN AMIA CALVA.

EDWARD PHELPS ALLIS, Junr.

CONTENTS.

The general course and position of the lateral canals in fishes have long been known, and short descriptions and diagrams, showing what is commonly accepted as the typical arrangement of the main canals, are given in nearly all modern text-books of vertebrate anatomy. More complete descriptions are given in numerous special works, most of which deal more particularly with other subjects, such as the structure of the skull, the development and distribution of the cranial nerves, or the histology and function of the sense-organs.

With a few exceptions, all these descriptions, so far as they relate to the cranial part of the lateral system, are of a general character only, giving little more than the course of the main canals. The development of the canals, the number and position of the organs, and their innervation, receive but scant attention. This has doubtless been largely due, as Merkel suggests, to the difficulties attending this part of the investigation before the introduction and perfection of modern methods of research ; but this cannot have been the only reason, for most of the work could easily have been done by any of the earlier writers. The purely descriptive part of the subject seems simply to have been neglected in the greater interest attaching to the histological and physiological sides, so that it is only within the last five or six years that the constant relations of the cranial canals to the dermal bones of the head, and their importance in determining these bones in doubtful cases, have been recognized. Both Sagemehl and Van Wijhe have called special attention to this, and Sagemehl further says (No. 12, p. 182, note) that the lateral canals seem to deserve a more careful study than has hitherto been given them.

In Amia calva the cranial canals have been oftener and more fully described than in any other form. Franque (No. 6), in 1847, in a dorsal view of the dermal bones of the head, shows some of the surface openings of these canals, but in the text he does not refer to them, these four words only being found, "Linea lateralis fere recta" (No. 14, p. 368). Bridge (No. 4, p. 620), thirty years afterward, in describing the skull, gave the course and position of the main canals, the connections they form with one another, and the bones they traverse, and the arrangement given by him agrees closely with that more fully detailed in the present paper. His work was mainly confirmed in 1882 by Van Wijhe (No. 17, p. 288), and in 1883 and 1884 by Sagemehl (No. 12, p. 183, and No. 13, p. 36) ; still later by Shufeldt (No. 15), in connection with his translation of Sagemehl's paper ; and finally Wright (No. 18) has called attention to the sensory tissue lying in the upper end of the spiracular canal, and belonging, by its innervation, to the general lateral canal system, though classed by him as hypodermal and exceptional.

Sagemehl's description is much the best and most complete of all; but he does not give the smaller branches of the system, simply saying of them that the main canals have numerous branches, arranged in many longitudinal rows and leading to minute openings on the outer surface of the head. These small branches are similarly disposed of in his description of the cranial canals in the Characinidæ, where he says they are too variable and irregular to have any morphological significance whatever.

A closer examination of Amia has shown that these small branches have as constant relations to the dermal bones as the main canals have, and hence may have as great significance. They also have constant relations to the sense-organs found in the canals, agreeing in this with the conditions described by Bodenstein in Cottus gobio (No. 3) and by Emory in Fierasfer (No. 5, p. 39).

The drawings for this paper have been made by Mr. Nomura, to whose patience and skill the plates bear witness.

I. ADULT FORM.

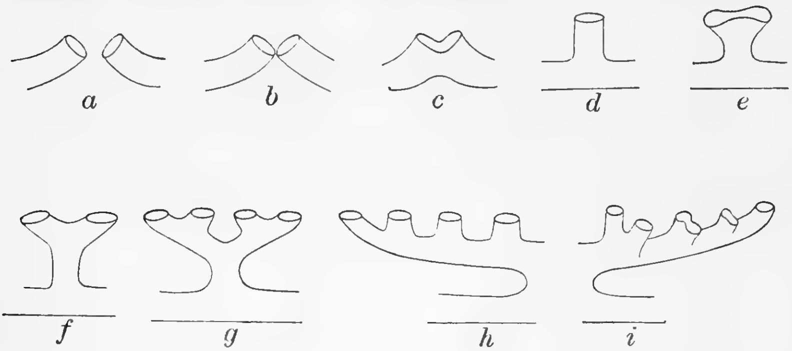
General Description.

If an adult specimen of Amia calva be examined, many hundreds of minute pores will be found, scattered to all appearance most irregularly over a large portion of the head (Figs. 20, 21, and 22, Pl. XXXVI.). Most of them lie directly superficial to the dermal bones; and they are found in greater or less number external to all these bones, excepting the prefrontal, maxillary and jugal, operculum, sub- and interoperculum, branchiostegal rays, and gular plate. They are also found in certain places beyond the limits of the dermal bones; as, for instance, near the posterior nasal aperture, in the fold of dermis immediately behind the pre-operculum, and in the thick dermis between the pre-operculum and the hinder and lower margins of the postorbitals. In these places they lie mostly near the edges of the bones, and are particularly numerous along the anterior edge of the pre-operculum.

Each pore, as is well known, is the external opening of a small epidermal tube which leads inward through the dermis into some one of the dermal bones. In its course it unites with similar canals from other pores, and increasing continually in size, finally becomes a trunk canal, which opens into one of the main lateral canals of the head. This trunk canal and its branches form what has been called a dendritic system, of which the surface pores are the external openings.

The arrangement of these pores varies greatly in different parts of the head. They are found either single or in pairs, in more or less irregular lines, or in irregular groups, the number and arrangement of them differing somewhat in every specimen, and even on opposite sides of the head in the same specimen. As many as thirty-seven hundred were counted on the head of a single large specimen, and the number apparently increases indefinitely with the age of the fish. This great multiplication is the result of a repeated dichtomous division of the pores formed in younger stages. The impulse leading to this division acts with much greater intensity in certain parts of the head than in others, but is felt in all parts; for, with the exception of the large pore at the hind edge of the supraclavicula (Fig. 39, Pl. XXXIX., $i^{22}ll^{1}p$), which marks the limit of the cranial system, there is not a pore on the head of the young fish that is not double in later stages.

In both fresh and alcoholic specimens, the pores have a well-marked whitish border, due mainly to the absence of inter-epithelial pigment cells; and when fully formed they are approximately round. When about to divide, the sides of the oblong and continually lengthening pore grow rapidly upward and toward each other, and the pore becomes hour-glass or dumb-bell-shaped. The projecting sides or lips finally meet and coalesce, and the pore is divided into two pear-shaped portions which lie in a small unpigmented oval space. In this process the canal leading to the pore is also divided into two portions, for an arch is formed across the end of it, and it becomes Y-shaped form as shown in the accompanying diagrammatic figure (Cut 1, *d*, *e*, *f*). The two newly formed pores are at first connected by a whitish cicatrice (Fig. 17, Pl. XXXV.); but the impulse which led to their formation continuing to act, they travel apart, the cicatrice disappears, and they become distinct and perfect pores. One or both of them may again divide in the same manner, and nearly in the same direction as at first, thus giving rise to a line of pores usually somewhat curved, and to a canal of the form shown in Cut 1, *g*. The division of the terminal pores of such a line may then proceed more rapidly than that of the intermediate ones, thus producing creeper-like canals of the form shown in *h*; or later, divisions may take place at an angle to the original direction of division as shown in *i*, the angle being usually a right one, or nearly so, and then again in the same direction, or in the original direction, thus giving rise to a series of intersecting, or parallel lines, and to a more or less complicated arrangement of pores in groups of different sizes and shapes. There is in this process of multiplication a strong tendency to keep the pores of the different lines and groups at about the same distance apart, so that when the groups become large, somewhat geometrical designs are formed, and any particular pore may appear to belong to one of two or more intersecting surface lines, either one of which might be taken, from surface indications alone, to be the line of formation of the series.



Cut 1.

Cut 1.—Diagrammatic representation of the formation and subsequent division of a primary pore or tube: *a*, *b* and *c*, two half-pores approaching each other and fusing; *d*, primary pore and tube; *e*, the same, undergoing its first division, which in *f* is completed; *g*, dentritic system after second regular division; *h* and *i*, forms of creeper-like branches.

This is the regular method of multiplication and formation of the pores and branch canals in Amia, none of them being formed by growth from beneath; that is, by the canals first forming there as diverticula, or prolongations of existing canals, and then forcing their way through to the upper surface. Not a single instance was found of such a growth from below, and but one of the reverse condition, — that of a tube leading blindly inward from the external surface toward a canal; and the conditions in this case seemed to indicate that the tube, after its regular formation, had been closed secondarily below the surface. The specimen in which this was found was taken in winter, through the ice, and having been frozen and frequently handled, the epidermis was so injured before the pit was discovered that it was impossible to tell whether there had originally been a regular surface pore or not.

The formation of the more or less complicated groups of pores resulting from this method of division is well shown in Fig. 17, Pl. XXXV., which represents the head of an Amia about fifteen months old and 11½ inches long. This specimen, which was raised in an aquarium, was much larger than other specimens two years old living in the same aquarium, and probably larger than fishes of the same age found in their native waters; for, according to Dr. Estes (No. 7, p. 659), Amia one year old, taken in the sloughs tributary to Lake Pepin, are only from three to six inches long. All stages in the division of a pore are shown in this figure. In some instances the pore is apparently dividing into three portions instead of two, but this is due to the accelerated re-division of one of the portions before the regular division has been completed. Nothing of this kind was found in any of the several adult fishes examined, but in the skeletons prepared, the openings of the canals on the upper surface of the frontal often presented a tri-lobate appearance, indicating that they had arisen in this manner (Pl. XL., Fig. 40, sg^5, sg^6).

The different groups of pores, although varying greatly in size and shape in different individuals, or even in the same individual on opposite sides of the head, are normally definite in number and general position. Each group when small is confined strictly to some particular region of the head; but in its growth it extends beyond this region, and becomes continuous with neighboring groups. It is necessary, therefore, in order to arrive at the proper number and arrangement of the groups in large and well-developed specimens, to trace the canal leading from each pore to the particular trunk or stem from which it arises.

The system of canals leading from the pores of any one group forms, as already stated, a dendritic structure, the trunk of which is the common connection of the group with some one of the main canals of the head. These main canals lie almost exclusively in the deeper, more porous layer of the dermal bones, near their under surface, and often project in the form of a ridge below the general level of this surface. Bridge (No. 4, pp. 607 and 608) considers this part of the bone in Amia an "adherent parostosis," resulting from the later ossification of the subcutaneous tissues lying immediately under the original ganoid plate, which is represented in the superficial, thinner, and denser layer of the bone. The development, however, shows that the dermal bones grow mainly by accretions to their upper surfaces, and that the deeper portion is the one formed first, the canals in young specimens lying in it or above it, and in no case below it.

In their passage from one bone to another, where the bones are not suturally connected, the canals lie in a dense connective tissue, which forms the deeper part of the cutis. This occurs particularly between the frontal and nasal on either side, and between the upper and lower ends of the pre-operculum and the squamosal and angular respectively.

The trunks of most of the dendritic systems and the proximal parts of their branches lie in the dermal bones, but in their upper denser layer. The openings of the branches on the upper surface of the bone present all the various stages between the single opening and two openings about to become separate that the pores do on the external surface of the head. The number of openings on the upper surface of the bone does not, however, usually correspond with the number of external pores; for where the dermis is thick, as on the end of the nose, around the posterior nares, and along the edges of the pre-operculum, there may be one or more series of branches lying in it, entirely above or beyond the bones; and where the dermis is thin, although some of the branches pass directly through it to the external surface, others, of the creeper-like form shown in Cut 1, *h*, are continued along the outer surface of the bone in long channelled lines, the bone not yet fully inclosing them.

Course of the Canals.

In tracing the canals through the dermal bones, the method used was the following. The head of a fish was boiled a few minutes, cleaned as much as possible, and then allowed to macerate until the tissues were thoroughly softened. The different bones that contained any part of the canals of the lateral system were then separated and carefully cleaned, the outside with a brush, and the canals by forcing water through them with a pipette. They were then heated in water and injected with a blue gelatine solution, and after a short exposure to the air, to allow the gelatine to set, cleaned and put in 50 per cent alcohol. The smaller tubes of the system, that the gelatine mass had failed to penetrate, were filled by forcing with a needle little plugs of the cold injection mass into them from the openings on the surface. Finally, the bones were scraped on the inner surface below the canals, until under the microscope every branch could be distinctly traced. In bones that had been simply macerated without boiling, the canals and branches were so filled with a chalk-like deposit that they could not be successfully injected.

All the dermal bones containing any part of the canals of the lateral system are shown in Figs. 40–43, Pl. XL. They are enlarged two diameters, and all, excepting the suprascapula and supraclavicula, placed in serial order as they occur in the fish. In these figures the canals and dendritic systems lying in the dermal tissues between the frontal and nasal, and at either end of the pre-operculum, are shown, as well as all the ramifications of the osseous canals, and the openings and channelled lines on the outer surfaces of the bones. In Figs. 45, 46, and 47, Pl. XLI., three views are given of the skull, natural size, with the dermal bones in place. In Figs. 46 and 47 the canals are, for fuller illustration, shown on both sides of the head, but the dissections were made on one side only, and the perfect bilateral symmetry shown in the drawing does not exist in nature.

The arrangement of the canals and dendritic systems shown in these figures is the normal one, from which there are, however, frequent variations. There are on each side of the head the three well-known canals: the infra-orbital, supra-orbital, and operculo-mandibular, and in addition a supratemporal or occipital cross-commissure.

1. *Infra-orbital Canal.* — The infra-orbital is the main canal of the system, and is directly continuous with the lateral canal of the body. It has four parts or regions, which develop somewhat independently: an antorbital, a suborbital, a squamosal or temporal, and a post-temporal, — all continuous in the adult. The antorbital part of the canal begins at a sharp bend in the suborbital portion, immediately in front of the eye and below the posterior nasal aperture. It runs forward and downward, and partly encircles the nasal tube (which in Amia is the anterior nasal aperture), running below and in front of it, and uniting, on the top of the snout between the nasal tubes, with the corresponding canal of the opposite side of the head. This antorbital portion, which is more properly an anterior cross-commissure connecting the two main infra-orbital lines, seems to be found in some other ganoids; for Traquair (No. 18, p. 181) describes a similar connection in *Polypterus bichir*, and Leydig (No. 9, p. 249) three of them in *Chimæra monstrosa;* but it is not found in the teleostei, so far as can be judged from the descriptions I have been able to find. According to Sagemehl (No. 14, p. 36), it does not exist in the Characinidæ, nor is it found in *Amiurus catus* (No. 21, p. 265), and from my own examinations I know it is not found in *Salvelinus namaycush*, *Micropterus dolomieu*, *Esox lucius*, or *Stizostedium vitreum*. In Salvelinus, a line of organs lying wholly in the external epidermis, occupies about the position of the canal in Amia. These organs belong to the same class as the canal organs. There are several other lines on the head of Salvelinus, and corresponding ones on that of Amia.

The suborbital part of the infra-orbital part is, in the adult, connected at its anterior end, immediately in front of the posterior nasal aperture, with the supra-orbital canal. There is no direct union of the two lines here, the connection being of the nature of a commissure formed by the anastomosis of two dendritic systems, one of which is the terminal system of the suborbital, and the other the fourth regular system of the supra-orbital canal. Starting from this point, the suborbital canal runs forward and downward to a point above the anterior end of the maxillary, where it is joined by the antorbital canal or anterior commissure; it then turns sharply backward, and lying above the upper edge of the maxillary and jugal and below the eye, it somewhat more than half encircles the orbit, extending to a point above and behind it, and a little in front of the blind upper end of the spiracular canal. The canal here turns sharply backward, and, as the squamosal or temporal portion, is continued backward and upward above the pre-opercular fold, to a point between this fold and the upper end of the opercular opening, where it gives off the supratemporal cross-commissure. The post-temporal portion lies behind this commissure, continuing at first in the line of the squamosal canal upward and backward, above the upper end of the opercular opening, and then downward and backward under the upper and posterior margin of the operculum, to the hind edge of the supraclavicula, where it joins the anterior end of the lateral canal of the body.

2. *Supra-orbital Canal.* — The supra-orbital canal begins a little median to and behind the nasal tube. It runs at first toward the median line, and then almost directly backward above the eye, ending near the hind margin of the frontal, and sending its posterior branches into the anterior part of the parietal and squamosal. Behind the eye it is deflected somewhat laterally, and anastomoses with the infra-orbital canal at the bend in that line where the suborbital portion joins the squamosal. The arrangement of the canals in the adult at this point is such that the supra-orbital has always been considered the direct continuation forward of the squamosal or temporal portion of the infra-orbital, the two together being described as the main lateral canal of the head, and the suborbital as one of its branches. The development of the canals in Amia shows conclusively that this interpretation is wrong, for the supra-orbital develops independently, its innervation is different, and it only acquires its connection with the main infra-orbital as an anastomosis after both canals have been fully inclosed.

That this independence of the supra-orbital canal is not peculiar to Amia is shown by the arrangement in the Characinidæ as given by Sagemehl (No. 14, p. 36). In these fishes the supra-orbital has, in the adult, the condition found in the larva of Amia; that is, it is separate and distinct from the main infra-orbital, broken off from it, as Sagemehl says, by the intrusion of the anterior end of the dilator operculi muscle, which has in this fish an unusual insertion on the upper surface of the post-orbital process. His description of the canal in the Characinidæ shows that it agrees closely in general course and position with that of Amia, beginning in both forms at the anterior end of the nasal, median to the nasal openings, and ending at the hind margin of the frontal, where one or more branches are sent backward into the parietal. The main canal in the Characinidæ also agrees closely with that in Amia, but Sagemehl describes the suborbital part of it as a branch given off downward behind the eye, from the extreme anterior end of what he considers to be the main temporal or posterior division of the supra-orbital.

3. *Operculo-mandibular Canal.* — The operculo-mandibular canal begins at the anterior end of the lower jaw, close to the middle line of the head and close to the anterior end of the canal of the opposite side, but without any connection whatever with it. Bridge (No. 4, p. 620), Sagemehl (No. 13, p. 183), Van Wijhe (No. 19, p. 288), and Shufeldt (No. 16) all agree in stating that here the two canals are continuous; but this was not the case in any of the many specimens I have examined.

Starting here as an independent line on each side of the head, the mandibular part of the canal runs backward along the lower inner margin of the ramus of the mandible, nearly to its hind end, where it turns upward and passes out of the mandible immediately in front of and above the articular process for the symplectic. It then turns sharply backward and is continued as the opercular part of the canal upward and backward through the pre-operculum in the curved line of that bone. Leaving the bone at its upper end it passes through a narrow strip of dermis, and joins the infra-orbital canal, near the hind end of the squamosal, turning forward at the point of union. The mandibular and opercular portions of the canal develop as two distinct canals, uniting later with each other to form a continuous line and then uniting with the main infra-orbital. These later connections in Amia are not always formed in other fishes. In *Esox lucius* for example, the two portions always remain, even in the adult, separate from each other and from the infra-orbital; and in *Polypterus bichir, Amiurus catus,* and *Cottus gobio,* although they unite to form a continuous line, they do not unite with the main canal.

4. *Supratemporal Cross-commissure.* — The supratemporal

cross-commissure lies in the temporal region. Leaving the main infra-orbital canal in the extrascapula it runs slightly forward toward the top of the head, and meets there the end of the corresponding canal of the opposite side, thus forming a second connection between the two main lines, the first or anterior one lying on the top of the snout, as already described. These two are the only connections that are formed in Amia between the lateral systems of the opposite sides of the head.

Leaving the several canals at irregular intervals, but at definite places, are the trunks of the different peripheral canal systems, each of which is represented on the outer surface of the bone by a distinct group of openings.

Topography of the Peripheral Canal Systems.

1. *Infra-orbital Canal.* — The infra-orbital canal, which is the direct continuation of the lateral line of the body, traverses in succession the supraclavicula, suprascapula, extrascapula, squamosal, postfrontal, post- and suborbitals, lachrymal, antorbital, and ethmoid, joining in this last bone the canal of the opposite side. Beginning at this point, in the middle line of the head, the canal first runs forward, outward, and downward to the outer anterior end of the arm of the V-shaped ethmoid, giving off at about two-thirds its course through the bone a branch which runs straight forward and upward to the surface of the bone, and has there a single large opening. This branch canal represents the second peripheral system of the line, the first system having disappeared at the middle line of the head, as will be described later. It may be designated as trunk 2 (Fig. 41, Pl. XL.), and the corresponding pore or group of pores on the external surface as group 2.

Leaving the ethmoid, the main canal turns sharply backward and upward, and entering the antorbital at its extreme anterior end, runs upward and backward along the middle line of the bone for about two-thirds its length. At this point, which is approximately above the articular end of the maxillary, it turns backward and leaves the bone at its hind margin. In the antorbital the canal gives off the trunks of four peripheral systems: trunk 3 at the beginning, trunk 4 at about one-third, and trunks 5 and 6 close together at about two-thirds its course through the bone. Trunk 3 runs forward and outward, and lies so far forward that it is not entirely inclosed in bone, leaving the canal between the ethmoid and antorbital, giving off no branches in the bone. Trunk 4 is directed downward, forward, and outward, and has a single large opening at the surface of the bone. Trunks 5 and 6 are given off almost at the same point, but on opposite sides of the canal, just before or at the horizontal bend in it. Trunk 5 is short, and is directed outward and downward. It sends one long branch forward with two single and one double opening, and one branch outward and downward which has two short branches with five openings, making in all seven single and one double opening in the system, all lying along the lower outer edge of the bone. Trunk 6 is a direct continuation upward and backward of the antorbital part of the main canal, and is comparatively long, extending from the bend in the canal to a point beyond the upper posterior margin of the bone and a little in front of the posterior nasal aperture. Here it runs directly into, and is continuous with, trunk 4 supra-orbital, the two trunks or some of their branches meeting and anastomosing, and so forming a direct connection between the two canals.

Trunk 6, infra-orbital, after leaving the antorbital bone at its hind end, enters the little strip of dermal tissue (near the lateral edge of which the posterior naris lies), which extends across the top of the head between the lachrymals, and between the frontals behind and the nasals and antorbitals in front. The canals that traverse this strip of dermis lie in a deeper, denser stratum of the corium, which corresponds in position to that of the dermal bones in other places. Trunk 4 supra-orbital lies entirely in this tissue, as does also 6 infra-orbital after leaving the antorbital bone at its upper end. This latter trunk usually sends one or more creeper-like branches forward, toward or into the hind margin of the nasal, and one or more backward, toward the median or anterior edge of the posterior nasal aperture; but these branches are given off so near the point of anastomosis that it is often difficult to determine to which one of the systems they belong. In the two systems combined, in the specimen used for illustration, there were on one side of the head twenty-six pores, and on the other twenty-seven, three on one side and five on the other being in the nasal.

The anastomosis of these two peripheral systems is not formed until the fish is well advanced in age. In the large 15-month specimen shown in Fig. 17, it is just forming. It is brought about in the following way: trunk 4 supra-orbital, which leaves its canal immediately in front of the frontal, runs forward and laterally until it reaches a point median to the anterior edge of the posterior nasal aperture. Here it turns backward, and runs toward the anterior edge of the frontal, often extending beyond this edge onto the upper surface of the bone. Trunk 6, infra-orbital, lies almost exactly in the line of the main part of trunk 4, supra-orbital, the two trunks and their system of pores and branches growing directly toward each other until either the trunks or some of their branches come squarely together and unite at or near the bend in trunk 4, enlargements being usually formed at the points of union. A remnant of the dividing wall remains, indicating the line where the two systems came together. *This is the only place in the entire lateral system of Amia where an anastomosis below the surface occurs;* for, even where terminal branches of the same or neighboring systems are united below the surface, as shown in Fig. 40, Pl. XL., ig^9, the union, so far as I have been able to determine, is always first formed at the surface by the fusion of two pores in a manner to be fully described in treating of the development of the system.

Leaving the antorbital at its hind edge, at about two-thirds the length of the bone, the main canal enters the upper anterior edge of the lachrymal, and, running backward along its middle line, gives off the trunks of three peripheral systems, — trunk 7, immediately on entering the bone, trunk 8, about half-way through it, and trunk 9, just before leaving it. All these trunks run outward, downward, and forward. Trunk 7, which is short, lies just above a small notch in the lower anterior corner of the lachrymal. Its system has three large openings along the upper edge of the notch, and five along a slender branch directed backward from it, making eight in all.

The openings of the next two systems, 8 and 9, are arranged along the entire lower, lateral edge of the lachrymal. No. 8 has three double and two single openings, and No. 9 two double and seven single ones. One of the double openings in this last system is formed by the anastomosis of two branches at their outer ends, an instance of the fusion of two pores in adult life already referred to. The posterior branch of this system is continued as a groove onto the outer surface of the first suborbital.

Leaving the lachrymal, the canal passes through the middle of the two suborbitals, and enters the lower postorbital near its lower anterior angle. Running upward and backward in this bone, to about one-quarter its length, the canal turns directly upward, traverses the rest of the bone, and enters the upper postorbital at the anterior quarter of its lower edge. Turning somewhat forward here, it passes through this bone, turning directly upward again and then backward, just as it leaves it, to enter the postfrontal.

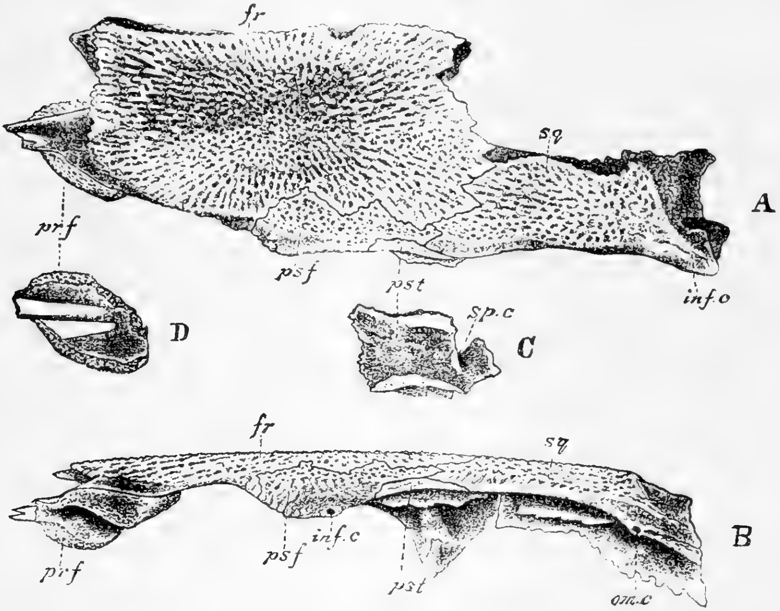
In its course through the sub- and postorbitals, the canal gives off the trunks of seven peripheral systems. The first one, trunk 10, leaves the main canal near the hind end of the first suborbital. Dividing immediately, it sends one branch forward, with five large openings near the lower edge of the bone, and one backward, ending in a groove on the anterior end of the outer surface of the second suborbital, making six openings in all, three of which at least are double. Trunk 11 is given off upward and outward near the hind end of the second suborbital. It sends one branch forward along the outer edge of this bone toward the end of the branch from trunk 10, and another backward into the lower postorbital, the two branches having sixteen openings in all, five, three of which are double, being in the suborbital, and eleven single ones in the postorbital. Trunk 12 leaves the canal where it turns directly upward at about the middle of its course through the lower postorbital. It is directed downward and backward, and gives off several branches, each of which divides again one or more times, the longer branches lying mostly parallel to the main trunk. It has in all thirty-seven openings, which lie in a group a little in front of and below the middle point of the bone. Trunk 13 is short, and is given off just as the main canal enters the upper postorbital. It divides immediately, sending one branch, with eight openings, downward and backward into the lower postorbital, and another, with twelve openings, upward and backward into the upper postorbital, making twenty openings in this system. Trunk 14 is given off at about three-quarters of the course of the canal through the upper postorbital, the bone here being very thick, and is directed backward and outward. It sends a large branch backward to about the middle of the bone, and another forward toward the eye, in front of the main canal, both of them branching several times, and having in all thirty-seven openings, all lying in front of the middle point of the bone, and extending almost to its extreme anterior edge.

The canal, after leaving the upper postorbital, enters the postfrontal, where it has a curved course, turning gradually backward till it reaches the median edge of the bone at about its middle point. Here it turns directly backward, and, running between the frontal and postfrontal, enters the squamosal at about the middle of its anterior end. It traverses this bone from end to end, running directly backward with a slight lateral bend near the hind end, where it is joined by the opercular canal.

In the postfrontal, the canal lies entirely in what Sagemehl (No. 13, pp. 184 and 185) considers merely the outer, denser, and harder part of the primary ossification of the postorbital process. This ossification, which is traversed by a canal of the lateral system, and the prefrontal, which is not, are both considered by him as exceptional instances of primary ossifications that have acquired secondarily the surface characteristics of true dermal bones. He calls attention to the earlier work of Bridge (No. 4, p. 607), who describes each of these bones as having an outer dermal component wholly separate from the underlying primary ossification; but he nevertheless strongly asserts that this separation can only be made by fracture.

In the several specimens which I have examined with special reference to this point, I have always found the prefrontal a single bone and the postfrontal in two parts. The prefrontal (Cut 2, *prf*) lies under the outer anterior corner of the frontal, projecting slightly beyond it, but in no place rising above the level of its under surface. The projecting edge is continuous with the edge of the frontal, which in this place is bevelled, and, although roughened, it has neither the character nor appearance of the outer surface of the dermal bones. In the unprepared head it is covered by thick dermis, and its roughened edge gives attachment to strong membranes. It lies deep and is not traversed by the main cranial canals or any of their branches.

The dermal portion of the postfrontal (Cut 2, *psf*) is a small bone, somewhat triangular in shape, exactly filling a large notch extending from the middle of the lateral edge of the frontal to the hind edge of the bone. Its small posterior end usually fits into a notch in the anterior end of the squamosal, which overlaps somewhat its lateral edge. It rests directly upon the deeper postorbital ossification, and is so closely connected with it, that in attempting to remove it in fresh specimens, one of the bones is usually broken, and a fractured surface obtained; but in skeletons properly prepared, — by maceration or by boiling, — the two bones are easily parted, leaving a clean and perfect surface of separation. The postfrontal projects beyond the postorbital ossification in front, and forms part of the roof of the orbit. The lateral edge of this part of the bone is thickened, frequently having a rib-like projection along its under surface, as if the edge of the bone had been turned down and a little under. The upper corner of this thickened edge and the corners of



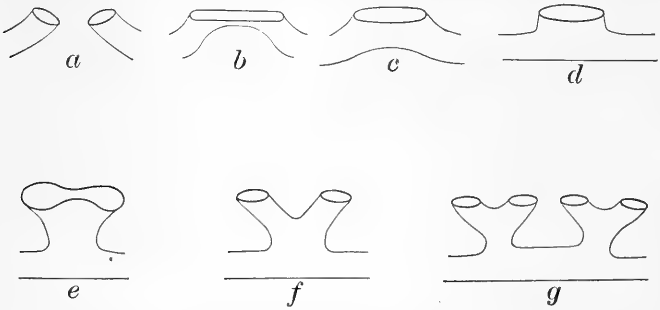
Cut 2.—*A*, top view of frontal, postfrontal, prefrontal, and squamosal bones, showing the postorbital ossification in place; *B*, side view of same; *C*, top view of postorbital ossification after removing the dermal bones; *D*, top view of prefrontal after removing the frontal; *fr*, frontal; *inf. c*, infra-orbital canal; *om. c*, operculo-mandibular canal; *prf*, prefrontal; *psf*, postfrontal; *pst*, postorbital ossification; *spc*, spiracular canal; *sq*, squamosal.

the bones immediately behind it are slightly bevelled, thus forming a shelving surface which looks upward and outward, and, when the cheeks are distended, serves as an articular surface for the overlapping edge of the upper postorbital. This lateral rib or thickening only extends one-half the length of the bone, which behind it is much smaller and narrower, the lateral edge and under surface being cut away by the postorbital process, a small portion of which here comes to the level of the outer surface of the dermal bones (Cut 2).

The postorbital ossification has roughly the shape of an inverted pyramid, one edge of which projects laterally and forms the hind boundary of the orbit. The upper outer angle of the ossification expands into an elongate cap-like piece, which overhangs the pyramid in front, behind, and laterally. Its outer surface is divided into two portions by a strong longitudinal line, which is continuous in front with the lower outer edge of the postfrontal, and behind with the corresponding edge of the squamosal. The part above this line is the small portion that forms a part of the external surface of the dermal bones, and it has in every particular the characteristic appearance of these bones. The part below the line lies at a deeper level and gives attachment to portions of the *levator arcus palatini* and *adductor mandibulæ* muscles. The line separating these two surfaces is sharp and strong, while that separating the upper surface from the dermal postfrontal is faint and indistinct, and might easily be overlooked.

The postorbital ossification gives support on its upper surface to the frontal and squamosal as well as to the postfrontal, but neither of these bones are closely attached to it. The squamosal projects slightly under the frontal and postfrontal, and separates the main lateral canal from the spiracular canal, which opens widely on the upper surface of the skull immediately below it. The spiracular canal has been fully described by Sagemehl (No. 13, p. 200) and by Wright (No. 20, p. 492).

The infra-orbital canal enters the postfrontal in front of the lateral edge of the postorbital ossification (Cut 2, *inf. c.*), and no branch is given off in its course through it. At the median edge of the bone it forms an anastomosis with the supra-orbital canal, and a double system is given off; that is, one formed by the complete fusion of two systems, one belonging to each of two anastomosing lines. There are seven such systems on the head of Amia, all of them essentially similar. Their pores multiply exactly as do those of a simple system, but the double trunk increases greatly in width along the canal, and the primary division of it is so deep that the trunk becomes practically a part of the canal (Cut 3, *e. f. g*), its two primary branches appearing as the trunks of separate systems. This is the condition found at the point of anastomosis of the infra-orbital and supra-orbital canals. The two systems that have fused here are Nos. 15 infra-orbital and 7 supra-orbital, and that part of the main canal lying between the frontal and postfrontal and extending as far as the anterior edge of the squamosal is in reality the trunk of the double system. The anterior primary branch of this system (Fig. 40. Pl. XL.) runs forward and outward into the postfrontal, sending one branch medianward into the lateral edge of the frontal, and having thirty openings in all, three of them in the frontal. The other issues at the anterior edge of the squamosal, sending one branch forward and another backward, with ten openings in the postfrontal and thirteen in the squamosal.



Cut 3. — Diagrammatic representation of the formation of a double pore and system: *a*, *b*, and *c*, two pores approaching and fusing; *d*, double pore and tube; *e* and *f*, the same, undergoing its first division; *g*, double system after second division of pore and tube.

Trunk 16, the next regular one, is given off in the squamosal beyond the middle line of the bone, and is a short trunk directed laterally. It sends one long branch forward, overlapping the posterior branch of trunk 15, and a shorter one backward. It has twenty-nine openings, all lying near the lateral edge of the bone. Behind this trunk the main infra-orbital is joined by the operculo-mandibular canal which comes up through the pre-operculum. At the point of union a double system is formed by the fusion of system 17 infra-orbital with 17 operculo-mandibular; but the trunk of this system has been pushed out of its proper place down into the opercular line, and lies with all its branches in the dermal tissue between the upper end of the pre-operculum and the lateral edge of the squamosal. Its primary branches are not so widely separated as those of the double trunk 15–7. They are directed one forward and the other backward, with all their branches running downward and with eighteen openings in all.

Leaving the squamosal at its hind end on the short shelving surface which is overlapped by the extrascapula, the main canal passes through a strongly raised portion on the under surface of the latter. It then traverses the suprascapula, entering it on its upper surface near its lateral edge, where it is overlapped by the extrascapula, and leaving it on its under surface, where it, in turn, overlaps the supraclavicula. Entering the supraclavicula on its upper surface at its upper end, it passes downward and backward through this bone, leaving it on its under surface to enter the first scale of the lateral line of the body.

The extrascapula overlaps the squamosal in front and the suprascapula behind, so that the canal only passes through the middle third of the bone, giving off trunk 18, with thirty-six openings, near its entrance, and trunk 19, with twenty-two openings, near its exit from the bone. Trunk 20 is given off in the suprascapula just as the canal leaves the bone. It runs backward and outward, and has thirty-nine openings, some of them double or triple. Trunk 21, given off soon after the canal enters the supraclavicula, runs backward, and, branching once, has two openings only at the hind edge of the bone. Trunk 22, the last one of the cranial system, is also trunk 1 of the lateral line. The supraclavicula overlaps the first scale of the lateral line, and the double trunk 22–1 is given off at the point where the main canal leaves the supraclavicula and turns inward to enter the scale. It is a long, open channel on the under surface of the bone, running downward and backward as a direct continuation of the main canal, and having a single large opening at the hind edge of the bone.

2. *Lateral Line of the Body.* — The first scale of the lateral line (Fig. 44, Pl. XL.) is always an irregular one. It is smaller than those immediately following it, much thickened, and roughly triangular in shape. It extends under the supraclavicula and lies in the direction of trunk 22–1, at an angle to the following scales of the line. The lateral canal enters it near its front edge, and leaves it on its inner surface, entering the next scale on its outer surface, and leaving it on the inner after traversing approximately its middle third. It passes in the same way through the other scales of the line normally, giving off in each a peripheral canal system, similar to those found on the head. The trunk of each of these systems is given off at the extreme posterior end of the section of canal contained in the scale to which the system belongs. It lies in the direction of the canal and soon branches dichotomously, sending one branch upward and one downward, each with one or more openings on the outer surface of the scale. These openings lie near the hind edge of the scale, and are approximately concentric with it. The system of the first scale of the line is very irregular. It always has fewer surface openings than that of the next following scale, or no openings at all; the trunk is present, but in a more or less aborted condition.

3. *Supratemporal Cross-commissure.* — The supratemporal cross-commissure is given off medianward from the main canal, between trunks 18 and 19, in the extrascapula; it traverses the length of this bone in about its middle line and joins, on the top of the head, the corresponding canal of the other side. In the full commissure there are two peripheral systems on each side and a double one in the middle. The two primary branches of this median system have become so widely separated in the adult that there are apparently three systems on each side of the head, the trunks of all of which run backward and laterally, with most of their branches directed backward and medianward. The median one of these three systems, although only a half-system, may be called No. 1, and it has in the specimen figured eight osseous openings. The next system, No. 2, has nineteen, and the lateral one, No. 3, twenty-five.

4. *Supra-orbital Line.* — The supra-orbital canal begins near the anterior end of the nasal. It runs for a short distance backward and medianward, and then, turning sharply backward,

continues in about the middle line of the bone to its hind edge, and then passing through the strip of dermal tissue, lying between the frontal and nasal, enters the frontal at about the middle of its anterior edge. It traverses this bone along its middle line for about half its length and then curves gradually outward until it reaches the lateral edge of the bone, where it meets and anastomoses with the infra-orbital canal, as already described. Leaving this canal immediately, it runs medianward and backward to the hind edge of the frontal, and then into the anterior and lateral part of the parietal, where it comes to the surface and ends.

Trunk 1 of this line leaves the canal at its extreme anterior end, and, running forward and laterally, has two openings at the outer edge of the nasal, immediately behind the notch made in this bone for the passage of the anterior naris. Trunk 2 leaves the canal exactly at the bend, and runs forward toward the anterior edge of the nasal, where it branches regularly, and has four openings on the surface of the bone, three single and one double. Trunk 3, given off near the middle of the bone, runs medianward and forward, and has eight single and six double openings arranged along the median edge of the bone. Trunk 4 is given off nearly opposite the posterior nasal aperture from that part of the canal lying in the dermal tissue between the nasal and frontal. It runs forward and outward, turning backward along the median edge of the nasal aperture, and anastomosing with trunk 6 infra-orbital, as already described. Trunk 5 is given off laterally at about one-third the length of the frontal, and trunk 6 medianward at about the middle of it: both are short and stout. No. 5 sends a long branch backward, overlapping the anterior branches of No. 6, and another forward almost to the anterior edge of the frontal. In front of this last branch, and also in front of several of the smaller branches, there are deeply channelled lines in which the epidermal canals of the system are continued onward along the upper surface of the bone, partly imbedded in it, and extending in some cases into the strip of tissue in front of it, reaching even to the hind edge of the posterior nasal aperture. System 5 has twenty single openings and eleven double or channelled ones, and system 6, thirty-three single and ten double or triple ones. Trunk 8 is a direct continuation backward of that part of the canal lying beyond the point of its anastomosis with the infra-orbital line; two of its branches lie in the frontal, both directed backward and laterally, one reaching to the extreme hind edge of the bone, and the other sending a short branch beyond this bone into the squamosal. The two branches have six single and three double openings in the frontal and two in the squamosal. A third and principal branch is sent backward, directly in the line of the trunk, into the parietal, near its anterior and lateral corner. It runs straight backward in this bone, sending six branches to the surface, making seventeen openings in the entire system.

5. *Operculo-mandibular Line.* — Close to the anterior end of each ramus of the mandible there is a single large opening which marks the beginning of the mandibular line. The tube from this opening leads backward and outward laterally into the anterior end of the mandibular canal, which, starting here, runs backward along the lower inner edge of the dentary. Leaving this bone, it enters the angular, and, turning upward near its hind end, passes out of it, and out of the upper surface of the mandible immediately in front of and above the articular process for the sympletic. It then turns sharply backward, and passing through the thick dermis between the angular and preoperculum, enters this last bone on the dorsal surface of its lower anterior end. It passes through the entire length of this bone, lying near its inner deeper edge, and then passing again through a strip of dermis it enters the squamosal and unites with the infra-orbital canal.

Along the mandibular part of the canal there are ten and a half peripheral systems, seven in the dentary and three and a half in the angular, most of them branching several times. Trunk 1 is a direct continuation forward of the main canal, which begins here, and has no connection whatever with the corresponding canal on the other side of the head. It has a large single opening at the front end of the dentary near the symphysis. Trunks 1 to 10 lie along the anterior horizontal part of the canal. No. 10 leaves it at the point where it turns upward near the hind end of the angular, and has one branch running straight backward as a direct continuation of the main canal. In these ten systems there are seventy-four openings, twenty-eight of them plainly double.

System II. is a double one formed at the point where the mandibular and opercular parts of the canal unite. Its primary branches are widely separated, one of them lying in the angular, near the upper end of the bone, and the other in the thick dermis between the angular and pre-operculum. The former has twenty-eight openings, eighteen in the angular and two in the supra-angular; and the latter, seven, all in the dermis, making twenty-seven in all for the entire system.

In the opercular part of the canal, the trunks of five peripheral systems are given off, Nos. 12 to 16, all of them running outward, and backward or downward, toward the outer edge of the bone, where each has several large irregular openings, approximately thirty-four in all. Trunk 17, the last one of the line, has united with 17 infra-orbital, as already described, to form a double trunk and system which lies wholly in the dermis between the pre-operculum and squamosal.

The mandibular canal in Micropterus dolomeus and in Salvelinus namaycush passes through the articular, and not through the angular, as in Amia and in Polypterus (No. 18, p. 182). In those two teleosts the angular is a small bone lying below or behind the articular, which is large and has the same position relative to the dentary that the angular has in the two ganoids. The articular in Polypterus is small, and lies below and behind the angular; and in Amia, what Bridge has called ossicle holds a corresponding position. This ossicle is, according to him, formed by the ossification of the hind end of Meckle's cartilage. It is covered by a small ganoid plate; and Bridge suggests that it may represent, at least in part, the articular of teleosts. But neither it nor the overlying dermal plate is traversed by a lateral canal, while the angular is. This last bone in the ganoids has doubtless been so called because it is entirely dermal, agreeing in this respect with the angular in teleosts, and differing from the articular, which has been supposed to be always pre-formed in cartilage. As the teleostean articular is in some forms traversed by a lateral canal, this distinction does not hold good, and the names now used for the bones in the ganoids should probably be changed.

6. *Summary.*—In this specimen, which is strictly a normal one, there are in all *ninety-three peripheral canal-systems, forty-six on each side of the head, and a median one in the supratemporal*

cross-commissure. This median system is a double one (Cut 3, *g.*), *and there are on each side of the head three other similar systems, making seven in all.* One is formed by the fusion of systems 15 infra-orbital and 7 supra-orbital; a second one by the fusion of 17 infra-orbital and 17 operculo-mandibular, and the third by the union of the two portions of the operculo-mandibular canal. This last system, being formed in the line of its canal, is called No. 11 of that line. The other two being formed at the points of anastomosis of two different lines, have each been given a double number which indicates the position of the system on each of the lines to which it belongs. Counting it this way, there are three peripheral systems along the supratemporal cross-commissure, eight along the supra-orbital line, seventeen along the operculo-mandibular, and twenty-one along the infra-orbital; but as a median double system has disappeared at the point where the two infra-orbital lines unite on the top of the snout, there are properly twenty-two systems along this line, seventeen of them up to the point where it is joined by the operculo-mandibular.

Surface Pores.

The peripheral canal systems are represented on the surface of the head by more or less distinct groups of pores. The number of pores in some of these groups can be easily determined by surface examination; but in many cases several groups are so run together that only the general position of each group and the total number of pores in the series can be ascertained.

For the following description three specimens were used: two males, one 17 in. and the other 20½ in. in length, and a female 27 in. long. The number of pores given in the different groups, unless otherwise specified, applies only to the left side of the head, a comparison being made in every case with the number of openings in the skeleton. The arrangement of the surface pores in the larger male is shown in Figs. 20, 21, and 22, Pl. XXXVI.

1. *Infra-orbital Line.* — The first group of the infra-orbital line, group 2, lies near the base of the nasal tube, a little in front of and median to it. It has usually one or two pores

only, arranged, where there are two, across the top of the snout. In the 17-inch specimen, which seemed an exceptional one in many ways, there were three pores in this group on each side of the head, the third pore lying a little in front of, and lateral to, the two regular ones. In no other specimen were more than two pores found. In the skull there was but one opening in the ethmoid corresponding to this group, showing that the division of the trunk lies in the dermis entirely above the bone.

Group 3 lies near the edge of the upper lip, below and in front of the nasal tube, and has but one pore, or two lying parallel to the edge of the lip. As the trunk of this system issues in the dermis between the ethmoid and antorbital, there is no corresponding opening in the skull.

Group 4 lies near the edge of the upper lip, lateral to and below the nasal tube, and usually has two pores in the adult. In the 17-inch male there were two pores in the group on each side of the head; in the 20½-inch male, two on one side, and four, arranged in a square, on the other; and in the 27-inch female, three, lying in a line parallel to the edge of the lip. In the skull there was a single opening only.

Group 5 lies back of and lateral to the nasal tube, and below the dermal crease which extends from the base of the tube toward the posterior nasal aperture. The number of pores in this group varies, as does also their arrangement, and they are nearly, if not quite, continuous with those of group 7. In the 17-inch specimen there were eight pores in the group; in the 20½-inch one, nine; and in the 27-inch one, nineteen. One or more of the anterior pores of the group lie close to the dermal crease before mentioned, and directly opposite the pores of group 1, supra-orbital. In the skull there were eight openings in this system.

Group 6 belongs in position to the supra-orbital line, and will be described with group 4 of that line, with which it is continuous.

Group 7 lies behind, and lateral to, group 5, considerably below the posterior nasal aperture, and immediately above group 8.

Groups 8 to 11 lie along the upper edge of a deep furrow which separates the maxilla from the side of the head. The maxilla, when the mouth is closed, shuts under the overhanging edges of the lachrymal and first suborbital, and over the lower edge of the second suborbital and the lower anterior corner of the lower postorbital, fitting into a depression on the outer surface of these two bones. The lower edges of the lachrymal and first suborbital, and the upper edge of this depression from the upper edge of the furrow, which is continued a short distance downward and backward behind the maxilla along the hind edge of the mandible. In young specimens the edge of this furrow, which may be called the *supramaxillary furrow,* is straight, and the pores of groups 8 to 11 are closely arranged in a line along it; but in the adult it is strongly ogee-shaped, and many pores may lie above the marginal row, especially immediately below or just in front of the eye. Group 12, which is usually continuous with group 11, lies immediately behind the maxilla, near the lower edge of the lower postorbital, and often extending beyond it. It is usually continuous with groups 13 and 14, which lie above and before it, directly behind the eye, superficial to the postorbitals and below the lateral edges of the postfrontal and squamosal. In these eight groups, Nos. 7 to 14 inclusive, there were in the 17-inch specimen one hundred and two pores, and in the 27-inch one, three hundred and thirty-three. In the 20½-inch male, either system 13 or 14 was wanting (probably No. 13), a condition frequently found, and there were accordingly only one hundred and one pores in groups 7 to 14, while in the skull, where the number of groups was normal, there were one hundred and forty-nine openings.

The pores of the double system, infra-orbital 15, supra-orbital 7, and those of group 16 infra-orbital, form a continuous line, extending from immediately above and behind the eye, nearly to the front edge of the extrascapula, which edge lies in line with the upper end of the pre-opercular fold. Some of the pores of these two groups extend laterally beyond the edges of the postfrontal and squamosal. In the 17-inch specimen there were eighty-nine pores in the two groups; in the 20½-inch one, seventy-eight; and in the 27-inch one, two hundred and eighty-eight. In the skull there were eighty-two openings.

Groups 18 and 19, and group 3 of the supratemporal commissure, form one large surface group. Groups 19 and 20, and 20 and 21, are also more or less continuous, but easily distinguishable, as seen in the figures. Groups 18 and 19 infra-orbital and the three groups of the supratemporal line all lie superficial to the extrascapula. They extend slightly beyond its margins, and form, with the same groups on the other side of the head, a nearly continuous series which lies behind the line of the pre-opercular fold and in front of the first row of scales. In the 17-inch specimen there were ninety-four pores in these five groups on one side of the head; in the 20½-inch one, one hundred and two; and in the 27-inch one, two hundred and fourteen. In the skull there were one hundred and ten openings.

Group 20 lies on a fleshy pad above, and immediately in front of, the upper end of the opercular opening, behind the extrascapula and opposite the first two or three scales behind that bone.

Group 21 is much smaller than No. 20, and lies on a similar but smaller pad above and behind the upper end of the opercular opening, above the upper edge of the supraclavicula and opposite the third and fourth, fourth and fifth, or fourth, fifth, and sixth scales, behind the extrascapula. The pores of this group often extend onto the bases of the scales, but when this occurs, the canals leading to them lie entirely in the dermis or epidermis, not entering the bony part of the scale at all. There were in groups 20 and 21, in the 17-inch specimen, thirty-nine pores; in the 20½-inch one, fifty; in the 27-inch one, ninety-one; and in the skull forty-one openings.

Groups 20 and 21 and those found on the first five scales of the lateral line in the 27-inch specimen are shown in Fig. 39, Pl. XXXIX. The hind edge of the gill cover is cut off in order to show the position of the supraclavicula and the arrangement of the scales immediately behind it. In this specimen, the pores of group 21 extended onto the base of the sixth scale, counting always from the hind edge of the extrascapula, and the lateral line began on the eighth. In the 17 and 20½ inch ones, group 21 only extended to the level of the fifth scale; and the lateral line began on the seventh.

2. *Lateral Line of the Body.*—The first scale of the lateral line is always irregular, and without the thin portion which extends beyond the bone in the other scales, and which gives them their rounded outline. Between it and the hind edge of the supraclavicula there is a single large opening (Fig. 39, Pl.

XL., p. 22, *i, ll*), which is the undivided original double pore formed by the fusion of the posterior peripheral system of the head with the anterior one of the lateral line. Although compressed and flattened and hidden from view under an overhanging fold of dermis, this pore is the largest one in the entire lateral system of Amia.

The peripheral system of the first scale is always more or less aborted. In the 27-inch specimen it had but two pores on one side of the body and four on the other, and in the 17 and 20½ inch specimens but one pore on each side. In several other specimens there were no pores at all in this system, the scale projected but little beyond the hind edge of the supraclavicula, the end of it being cut squarely off across the line of the canal so that the exposed portion was triangular in shape, with a straight edge behind.

There were, in the several specimens in which they were counted, sixty-seven or sixty-eight full scales in the lateral line. In the second scale of the line there were, in the 17-inch specimen, seven openings; in the third, six; and in the fourth, seven. In the 27-inch one (Fig. 39) there were eight in the second scale, twelve in the third, and eleven in the fourth. In the following scales, for about half the length of the line, the peripheral systems are fairly constant and regular; but behind that there is great irregularity, some of the scales, and often several in succession, having no pores at all, and nearly all of them having a much smaller number than those in the first half of the line. Toward the tail there are usually but one or two pores in a scale (Fig 3, b, Pl. XXX.), and the development here is often so greatly arrested that the lateral canal, through one or more scales, is an open channel.

Behind the last full scale of the line the canal turns slightly downward, and enters the tail fin between two of its rays. It then runs straight backward about three-fourths the length of the fin, and ends in a single terminal pore, which is usually closed secondarily. Along this part of the canal there is only a single row of pores, those toward the end of the line being small, and often closed.

3. *Supra-orbital Line.* — Group 1 of the supra-orbital line lies near the base of the nasal tube, close to the dorsal edge of the dermal crease, which extends backward from it. There are

usually only one or two pores in this group; but in the 27-inch specimen there were six on one side and five on the other, all lying along the edge of the crease. As already stated, this group lies close to group 5 infra-orbital, the two being separated by the crease. There were two openings in the nasal bone corresponding to this group.

Group 2 has usually four pores, which form a slightly curved line, extending backward and medianward from the anterior edge of the nasal tube, and lying nearly in the line of the hind edge of the ethmoid. The group is a prominent one, and is most regular and constant in shape and position. In the 27-inch specimen it contained seven pores on each side of the head, all arranged in line as usual; but on the left side the median pore of the group, which approached closely the anterior pore of group 3, was dividing at right angles to the line of the group, the new pore lying in front of the line of the rest of the pores. In the 17-inch specimen the lateral pore of the group, on the right side, had undergone a complete division at right angles to the line of the group. These two instances were the only ones noted of a pore lying out of the regular line.

Group 3 lies near the middle line of the head, directly above the nasal sack. In the 17-inch specimen it had nineteen pores; in the 20½-inch one, twenty-four; and in the 27-inch one a still greater number; but in this specimen the group was so continuous with groups 4 supra-orbital and 6 infra-orbital that the exact number of pores in each could not be determined.

The double group, 4 supra-orbital and 6 infra-orbital, lies close to the posterior naris. A part of the pores lie in a half-circle along the median edge of the aperture, and the rest of them form two groups, one lying in front of and median to the aperture, and the other behind and median to it, or directly behind it. This last group belongs entirely to system 4 supra-orbital, and the other entirely to system 6 infra-orbital; while the half circle of pores belongs partly to each of these systems. The group is usually continuous with group 5 supra-orbital. In the 17-inch specimen it had twenty-eight pores; in the 20½-inch one, twenty-four; and in the 27-inch one, a much larger number, but it was so continuous with groups 3 and 5 that the number of pores could not be determined. The two systems lie almost entirely in the dermis, so that in the skull there were only five openings, all in the nasal, and all belonging to group 6 infra-orbital.

Groups 5 and 6 are almost always continuous, both lying between the eyes on top of the head, No. 5 almost directly behind the posterior nasal aperture, and No. 6 much nearer the middle line of the head, and extending somewhat behind the eye. In the 17-inch specimen there were in these two groups one hundred and nine pores; in the 20½-inch one, one hundred and sixteen, and in the skull eighty-two openings. In the 27-inch specimen these groups were continuous with 3 and 4 supra-orbital and 6 infra-orbital. The total number of pores in the five groups in this specimen was three hundred and fifty-four; in the 17-inch one, one hundred and fifty-six, and in the 20½-inch one, one hundred and seventy-four.

Group 8 lies behind group 6, not so near the middle line of the head, and about half way between that group and the supra-temporal cross-commissure. It had in the 17-inch specimen twenty-nine pores; in the 20½-inch one, thirty-two; in the 27-inch one, ninety-three; and in the skull, seventeen openings.

4. *Operculo-mandibular Line.* — Group 1 of the operculo-mandibular line in all the numerous specimens examined, excepting only the unusually large 27-inch one, had only a single large pore belonging to it; the two pores, one on each side, lying directly in front of the gular plate, near the tip of the lower jaw and close to its middle line. In the 27-inch specimen there were two pores on each side of the head, lying in a line transverse to the direction of the trunk of the system as seen from below.

The pores of group 2 and those of the succeeding groups to No. 10 are arranged in regular lines, approximately parallel to the inner edge of the mandible, but the lines of the different groups are broken, and overlap, or are continuous with each other, so that the number of pores belonging to each cannot be determined. In groups 1 to 10 inclusive, in the 17-inch specimen, there were sixty-six pores; in the 20½-inch one, seventy-two; and in the 27-inch one, one hundred and twenty-five. In the skull there were seventy-four openings, many of them double.

Group 11 lies at the hind end of the mandible, in front of and above group 10, and about half way between the maxilla and the lower end of the pre-opercular fold. It lies on both sides of the posterior prolongation of the supramaxillary furrow. The part below the furrow lies superficial to the angular element of the mandible, and is much larger than the other part which lies wholly in the dermis. In the 17-inch specimen there were sixteen pores in this group, thirteen of them in the lower portion of it; in the 20½-inch one, twenty-four, eighteen below the furrow; and in the 27-inch one, sixty-four, with fifty-eight below the furrow. In the skull there were twenty-seven openings in the angular and supra-angular, corresponding to the lower portion of this group.

Groups 12 to 17 extend from the lower end of the pre-opercular fold almost to the lateral edge of the dermal bones of the top of the head. The pre-operculum lies just in front of the surface fold, and the pores of the different groups lie mostly in lines transverse to and extending on both sides of it. Some of them extend to the very edge of the fold, and others, at the upper end of the series, reach onto the surface of the upper postorbital. In this series of groups, in the 17-inch specimen there were one-hundred and fifty-two pores; in the 20½-inch one, one hundred and fifty-five; and in the 27-inch one, two hundred and five; while in the skull there were only eighty-four large and irregular openings, showing that the branches of the different systems lie mostly in the dermis.

The total number of pores on one-half of the head of the 17-inch specimen was seven hundred and sixty-two; of the 20½-inch one, seven hundred and twelve; and of the 27-inch one, eighteen hundred and thirty-one. Other adult specimens examined had intermediate numbers, showing that the pores continue to divide, the canals leading to them increasing correspondingly in number and extent, up to a late period, if not throughout life.

II. POSTLARVAL FORMS.

1. Primary Pores.

As all the pores and branches of the peripheral canal-systems arise by the repeated dichotomous division of previously existing pores and branches, it is evident that at some stage of growth each system must have been represented by a single primary pore with a single unbranching tube leading to it from one of the central canals. This condition is found in fishes about one month old, or from 40 to 60 millimetres long; but as the different systems pass through it at slightly different times, no single specimen or age fully represents it.

There are normally at this stage ninety-three primary pores and tubes on the entire head, — forty-six on each side and a median one in the supratemporal cross-commissure. This median pore is the last one developed, and its formation marks the end of a first period, in which the canals and the primary tubes and pores are developed, and the beginning of a second and last in which the tubes and pores begin the dividing, shifting, and multiplying which result in the complicated arrangements found in the adult. Fig. 49, Pl. XLII., is a diagrammatic representation of this stage, showing the course of the canals and the position of the primary pores and tubes. Fig. 13, Pl. XXXIV., shows the arrangement of the pores on the head of a fish 30½ millimetres long, in which the lateral system is in a somewhat earlier stage of development; and Figs. 14, 15, and 16, Pl. XXXV., that on the head of a fish 78 millimetres long, in a more advanced condition.

At the stage represented in the diagram, pores 1 and 2 supra-orbital, and 2, 3, 4, and 5 infra-orbital, are arranged nearly in a circle around the nasal tube, No. 5 infra-orbital lying somewhat out of the circle, directly in line with pores 1 and 2 supra-orbital in front, and 7 and 8 infra-orbital behind. A dermal depression separates pores 1 supra-orbital and 5 infra-orbital as in the adult. Pore 8 infra-orbital lies in a well-marked corner formed by the anterior end of the supramaxillary furrow, which turns sharply upward in a curved line. Pores 9 to 12 lie below the eye, forming with No. 8 a straight line extending directly backward. Pores 13 and 14 lie behind the eye, and above and behind it is the double pore, 15 infra-orbital and 7 supra-orbital, which, in the 67½-millimetre specimen has undergone its first division. Pore 16 is in process of division in this specimen, lying about mid-way between the double pores, 15–7 and 17–17, formed at the point where the infra-orbital and operculo-mandibular canals unite. Then follow pores 18 and 19 as a pair a little in front of the upper end of the opercular opening, and pores 20, 21, and 22–1 above this opening.

Pore 3 of the supra-orbital line and the corresponding one of the opposite side form a prominent pair about half way between the nasal apertures. Pores 6 infra-orbital and 4 supra-orbital lie close together near the posterior nasal aperture, No. 6 in front of, and No. 4 median to, it. No. 5 supra-orbital lies immediately behind No. 4, about on a level with the anterior edge of the eye; No. 6 nearer the middle line on the top of the head, between the eyes; and No. 8 behind and median to the double pore 15–7.

Pores 1 to 10 of the operculo-mandibular line lie along the lower edge of the jaw, No. 1 markedly in front of the curved line of the others. No. 11 lies almost directly above No. 10, and has in the 67½-millimetre specimen undergone its first division, the two secondary pores lying, as in the adult, one on either side of the end of the supramaxillary furrow. Pores 12 to 16 lie along the edge of the pre-operculum, Nos. 13 and 14 already double in the larger specimen.

In the supratemporal cross-commissure there are two pores on either side, and one in the middle line of the head.

The central canals at this age are inclosed in thin, bony tubes which in certain places, as in the suborbital series (Cut 9), represent the entire bone of the adult. In others, as in the squamosal and frontal, the tube lies along the edge or toward the middle of a thin, bony plate of the same thickness as the wall of the tube, and the tube and plate together form the bone. In young larvæ, where the bones are just beginning to develop, they are represented by short, semi-cylindrical pieces lying immediately below each organ. At this stage they correspond to the short, bony scales which, according to Bodenstein (No. 3, p. 131), partly inclose each organ of the lateral line in the adult of Cottus, and to the bony half-rings which, according to Leydig (No. 9, p. 251) and Solger (No. 14, p. 111), support the walls and protect the organs in the cranial canals of Chimæra monstrosa. These semi-cylindrical pieces in Amia increase in length and soon become open gutters or channels. The plate then appears along the sides or toward the bottom of the channel, always continuous with it and growing from it on either side. The canal and the gutter in which it lies are always at this stage on the upper surface of the bone, thus corresponding to the conditions described by Bodenstein (No. 3, pp. 132 and 143) in the *os mastoideum* of the adult Cottus. The gutters then become tubes, lying at first on the upper surface of the bony plates, and corresponding to the conditions found in the adult of some of the bony fishes.

The relations of the primary tubes to the various dermal bones in Amia are easily determined in a series of sections. They differ slightly from the relations of the trunks of the corresponding systems to the bones in the adult.

Trunk No. 2 infra-orbital enters its canal through the ethmoid; No. 3 between the ethmoid and the antorbital; Nos. 4 and 5 through the antorbital, and No. 6 at its upper posterior edge; No. 7 between the antorbital and lachrymal; No. 8 through the lachrymal; No. 9 between the lachrymal and first suborbital; No. 10 between the first and second suborbitals; No. 11 between the second suborbital and lower postorbital; No. 12 through the lower postorbital; No. 13 between the postorbitals; No. 14 between the upper postorbital and the postfrontal.

The double trunk 15–7 lies between the frontal and postfrontal and between the two anastomosing canals, which, at this point, change sharply their direction. The infra-orbital lies entirely in the postfrontal, and the supra-orbital entirely in the frontal; both of them along the open edges of the bones. The trunk of the system at this age is a large shallow pit into which the two canals open. In the further development of the system it deepens, becomes narrower, and lies over the point of anastomosis of the two canals instead of between them as at first. In the first division of the system the trunk divides after the manner shown in Cut 3, p. 18, *f* and *g*. One of the primary branches resulting from this division retains its position at the point of anastomosis of the two canals. The other travels backward along the infra-orbital canal till it reaches the anterior edge of the squamosal, where it is found in the adult (Fig. 40). The trunk of the system disappears.

Trunk 16 infra-orbital enters its canal through the squamosal. Immediately behind it is the double opening, 17–17, which lies at the lateral edge of the squamosal, between it and the upper end of the pre-operculum, and resembles closely the double pore 15–7. The upper end of the opercular line opens directly into the pit on its lower wall, and on the upper wall a small opening, much smaller than the openings of the other pores, leads into the infra-orbital canal, which at this point is deflected toward the lateral edge of the squamosal. In the first division of this double system the trunk disappears, and the two primary branches travel downward along the opercular canal, at the same time separating somewhat along the line of that canal. The two secondary pores formed by this division also separate antero-posteriorly. From one of them arises the half-system lying in the adult in front of the canal (Fig. 40), and from the other that lying behind it.

Trunks 18 and 19 enter the main canal on either side of the extrascapula, between it and the squamosal and suprascapula respectively; No. 20 enters it between the suprascapula and supraclavicula; No. 21 through the supraclavicula, and No. 22–1 between the supraclavicula and the first scale of the lateral line.

In the supra-orbital line trunks 1, 2, and 3 all enter the canal through the nasal; No. 1 on its lateral edge; No. 2 on the anterior edge; and No. 3 through the top of the bone. Trunk 4 enters the canal between the nasal and frontal; Nos. 5 and 6 through the frontal; No. 7, as already described, between the frontal and postfrontal; and No. 8 between the frontal and parietal.

In the operculo-mandibular line, trunks 1 to 7 enter the canal through the dentary; No. 8 between the dentary and nasal; Nos. 9 and 10 through the angular; No. 11, a compound or double trunk, between the angular and pre-operculum; Nos. 12 to 16 through the pre-operculum; and No. 17 between the upper end of this bone and the lateral edge of the squamosal.

In the supratemporal cross-commissure the two lateral trunks on each side enter the canal through the extrascapulæ, and the large double median one between the two bones. By the first division of this median pore the two primary branches are formed, which, in the adult, become the trunks of the half-systems lying one on each side of the middle line of the head.

The conditions existing at this age and a little earlier show that a primary tube originally leaves each of the main lateral canals along its entire length between each two consecutive dermal bones, and that at every point of union of two canals, whether of the same or of opposite sides of the head, a double pore and trunk is formed, which give rise at this point to a double dendritic system.

If the bones containing the two anastomosing canals have anchylosed, or the two canals lie in the same bone, then both the pore and the trunk belonging to it entirely disappear.

The ethmoid in Amia is formed by the union of the two bones usually found in other fishes. At the line of union of these two bones, where the main infra-orbital canals of opposite sides unite, a single median pore and trunk have been formed and disappeared, as younger stages show. In like manner a pore and trunk have disappeared on either side at the point where the supratemporal commissure joins the main infra-orbital, these two canals here lying in the same bone, the extrascapula. *These two are the only trunks and pores that have disappeared in the entire system in Amia. In the adult, with two exceptions only, all of the primary tubes, which at younger ages issue from the main canals between consecutive bones, become partly or entirely inclosed in one or the other of these bones.* The two exceptions are trunk 4, supra-orbital, and the double trunk 17–17, which, even in the adult, lie wholly in the dermis.

2. Number and Position of the Canal Organs.

Between every two consecutive trunks, along the entire length of each canal, counting the double trunks twice, once along each of the anastomosing lines, and also counting the trunks that have disappeared, there is a single sensory spot or patch containing either a single well-developed organ of the kind called by Merkel (No. 12, p. 5) nerve-hillocks, and by Wright (No. 20, p. 480, note) neuromasts, or such an organ with one or more smaller ones developing at either end of it (Fig. 48, Pl. XLI.).

These sensory patches always lie inside the dermal bones, and there are along the infra-orbital line two in the ethmoid, four in the antorbital, two in the lachrymal, one in each suborbital, two in the lower postorbital, one in the upper postorbital, one in the postfrontal, three in the squamosal, one in the extrascapula, one in the suprascapula, and two in the supraclavicula. Along the supra-orbital line there are three in the nasal, and four in the frontal; along the operculo-mandibular, seven in the dentary, three in the angular, and six in the preoperculum; and in each half of the supratemporal cross-commissure three, all in the extrascapula, making forty in all on each side of the head.

The position of these organs in the canals, and their method of innervation, is shown in the diagrammatic drawing, Fig. 49, Plate XLII.

In this diagram two sense-organs, or groups of organs, are shown between the first trunks of the supra-orbital line on either side of the head, and one in this same line between trunks 18 and 19, directly opposite the point where the supratemporal cross-commissure joins it, with no trunk system between it and the first group of organs in this commissure. These two trunks and pores have disappeared, the position of the organs and the development of the system alone showing that they at one time existed. There is but one group of organs in the infra-orbital canal on each side of the double trunk 17–17, and only one between it and trunk 16 operculo-mandibular, showing that the double trunk, although displaced in the adult, belongs primarily at the point of union of the two canals. There is one group of organs on each side of the double trunk 15–7, between it and the next trunk, in the infra-orbital and supra-orbital canals, showing that the displaced primary branch, which in the adult issues between the squamosal and postfrontal, is in reality a part of the double trunk, and not a separate system. There is also but one group on each side of the compound trunk 11 of the operculo-mandibular line, between it and the next trunks of that line, and but one on each side of the median system of the supratemporal cross-commissure.

The fifth group of the infra-orbital line is apparently out of place, lying in what seems to be the trunk of system 6, above the point where the anterior commissure joins the suborbital part of the main canal. This is due to the fact that the end of the suborbital canal, beyond the point where the commissure joins it, has taken the direction of the commissure instead of retaining that of its own canal; so that what appears as the trunk of system 6 is in reality this trunk and the extreme anterior end of the main canal, and it is in this anterior end, and not in trunk 6, that group 5 lies. Moreover, system 6 being properly a terminal system in which the trunk continues the line of the main canal, there is nothing to indicate where it begins and the canal ends. Organs 1 and 7 supra-orbital and 1 operculo-mandibular occupy strictly analogous positions, apparently lying in the trunks of the neighboring terminal systems.

3. Sense-organs of the Spiracular Canal.

Wright (No. 20, pp. 481 and 489) has described a patch of neuro-epithelium at the upper end of the spiracular canal in both Amia and Lepidosteus. It is supposed by him to have developed in this canal, and hence to be of hypodermal origin. In the young of Amia this sensory patch is a group of organs exactly like the regular organs of the lateral canals, consisting, as they do, of a large central organ and two or more smaller terminal ones. The group lies in the median wall of the membranous spiracular canal near its blind upper end.

The spiracular canal in Amia (No. 20, p. 492) opens widely on the upper surface of the cartilaginous cranium, at the extreme anterior end of what is rather a diverticulum of the temporal groove of Sagemehl (No. 13, p. 188) than a part of the groove itself. The main groove lodges the anterior end of the trunk muscles, while the diverticulum, which lies wholly lateral to it, connected with it along its edge, lodges no muscles whatever. It contains only loose, fatty tissues, vessels, and nerves. The squamosal portion of the infra-orbital canal lies directly above this diverticulum, and that branch of the R. *oticus facialis* that supplies organs 15 and 16 of that line lies in it, running backward from the point where the nerve issues through the roof of the cranium median to and about on a level with the opening of the spiracular canal. A branch of this same nerve, given off just as it leaves its foramen, turns outward and downward into the upper end of the spiracular canal, and is distributed to the group of organs there in the same way that the nerves of the lateral canals are distributed to the organs they supply.

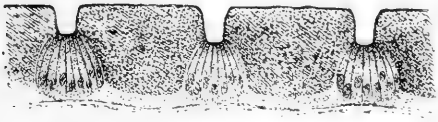
When it is remembered in connection with the innervation and position of this group of organs, that all the sense-organs which at this stage lie inside the canals of the lateral system, are in earlier stages found on the external surface of the head, it seems reasonable to suppose that this particular group in Amia, apparently so anomalous in position, was regularly developed in the epidermal covering of the head along with the other organs of the infra-orbital line, but, lying near the edge of the spiracular cleft, it wandered into this cleft as it was closed, and so acquired its present position. If this be so, the lining membrane at the upper end of the spiracular canal must be ectodermal rather than entodermal in origin. No positive evidence of this method of development has yet been found, for in none of the postembryonic forms to which the present work has so far been confined has the spiracle been open. In some of the youngest specimens, however, certain appearances seemed to indicate that it had only recently been closed. In specimens from one to five days old there is always a strong depression immediately above the upper end of the opercular line (Figs. 1 and 3, Pl. XXX., *spr*). The developing infra-orbital line crosses this depression, and organs 15 and 16 lie in it. In freshly prepared one-day-old specimens there is in the bottom of the depression, immediately below these organs, a dark spot indicating the position of the blind upper end of the spiracular canal. This spot in some specimens is strongly marked, and if the tissues are fresh and somewhat transparent, has the appearance of being an opening with a part of the sensory tissue of the infra-orbital line extending into it or across its edge.

4. Lines of Pit Organs.

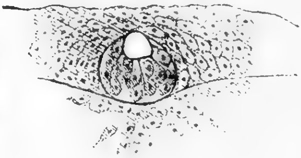
There are in Amia, in addition to the sense-organs found in the lateral and spiracular canals, several surface lines of somewhat similar organs, which, although belonging to the same general class of nerve-hillocks (Merkel), differ greatly from the canal organs in shape, arrangement, and method of multiplication. These organs are somewhat conical in shape, and, like the canal organs, represent the entire thickness of the epidermis at the points where they occur. In young fishes, and on the body in the adult, they project slightly beyond, or come nearly to the level of, the outer surface; but on the head of the adult they lie at the bottom of little pits, and therefore they may be called pit organs. They are found close together, in regular lines on slight dermal papillæ, and are connected by a special cord of cells which extends beyond the end of the line, and is lost among the general epidermal cells. They appear to develop independently along this cord.

Cut 5 represents a section through one of these surface lines in an adult; and Cut 4, one in a fish 45 millimetres long. Cuts 4 to 9 are semi-diagrammatic, but the outlines are taken from actual sections. In Cut 4 is seen the cord along which the organs lie, and an organ developing in it. The organ at this

Cut 4.



Cut 5.

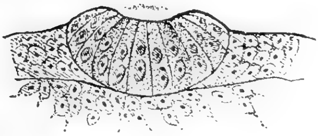


Cut 6.

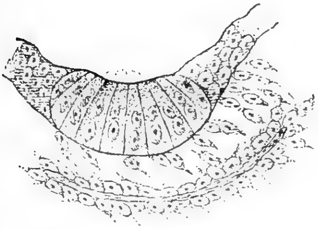
Cut 4. — Longitudinal section through a line of pit organs in a fish 45 millimetres long, showing four organs, one of which is just forming, all connected by a cord of cells in the deeper layers of the epidermis.

Cut 5. — Longitudinal section through a line of pit organs in the adult, showing three organs and the connecting cord.

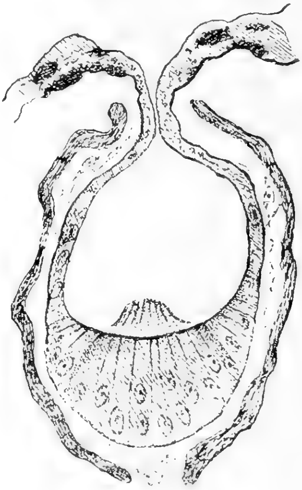
Cut 6. — Section through a developing organ of the suborbital line in a fish 11½ millimetres long, showing large vacuolar space at top of organ.



Cut 7.



Cut 8.



Cut 9.

Cut 7. — The same in a fish millimetres long, where the organ has reached the other surface.

Cut 8. — The same in a fish millimetres long, where the organ is beginning to sink below the surface and the osseous canal is forming.

Cut 9. — The same in a fish millimetres long, where the canal is just closing over the organ, showing the nearly formed osseous canal and the nerve leading through it to the organ.

stage of its development has the appearance of a flat dome with a large, vesicle-like space, set like a keystone at the top of the structure. Toward this space the cells of the organ are directed, and as they increase in length, and the organ in height, the latter pushes its way, wedge-like, through epidermal cells, crowding them to either side, until it reaches the outer surface, where its upper central portion becomes exposed. It has now the shape of a cone with rounded summit (Cut 4); and its exposed upper end, which contains the compressed outer ends of all the sensory cells, reaches to the general level of the outer surface, or even projects beyond it. On the body, and particularly toward the tail, the organs retain nearly this condition even in the adult; but on the head they are later so much withdrawn from the surface that only a series of minute holes indicates their position (Cut 5).

Cut 6 is a section through the suborbital line in a fish 11½ millimetres long. It shows one of the canal organs in a stage corresponding to that of the young pit organ in Cut 4, and also to that of the organs of the lateral line in Salmon embryos before the organs have reached the outer surface, as shown by Hoffman (No. 8, Pl. V., Fig. 29). There is at the top of this canal organ the same vacuolar space that is found in the developing pit organ, and there are apparently no support cells. These appear later, after the organ has reached the outer surface, as shown in Cut 7.

In these early stages the different organs of a canal line are connected by a special cord of cells similar to that connecting the organs of a pit line. In Cut 8 the organ has begun to sink below the surface, and in Cut 9 the canal is just closing over it. As development progresses, the connecting cord of cells disappears, except immediately adjoining the organ, where it was present in the oldest specimen in which it was examined, one about 80 millimetres long. Along this remnant of the cord, and immediately adjoining the primary organ, the other organs of the group appear, at first as small bud-like organs, inclined away from the larger central one (Fig. 48, Pl. XLI). These new organs grow rapidly, and others soon appear in succession along the cord beyond them, all at first in contact at their bases, but separated above by projecting ridges of indifferent cells, exactly as figured and described by Blaue (No. 2), in the olfactory epithelium of Exocœtus and other forms. The groups which thus arise are doubtless the beginnings of what Merkel has called nerve-ridges (No. 12, p. 20), for under this name he includes all organs found in the adult inside the canals of the lateral system (No. 12, p. 23). He also finds nerve-ridges on the surface in some fishes that have no canals, as Petromyzon, Squatina, etc., and describes them as simply an elongated form of the regular conical nerve-hillock, containing exactly the same histological elements, but with a larger proportion of support-cells. He further says, that in the teleosts the conical hillocks are always found on the surface or in slight depressions; that they may either be arranged in lines and groups, or scattered irregularly over the whole body; that they are most numerous in those forms that have but few openings to the lateral canals, or have no canals at all; and that where the canals branch freely, and there are many pores, the conical hillocks may entirely disappear, as on the head of Mullus. In the Selachians they are, according to him, found only on two species, Mustelus and Squatina, being entirely replaced in other forms by another kind of sense-organ, the nerve-ampulla (No. 12, p. 39); and in the Ganoids, he says, they are not found at all, being entirely replaced by still another kind of organ, the nerve-sack (No. 12, p. 36). This certainly is not true of all the Ganoids, for in Amia I have not been able to find any of the nerve-sacks which he considers peculiar to the Ganoids, and I have always found seven different lines of pit organs (his conical hillocks) on each side of the head, and two series of lines of organs on each side of the body.

Of the seven lines found on the head, three lie on top of it, two on the cheek, one on the side of the mandible, and one on the gular plate (Figs. 21, 22, and 23, Pls. XXXVI. and XXXVII.). Of the two on the body, one lies parallel to the lateral line, and the other on the top of the body close to the dorsal fin. Each of the lines on the head is a continuous series of organs, while those on the body in the adult are each made up of a series of such lines, one approximately to each segment of the body. No ventral body line could be found.

a. Head Lines. — The first or anterior one (Fig. 21, *al*) of the three dorsal lines of the head runs backward and medianward from group 8 supra-orbital; and the third or posterior one

(Fig. 21, *pl*) forward and medianward from group 2 supra-temporal. The second or middle one (Fig. 21, *ml*) lies between the other two, and extends almost direct medianward from near the double group 17–17. The first line lies superficial to the parietal. It begins close to, or among, the pores of group 8 supra-orbital, sometimes starting in or running across the edge of a pore so that one of its organs lies partly inside it. The second one lies superficial to the squamosal and parietal, just in front of the anterior edge of the extrascapula. It often ends close to the posterior end of the first line, the two almost meeting to form an angle. The third one lies superficial to the parietal and extrascapula, and usually extends much nearer the middle line of the head than the other two. In many specimens these six lines, three on each side, seem to radiate from a clear space directly on the crown of the head. This appearance is most marked in young specimens (Figs. 14, 15, and 16, Pl. XXXV.), in which *the anterior line begins close to pore 8 supra-orbital, and is a direct continuation of the line of that canal. The first organ of the pit line often lies partly inside the tube of pore 8, and in one set of sections was entirely inside it, somewhat modified in shape and about midway between the next following pit organ and the regular terminal organ No. 7 of the canal.* This organ No. 7 is inclosed in its canal much later than the other organs of the line, and is in specimens up to 45 millimetres in length much smaller, being still single while they are represented by groups of three or five.

The horizontal line on the cheek (Fig. 22, *hl*) begins among the pores of groups 14 or 15 of the opercular line, and ends among those of group 12 infra-orbital. It lies partly superficial to the lower postorbital, somewhat behind the centre of the bone, *and frequently runs directly into a pore of group 12, just as the anterior dorsal line does into the pores of group 8 supra-orbital. These two lines are the only ones in which this occurs, the other lines beginning at some little distance from the pores of the groups near which they arise.* The vertical line (Fig. 22, *vl*) begins behind or among the pores of group 12 infra-orbital, near the anterior end of the horizontal line, and, lying partly superficial to the lower postorbital, runs downward toward the pores of group 11 operculo-mandibular, or a little behind them. The mandibular line (Fig. 22, *mdl*) lies superficial to the angular, and runs, in the shape of a letter S, from the anterior part of group 11 toward group 9 operculo-mandibular. The gular line (Fig. 23, *gl*) runs transversely across the gular plate between groups 7 and 8 on either side.

In the adult the bones immediately beneath these pit lines are slightly furrowed, and the lines are often broken.

Body Lines. — In the adult there is, on nearly every scale of the first two-thirds of the lateral line, a line of pit organs running across the scale immediately in front of the group of pores (Fig. 39, Pl. XXXIX., *all*). In young specimens these lines are each represented by a single organ lying immediately above the corresponding organ of the lateral line. In the development of the pit line these single organs are apparently connected by a cord of cells, not only with each other, but also with the corresponding organs of the lateral line. The line grows backward in the same way that the main line does, and may be called the accessory lateral line, a name already used by Solger (No. 17, p. 380) and others. In the adult the first series of pit organs is found on the third, fourth, or fifth scale of the line; in one specimen which was examined for this purpose no organ could be found behind the forty-fifth scale, there being in all sixty-seven scales in the lateral line. Toward the head there are always more organs in each series or line, some of them having as many as eight.

The first series of organs of the dorsal body line is usually found on the second row of scales, above and behind group 21 infra-orbital (Figs. 15, 16, and 17). This row of scales is the second or third row of the body, counting backward along the middle line of the back, or the second row, counting along the lateral line. Considering the rows transverse to this, — that is, those that run upward and backward, — the dorsal body line begins on the sixth or seventh row of scales and on the second row in front of the first scale of the lateral line. Still considering these transverse rows, the second series of organs lies on the row following that on which the first series is found, and on the second scale dorsalward along that row. The third series lies on the next row, usually four scales dorsalward from the second series, and on the second scale from the middle line of the body. It lies in the same row as the first scale of the lateral line. From this point the pit line runs directly backward, and ends about opposite the anus. The different series of organs, after the third, lie one behind the other on the second or third scale from the middle line of the body, or on the second scale from the base of the dorsal fin ; and there is normally a series on each row of scales, the rows corresponding to the scales of the lateral line. The series or lines in front of the dorsal fin are transverse to the body, while those along either side of it are longitudinal.

In 55-millimetre specimens the different lines or series of the dorsal line, as well as those of the accessory lateral line, are still represented by single organs (Figs. 12 and 13, Pl. XXXIV.).

In both Lepidosteus and Polypterus the canal of the lateral line extends to the tail fin ; and in both there seem to be, from the descriptions given by Solger (No. 14, pp. 368 and 369), series of organs corresponding to the pit lines of the body in Amia. In neither form are the organs themselves described, but their distribution, as indicated by well-marked furrows, is fully given. In Lepidosteus the furrows are transverse, as they are in Amia ; and there are only two series, one on the back extending as far as the dorsal fin, and the other accompanying the lateral canal, and extending as far as the tail fin. The furrows of this last line lie, as in Amia, just in front of the pores of the lateral canal, and they are found on about one-half the scales of the line.

In Polypterus the furrows are longitudinal. The dorsal series extends as far as the tail fin, and a number of irregularly scattered furrows lying below the lateral line and immediately behind the pectoral fin represent what Solger considers a ventral series, not found in Amia. A third series of furrows is found on the scales of the lateral lines, but it is impossible to tell from Solger's description whether they represent lines of pit organs or the lateral canal itself not fully inclosed. Each furrow cuts through the hind edge of the scale on which it lies, and they are found on nearly every scale of the line. Immediately above them there is a series of depressions, which differ somewhat in appearance from the furrows of the lateral line while they closely resemble the transverse furrows in Lepidosteus. They doubtless represent the accessory lateral line of Amia.

In Fierasfer also there are several lines of organs which seem, from the descriptions given by Emory (No. 5, p. 40), to correspond to the pit organs in Amia. They lie at the bottoms of flask-shaped epidermal pits, each of which contains a single organ. The external opening of the pit is about the size of the exposed upper end of the organ, and the organ which is smaller than, but similar to, those found in the lateral canals does not come in contact with the sides of the pit. They are found in lines or irregular groups on the head, and on the body in four lines or series of lines, a dorsal line, two accessory lateral lines, one immediately above and one immediately below the lateral canal, and a ventral line. The pits of the ventral line and those of the dorsal accessory line are all connected by small longitudinal canals formed in the deeper layers of the epidermis, and those of the ventral accessory line that are formed on a single segment of the body are similarly connected. The organs of the dorsal body line are not so connected; but canals extend transversely on either side of them, and end blindly in the epidermis, often branching toward the end. These epidermal canals have not been described in other fishes. They agree exactly in position with the cords of cells connecting the pit organs in Amia; and if these cords should be replaced by canals, or canals should be formed in them by deliquescence or otherwise, as the lateral canals themselves are formed in Selachians, the arrangement described by Emory would arise. The artificial separation of the cord from the overlying epidermal cells would probably produce a somewhat similar appearance.

5. Surface Sense-organs.

Under the name Terminal Buds Merkel includes a large class of organs, which, in Amia, always come to a level with or project slightly beyond the outer surface of the membrane in which they lie. They are found in great numbers on the external surface of the head, including the operculum, gular plate, and branchiostegal rays. They also extend on the top of the body as far as the dorsal fin; but behind this, and along the sides and belly, none could be found by surface examinations of the adult or by sections in young specimens, and none were found on any of the fins. They are also found in the mouth and branchial cavities.

In the adult they are scattered irregularly over the surfaces where they occur; but in young specimens they are found in lines or series, connected more or less distinctly in hardened specimens by a whitish cord similar to that connecting the pit and canal organs at this age. They are first seen in specimens of from one to two days old as faint whitish spots adjoining a canal line, as shown in Fig. 4, median to the line of the supra-orbital canal. This spot soon breaks up into, or is replaced by, a series of spots, as shown in the four-day-old specimen represented in Fig. 5. In this specimen similar rows are also seen on the other side of the supra-orbital and on each side of the infra-orbital line, while faint markings on the cheeks, median to the squamosal and post-temporal part of infra-orbital, indicate still other places where they will soon appear. After this age the organs develop rapidly, and in specimens five days old (Figs. 6 and 7, Pl. XXXI.) they are already numerous on the anterior half of the head. In specimens ten or twelve days old (Figs. 8 to 11, Pls. XXXII. and XXXIII.) they appear on the operculum; and when the fish is from three to four weeks old (Fig. 13, Pl. XXXIV.), they have spread over the entire head and part of the body. In these older specimens the serial arrangement of the organs has disappeared, except in those parts of the head where they are just beginning to appear. In such places (Fig. 9, Pl. XXXII.) they are still found in rows, and more or less distinctly connected by a cord.

6. Innervation.

It is now well known that all the sense-organs belonging to the canals of the lateral system are innervated by dorsal branches of the cranial nerves. For these organs Beard has recently proposed the name branchial sense-organs, because of their development in early embryos from thickenings of the epiblast over each branchial cleft, and for the nerves the name suprabranchial nerves (No. 1, pp. 171 and 174).

According to his general scheme of development in Elasmobranchs, based largely on the researches of Balfour, Marshall, and Van Wijhe, the dorsal root of a cranial nerve grows outward and downward from the neural crest, toward a local thickening of epiblast already formed over the cleft of its segment. At the level of the notochord, it fuses with the epiblastic thickening, a part of it, however, passing on as the future postbranchial nerve to the lateral muscle-plate of the segment. At the point of fusion, cells are rapidly proliferated. The deeper part of the mass which thus arises is the rudiment of the ganglion of the dorsal root, and the superficial portion, the rudiment of a branchial sense-organ. The deeper portion soon separates from the rest of the mass, leaving a nerve strand connecting it with sensory portion, and, lying deeper in the mesoblast on the root of the nerve, apparently at first distal to the point of separation of the post-branchial branch, becomes the ganglion of the nerve.

The superficial sensory part of the thickening may remain very small, or it may increase to a very considerable length, pushing its way either backward or forward, as the case may be, between the general epiblast cells, and connected in every case with the ganglion of the segment by the supra-branchial nerve, which is split off from under side of the thickening simultaneously with its growth. Along this thickening, concomitantly with the splitting off of the nerve, different organs arise, according to Beard, by the simple and repeated division of the single organ formed over the cleft, each organ so formed being connected by a separate branch with the main supra-branchial nerve.

This method of origin differs somewhat from that of the lateral line of Salmo, where, according to Hoffman (No. 8, p. 88), the different sense-organs arise independently after the lateral nerve has been split off from the under part of the epiblastic thickening which represents the line. As the nerve separates, a strand is left at each intermuscular septum connecting the nerve with the cells of the deeper part of the epidermis where later the organ will arise.

Beard's work was mainly confined to Torpedo ocellata, but he confirmed the results obtained in this form by comparison with the embryos of Mustelus and Pristiurus, and of certain Teleostei and Amphibia. In all these forms he finds seven supra-branchial nerves and seven corresponding lines of branchial sense-organs; but the position of these organs in the embryos is not fully detailed, and the adult conditions are not noticed at all, so that it is impossible to tell what becomes of the seven thickenings, and where, in the adult, the organs developed from each are to be found.

The seven supra-branchial nerves, as given by Beard, are the following:—

1. Ophthalmicus profundus,
   belonging to the ciliary ganglion and hypophysis cleft.
2. Ophthalmicus superficialis less portio facialis,
   of the gasserion ganglion and mouth cleft.
3. Portio facialis of Ophthalmicus superficialis.
4. Ramus buccalis,
   of the facial ganglion and two clefts, the hyoid and an absent one.
5. Supratemporal branch of the glossopharyngeal,
   of the glossopharyngeal ganglion and the first branchial cleft.
6. Supratemporal branch,
   of the first vagus ganglion and second branchial cleft.
7. Lateral nerve,
   of the second, third, and fourth vagus ganglia, and the third and following visceral clefts.

Of these seven nerves, the ophthalmicus profundus and ophthalmicus superficialis less portio facialis innervate, according to him, sense-organs lying over the snout; the portio facialis and ramus buccalis, the organs of the supra- and infra-orbital lines respectively; the glossopharyngeal and first vagus branches, the supratemporal organs; and the rest of the vagus, or nervus lineæ lateralis, the organs of the lateral line of the body.

The arrangement of the organs of the lateral system in Amia calva and their method of innervation, as determined by the examination of larval stages by sections, does not agree with Beard's scheme, for the trigeminal and ophthalmicus profundus take no part with any of their branches in the innervation either of the canal or pit organs. Moreover, there is the large and important operculo-mandibular line of organs, which Beard seems to have overlooked, for he does not mention it, and none of the suprabranchial branches given in his scheme of the sensory nerves could take any part in its innervation, unless the conditions in Torpedo and the other forms used by him for comparison are markedly different from those found in Amia.

In Amia the trigeminal, although it takes no part in the innervation of the regular canal or pit organs, has a large and important part in innervating the surface sense-organs, or terminal buds. Its ophthalmic and superior maxillary branches are largely devoted to this purpose. They supply no muscles, and numerous branches can be traced in sections from each of them directly to the surface organs which they supply. The inferior maxillary is partly sensory and partly motor, several important branches of it being distributed entirely to the surface sense-organs and other non-muscular tissues.

The ophthalmicus profundus is also entirely sensory. A small branch pierces the choroid coat of the eye, accompanied by a branch of the external carotoid artery, while the rest of the nerve fuses completely with the ophthalmic division of the trigeminal, so that its special distribution cannot be determined. In one set of sections only of all those examined did there seem to be a separation of these two nerves on the top of the snout, the ophthalmicus profundus being lost in the general tissues above the nasal sacks, and doubtless taking part there, along with the trigeminal, in the innervation of the surface organs.

The facial is the first one of the cranial nerves that takes any part in supplying the regular organs of the lateral canals, and it has a large and important part not only in their innervation, but also in that of the different lines of pit organs. Four of its branches, the ophthalmicus superfacialis, buccalis, oticus, and mandibularis externus, are entirely devoted to this purpose.

The R. ophthalmicus superfacialis facialis supplies all the organs of the supra-orbital canal, a separate branch being sent from the main nerve to each group of organs. This branch pierces the bony canal of the line immediately below the central organ of the group, and after entering the canal sends a branch to each organ. This is the method of innervation in all the canals. Posterior to all the branches sent to the different groups of supra-orbital organs, still another branch — the most posterior one of the R. ophthalmicus — is sent to the organs of the anterior dorsal pit line, a separate, smaller branch being sent from it to each organ of the line. This nerve alone, or together with the branch to organ 7 supra-orbital, which leaves the main nerve close to it, probably represents the branch which, according to Wright (No. 26, p. 483), supplies the organs of the transverse commissure in Mustelus. Wright is inclined to consider this most posterior of the dorsal twigs of the seventh in Mustelus as homologous with the ramus oticus in Ganoids and Teleosts (No. 20, p. 490).

The ophthalmic branch of the facial is closely associated throughout most of its course with the ophthalmic branch of the trigeminal, but there is apparently no interchange of fibres between them; and in the youngest specimens examined, the two nerves were wholly separate, although lying close together.

The R. buccalis facialis supplies the first thirteen organs of the infra-orbital line, and the R. oticus facialis the next three, making sixteen organs in all of this line supplied by the facial, or all those in front of the line of the opercular canal. The remaining organs of the infra-orbital line are innervated by the glossopharyngeal and vagus.

The sixteen infra-orbital organs supplied by the facial are separated by their innervation into four distinct groups. The first four, all belonging to the anterior commissure, form the first of these groups. They are supplied regularly by separate, consecutive branches given off from the anterior portion of the R. buccalis, which ends in the first one of them. The next six organs, from 5 to 10 inclusive, form the second group of the line, and they are also supplied by separate branches of the R. buccalis; but the branches to organs 5 and 6 are given off close together, the one to No. 6 passing outward behind the fifth division of the M. levator arcus palatini (McMurrich, No. 10, p. 122), and the other to No. 5, internal to, and in front of, this muscle. The origin of these two nerves close together from the main R. buccalis is easily explained by supposing the first four organs of the canal in Amia to have belonged to a line of pit organs in some earlier form. As the separate organs of such a line are always much smaller than those found in the canals, and as the nerve that supplies a whole line of them, where still found in Amia, is no larger, or not so large, as the branch sent to a single canal organ, the main part of the ramus buccalis would, in such an earlier form, have ended in the terminal organ of the canal; that is, in organ 5 of the line in Amia; and what is the anterior part of the nerve in Amia would, in that form, have been simply a smaller branch sent to the organs of the pit line, and given off beyond and rather close to the branch to organ 6, just as a similar branch, destined to supply the organs of the dorsal pit line, is still given off in Amia from the end of the nerve supplying the organs of the supratemporal commissure. As this anterior branch became larger and more important, concomitantly with the change of the pit line to a canal, it would become the anterior part of the main nerve, and the branches to organs 5 and 6 would arise close together from it, as they do in Amia.

Organs 11, 12, and 13 form the third group of the line. They are innervated in different specimens by one or by two branches of the R. buccalis, the branches, where there are two of them, arising close together and close to the origin of the main nerve from its ganglion, and one of them supplies organs 11 and 12; where there is but one, the branch to organ 13 arises close to the origin of the nerve from the main R. buccalis; thus representing a stage in which the division of the nerve has not proceeded far enough to give rise to a separate branch. The branches to the different organs enter the bony canal of the suborbital line by separate passages, immediately below the proper organ.

The next three organs, Nos. 14, 15, and 16, form the fourth group of the line, and vary somewhat in their method of innervation. Organs 15 and 16 are always supplied by branches of the R. oticus facialis. This nerve arises directly from the facial ganglion. It runs upward and outward without entering the orbit, and, piercing the cranial cartilage, issues on the top of the chondrocranium at the extreme anterior end of the diverticulum of the temporal groove. It here separates into three branches, two of which supply organs 15 and 16, and one the organ at the upper end of the spiracular canal.

Organ 14 is sometimes supplied by a branch given off by the ramus oticus after it makes its exit on top of the cranium; but oftener, in the specimens examined, it was innervated by a branch which left the nerve close to its origin, or even from the facial ganglion itself, near the root of the oticus, but a little in front of it. This branch, after making its exit into the orbit through the regular foramen for the ophthalmic nerves, turns upward and reaches its proper organ without piercing the cranium at all, or passes through a special perforation in the overhanging cartilaginous roof of the orbit.

In young specimens the buccal and ophthalmic branches of the facial arise from a Y-shaped mass of ganglion cells, formed on the dorsal root of the facial nerve, and lying on top of the rest of the trigemino-facial ganglionic complex, closely applied to it, but quite separate from it. The ophthalmic branch of the facial arises from the inner and upper arm of the Y, and the buccal from the lower and outer one. The otic and the branches to organs 11 to 14 infra-orbital, when they are not given off by the buccal, arise from the external side of the Y, and hence seem properly a part of the buccal. If this be so, and Beard's theory is to be accepted, then the original epiblastic thickening from which the infra-orbital line to organ 16 is developed, must have grown both forward and backward, the buccal being split off concomitantly with the growth of the anterior part, and the otic with that of the posterior, a few uncertain branches lying between them.

Organ 17 is supplied by the dorsal branch of the glossopharyngeal. This branch arises by a separate root, which passes out of the cranial cavity immediately behind the root of the main nerve, and often at this age by a separate foramen, or through a special part of the main foramen. On this root a separate ganglion is formed close to, and more or less intimately connected with, the main ganglion, and from it the dorsal nerve mentioned by Wright arises (No. 17, p. 489). This nerve runs upward through a special perforation of the chondrocranium, and, issuing on the bottom of the temporal groove, sends one branch to organ 17, the only canal organ supplied by it, and another to the middle dorsal pit line. This last branch runs medianward to about one-third the length of the pit line. It then turns upward and outward through the dermal bone, and dividing somewhat dichtomously, sends one branch medianward and another outward, both of them lying immediately underneath the line. From these branches smaller ones are given off directly to the separate organs. The innervation of this line indicates that it has grown in both directions from the original sensory spot found in younger specimens, and also that, although supplied by the same dorsal nerve that supplies canal organ 17, it is not a continuous growth from the epithelial thickening which was the rudiment of that organ. In this it differs from the other two dorsal head-lines, which grow from, and are directly continuous with, the rudiments of the canal organs from which they start.

The remaining organs of the infra-orbital canal, and those of the supratemporal cross-commissure, as well as the organs of the lateral line, are all supplied by branches arising from the ganglion formed on the root of the N. lineæ lateralis, or from that nerve itself. The arrangement here apparently departs somewhat from that given by Beard. The root of the N. lineæ lateralis receives its most anterior fibres at this age close to and a little above and behind the root of the N. acousticus. Piercing the membranes that separate the cranial cavity from the labyrinth, it runs directly backward, close to their outer surface and just above the posterior branch of the N. acousticus, in which there are numerous ganglion cells. It passes through the upper part of the main root of the glossopharyngeal, receiving there an important addition to its fibres, and, continuing backward immediately external to the origins of the anterior roots of the vagus, it issues through the main foramen of that nerve. In its passage through this foramen, it runs backward and outward, crossing the main root of the vagus at a considerable angle, and lying immediately above and closely applied to it. It probably receives here also an important addition to its fibres, but this could not be traced.

Immediately outside the foramen it forms a large, well-rounded ganglion, which lies directly above, and partly embedded in, the first vagus ganglion, but has no commissural connection with it, the line separating the ganglia in sections being perfectly sharp and distinct. From the proximal part of this ganglion, at its extreme anterior end, and almost from the root itself of the nerve, a large nerve is given off upward and outward. From it a branch is sent to organ 19 infra-orbital, and another, arising close to it, to organ 18, the rest of the nerve passing upward and medianward to supply the organs of the supratemporal commissure and those of the posterior dorsal pit line. The branch supplying the pit line is given off immediately beyond the branch to organ 2 of the commissure, thus agreeing in its relation to the other branches with that of the large branch sent by the R. buccalis to supply the organs of the anterior commissure, which branch is given off immediately beyond the branch to organ 6 infra-orbital, the second one of the suborbital line.

This dorsal nerve is described by Beard as the supra-branchial nerve of the first vagus ganglion. In Amia it is the first dorsal or supratemporal branch of the lateral nerve. It is joined soon after leaving its ganglion by a branch arising inside the cranial cavity, either from the root of the lateral nerve or from the root of the vagus, which here contains numerous ganglion cells. This branch, although closely applied to the regular dorsal nerve, is wholly separate from it. It is distributed entirely to the general tissues of this part of the head, including doubtless the surface organs, although the direct connection with any of them was not determined.

The next or second regular dorsal branch of the lateral nerve is given off near the base of the nerve, and not from the ganglion. It supplies organ 20 infra-orbital and the dorsal pit line of the body, branches being sent in succession to each organ or series of organs of that line. Other dorsal branches of the lateral nerve are then sent in succession to organ 21 infra-orbital and the organs of the lateral line of the body.

The lateral nerve has an undulating course, as shown by longitudinal horizontal sections (Fig. 48, Pl. XLI.). Each full undulation of the nerve corresponds to a muscle segment, and from the outer crests of each the branches sent to the organs of the lateral line arise. Running outward along the intermuscular septa, they pass through the corium, and then backward along the under surface of the scale they supply. Reaching the anterior end of the section of canal contained in this scale, the nerve enters it through a special passage, and supplies the single organ or groups of organs found there in the same way that the organs of the head are supplied. Each of these nerves, before reaching the under surface of the dermis, sends a branch upward and outward through the corium, a little dorsal to the point where the main nerve pierces it. Arriving under the same scale, this branch runs backward, dorsal to and parallel to the main nerve, and, piercing the scale about opposite the regular canal organ, supplies the corresponding series of pit organs.

The organs of the operculo-mandibular line are all innervated by branches of the R. mandibularis facialis externus. The first one of these branches is given off before the externus has separated from the main truncus hyoideo-mandibularis facialis. Leaving the truncus immediately after its passage from the facial canal through the hyomandibular, or even while still in that canal, it runs outward, backward, and upward, and enters the bony canal of the opercular line immediately under organ 15. It sends a branch to this organ, and then continuing upward inside the bony canal, immediately underneath the epidermal lining, ends in organ 16, the last one of the line. Organs 14 and 13 are supplied by separate branches, given off either from the mandibularis externus or from the main ramus mandibularis before it has separated into an external and internal portion. Organs 12 and 11 are supplied by a single branch, which, as in the case of the branch to organs 15 and 16, enters the bony canal under the first organ supplied, No. 12, and then passes on inside the canal to the second one, No. 11. Where these branches are given off from the main ramus mandibularis or the main truncus, it is from that part of the nerve that contains the fibres which afterward separate as the externus. Beyond the branch to organs 12 and 11, separate branches are sent in succession to each organ up to No. 4. The nerve then enters the bony canal, and running forward inside it, supplies in succession organs 3, 2, and 1.

Between the single branch that supplies organs 15 and 16, and the next regular one to organ 14, a branch is sent outward through the adductor mandibulæ muscle and then forward along its outer surface, immediately underneath the horizontal cheek line, branches being sent in succession to each organ of the line. A similar nerve is given off between the branch to organ 13 and the one to organs 12 and 11. This nerve also passes outward through the adductor muscle, and then forward along its outer surface, but it soon separates into two parts, one of which goes to supply the vertical cheek line, and the other the pit line on the mandible. In both cases the nerve arrives near the middle of the line it supplies, and there separates into two parts which run toward either end of the line, sending separate branches to each organ. In one specimen the nerve supplying these two pit lines was not given off as a separate nerve from the externus, but as a branch from the nerve supplying organs 12 and 11.

The innervation of the line of the gular plate could not be fully determined. Branches can be traced from the different organs of the line to a single nerve which runs backward internal to the plate. At the hind edge of the bone the nerve turns dorsalward, and, lying close beneath the epidermal lining of the dorsal side of the gular plate, runs forward dorsal to the hind edge of the geniohyoid muscle. Here it turns upward and backward, and then immediately upward and forward toward the front edge of the hyohyoideus muscle, round which it turns upward and backward, and, passing external to the front end of the sternohyoid muscle, enters the first branchial arch, and joins a part of the main nerve of that arch. This main nerve, so far as could be determined, is formed by the union of the postbranchial branch of the glossopharyngeal and the prebranchial branch of the first vagus ganglion. At the point where it is joined by the nerve of the gular line it has just separated into two parts, one of which runs downward and inward, and the other upward and inward, to be distributed to the tissues on the upper surface of the hyoid apparatus. It is this last branch that is joined by the nerve of the gular line.

7. Review of Nerves and Organs.

Reviewing briefly the arrangement of the nerves and organs, there are in front of the double pore 17–17, where the opercular and infra-orbital lines unite, sixteen separate canal organs or groups of organs along each line. The last two organs on each line, Nos. 15 and 16, are supplied by branches of a single nerve, which is directed posteriorly along the canal. Organs 11 and 12 of each line are also supplied by branches, directed anteriorly, of a single nerve; while the intermediate organs, Nos. 13 and 14, are in most cases supplied by independent branches. On the infra-orbital line a branch of the otic, anterior to organ 15, supplies the organ or group of organs of the spiracular cleft; while on the opercular line a branch of the mandibularis given off next in front of the single nerve to organs 15 and 16, and hence in a corresponding position, supplies the organs of one of the surface lines of the cheek. The other cheek line and the surface line on the mandible are supplied by a single nerve, which, in one of the two sets of sections in which it was traced, arose as a branch of a nerve supplying a regular canal organ. The possible significance of this will appear in considering the arrangement of the dorsal nerves behind the facial. The horizontal cheek line ends close to organ 11 infra-orbital; and the vertical cheek line, close to organ 11 operculo-mandibular. In front of this the canal organs on both lines are innervated by separate branches from the main nerve of the line.

Behind the point where the infra-orbital and opercular lines unite, organ 17 is supplied by the dorsal branch of the glossopharyngeal, which also supplies a line of surface organs lying dorsal to it. The next dorsal nerve, the first branch of the lateral line nerve, supplies organs 19 and 18, the organs of the supratemporal commissure, and a line of pit organs dorsal in their innervation to all of these. The second branch of the lateral nerve supplies organ 20 and the dorsal body line of pit organs. The next branch, so far as could be determined, supplies organ 21 alone; but each of the following branches for nearly the full length of the line normally supplies an organ of the lateral line and a corresponding line of pit organs.

The supratemporal cross-commissure, in the Characinidæ (No. 13, p. 36), lies in the parietals, and according to Sagemehl is an independent formation not to be compared with the commissure in Amia. So far as can be determined from his description, it occupies about the position of the middle dorsal pit line on the head of Amia. If it has the same innervation as this pit line, that is by the glossopharyngeal, a not improbable supposition, its exceptional position can easily be explained; for a canal line in one form is often represented by a pit line in another, as for instance, the anterior commissure in Amia and the corresponding pit line in Esox or Salvelinus; and probably also the anterior dorsal pit line in Amia and the cross-commissure in Mustelus, which has a corresponding position and apparently the same innervation.

In Fierasfer (No. 5, p. 38) the arrangement of the canals in this part of the head is markedly different from that in Amia. The cross-commissure leaves the main canal near the hind end of the squamosal directly opposite the upper end of the opercular canal, apparently as a direct continuation of that canal. It is innervated by the "ramus ascendente" of the lateral nerve, a branch which corresponds to or comprehends, according to Emory, both the supratemporal (probably of vagus) and opercular branches in other fishes. The "ramus ascendente" innervates not only the organs of the commissure, but also those in the temporal part of the main canal and in the upper end of the operculo-mandibular. The glossopharyngeal, which in Amia supplies a canal organ and line of pit organs lying almost directly above the end of the opercular canal, is in Fierasfer distributed entirely to the first branchial arch, and takes no part in the innervation of the lateral system.

Variations. — The arrangement of the canals and organs of the lateral system given in the preceding descriptions is the one most commonly found; but there are frequent variations, due either to the complete disappearance, or to the addition, of one or more peripheral systems. A group of sense-organs and its nerve appear or disappear with the addition or disappearance of a system. No exception to this rule was found in Amia; but in one specimen of Amiurus, a primary tube was missing in the mandibular line without the disappearance of a corresponding nerve and organ, thus leaving two separate organs or groups of organs between two consecutive tubes. This was doubtless due to the abnormal closing of a tube after its regular formation.

In Amia the most frequent variation from the normal type was the disappearance of one sense-organ and corresponding primary tube in the mandibular canal, leaving nine organs, tubes, and pores along the lower edge of the mandible instead of ten. The missing system was always one of those normally found in the angular. Less frequently there was the addition of one system, or the disappearance of two, along this same canal, the number along the opercular part of the line always remaining constant.

Other variations were the addition or disappearance of a single system along that part of the suborbital canal that lies in the postorbital bones, and the addition or disappearance of one in the one-half of the supratemporal cross-commissure, the other half of the commissure often varying inversely, so that the total number of systems in the full commissure remained the same. The organ that is missing when there is one system short in the suborbital line is either No. 11 or No. 12, both of which normally lie in the lower postorbital, and are innervated by a single branch of the R. buccalis. No variations were found in the supra-orbital line.

Van Wijhe (No. 19, p. 285) has called attention to the regular correspondence of each scale of the lateral line in Amia to a segment of the body, and has suggested the possibility of some sort of relation between the dermal bones of the head and the cranial segments. The arrangement of the sense-organs and nerves of the lateral system, the regular occurrence of primary tubes between consecutive dermal bones of the head, as well as between consecutive scales of the lateral line, and the singular correspondence between the infra-orbital and opercular canals is further evidence in this same direction.

III. LARVAL FORMS.

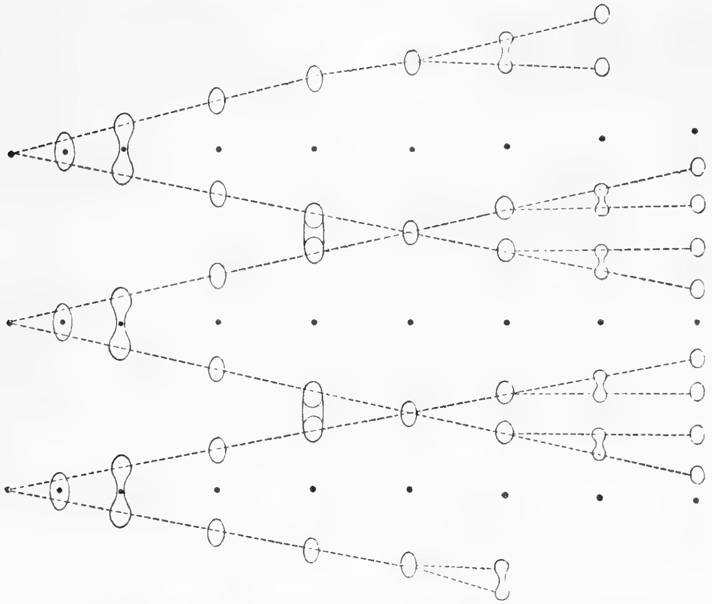
1. Formation of the Canals.

The inclosing of the lateral canals and the formation of the ninety-three normal primary pores and tubes is essentially a simple and regular process, but in most parts of the head marked abbreviations take place, which greatly obscure it. Where the process is regularly and fully carried out, the canals arise in separate sections, each of which contains a single sense-organ, and hence corresponds to the part between two primary tubes in the developed canal. This has already been described by Bodenstein in the lateral line of Cottus (No. 3, p. 142) and by both Schulze (No. 16, p. 69) and Solger (No. 18, p. 386) in Plateria.

If young Amia, in which the canals have not yet begun to develop, are hardened in chromic or picro-sulphuric acid, the organs of the lateral system, still below the surface, appear as whitish spots, with indistinct outlines, strung along more or less continuous whitish lines. These lines mark general and extensive surface depressions. After a developing canal organ has reached the surface at the bottom of one of these depressions, it begins to sink, carrying with it the surrounding tissues, thus forming a small pit, at the bottom of which the organ lies. A series of changes now begin, which, on an exaggerated scale, are a repetition of those which lead to the division of a pore. Lips grow upward and inward from the edges of the pit, and, meeting above the organ, form a short section of canal, the openings of which are inclined to the general surface, and give to the canal a tunnel-like appearance. A narrow shallow channel, pigmented like the rest of the outer surface, has meantime formed between the organs along the bottom of the general depression. It is deepest near the newly formed section of canal; and into it the canal opens, the sides of the openings passing gradually into the walls of the channel. The limits of the canal are clearly defined by a sharp change in direction of the bottom of the channel, the canal leading inward at something of an angle, the walls of the canals and pits always being much lighter in color than the outer surface.

The openings of these short sections of canal may be called half-pores because, with a few exceptions, all the primary pores in the developed system are formed by the fusion of two of them. After its formation the short canal increases in length by the continued coalescing of the edges of the channel immediately beyond it, and the two half-pores are pushed apart along the line of the canal toward other pores which are in a similar way approaching them from adjoining sections. This process in Amia is continued until the pores meet and unite, thus forming a continuous canal with a primary pore and tube between every two consecutive organs; but it may be arrested, in which case an interrupted canal will be formed, as in the post-temporal part of the infra-orbital in Esox lucius and along the canal of the lateral line in Ophidium (No. 5, p. 39). At each end of a continuous canal formed in this manner it is evident there must be a pore, which, if it cannot unite with a pore of some other line to form a double system, must always remain a half-pore or terminal opening. Such terminal openings are retained in Amia in pores 1 and 8 supra-orbital and 1 operculo-mandibular. The other terminal opening of the opercular line, pore 17, unites with pore 17 infra-orbital to form a double system. In the infra-orbital line pore 6 is a terminal one, and pore 22–1 a double one, formed at the other end of the line where it joins the lateral canal of the body. In the anterior commissure one terminal opening has disappeared on the top of the snout where the two lines meet, and the other has fused with the second pore of the main canal to form what has been called pore 5 infra-orbital.

Cut 10 is a diagrammatic representation of the formation and subsequent subdivision of a primary pore. These two processes are continuous and essentially similar; for even in the adult, two pores if forced together from want of space fuse, as frequently happens along the lower edge of the lachrymal. Double pores of this kind, formed in the adult, usually undergo no further division; but the conditions shown at *omg''* in group 11 operculo-mandibular (Fig. 20, Pl. XXXVI.) can only be explained on the supposition that this pore has afterward subdivided and multiplied exactly as do the simple pores.



Cut 10.—Diagrammatic representation of the formation of pores and groups of pores. The small black spots indicate organs, and the curved outlines openings of pits or pores in different stages of formation and division.

All phases in the formation of half-pores, as well as of the primary ones, are shown in Figs. 23 to 34, which fully illustrate the development of that part of the infra-orbital canal lying immediately behind the eye. The formation of the first few pores of the lateral line and the last three pores of the infra-orbital are shown in Figs. 35 to 38.

In Fig. 23, which represents a specimen 19 millimetres long, and from twelve to fifteen days old, organ 16 infra-orbital is just inclosed, an unpigmented line still marking where the sides of the canal have come together above it. Organ 15 lies in a deep groove continuous with the canal at organ 16, and is about to be inclosed. The inclosing of these two organs is an abbreviation of the regular method. They lie relatively close together, and the pits in which they lie become a continuous groove, as shown in Fig. 12, before the canal closes over either of them. The canal is formed as usual, but a relatively long section of it is inclosed at once so that the two half-pores which go to make pore 16 are formed facing each other and already partly fused. The different steps in this process are shown in Figs. 23, 24, and 25, in the last of which pore 16 is fully developed. This abbreviated method occurs wherever the organs lie close together, or where the canals are relatively large, as in young larvæ.

In Figs. 23 and 24, organ 8 supra-orbital lies on the surface, and is hardly to be distinguished except by position from the following organs of the anterior dorsal pit line. In Fig. 25, which represents a 23½-millimetre specimen, it is just being inclosed, and in Fig. 27, a 29-millimetre one, is entirely so, pore 8 appearing as a small terminal opening immediately in front of the first organ of the pit line.

In Fig. 23, organs 14 and 15 infra-orbital can both be seen; in Fig. 24 they are just inclosed; and in the succeeding figures up to 28 the principal phases in the formation of pore 15 are shown. This pore lies at a sharp bend in the infra-orbital line close to pore 7 supra-orbital, which also lies at a bend in its line. The two lines are approaching each other at these bends, and the surface between them is strongly depressed, just as it is between successive organs on a regularly developing line. Along this depression pores 15 and 7, once formed, approach each other and coalesce, exactly as half-pores do along the line of a canal. In Figs. 29 and 30 they are shown partly united, and in Fig. 31, a 40-millimetre specimen, they have already united and begun their primary division, which is completed in Fig. 33, a 54-millimetre specimen. In Fig. 34, a specimen 135 millimetres long, the double pore has undergone its secondary division, and is represented by a group of four.

In Figs. 23 and 24, organ 16 operculo-mandibular and all the organs of the infra-orbital line behind organ 16, lie on the surface or in small pits along the strong channels which mark the course of the canal. In Fig. 25 the canal is closing over organs 17, 19, and 20. In Fig. 26 it has fully closed over organs 17 and 19, but organ 20 is still visible in a large double pit common to it and to organ 21. In Fig. 27 the canal has closed over organ 20 and is about to close over organ 21, the process being so greatly abbreviated that pore 21 is formed at once in place. The two halves of pore 20 are always formed at some distance apart, as shown in Figs. 26, 27, and 28.

In Fig. 26 the two half-pores that go to form pore 17 infra-orbital are some distance apart. In Fig. 27 they are nearing each other, and in Fig. 30 they have united. The pore so formed is also beginning, in this figure, to travel down the opercular canal toward the terminal pore 17, which is formed by the closing of the canal over organ 16. In Fig. 33 the double pore 17–17 is nearly formed, and in Fig. 34 it has undergone its first division.

The formation of pores 18 and 19 infra-orbital is somewhat irregular. Organs 2 and 3 of the supratemporal commissure are usually the first ones inclosed, but in Fig. 27 the canal has formed over organs 1 and 3, and not over organ 2. The lateral terminal opening of the commissure, pore 4, lies directly opposite organ 18 infra-orbital, and a little in front of and behind this organ are the anterior and posterior halves of pores 18 and 19. In Figs. 28 and 35, which represent the same specimen, the canal is beginning to close over organ 18, the upper lip of the canal forming at the end of the commissure directly above its terminal opening. In Figs. 29 and 36, which also represent the same specimen, the canal has nearly closed over organ 18, and in Figs. 30 and 31 the process is completed, the terminal opening of the commissure being entirely shut off from the exterior,—transferred, in fact, from the exterior to the inner wall of the infra-orbital canal. In two of the specimens examined by section there was an extra pore and tube at this point, both small, the tube leading forward and medianward from the point where the commissure joined the main canal.

In Fig. 34 pores 18 infra-orbital and 3 supra-orbital have undergone their first division. In this figure the median terminal openings of the half-commissure of each side have united and undergone their first division. This division frequently takes place before the two terminal pores have fully united, and in such cases the median pore never gets beyond the oblong shape shown in Figs. 32 and 33. The same thing often occurs in pore 17 infra-orbital, which may undergo its first division before it is fully formed and before it has united with pore 17 operculo-mandibular, as shown in Fig. 13. In this case only the anterior one of the secondary pores takes part in the fusion with the opercular line.

The canal of the lateral line, like the canals of the head, is first formed in short sections, which afterward become continuous. The rudiments of the different organs of the line are formed on the intermuscular septa, as described by Bodenstein and others in the bony fishes; but as the organ develops, it travels backward, and before being inclosed lies in the middle of the segment, as shown in Figs. 35 and 36, and as found by Malbranc in the Amphibia (No. 11). The organ then sinks into a little pit, and on its dorsal and ventral sides lips are formed which coalesce, forming a short canal about the length of a body segment, as seen in Figs. 36 and 37. The primary pores formed by the union of the terminal openings of these short sections lie at first opposite the intermuscular septa and between consecutive scales, which at this age have only the length of a body segment and no free edge (Fig. 37, *llp*^{1} and *llp*^{3}). As the scale grows its free hind edge pushes backward on either side of the primary tube and, uniting beyond it, leaves the pore on its outer surface (Fig. 38) and the tube at the point where the canal passes from one scale to the next (Fig. 48). The tube at first runs directly outward through the scale, but later it acquires a longitudinal position, extending backward almost as a prolongation of the short canal, and having on the outer surface of the scale one or more pores (Fig. 44).

Toward the front of the head and along the mandibular line the canals are inclosed much earlier than in the parts behind the eye. The process in this part of the head is always greatly abbreviated after the manner detailed in describing the formation of that part of the infra-orbital canal containing organs 15 and 16. The development also proceeds so rapidly here that the canals in this anterior part of the system are fully formed before those behind it have much more than begun to develop. This anterior part includes the first six organs of the supra-orbital line, the first ten of the infra-orbital, and the first nine of the operculo-mandibular. The canals inclosing these organs appear in specimens only five or six days old, and when the fish is from twelve to fifteen days old they are fully formed.

Figures 6 to 12 show the formation of these canals in three specimens, —one 11½ millimetres long (Figs. 6 and 7), one 14 millimetres long (Figs. 8 to 11), and one 18 millimetres (Fig. 12). As shown in these figures, the supra-orbital canal in front of organ 7 is inclosed in two sections containing three organs each, and the mandibular canal in a single section containing the first nine organs of the line. In the infra-orbital line organs 3 to 7 are inclosed together in a Y-shaped section of canal, and then organs 1 and 2, and 8, 9, 10. The median pore No. 1 formed in this process is shown in Fig. 11. It afterwards entirely disappears.

Organ 5 infra-orbital is normally the first one in the whole lateral system to be inclosed, and the formation of that part of the canal in which it lies is closely associated with the development of the nose. In Fig. 1 the nose is shown as a simple pit lying beyond the line of the infra-orbital canal. It is at first round and deep, but it soon becomes oblong, as shown in Fig. 4, and is then inclosed exactly as the canals of the lateral system are, a short section of canal being formed open at both ends and continuous behind with the Y-shaped open depression of the infra-orbital line. This stage is shown in Fig. 6, an unpigmented surface line still showing where the canal has closed over the nasal pit. The whitish cord of the infra-orbital line extends beyond organ 5 toward and partly into the posterior one of the two openings. In the 14-millimetre specimen, Fig. 8, organ 5 has been inclosed, and the half-opening, destined to become pore 6, stands facing the posterior naris, connected with it by a deep depression. At this stage these two openings appear like two half-pores about to fuse, but this resemblance soon disappears. In the 18-millimetre specimen, Fig. 12, the two pores still open into a large common depression, but it is becoming shallower; in Fig. 13, a 31-millimetre specimen, it has nearly disappeared; and in Fig. 14, entirely so, pore 6 now having a position in front of the naris instead of below it as at first. The formation of pore 5 infra-orbital from three half-pores is shown in Fig. 8.

In the opercular line the central part of the canal is formed at an early age. Organs 13 and 14 are the first to be inclosed (Fig. 12), then organs 12 and 15, and finally, at a much later period, organs 11 and 16. During this stage of its development the opercular canal is an independent canal not connected with the mandibular portion, or with the main line, a condition which is permanent in Esox lucius.

The lateral canals of Amia present a more highly developed arrangement than those of the bony fishes. Lepidosteus, judging from a most cursory examination, resembles Amia; Polypterus, except in the possession of large dermal plates, has essentially the arrangement found in Amia immediately after the formation of the primary pores and tubes, and before the opercular line has joined the main canal. This larval arrangement in Amia also corresponds to that found in the adult of most bony fishes, but in many teleostean forms still more primitive conditions exist.

Sagemehl has advanced the theory that the teleostean condition is derived directly from that found in the adult of Amia by the gradual growth of a thicker cutis from the edges of the dermal bones toward their centres. As a result of this growth, the bones lose their superficial position, and finally lie beneath a thick dermis. The lateral canals, however, in order to maintain their communication with the exterior, do not sink in a corresponding degree, and they are accordingly found in the Teleosts much nearer the upper surface of the bone than in Amia. In many species they project in ridges above it, and in Gymnotus, many of the Muræniðæ, some Cyprinoids and others, they lie entirely above the bones of the head inclosed in bony tubes and forming the "nervenskelet" of Stannius. In Polyodon Spathula, also, clearly a more primitive form in this respect than Amia, a somewhat similar arrangement exists; for, according to Van Wijhe, the canals lie in the flesh in open, bony channels. These different conditions both in the Teleosts and in the Ganoids would also be obtained if the development, as shown in Amia, was simply arrested instead of undergoing retrogression; that is, by supposing that the Teleosts had never attained the Amia condition instead of having passed through it as indicated by Sagemehl.

In Salvelinus the canal of the lateral line is never developed, and the peripheral systems of the cranial canals have, in most cases, only a single surface opening corresponding to the primary pores of Amia; but in one very large specimen, two of these systems had undergone a primary division similar to that which takes place in Amia, and the two pores, always found single in other specimens, were each represented by a group of two.

2. Origin of the Canal Organs.

The discussion of the origin and growth of the sensory thickenings from which the different lines of the lateral system arise, and the origin of the sense-organs along these lines, lies wholly beyond the scope of the present paper, but the order and manner of their appearance, as determined from surface examinations, lies fairly within it. Most of the specimens used in this part of the work were killed in picro-sulphuric acid or chromic acid, with, or without, a trace of osmic, or in the vapor of osmic acid, and then transferred to chromic. Chromic acid was found to emphasize the continuity of the whitish lines which represent the sensory tissues, while picro-sulphuric produced a somewhat opposite effect, making evident a want of continuity, or at least a difference in the composition of the lines in those places where the innervation changes. Freshly killed specimens were found to give much the best results, for the use of alcohol obscured the markings which in certain places are indistinct even in the best preparations.

In fishes just hatched, the lines of the infra-orbital, supra-orbital, and lateral line canals are the only ones that can be distinguished. They are all represented by short, straight, raised lines of about the same length. That of the lateral canal starts immediately above the opercular opening, and those of the other two close together (if not from a common point), immediately behind the eye and directed, like the arms of a letter V, one above and the other below it. In somewhat older specimens the infra-orbital line extends under the eye to the level of the hind edge of the nasal pit, where it ends in an enlargement, from which later (Fig. 1, Pl. XXX.) the anterior commissure is given off downward and forward, the main line continuing upward toward the nasal pit. Behind the infra-orbital line, and immediately above the opercular opening, there are at this age two short, curved, comma-like lines directed upward and backward with their enlarged ends behind. The anterior one is the rudiment of organ 17 and the middle dorsal pit line, and the other the rudiment of the supratemporal and posterior dorsal pit lines. They both lie on the anterior end of a raised surface which is continuous with the dorsal part of the body muscles, and is faintly indicated in Fig. 1. The dorsal outline of this raised portion curves downward, leaving a semi-transparent space in front of it, between it and the hind edge of the cerebellum. Its curved surface forms an angle behind with the curved surface of the yolk, the line of the angle extending backward and upward from the hind edge of the opercular opening to the anterior end of the line of depression between the dorsal and ventral muscle segments of the body. At the angle formed by these two lines of depression, at some distance behind the supratemporal line, the lateral line begins, as does also the accessory lateral line.

In specimens less than a day old, or even in those a little older, the lines or regions supplied by different nerves are distinctly separate in picro-sulphuric preparations, but in chromic acid ones much less so, particularly when first killed in the vapor of osmic. In such specimens the infra-orbital line is somewhat continuous throughout its length. In fishes two and one-half days old this appearance is still more marked, as shown in Fig. 1, which is drawn from a chromic acid preparation. The sense-organs of the different lines in this specimen are not yet sufficiently developed to show on the surface; but the raised whitish lines, which indicate the positions of the cords of cells along which they arise, are strongly marked. The line of the supra-orbital canal is continuous with that of the anterior dorsal pit line, and widely separated from the infra-orbital at the point where later the anastomosis with it will take place. Both ends of the line are enlarged where, according to the theory of Beard and others, it is pushing its way through the surrounding indifferent epithelial cells. The infra-orbital line is continuous throughout its length, and continuous with the lateral line which extends beyond the pectoral fin nearly to the level of the hind edge of the yolk. The accessory lateral line, which has just begun to develop, starts from the lateral line immediately behind the line of the supratemporal commissure, and is pushing backward through the surrounding cells exactly as the lateral line does. The ends of both these lines are enlarged, that of the lateral line sometimes forming a large and prominent swelling. The dorsal body line has not yet appeared. The posterior dorsal pit line of the head is continuous at an angle with the line of the supratemporal commissure, which is represented by a single whitish spot connected by a cord with the infra-orbital line. These two lines are short and indistinct. They lie behind the upper end of the opercular opening and immediately behind the slight prominence of the auditory vesicle. The middle dorsal pit line is represented by a large spot lying immediately superficial to the auditory vesicle, and connected by a faint cord with the line of the infra-orbital.

Just in front of the auditory vesicle, the infra-orbital line runs across a depression, in the bottom of which, immediately below the line, is a dark spot marking the blind upper end of the spiracular canal. Above and in front of this point the line is enlarged; and from this enlargement organs 14, 15, and 16 arise. No opening into the spiracular canal could be found at this age or in one-day-old specimens. Behind and below the eye, the infra-orbital line is small; but in front of it, where organs 7 and 6 arise, it is enlarged again. In front of this enlargement it again narrows; and the line of the anterior commissure is given off, the main line continuing on toward the nasal pit, and ending there in an enlargement which is indistinctly continuous with the whitish border of the pit.

The operculo-mandibular line is a slender and faint but continuous line, lying along the anterior edge of a depression which marks the boundary between the operculum and branchiostegal rays on one side and the pre-operculum and mandible on the other. Its upper end lies in line with the spiracle, but is separated from it and from the infra-orbital by a strong prominence. A slight depression indicates the position of the horizontal cheek line, and another that of the vertical one.

The raised whitish lines which in these early specimens represent the growing sensory tissues disappear as the separate organs of the line develop, and there is left a slender white cord connecting them. This cord is doubtless the one found by Bodenstein in the adult of Cottus gobio (No. 3, p. 136), where it must be much more strongly developed than in Amia, for even in specimens only 40 millimetres long (or from twenty to thirty days old) it is traced with difficulty in sections. It is apparently the remnant of the cord along which the organs develop. In the four-day-old specimens, shown in Figs. 4 and 5, these cords are well defined, and most of the canal organs recognizable. The organs of the supra-orbital line are well developed, the first six being widely separated from the seventh and last, which cannot be distinguished in outward appearance from the pit organs lying immediately behind it. The cord connecting the canal organs is continuous with that connecting the organs of the pit line. On the infra-orbital line all of the organs up to No. 16 have appeared; and all, excepting Nos. 1, 6, 11, 12, and 13, which are always the last ones in this section of canal to be fully developed, have reached the outer surface. Organ 5 lies above the point where the anterior commissure and suborbital canal unite, and may from its position belong to either line. Up to No. 16 the cord of the line is continuous, but behind this it is broken or very faint. At the spiracular depression it begins again, and is continued back into the lateral line. Organ 17 is the only one in this length of canal that can be distinctly recognized. The lateral line extends beyond the anus, and the accessory lateral line not quite to it, as shown in Fig. 2. The dorsal body line begins opposite a bend in the main line a little in front of the point where the first organ of the lateral line will appear, and has already reached the top of the body, and turned backward along the edge of the dorsal fin. The end of the line is strongly swollen. Neither this line nor the supratemporal or middle dorsal pit lines are continuous at this age with the main lateral line. The supratemporal line shows two enlargements, from the median one of which the posterior pit line starts at a sharp angle. The middle dorsal pit line has a single well-developed organ, with the cord of the line extending on either side of it. The line of the mandibular canal is regularly developed to organ 10, the first two or three organs still being indistinct. The opercular part of the line is broken. Organ 15 and the rudiment of organ 16 lie above the horizontal cheek line, and separated from it and from organs 12, 13, and 14, none of which are fully developed. Organ 11 has not yet appeared. The vertical cheek line and mandibular surface line form a nearly continuous line, extending between organ 8 mandibular and 12 infra-orbital. The gular line could not be found.

In the 11½-millimetre specimen (Fig. 6, Pl. XXXI.) the cord of the infra-orbital line extends the whole length of the line, and is continuous with that of the lateral line. In this specimen the dorsal body line is also continuous with the cord of the lateral line; the cord of the supratemporal line, with organ 18; and the cords of the three dorsal pit lines and the lines on the cheek, with the canal organs, near which they arise. In slightly older specimens these connections disappear, and in still older ones even the cord connecting the organs of each line is traced with difficulty. In the 11½-millimetre specimen there are, behind organ 18 infra-orbital, five faint transverse markings, as shown in Fig. 6. The first one marks the hind edge of the extrascapula, and the others the lines of intermuscular septa. Between the fourth and fifth lies the first regular organ of the lateral line. Between the others, organs 19, 20, and 21 will doubtless appear; but this could not be established, for when these organs are first seen, the intersegmental markings have disappeared.

General Summary.

The sense-organs of the lateral system in Amia are separated by their position and by their innervation into distinct groups. Each group develops from a special cord of cells lying in the deeper layers of the epidermis, and each cord from a special sensory thickening, which when first seen from the surface in specimens hardened in chromic or picro-sulphuric acid, appears as a large, whitish, and slightly raised spot. These spots are the rudiments, not only of the different groups of organs, but also, according to the theory of Beard and others, of the nerves supplying them. They are all distinctly recognizable before the close of the first day after hatching. From them are developed the following groups of organs: —

1. The first sixteen organs of the infra-orbital canal, and the one organ of the spiracular canal, all innervated by the *R. buccalis facialis*, and its posterior division, the *R. oticus*.

2. The seven organs of the supra-orbital canal and those of the anterior dorsal pit line, all innervated by the *R. ophthalmicus facialis*.

3. The sixteen organs of the operculo-mandibular line and those of the two pit lines on the cheek and the one on the mandible, all innervated by the *R. mandibularis externus*.

4. Organ 17 infra-orbital and those of the middle dorsal pit line, all innervated by the dorsal branch of the *N. glossopharyngeus*.

5. Organs 19 and 18 infra-orbital, the three organs of the supratemporal cross-commissure, and those of the posterior dorsal pit line, all innervated by a dorsal nerve arising from the ganglion or root of the *N. lineæ lateralis.*

6. The organs of the lateral line of the body, organs 20 and 21 infra-orbital, and those of the accessory lateral and dorsal pit lines of the body, all innervated by branches of the *N. lineæ lateralis.*

All these organs in the early stages of their development lie below the surface, but they soon push through the overlying epidermal cells, and their upper central portions become exposed. Each pit organ subsequently sinks slightly below the surface, and a little epidermal pit is formed above its central portion. The canal organs also sink below the surface, but they carry with them the surrounding tissues and by a process of infolding become inclosed in short canals, each containing a single organ. These short canals then become continuous, a single surface opening being left between every two consecutive organs along each line. These simple openings, or primary pores, may be retained in the adult, but most of them undergo a repeated dichotomous division, thus giving rise to groups of surface pores and to corresponding dendritic systems of canals.

By the union of the primary groups of short canals three principal canals are formed and two cross-commissures; namely, the infra-orbital or main canal, which is continuous with the canal of the lateral line of the body, the supra-orbital and operculo-mandibular canals, and the anterior and supratemporal cross-commissures. The anterior commissure has, following the terminology of other writers, been considered as a part of the infra-orbital canal. It lies over the snout, and connects the infra-orbital lines between organs 5 and 6, which are properly the first two organs of the line. The supratemporal commissure lies in the temporal region, and connects the main lines between organs 18 and 19, or directly opposite organ 18. The supra-orbital and operculo-mandibular canals have no connection with the corresponding canals of the opposite side. They arise as independent canals, but the supra-orbital, soon after its regular formation, anastomoses between organs 6 and 7 with the main canal between organs 14 and 15; and the operculo-mandibular, by its terminal opening, with the main canal between organs

16 and 17. These two anastomoses, and those of the anterior commissure with the infra-orbital, and the supratemporal commissure with the corresponding canal of the other side, are the result of the fusion of two primary pores which coalesce to form double pores, in the same way that two half-pores unite to form the primary ones. Double pores are formed in this way, and then disappear at the point where the anterior commissure joins the canal of the other side, and where the supratemporal commissure joins the main infra-orbital. One other anastomosis, formed in a somewhat different way between systems 6 infra-orbital and 4 supra-orbital, establishes a second connection between these two canals, and completes the circuit of the orbit.

There are on each side three lines of pit organs on top of the head, besides two on the cheek, one on the mandible, and one on the gular plate. The anterior and middle pit lines on top of the head lie nearly above the anterior and posterior semicircular canals. On the body there are two series of pit lines, one on the back and one accompanying the lateral canal.

In the adult the main canals lie in the deeper layers of the dermal bones. In larval stages they lie in open channels, or in bony tubes on the upper surface of these bones. Although some of the primary tubes issue through the bone, one always issues between every two consecutive bones along each line.

The sense-organs always lie inside the bones. They are at first single, but by the formation of bud-like organs at each end of the original one, large groups are formed, which in certain stages resemble the nasal epithelium of Exocetus and other forms, as given by Blaue.

The nasal pits are inclosed in the same way that the lateral canals are, and the short canal so formed is at first continuous with the canal inclosing organ 5 infra-orbital.

The head, gill-covers, and gular plate are thickly covered with the surface sense-organs called by Merkel terminal buds, which extend also onto the body. They are innervated in large part by the trigeminal, but probably also by the ophthalmicus profundus, facialis, glossopharyngeus, and vagus.

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EXPLANATION OF PLATES.

INDEX LETTERS.

a.	anal fin.
al.	anterior dorsal pit line of head.
all.	accessory lateral line.
allo.	sense-organ of lateral line.
an, an.a.	anterior nasal aperture.
ANG.	angular.
ANT.	antorbital.
av.	auditory vesicle.
b., bf.	ramus buccalis facialis.
c.	caudal fin.
c.ll.	canal of lateral line.
c.md.	mandibular canal.
D.	dentary.
dl.	dorsal pit line of body.
dlo.	sense-organ of dorsal pit line.
ep.	epiphysis.
ETH.	ethmoid.
ESC.	extrascapula.
f.gl.	facial ganglion.
FR.	frontal.
G.	gular.
g.gl.	glossopharyngeal ganglion.
gl.	gular pit line.
gu.	gular plate.
hf.	ramus hyoideus facialis.
hmf.	truncus hyoideo-mandibularis facialis.
hl.	horizontal line pit of cheek.
IOP.	interoperculum.
ig.	infra-orbital groups of pores.
io.	infra-orbital sense-organs.
ip.	infra-orbital primary pores.
i^{17} om^{17} *p.*	double pore at union of infra-orbital and operculo-mandibular canals.
i^{17} om^{17} *g.*	double group of pores at union of infra-orbital and operculo-mandibular canals.
i^{22} ll^{1} *p.*	double pore at union of infra-orbital and lateral line canals.
i^{15} s^{7} *p.*	double pore at union of infra-orbital and supra-orbital canals.
i^{15} s^{7} *g.*	double group at union of infra-orbital and supra-orbital canals.
i^{6} s^{4} *g.*	double group at union of infra-orbital and supra-orbital canals.
JG.	jugal.
LA.	lachrymal.
lb.	surface organs.
li.	line of infra-orbital canal.
l.md.	mandibular line of pit organs.
l.om.	line of operculo-mandibular canal.
l.p.	line of antorbital cross-commissure.
l.s.	line of supra-orbital canal.
l.st.	line of supra-temporal cross-commissure.
ll.	lateral line.
llg.	lateral line group of pores.
llo.	lateral line sense-organs.
llp.	lateral line primary pores.
md.l.	line of mandibular canal.
mef.	ramus mandibularis externus facialis.
mif.	ramus mandibularis internus facialis.
mf.	ramus mandibularis facialis.
ml.	middle dorsal pit line of head.
mx.	maxilla.
MX.	maxillary.
NA.	nasal.
nll.	nervus lineæ lateralis.
np.	nasal pit.
nt.	nasal tube.
omg.	operculo-mandibular group of pores.
omo.	operculo-mandibular sense-organs.
omp.	operculo-mandibular primary pores.
OP.	operculum.
opf.	ramus opthalmicus facialis.
p.	pectoral fin.
PA.	parietal.
pl.	posterior dorsal pit line of head.
pn., pna.	posterior nasal aperture.
popf.	pre-opercular fold.
POP.	pre-operculum.

POR.^{1}	first postorbital.
POR.^{2}	second postorbital.
PSF.	postfrontal.
S$^{1\text{-}3}$.	scales of lateral line.
S.ANG.	supra-angular.
SC.	suprascapular.
SCL.	supraclavicula.
sg.	supra-orbital group of pores.
so.	supra-orbital sense-organs.
sp.	supra-orbital primary pores.
smf.	supramaxillary furrow.
SOP.	suboperculum.
SOR.^{1}	first suborbital.
SOR.^{2}	second suborbital.
spr.	spiracle.
sp.o.	spiracular sense-organ.
SQ.	squamosal.
stg.	supratemporal group of pores.
sto.	supratemporal sense-organs.
stp.	supratemporal primary pores.
st.gl.	supratemporal branch of glossopharyngeal.
st.v^1.	supratemporal branch of vagus.
v.	ventral fin.
vl.	vertical pit line of cheek.
x.	nerve to gular line of pit organs.

The numerals affixed to the index letters *g*, *i*, and *p*, along the infra-orbital line, should be increased by one, except in Pl. XXXVI., where the correction has been made by the lithographer.

For	$ip^{1\text{-}20}$	read	$ip^{2\text{-}21}$.
"	$ig^{1\text{-}20}$	"	$ig^{2\text{-}21}$.
"	$i^{14}s^{7}$ *p* and *g*	"	$i^{15}s^{7}$ *p* and *g*.
"	$i^{16}om^{17}$ *p* and *g*	"	$i^{17}om^{17}$ *p* and *g*.
"	ip^{21} and ig^{21}	"	$i^{22}ll^{1}$ *p* and *g*.

EXPLANATION OF PLATE XXX.

FIG. 1. Larval Amia, one day old, showing a stage in the development of the lateral line, preceding the appearance of definite sense-organs. × 40.

FIG. 2. Larva four days old. Sense-organs beginning to appear along the sensory lines of the head. The double line of the body has not yet completed its growth backward. Length 10^{mm}. × 15.

FIG. 3*a*. Larva 40^{mm} long. Lateral line has reached the rays of the caudal fin; and while the formation of sense-organs now begins to advance along the body lines, the more anterior organs of the head have already disappeared by inclusion in their respective canals. × 15.

FIG. 3*b*. Tail of a larva 21^{mm} long, showing the extension of the lateral-line organs onto the caudal rays. × 15.

FIG. 3*c*. Tail of an adult ♀ 22½ inches long. Half natural size.

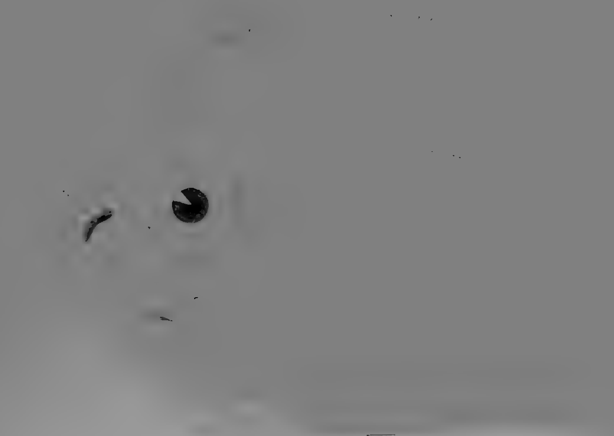
EXPLANATION OF PLATE XXXI.

FIG. 4. Side view of larva four days old (10^{mm} long). The surface organs appear in a line above and below the eye. × 40.

FIG. 5. Front view of same larva.

FIG. 6. Side view of larva six days old (11½^{mm} long). Lateral-line organs of head lying in half-closed canals. Surface organs multiplying. × 40.

FIG. 7. Front view of same larva.

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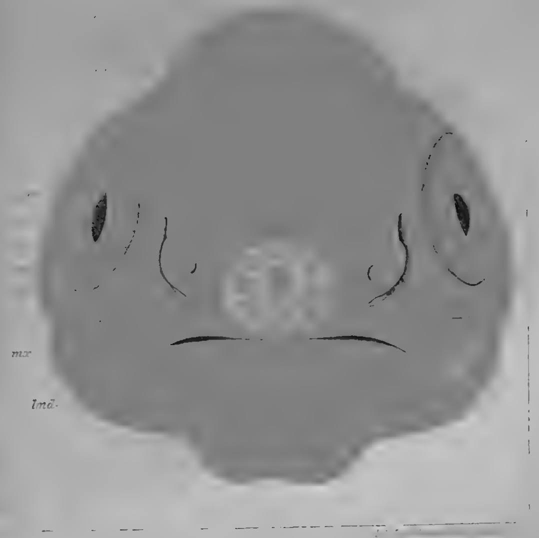
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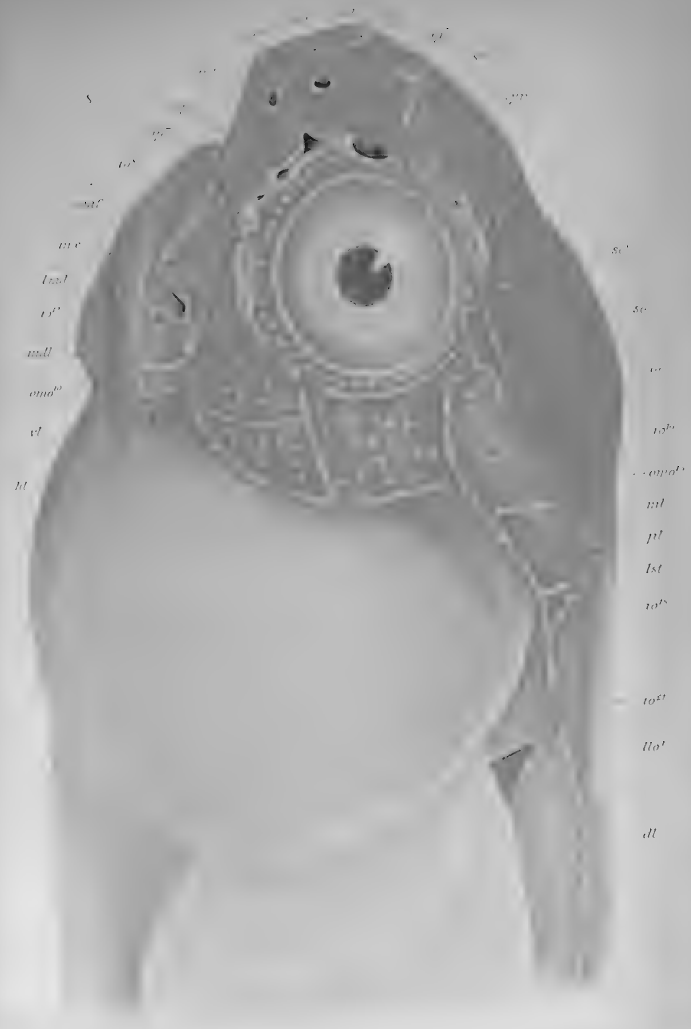
EXPLANATION OF PLATE XXXII.

FIG. 8. Side view of larva 14^{mm} long, showing canals of head in various stages of formation. Surface organs have become numerous. ×40.

FIG. 9. Dorsal view of same larva.



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EXPLANATION OF PLATE XXXIII.

FIGS. 10 and 11. Ventral and front views of the same larva. × 40.

10


an
omo^1
omo^2
m.r
gl
omo^3

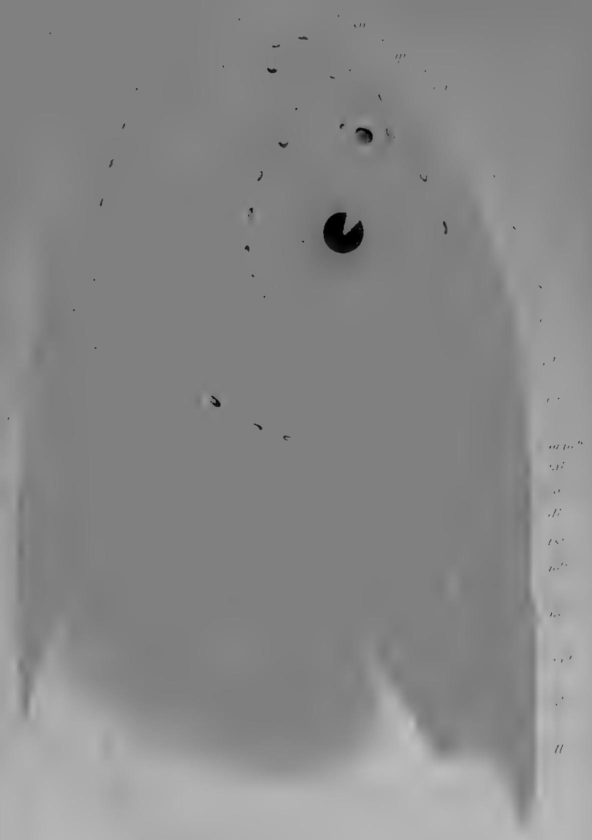
11

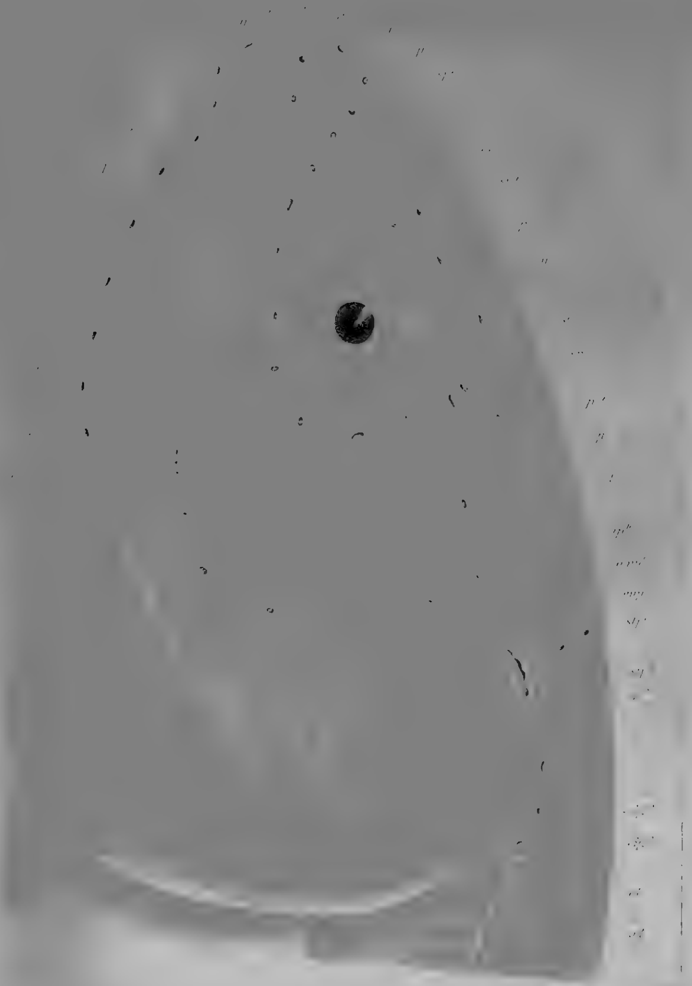

so^2
pn
ip^2
so^1
an
ip^2
ip^1
io^2
io^3
mx
cmd
gl

EXPLANATION OF PLATE XXXIV.

FIG. 12. Larva 18^{mm} long, showing the primary pores in various stages of formation. × 30.

FIG. 13. Larva 31^{mm} long, showing the primary pores of the head. × 30.



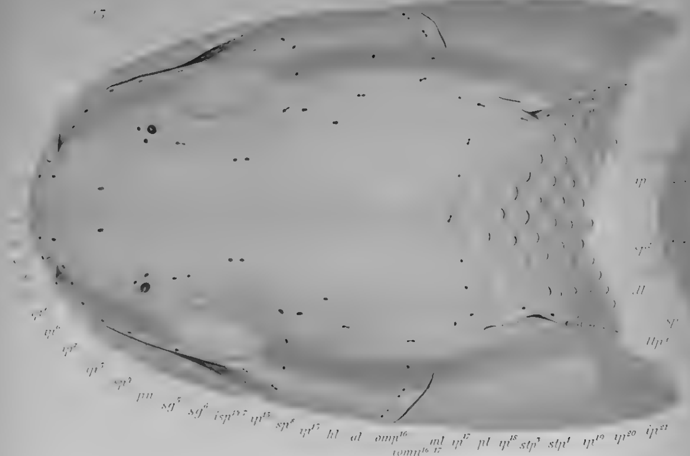


EXPLANATION OF PLATE XXXV.

FIGS. 14–16. Three views of a young Amia 78^{mm} long. The pores have begun to multiply by division. × 5.

FIG. 17. Young Amia 25^{cm} long. The primary pores are now represented by irregular groups of pores in different stages of division. × 3.

13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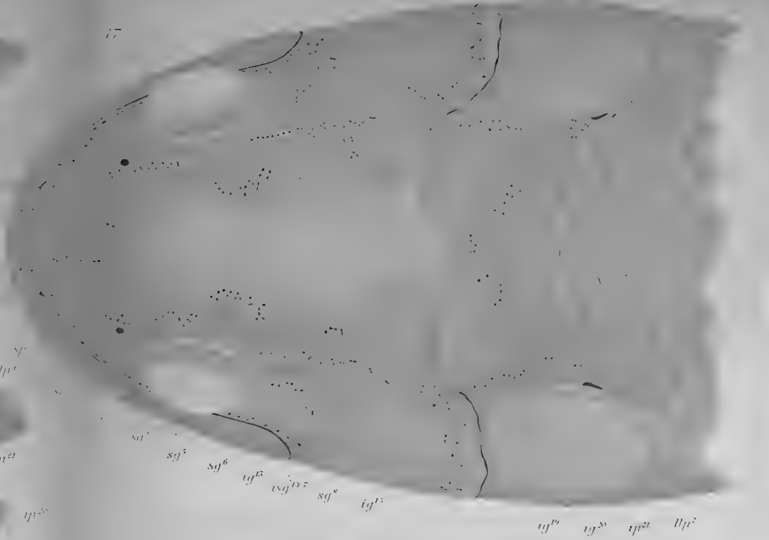
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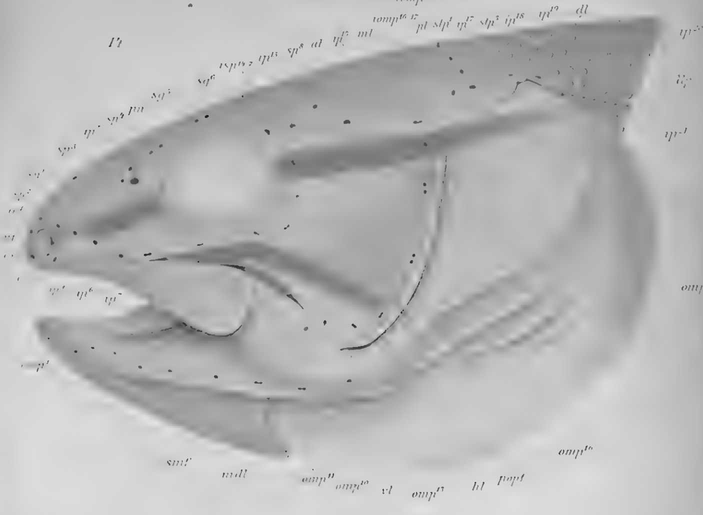
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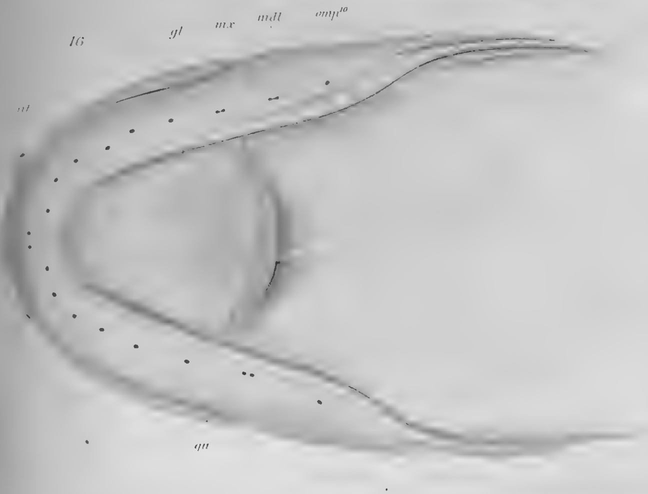
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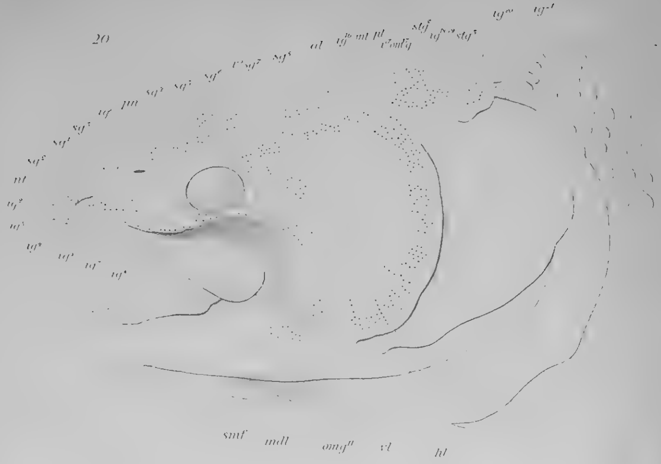
EXPLANATION OF PLATE XXXVI.

FIGS. 18 and 19. Young Amia, 13.6^{cm} long, shows most of the pores of the head divided into two, a few pores (*ll*) of the lateral line still single, and the surface organs of the dorsal line (*dl*). × 2.

FIGS. 21 and 22. Three views of the adult head. Natural size.

20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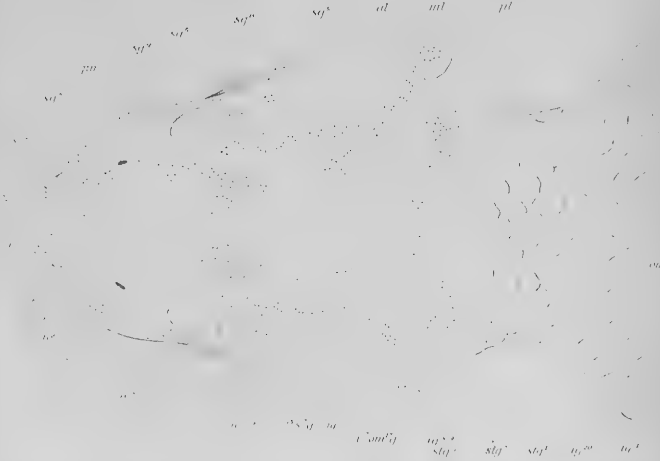
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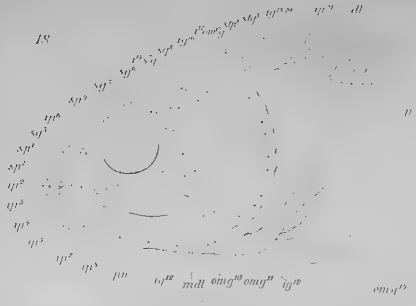
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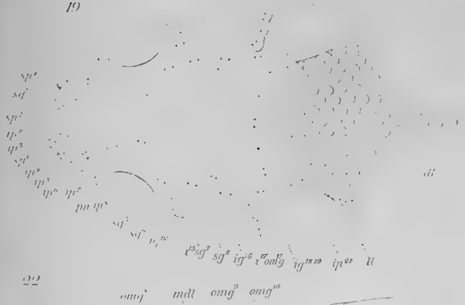
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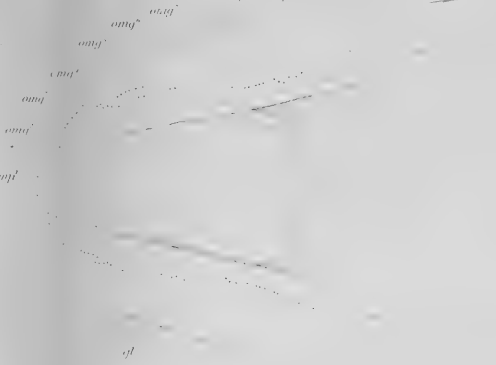
omg¹⁰

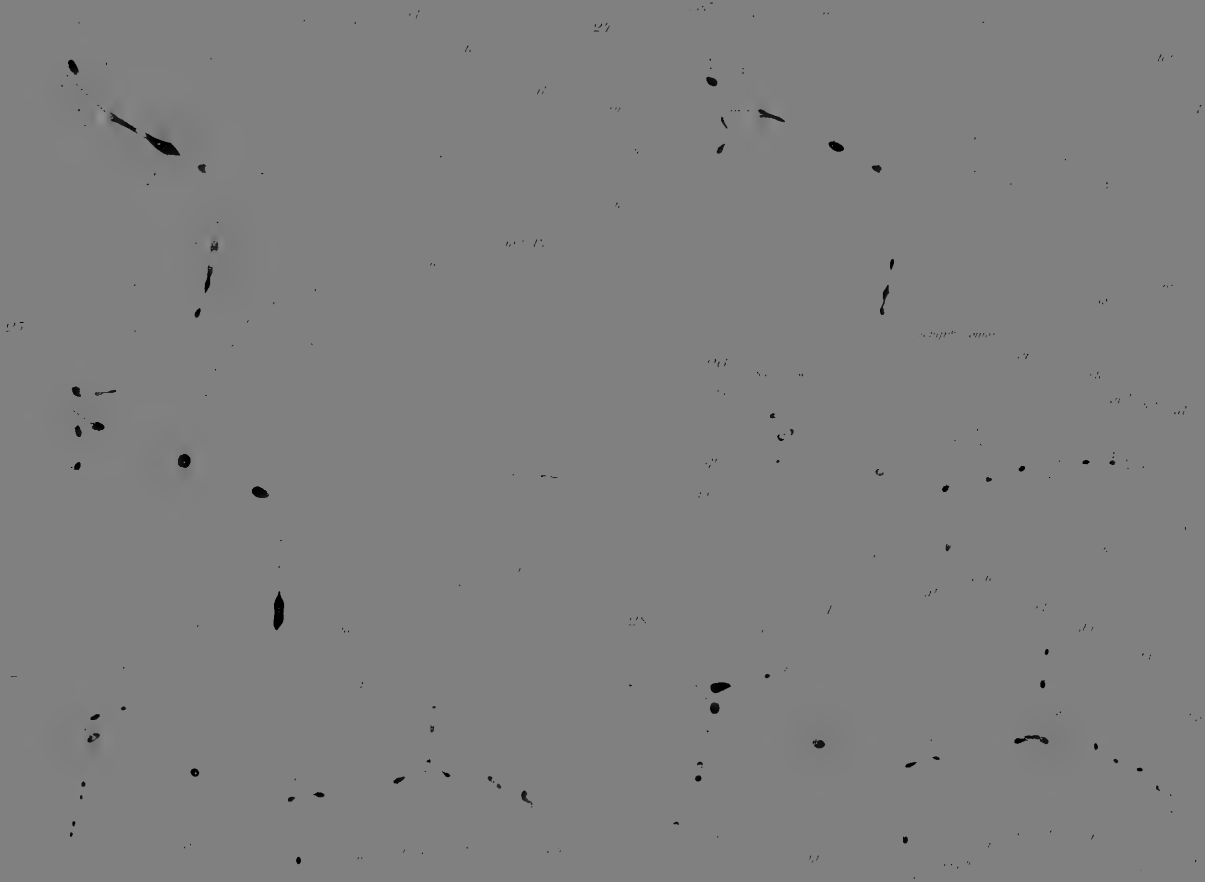
22


omg⁸
omg⁷
omg⁶
omg⁵
omg⁴
omg³
omg²
omg¹
gl

EXPLANATION OF PLATE XXXVII.

Surface views of the area between the eye and the first scales of the lateral line, taken at different ages, to illustrate the formation of the canal in sections, and the establishment of continuity between the sections by bringing two openings together to form one pore.

FIG. 23. From a specimen 19^{mm} long. × 40.
FIG. 24. From a specimen $20\frac{1}{2}^{\mathrm{mm}}$ long. × 40.
FIG. 25. From a specimen $23\frac{1}{2}^{\mathrm{mm}}$ long. × 40.
FIG. 26. From a specimen 26^{mm} long. × 40.
FIG. 27. From a specimen 29^{mm} long. × 40.
FIG. 28. From a specimen $30\frac{1}{2}^{\mathrm{mm}}$ long. × 20.

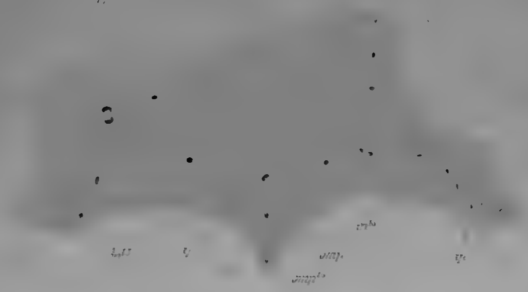

24
25
26
28

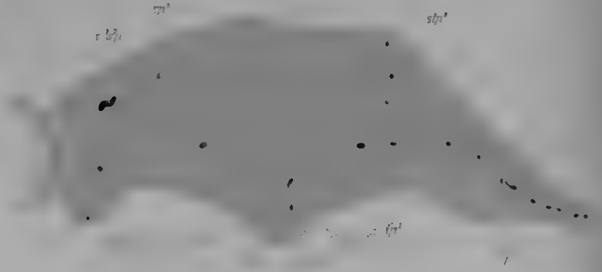
EXPLANATION OF PLATE XXXVIII.

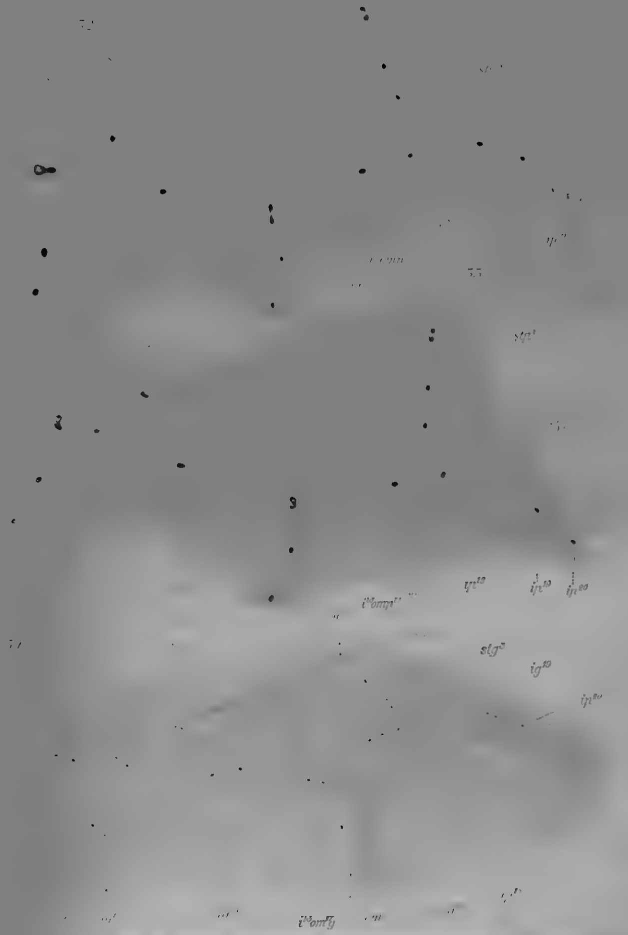
FIGS. 29–33 illustrate still later stages in the formation of the primary pores; and Fig. 34, the first division of these pores.

FIG. 29.	From a young Amia 35^{mm} long.	× 20.
FIG. 30.	From a young Amia 37^{mm} long.	× 20.
FIG. 31.	From a young Amia 40^{mm} long.	× 20.
FIG. 32.	From a young Amia 50^{mm} long.	× 20.
FIG. 33.	From a young Amia 54^{mm} long.	× 20.
FIG. 34.	From a young Amia 134^{mm} long.	× 8.

In Fig. 33, read sp^8 for ip^8.


omp
ip


stp¹
ip¹

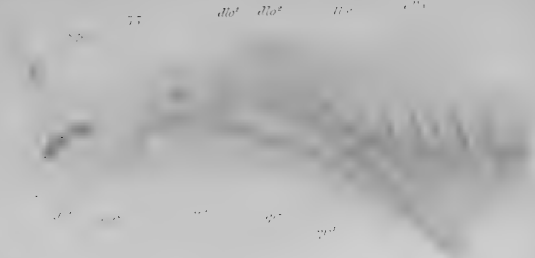

stp¹
ip¹⁰
ip²⁰
stg⁵
ig¹⁰
ip²⁰

EXPLANATION OF PLATE XXXIX.

FIGS. 35–38, illustrate the formation of the lateral-line canal; and Fig. 39 shows the primary pores replaced by a group of pores in each scale.

FIG. 35.	From a specimen 30½^{mm} long.	× 40.
FIG. 36.	From a specimen 35^{mm} long.	× 40.
FIG. 37.	From a specimen 40^{mm} long.	× 40.
FIG. 38.	From a specimen 60^{mm} long.	× 20.
FIG. 39.	From a specimen 69^{cm} long. Natural size.	

55



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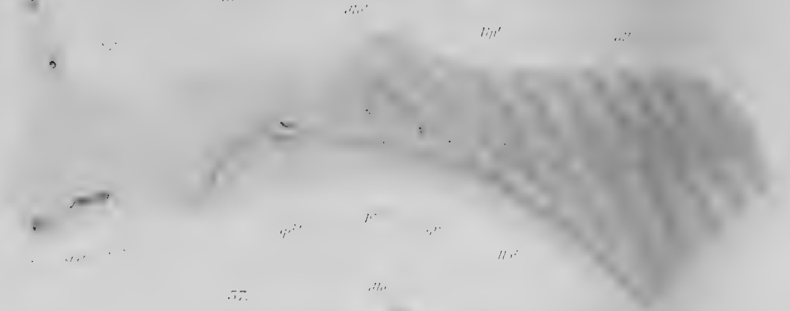
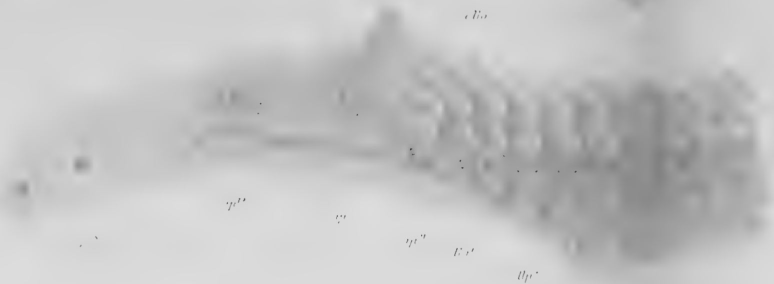


57.



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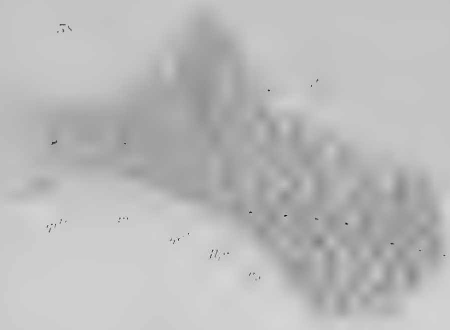

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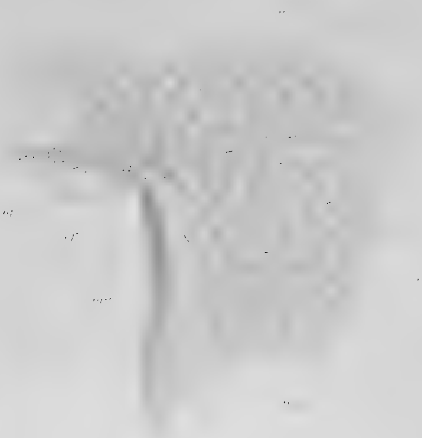
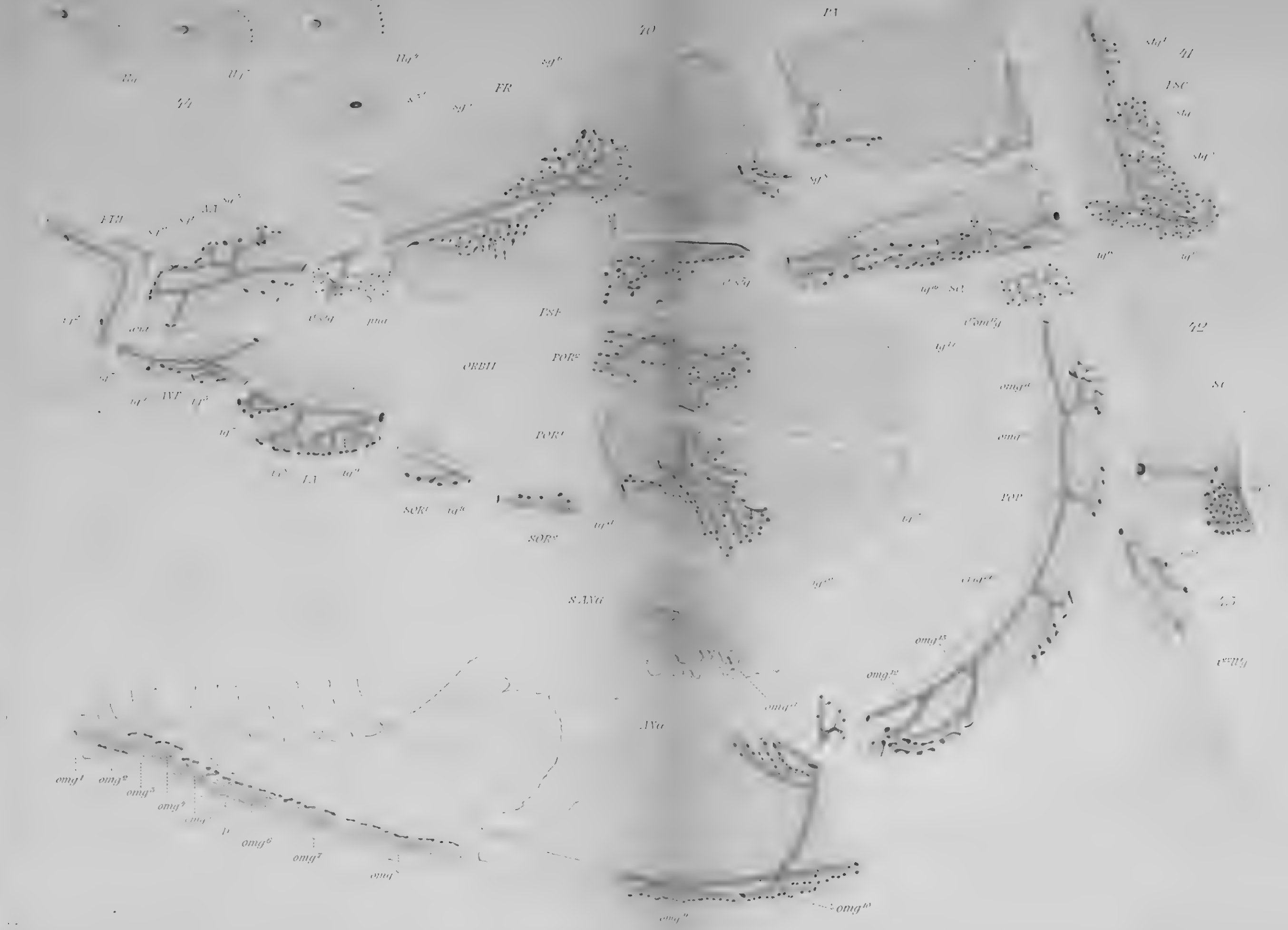


EXPLANATION OF PLATE XL.

Illustrating the osseous canals and pores in the adult. × 2.
FIG. 40. Bones of the head separated, but in serial order.
FIGS. 41–43. Scapular arch.
FIG. 44. First four scales of lateral line.

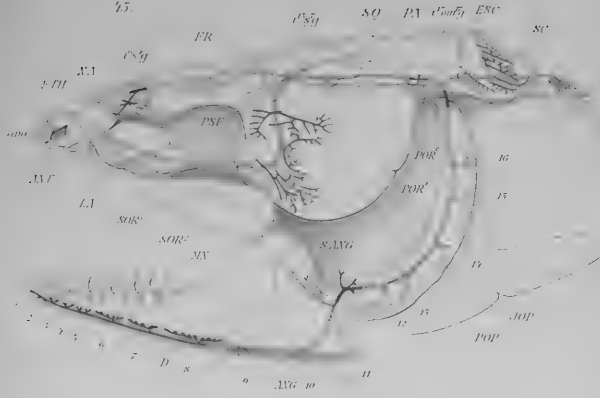

44
Ha
Hf
Hq
sg
FR
40
PA
sg1
41
ISC
sa
sg
ETH
NA
ena
pna
PSP
ORBIT
POR2
POR1
INT
LA
SOR1
SOR2
SANG
ANG
SO
42
St
POP
43
omg1
omg2
omg3
omg4
omg5
omg6
omg7
omg8
omg9
omg10
omg11
omg12
omg13
omg14

EXPLANATION OF PLATE XLI.

FIGS. 45–47. Three views of the skull with the bones *in situ,* showing the course of the lateral canals and the dendritic systems of peripheral canals. Natural size.

FIG. 48. A longitudinal section of a portion of the lateral line. × 140.

45.


v^5s^2g
SQ
PA
v^5om^2g
ESC
SC
FR
v^5s^1g
NA
ETH
SCL
PSF
ant
ANT
POR^2
POR^1
16
15
LA
SOR^1
SOR^2
MX
S.ANG
14
13
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2
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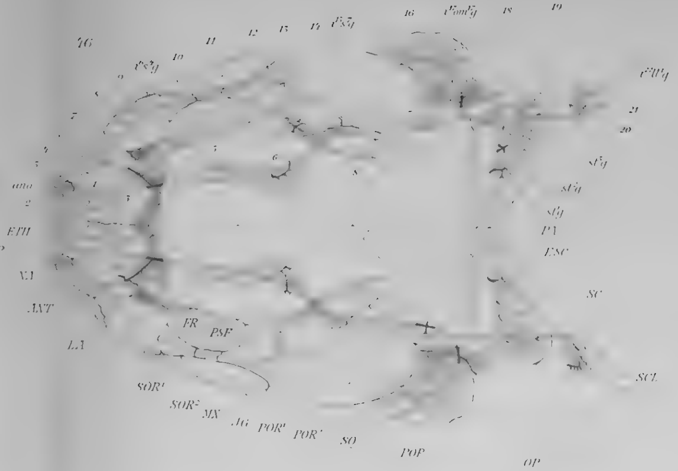
4
5
6
7
D
8
9
ANG
10
11

46


16
v^5om^2g
18
19
9
v^5s^2g
10
11
12
13
14
v^5s^2g
v^5ll^2g
21
20
7
4
5
6
3
8
ant
1
2
s^1g
s^2g
s^3g
PA
ETH
ESC
OP
NA
SC
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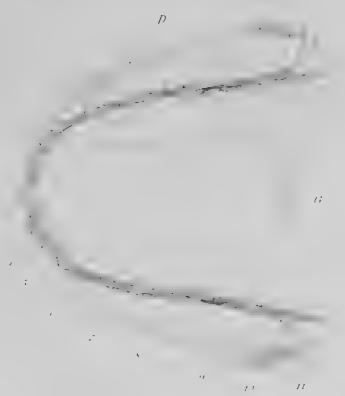
SOR^1
SOR^2
MX
AG
POR^1
POR^2
SO
POP
OP

47


D
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9
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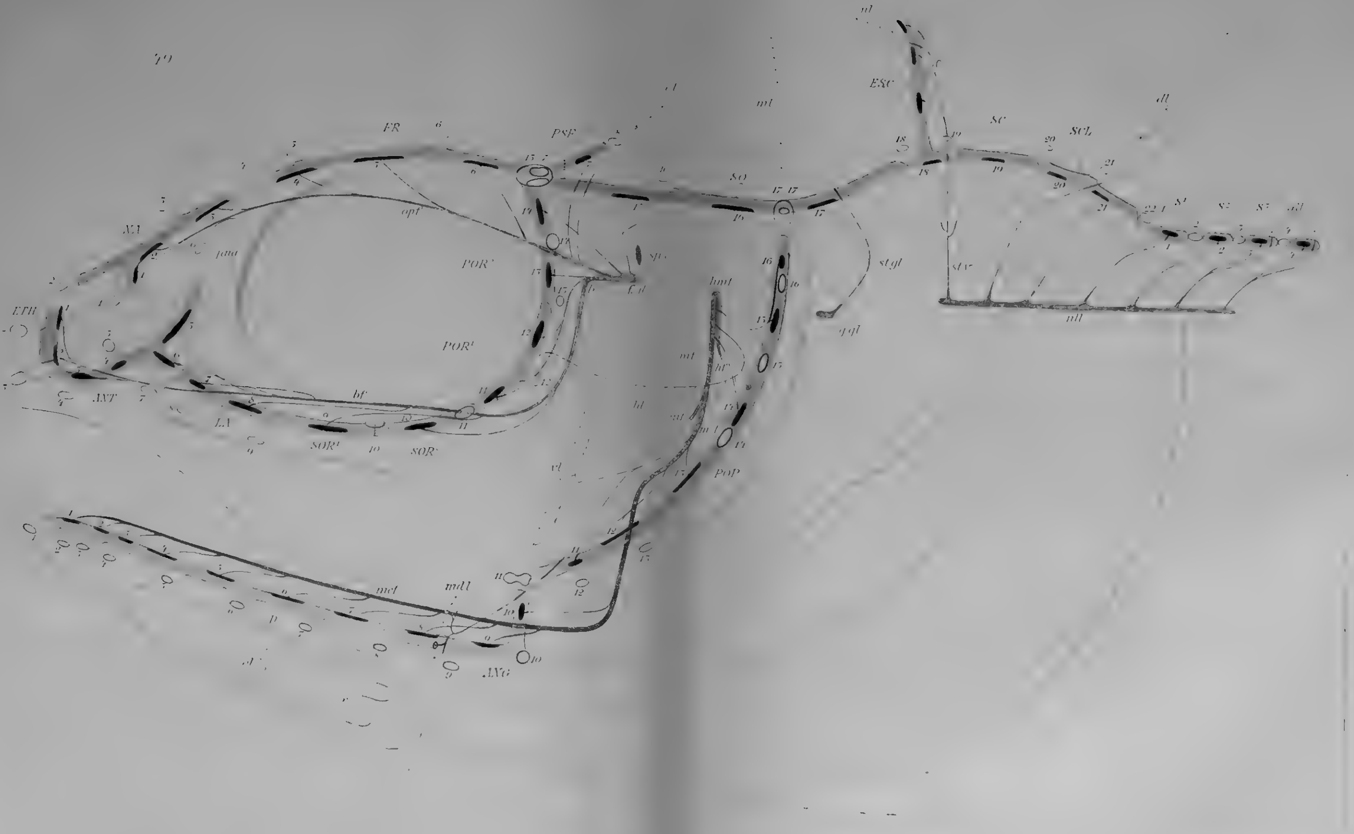
11

48


llo
llp
cll
S
nll

EXPLANATION OF PLATE XLII.

FIG. 49. A diagram showing the innervation of the lateral-line organs.


79
ml
ESC
ml
FR
PSF
SC
SCL
dl
SO
opt
NA
POR¹
POR²
ETH
ANT
LA
SOR¹
SOR²
bf
sp
hmf
mt
POP
stgl
qgl
stv
S¹
S²
S³
mll
md
mdl
ANG

ON THE ORGANIZATION OF ATOMS AND MOLECULES.

PROF. A. E. DOLBEAR,

College Hill, Mass.

In his dialogues on *The Plurality of Worlds*, Fontenelle represents the sages of antiquity as being spectators at the opera, watching the play of the Universe. The subject is supposed to be Phaeton carried away by the winds. The dancer who represents Phaeton is made to fly away through the upper part of the scenes, much to the admiration of the lookers-on. The wise ones now begin to speculate, and attempt to explain the extraordinary movement of Phaeton. An Aristotelian says, "Phaeton has an occult quality which carries him away." A Pythagorean says, "Phaeton is composed of certain numbers that make him move upwards." Another one says, "Phaeton has a longing for the top of the theatre, and is not easy until he gets there." He explains the universe by love and hate. Another one says, "Phaeton has not a natural tendency to fly, but he prefers flying to leaving the top of the theatre empty," — which is the doctrine of Nature's abhorrence of a vacuum. After all these come Descartes and some other modern philosophers; and they say, "Phaeton goes up because he is pulled up by a weight that goes down behind the scenes."

This is the mechanical philosophy that has been employed so successfully in the unravelling of phenomena once thought to be altogether occult. It is the philosophy that explains every phenomenon of *visible* motion as due to some antecedent motion, which may or may not itself be visible. Since the time of Sir Isaac Newton and the discovery of the laws of motion, there has been no room for mysterious forces operating to give movements to matter of visible magnitude. Guiding spirits like Kepler's are no more thought of as being necessary to account for them than are Arabian genii.

When, however, we come to the phenomena manifested by atoms and molecules, it is plain that the mechanical philosophy has not only not been applied, it has not even been assumed: and all sorts of visionary entities and special forces have been summoned to explain their behavior. Phlogiston and Caloric for heat, fluids for electricity; crystallizing force and vital force for the phenomena of organization in crystals and living things, — a continuation of the philosophies of the pre-Newtonian period, which proved to be inappropriate, inadequate, and unnecessary when applied to larger masses. The assumed explanation was more mysterious, and needed explanation more than the phenomenon to be explained by it; for the latter are admitted to be mechanical, while the assumed explanations are of a super-mechanical sort, for which there is no evidence apart from its implied necessity for accounting for the special movements observed.

Another Fontenelle might fairly make game of modern philosophers who offer such inappropriate explanations of the movements of matter, whether they be large or small, and who refuse, in any case, to assume a mechanical cause for any mechanical operation. To be sure, Caloric and Phlogiston and electric fluids are no longer serviceable in physics, for it is conceded that *heat is a mode of motion;* and as for electricity, it is also conceded that, whatever it may be, it is certainly not a fluid; and many are not ashamed to admit being electrical agnostics, and say they don't know what it is.

It is certainly the business of physical science to explain physical phenomena; and there are certain fundamental principles sufficiently well attested which may be assumed at the outset of every investigation; namely, the laws of motion, and that these laws are always operative and quantitatively never change. Hence every change in the position or collocation of a mass of matter of any magnitude is referable to the laws of motion of matter, is purely mechanical, and is to be explained solely upon the assumption of antecedent motion.

Even the so-called properties of matter are amenable to this principle. Physical terminology is, perhaps, to blame for not a little of the incoherence, as is the case when the expansibility of a gas or its pressure upon the walls of a containing vessel are explained as due to molecular *repulsion,* seeming to endow the molecules with an unmechanical property. When a base-ball rebounds from the side of a house against which it has been thrown, no one thinks of saying that the house and ball repel each other; instead, it is recognized as the result of the impact of elastic bodies. In like manner, the impact of elastic molecules upon the sides of the containing vessel produce a pressure upon it proportional to the momentum of the molecules; and when molecules collide, they have their direction of movement changed, and they separate.

Chemical affinity is another term that seems to imply that atoms are endowed with essential selective properties by which they are enabled to combine in definite ratios. In late years chemists have adopted the term *Chemism* in place of chemical affinity, and have given to it a greater range of proclivities, finding no difference but one of degree between it and cohesion. It makes but little difference to one who uses it who is concerned solely with chemical reactions; but it makes a good deal of difference to one who is to explain the relations of chemical changes to other physical changes, whether or not, as soon as he touches atomic phenomena, he has to import into his discussion a factor which has no physical antecedent that can move and arrange atoms and molecules thus and thus, and yet itself not be subject to the laws that obtain among larger masses. As chemists no longer contend for a chemical force that is not derived from antecedent physical conditions, it is alluded to here for the double purpose of calling attention to the positive mischief that often comes from inappropriate terminology, and to the fact that, so far as my knowledge goes, chemists have not attempted to give a physical explanation of the cohesion of atoms into molecules, but have stopped with chemism, as if it were an ultimate fact or property.

To give such a physical explanation of chemism or atomic cohesion, and to extend it to the building up of geometrical crystalline forms, is the object of this paper. It is not claimed to be demonstrated, but as a hypothesis having a good degree of probability in its favor. But even if it be inadequate, at least it gives one a mechanical idea of how such forms necessarily result from mechanical conditions.

Investigations into the relations of chemical reactions to heat have developed the fact that all chemical changes involve definite quantities of heat, either absorbed or evolved. That all such changes are absolutely dependent upon the exchanges in motion that constitute what is called heat, and are therefore measurable in heat units. As a heat unit can do a definite amount of mechanical work, namely, raise 426 kilograms a metre high, this latter quantity is called the mechanical equivalent of heat. Chemical work is therefore expressible in mechanical units. For example, when a kilogram of hydrogen combines with oxygen to form water, there are given out in the operation 34,000 heat units, capable of doing $426 \times 34{,}000 = 14{,}484{,}000$ kilogrammetres of work. A kilogram of coal when burnt gives out 8080 such units, and the elements thus combined can only be separated again by the expenditure of as much energy upon them as they gave out when combining. This department of chemistry is known as Thermo-Chemistry. The relation between heat and work, as explained above, is known as the first law of Thermodynamics.

Again, from the second law of Thermodynamics it may be shown that the total heat energy of a body, or its ability to do work, is proportional to its absolute temperature. Hence at absolute zero no chemical work could be done; that is, chemism does not exist, and no work would be spent against cohesion to separate the elements in a molecule. From this it may be inferred that chemism is a derived property, and is the *result* of heat; and also that Chemistry itself is a department of Thermodynamics.

In order to understand more definitely how heat can bring about such phenomena as selective combinations and the organization of atoms into molecules and crystalline forms, it becomes necessary to know more precisely what the nature of heat motions is that enables it to produce such mechanical effects.

If one turns to the text-books for a definition of heat, he will quite likely be perplexed by the different statements to be found in them. One may say that heat is energy; another, that it consists of ether waves; a third, that it is a mode of motion; and still others treat it in all three senses. The trouble comes from the failure to distinguish between heat and some of the effects of heat. Really they all agree that heat is a kind of atomic and molecular vibration, as distinguished from oscillatory, rotary, or free-path motions, and that is the meaning of it as applied here. It is a necessary *change of form* of the atoms or molecules, and will be easily understood by considering the diagram, Fig. 1.

The heavy-lined circle represents the atom, which is certainly an elastic body, whatever may be its dimensions; and if it be subjected to pressure or impact, will yield like the prong of a tuning-fork or the mouth of a bell; and if spherical or circular, will assume an elliptical outline; and if free to move, will execute a series of elliptical phases at right angles to each other, as represented by the dotted lines in the figure. This change of form is a mechanical necessity when bodies are elastic, and that quite independent of what the form of the body may be. The evidence for the statement that this is the real character of the motion that constitutes what is called heat comes from Spectroscopy, especially that of heated gases, where molecules have time to execute vibrations between impacts, in which case they give out radiations of definite wave lengths, and in harmonic series, which of course must be derived from the harmonic vibrations of the particles of matter that are heated. It has been demonstrated that the ultimate particles of matter, atoms, cannot be spherical in shape; and to-day the only theory of the constitution of matter we have is the *Vortex Ring Theory* of Sir William Thomson. One must either adopt that or be without any; but evidence for its being a true theory is fast accumulating, and there has as yet no serious objection been offered to it from either physics, chemistry, or mathematics.

Fig. 1.

It will be adopted for the purposes of this paper, and hence the diagram, Fig. 1, may be considered as a vortex ring capable of changing its form and vibrating with an amplitude determined by its size, thickness of ring, etc. Such an atom has a definite fundamental rate of vibration, and a series of harmonic rates which are 2, 3, 4 . . . *n* times the fundamental rate, which is the one represented. It is to be noted that where such vibrations are taking place there are certain places upon the vibrating body where the motion is at a maximum, called the *loops*, and also intermediate places where the motion is least, called *nodes*. In the diagram there are four of each. If the body has a series of harmonic vibrations, there will then be 2, 3, 4, and so on, number of times the nodes of the fundamental. The number of times such vibrations can occur among the atoms of matter is determined by dividing the velocity of light by the wave length of any particular ray that is produced by the vibration. Thus, if the red hydrogen rays have a wave length of 0.000656 of a millimetre, the frequency of vibration of the hydrogen atom that produces it is 457,000,000,000,000 times per second. This particular vibration is the 20th harmonic of hydrogen. What is of most moment here is to bear in mind that waves of so-called light, having definite and constant wave lengths, are the result of the heat vibrations of the atoms and of molecules, which must therefore be vibrating at a constant rate, not irregularly; and to vibrate thus is one of the fundamental mechanical properties of atoms as elastic bodies.

In order now to see what must follow from such motions, it will be best to consider some of the phenomena of vibrations as manifested in bodies of visible magnitude, say a tuning-fork. If a light body like a pith ball be brought near the prong of a vibrating tuning-fork, it will move towards the prong as if the latter attracted it, and this is explained as being due to the fact that a vibrating body reduces the air pressure adjacent to it. How a vibrating body can reduce the pressure of the medium about it may be understood by remembering that the pressure is proportional to the density. If the vibration lessens the density, it lessens the pressure. Let the inner circle of the diagram, Fig. 2, represent an elastic sphere capable of extension to the dimension of the outer circle. When it is thus expanded, of course it excludes the air from the space it occupies. When it contracts again, the air must follow. Suppose the contraction should take place at a rate greater than the air could move; then there would be a vacuum between the surface and the advancing air, and that would be the condition all about the sphere; but at whatever rate the contraction took place there would still be a partial vacuum next the surface of the sphere, else there would be no movement of the air towards it; that is to say, the pressure is less next to the sphere than at a distance from it. Suppose the sphere to contract and dilate between the limits of the lines in the figure, say one hundred times per second; then the density would be less between those limits than it would be beyond the outer one, with the consequence that the lessened density would lessen the pressure upon the sphere in every

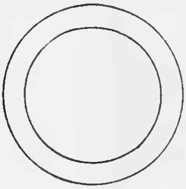


FIG. 2.

direction about it, and this condition would be maintained as long as the vibration was maintained. Another body near the vibrating sphere would be subject to a pressure on its further side greater than on the side adjacent to it, and as a consequence would be pushed towards the sphere. It would appear as if the latter attracted it. The space about the vibrating body within which such lessening of pressure occurs, may be called its *mechanical field*, because the effects noted are mechanical effects. This expression is in accordance with usage in electrical and magnetic phenomena. The magnetic field is that space about a magnet within which magnetic effects take place. In the case of the sphere the shape of the field would be spherical; but if the vibrating body was a rod or fork or disk or ring, the shape of the field would be different, and evidently would depend upon the shape of the body as well as upon its characteristic vibrations. A tuning-fork does not have such a uniform field as the imagined sphere, but presents two nodes, radiating from the outer edge of each prong. These nodes, or spaces of no vibration, may easily be detected by holding the fork near the ear and rotating it with the fingers while it is vibrating. As the lessening of density depends upon the amplitude of vibration, it is plain that the greatest disturbance and least pressure will be in the plane of vibration of the fork and near the ends of the prongs, and here is where it makes itself obvious by its apparent attraction of other bodies. If a paper wind-mill three or four inches in diameter be held by a thread near to a vibrating Chladni plate, it will be made to rapidly rotate by the difference in pressure above and below the arms of the mill. A smaller one that may be moved to different parts of the plate will be found to be but little affected at the nodal points and lines. This mechanical field of the Chladni plate extends an inch or more from its surface both above and below, and its form, of course, varies with the number of vibrations the plate is making and the energy of the components of the sound.

It is here assumed that vibrating atoms must have a *field* in the same sense as larger bodies, and that mechanical effects must be produced in them not dissimilar to what takes place in larger masses. The atoms, however, vibrate in the ether; but we know from various other phenomena presented by atoms, molecules, and ether, that the latter is affected by motions of the former because they spend their energy upon it in some cases, and in others receive energy from it. This is true for light, for magnetism and electricity, and these are explained as setting up undulations or special stresses in the ether. If one considers the space affected by a heat vibration of an atom as its field, it appears to be as large as the universe, for the undulation travels on in straight lines to an indefinite distance, as do sound vibrations in the air; but the maximum displacement or change in the density or stress in the medium must necessarily be greatest where the amplitude of motion is greatest; namely, immediately adjacent to the vibrating body itself. Assume that the vibrating atom lessens the density of the ether adjacent to it, and at once it is seen that other atoms near by will be crowded towards the one thus vibrating — there is an apparent attraction within its field. But the heat vibrations of an atom, as represented in Fig. 1, will have a field somewhat like that of a tuning-fork; for, as shown, there are four nodes where there would be no lessening of the pressure, and four parts where such lessening would be at its maximum. Consider, then, two atoms adjacent to each other, but not in contact, and one of them vibrating in its fundamental rate, Fig. 3. The nodes are at 1, 2, 3, and 4; and if the spaces marked 5, 6, 7, and 8 represent the variable pressure spaces or the field of the atom, it is shown that the other atom will be in a space of less pressure at 6 than at 9, and consequently will be crowded towards 6, where the amplitude is greatest; but because it is greatest, it will be in unstable position, and will move to one or the other nodes, 1 or 2, where it will be held while the vibration is kept up. If the second atom vibrates also, that will only double the strength of the field at 6 and make the pressure towards each other stronger than before, and the two will join nodes at 1 or 2. But there are four nodes, and consequently as many places

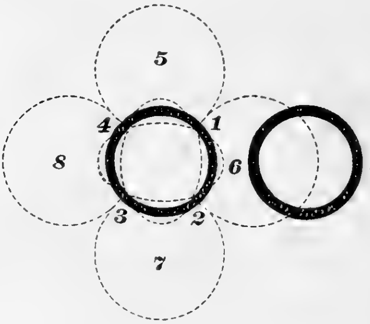


FIG. 3.

where other atoms can join, in which case, if all were vibrating similarly, there might be a conjunction, as shown in Fig. 4, — an atom at each one of the nodes; but such an arrangement in one plane would not be a stable arrangement. The point of attachment of any one might be considered as a kind of hinge, allowing a swing to and fro. Imagine two opposite ones, as 2 and 4, to swing upwards so as to touch each other. If these be vibrating, their points of contact will be nodes. They will, therefore, cohere by another bond, and such an atomic arrangement will be a stable one. If the rings have equal dimensions, an edge view would show them as an equilateral triangle with nodes at the apices, Fig. 5. We might call such a combination a molecule, and say it was held together by chemism. Each molecule thus constituted must have a mechanical *field*, which will be the resultant of all the atomic fields that compose it; and indeed this will be true for such molecules of every degree of complexity. Molecules having similar fields fit together for obvious mechanical reasons, and cohere because they are pressed together by the medium they vibrate in. If similar triangular forms to the one above unite, they may form hexagonal prisms, as Fig. 6 shows, in cross-section, and such as is the crystalline forms assumed by water, silica, and some other minerals having three atoms in the molecule.

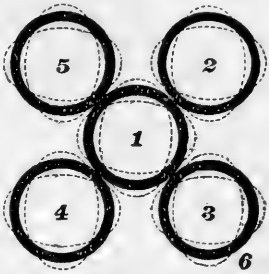


FIG. 4.

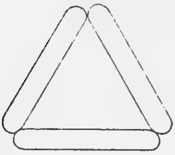


FIG. 5

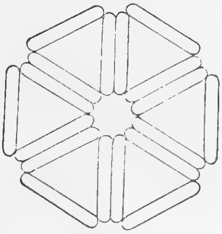


FIG. 6.

Now let 2, 3, 4, and 5 of Fig. 4 swing upwards; they too will touch each other at their sides and at nodes, so as to form a stable figure held by eight bonds, — an atomic box without a lid, — yet having four nodes on the open end to which another similar atom could be attached by its four bonds, forming a cubical box having a high degree of mechanical stability. It will have a symmetrical, but not a uniform, field; the corners being the places having maximum displacements, and the middle of each edge the minimum, as the nodes are all in such positions. Hence other similar cubes would be moved to assume symmetrical positions when in contact, and thus a cubical structure, or prismatic form, would be built by aggregation of similar molecules. This is on the supposition that all the atoms combining thus together are equal in size as well as uniform in their vibrations; and this cubical form is one in which not a few of the elements crystallize; for example, gold, iron, copper.

If one would see more clearly how these nodes and loops fit together in such structures, let him make paper models, drawing a set of circles with their peripheries touching at one point, as shown in Fig. 4. Make points upon each circle to indicate the nodes, and then bend them up as described. If another one similar to 3 be made hinged at 6, it will form the cover to the cube, and all the nodes will be adjacent.

So far such vortex atoms have been considered as being all of one magnitude, or as all having a similar rate of vibration; but the different elements have different masses, and therefore vibrate with different rates; the greater the mass, the slower the rate, according to the laws of motion. When two elementary atoms come into contact with each other while vibrating at their individual rates, whether they can cohere or not will depend upon whether the vibratory rates are commensurate or not. If they are not, there will be what is called interference in their respective fields, and each will tend to destroy the other's field. When the vibrations of two tuning-forks not in unison or in a harmonic series are heard together, their interferences are audible, and are called *beats*. They are in opposite phases a portion of the time. Vibrating atoms must be subject to the same conditions. One ought, therefore, to expect that elements with different masses would show different degrees of coherence, as indeed they do. There are all degrees of these incompatible movements from that exhibited by oxygen and fluorine, which have never been made to combine at all, through the slight cohesions shown by gold, platinum, etc., for other elements, up to that exhibited by carbon for itself in the diamond, and oxygen and aluminium in the ruby. Furthermore, an element having but a small mass like hydrogen could produce a field of slight strength compared to that of an element moving with the same velocity, yet having decidedly a greater mass, so that when it combined with any other element, it would be because of the greater energy of the other's field; that is to say, oxygen holds on to hydrogen rather than hydrogen to oxygen, and one would expect that hydrogen could be replaced by some other element in a compound more readily than any other element. Hence, whatever might be the relative rates of vibration when compared with other elements, one might infer it could be associated with them. One might explain its weak affinities by its small mass and consequent small vibrating energy. With larger masses, however, the case would be different. If one made five vibrations while the other made but one, they would be in the same phase but one-fifth of the time, and in more or less interference the other four-fifths; and unless there was a considerable disparity in their masses, there would apparently be but slight cohesion. If one made four while the other made one, they would be in similar phases three-fourths of the time, and could thus form a more stable alliance.

As has already been said, atoms vibrate in harmonic series, and this must frequently modify the position of the nodes when adhesions can occur. Now the harmonic series is 2, 3, 4, and so on, times the fundamental rate. If one will imagine such a vibrating ring to be cut at one of the nodes, and the two ends straightened out, it will be seen that there are really two vibrations, or stationary waves, as they sometimes are called, in the ring, and the harmonics are the fractional parts of one wave. Suppose each of these waves to be divided into three parts, — that is, to be accompanied by the second harmonic; then the circumference of the ring would have twelve nodes, — an arrangement that would permit three other rings to be hinged at angles of 120° apart; and if these were swung upwards until they touched each other, they would form a stable combination, but the angle made between the base and the side of this pyramidal structure would depend upon the relative diameters of the ring composing the base and sides. The smaller the latter, the greater the inclination. With similar structure there could grow up another hexagonal system, having a differently distributed field from the other, but still symmetrical, and therefore capable of growing a symmetrical shape.

This has probably been carried far enough to show what was intended; namely, that because the atoms of matter are vibrating, and for all matter within our experience a long way above absolute zero, and because the motions of matter are known to affect the ether in a manner that depends upon the character of the motion, it follows that each atom has a field the shape of which, and the strength of which, must depend upon the kind of motion it has and the energy involved; that vibrating motions affect the density of the ether in different directions about the atom, and result in a pressure towards it, and on account of the harmonic motions, there are stationary nodes where atoms may cohere together, forming symmetrical figures of molecules and larger masses of crystals, each of which in its turn has a field which is the resultant of the combined fields of its constituents. It is the reaction of this field upon other molecules that organizes them into the larger geometrical shapes, and tends to replace upon imperfect crystals the parts that have been removed or which are not symmetrical with the rest — a phenomenon that has been observed.

The reaction of a field upon a body within it is recognized in the familiar phenomena of heat; for the ether waves that have been produced by a hot body compel other molecules, which these waves meet, to vibrate like those that produced the waves. The earth is heated by the sun for this reason.

Whenever the ether is put into a condition of motion or of an abnormal stress through the motions of atoms and molecules, other atoms and molecules must adapt themselves to the abnormal condition by adopting the motions, or changing their position, or both, the tendency always being to assume the condition of the original disturbing body. This explains why it is that a certain molecular combination possesses the ability to aid in the formation of other similar molecules, a property exhibited by the simplest as well as the most complex molecules, in nonliving as well as living organisms.

The foregoing explanation of the organization of atoms into molecules, and molecules into crystalline forms, is made to depend upon the freedom of such bodies to assume their geometrical positions, such as gases and liquids permit; but it must not be inferred that molecules could not cohere except at such nodal points. So long as the atoms vibrate, they produce fields; and this compels the molecules to assume a degree of compactness that depends upon the strength of the fields, and this may take place in the most irregular manner and without any special order. A piece of wrought iron may be made crystalline by repeated jarring, as it gives to the molecules a transient degree of freedom to assume any new position they have any tendency to take. In like manner, a bar of iron held in the proper position in a magnetic field will, if jarred by the stroke of a hammer, assume polarity; for the jar assists the molecules to rotate to the magnetic position induced by the field. But the strength of cohesion in crystals is generally less than in amorphous bodies, probably from the fact that when the molecules have moved to the vibratory nodes, forming geometrical figures, they have moved somewhat away from the place of greatest pressure, which is where the amount of motion is greatest, the atomic impacts at such places tending to move them towards less disturbed points. When molecules are very compact, such change of position is mechanically difficult, and vigorous jarring aids somewhat to the rearrangement. Hence the crystallization that often takes place in solids like iron.

Perhaps most who have read this so far have already foreseen the bearing it has upon organization as manifested in living things, rendering it unnecessary to do more than briefly to apply it.

Chemically, protoplasm is made up of complex molecules, not of so great a variety of elements, yet a thousand or more atoms in one molecule. As molecules increase in complexity, they become less stable, the interior atoms being in a much more uniform field than the outer ones, and therefore more easily displaced; but every such protoplasmic molecule, whether with or without a cell structure, must have a *mechanical field*, and therefore must compel other matter in proximity to it to assume the same arrangement as its own. If all the elements necessary are available, it will be done; that is to say, the protoplasmic mass *grows*. But this process is called life, or the results of life.

As the mechanical relation to the *field* is different for an atom deeply imbedded in a molecule from that of one on the surface, as was pointed out a little way back, it follows that a greater degree of stability would be looked for in the materials upon the outside than upon the inside; and hence the cellular structure itself is a result of the mechanical relations between the molecules and their field.

The field of a given cell must depend upon the elements of its composition, their number and arrangement; and for any one of visible magnitude must be so complex that, at any rate, now it would be quite a hopeless task to attempt to describe it, yet there does not appear to be a good reason for not having a well-grounded conviction that in fact there must be such a field, and some sort of a mental picture of what it must be like.

As its source is purely mechanical, its properties must also be purely mechanical, the form assumed and the order exhibited being but an extension to complex molecules of the form and order displayed among relatively simpler bodies called crystals.

Now, vital force as an entity has been quite given up by all, except a few of the old school of biologists who have not yet, and probably never will learn that such a view is incompatible with almost everything we do know, as science, about the matter. The foregoing presentation shows that such an assumption is an unnecessary one, as fundamental mechanics will explain the phenomena without its aid. Its bearings upon some of the problems of biology must be apparent, as a prime factor in evolution, in explaining heredity, and in giving a very distinct answer to the question as to the cause of variation; for an extra molecule, even accidentally imbedded in a mass of other molecules, must change the configuration of the field, and hence the direction of growth. One does not need to go further than the formation of a cell that can organize a similar one, animal or vegetable, for the purposes of this article; but the next question to be asked by every one interested in the problems of life is, What is to be said of mind, consciousness? Has that, too, a mechanical antecedent, a mechanical equivalent, and does it depend solely upon mechanical conditions? Not long ago it was the custom to speak of *higher* and *lower* forces. These were mechanical forces on the lowest plane, then chemical, then vital and mental forces highest of all. Now two of these, the chemical and vital, have absolutely been absorbed into the mechanical one. In fact, it now seems absurd to speak of higher and lower in physical phenomena in any philosophical sense. There is matter and its motions, rectilinear, rotary, vibratory, and vortical, each kind changeable into the other under proper mechanical conditions; and there is no sense in speaking of one of them as being higher than another. Each one of them has mechanical possibilities that do not belong to the others, and no one of them can be treated as first in order.

When it is ascertained that heat is a vibration, that light is an undulation, that electricity is a rotation, that is, that they are only conditions, it is seen that the questions *what is heat, what is light, what is electricity*, are philosophically improper questions, and the whole scheme of the universe mechanically considered is on one plane, and there is nothing common or unclean in it. This is to meet the objections of those who think that matter and its phenomena are of a low grade. As a matter of fact, mind is in some way associated with matter, and depends for its development upon matter and its properties. As it is associated with a certain cell structure, there is at the outset a presumption that the mechanical relations are not so different as they seem to be, and the explanation is to be found sooner or later in entire accordance with all other physical phenomena. If one is to attempt an explanation, it must be in accordance with what we do know, and not in accordance with what we don't know.

Suppose, then, there be in the universe a mental field, no matter how that was produced. Wherever there should chance to be a collocation of matter, with a field upon which the first could react, the second would be mechanically endowed with the property that maintained the field; that is to say, mental phenomena would manifest themselves for precisely the same reason that other properties manifest themselves. The character of the mental manifestations would in such a case depend upon the character and complexity of the material structure that was acted upon, giving scope for all the degrees of intelligence exhibited by the animal creation including man.

Perhaps most persons would say I have now invoked the *deity*, to which I do not object; but as my purpose is to show how things can be so and so in accordance with mechanics, I have spoken of the *mental field* without regard to other than its mechanical relations to such matter as makes up the nervous matter of animals. When the needle of a compass turns from its normal position, we know that a new magnetic field is acting upon it, and we do not need to know whether that was produced by a permanent magnet or a current of electricity in a neighboring conductor. Its behavior is explained without regard to the antecedents of the field.

REMARKS.

As the foregoing article cannot be said to come strictly within the scope of this JOURNAL, a note of explanation is here appended. The nature of formative energy was briefly adverted to in a previous number, and the views there presented elicited some critical comments by letter from Professor Dolbear. The outcome of the correspondence was that Professor Dolbear prepared, at my solicitation, a paper for the JOURNAL, in which the question is treated from the physicist's standpoint. An article of such exceptional interest, bearing directly on a problem underlying all animal and vegetable morphology, can hardly be regarded as out of place in these pages, and I am confident that its perusal will not leave the reader over-solicitous on such a point.

It is not my purpose here to discuss the bearings of the mechanical hypothesis presented by Professor Dolbear, but a brief comment or two may not be amiss.

According to this hypothesis, the formative agency is ether-pressure, acting under conditions induced and maintained, not by unit-action of the organism, but by vibratory motions of its constituent elements mechanically associated. Attraction is banished from the universe. Chemism and cohesion, and presumably gravitation too, are but different degrees of ether-pressure. Crystallization, development, growth, are all mere expressions of the interaction of atomic vibration and ether-pressure.

Now consider the elements out of which the organic world is to be evolved: *Atoms*, absolutely inert, and utterly destitute of all *qualitative* distinctions; impressed, vibratory *motions*, measured and timed by the magnitude of the atoms; and *ether-pressure*, compelling purely mechanical associations. Then we have the *mechanical field*, and with this captivating conception, we rise to that of an automaton in the *form* of man. But alas! the all-important psychical qualities are missing. We have just what we started with — unconscious, inert atoms, played upon by ether-impressions. Of course we had no right to expect more;

for if qualities are left out at the beginning, they will not turn up at the end. *Ex nihilo nihil fit.* Now I may be mistaken, but I think there are few biologists to-day who will object to an hypothesis because it is mechanical; but there are at least some who find it difficult to accept any hypothesis that ignores qualities. The evolution of function proceeds *pari passu* with that of structure, and the basis for both must be postulated at the outset. There is no place anywhere for the sudden apparition of qualities for which no basis previously existed. And here the question forces itself upon us: If it be inadmissible for a physicist to import into his discussion of atomic phenomena anything which has no physical antecedent, how much has he lessened the difficulty by postponing the forbidden act till after his automaton has been constructed? And yet we are told that the psychical factor, once introduced, transforms the machine into a microcosm, and henceforth exhibits itself in vibrations that do not upset the previous mechanical harmony. If the mechanical field be the avenue of admission for the psychical factor, then why may not our mechanical hypotheses endure its presence at one stage with as much composure as at another? If the doctrine of the conservation of energy allows a "mental field," impressing itself upon a mechanical field, then it surely will not break down under the burden of a few qualitative distinctions imported into our atoms and molecules. Then, too, I am tempted to ask, is not the "mental field" a needless invention? It claims to add nothing to the organism except motion, and if qualitative distinctions need no other basis, why seek an unknown source for what is furnished in the elements with which we have to deal?

But there is no end to questions, and my interest in Professor Dolbear's admirable exposition has already carried me beyond the first intention of my comments, and perhaps beyond the forbearance of the reader.

C. O. Whitman.

SOME NEW FACTS ABOUT THE HIRUDINEA.

C. O. WHITMAN.

A FEW facts and conclusions are here briefly stated in advance of several papers on the *Hirudinea*, which are now nearly completed, and which I hope to see published in the third volume of this JOURNAL.

1. The *Hirudinea, as a group*, are characterized by the possession of *segmental* sense-organs on the first ring of every somite. The plan of arrangement is everywhere essentially the same as I have already described in detail for the ten-eyed leeches. The statement by Mr. Apàthy that such organs do not mark the somites in *Aulastoma* is incorrect; and inexcusably so, as their topography has already been made known. I do not deny that some forms are found, like *Nephelis, Clepsine bioculata, and Pontobdella*, in which the segmental arrangement has been much obscured, or perhaps entirely obliterated. It is plain that such conditions might be reached in two ways: either by the loss or the multiplication of organs.

2. As the metameric arrangement of these sense-organs characterizes marine as well as fresh-water and land leeches, and as they everywhere agree in certain remarkable details of number, topography, and structure, I am led to believe that the diffuse, or non-metameric arrangement, exemplified in *Nephelis* and some other forms, has been secondarily acquired. *Nephelis* is an instructive example, for it shows an analogous departure from the typical arrangement in the multiplication of its testicular organs. The lateral-line organs of some fishes and amphibia illustrate the same point. Obscuration of the metamerism of organs through multiplication is too well known to require further illustration here. The presence of well-developed eyes in *Nephelis, segmentally* disposed, points unmistakably to the former possession of the ordinary segmental sense-organs.

3. I have brought together a large amount of evidence to prove that in all ten-eyed leeches, including many widely scat-

tered species of both land and fresh-water forms, the eyes represent enlarged and more or less modified segmental sense-organs. The question remains to be answered, whether the same holds true of other leeches. If this be conceded, then I see no easy escape from the conclusion that the metameric sense-organs are earlier in origin than the non-metameric ones. If the scattered organs were first in order of development, we ought at least to find some cases in which the eyes are not segmentally arranged. There are some cases in which the serial homology of the eyes with the segmental sense-organs is not at first sight apparent. This is true of some species of *Clepsine.* The development of the eyes in these cases, as will be shown in one of my papers, settles, *beyond dispute*, the fact that the eyes are segmental in origin, and strictly homologous with the segmental sense-organs.

4. In the case of *Clepsine parasitica* and *C. chelydræ* (*n.sp.*), I have satisfied myself that the segmental sense-organs appear very early in the embryo, before the time of hatching, while the scattered organs arise later. Another evidence in support of the above-stated conclusion.

5. In *Hæmenteria* (commonly, but incorrectly, *Hæmentaria*), and in several species of *Clepsine* from Japan and America, there is one somite clearly marked by *segmental* sense-organs in front of the eyes. This makes twenty-six somites in front of the acetabulum, not counting the narrow tip of the cephalic lobe. Mr. Apàthy insists on counting this tip as the first somite, but he has not yet produced any satisfactory grounds for so doing. The difference between us is, not that I deny the possibility of finding one, or even more than one somite in the "prostomial," but that I question the propriety of calling it *one*, while it still remains undetermined whether it represents one, two, three, or none at all. The argument from the number of segments in the brain will be worth considering when we know precisely how many somites are there represented. The question is beset with some difficulties, which are not likely to be removed by anything less than thorough embryological research. The argument from the labial sense-organs, as will be seen in the next paragraph, is likewise premature.

6. The labial sense-organs — prostomial sense-organs of Apàthy — are serially homologous with *ventral* segmental sense-

organs, as I shall be able to show very clearly in *C. chelydræ* and in a Japanese species. They do not therefore represent *one* somite, as supposed by Mr. Apàthy, but merely the ventral organs of as many somites as belong to the cephalic lobe. Their *dorsal* counterparts have preserved their segmental arrangement. If any dorsal organs are represented in these labial organs, the development ought to show it. I once thought I had found some evidence of this nature, but I have since followed the history of these organs farther, and find reason to modify my view.

7. Systematists have usually concluded that where no eyes could be recognized by surface examination, none were present. My experience leads me to suspect that most of our reputed blind leeches will yet be made to bear testimony to the blindness of their observers. To all outward appearance, *Branchelliopsis* (*gen. nov.*), a Japanese marine leech, has no eyes. I made a careful examination of the head, first in a fresh and then in a hardened state, and finally by sections, but found no eyes. Returning to the study of this leech recently, after having learned in what the eye of a leech consists, I succeeded in finding at least two pairs of eyes. These eyes have so little pigment that they cannot be seen from the surface; and any one in search of pigment-spots would find little in sections to arrest the eye. The visual cells, however, are there; and their form and relation to a thin, open background of pigment would, on close examination, entitle them to rank as eyes in the ordinary acceptation of that term as applied to leeches. In form they remind one of the eyes of *Piscicola*; in structure, the eyes of *Clepsine*; and in position, the eyes of *Nephelis*. They are in fact so little removed in general make-up and appearance from the ordinary segmental sense-organ, that I had to examine sections made in the three principal planes before fully satisfying myself that they would pass as veritable leech eyes.

8. *Piscicolaria* (*gen. nov.*), a parasite of fishes in the smaller lakes of Wisconsin, about the size of *Piscicola*, and intermediate in form and structure between *Piscicola* and *Branchelliopsis*, comes nearer to being blind than any other leech I have yet examined. The only evidence of an eye is a single large visual cell, on either side of the head, without a trace of a pig-

ment investment. In view of these facts, and others yet to be noticed, we can no longer regard pigment as an essential element of the leech eye. It will not do to fall back on the hypothesis of degeneration, and assume that these eyes supplied with little or no pigment are functionless rudiments. The visual cells are here as perfectly developed as in the pigmented eyes, and the same is true of the optic nerves.

9. The test of a leech eye, then, is the presence of visual cells. Now what are the visual cells, and how are they to be recognized? After spending a good deal of time in the study of the structure and development of the sense-organs of the leech, I feel quite confident of having reached a point in the investigation where I can safely answer these questions. The visual cells are the "*large clear cells*" of Leydig, the so-called "*Glaskörper.*" The proof of this lies in a variety of facts, only a few of which can here be presented in a summary way. The leading points are as follows: 1. These cells always make up the bulk of the eye, and in the Hirudo pattern *they are the only cells supplied by the optic nerve.* 2. The main axis of these cells — that passing through the centre of the cell and the eccentric nucleus — is generally, though not invariably, parallel with the axis of the eye. This is most clearly seen in some species of *Clepsine*, and is very evident in *Branchelliopsis.* 3. In these genera, the nucleus lies on the side exposed to the light, the clear rod-like part of the cell being directed towards the pigment. The cells are practically inverted, the nerve-fibres entering at the nucleated pole. 4. A comparison of the different patterns of eye represented in *Hirudo, Nephelis, Clepsine,* and *Branchelliopsis*, with the typical segmental sense-organ, shows that the chief distinction between the two classes of organs lies in the relative abundance of the clear cells.

10. The segmental sense-organs are *double organs, both in structure and in function.* There is an axial cluster of elongated cells, terminating at the surface in minute hairs, and representing most likely a tactile organ. Around and beneath the *tactile* cells, are the large, clear *visual* cells, so characteristic of the eye. Thus we have a visual and a tactile organ combined, both derived from a common mass of indifferent epidermal cells, and both supplied by fibres from a common nerve branch.

11. Incredible as the double nature of these organs may at

first appear, there is no escape from the fact, when we once understand the structure of the eye in *Clepsine.* A vertical section in the plane of the optical axis reveals the compound nature of the eye, and the identity of its structure with that of the segmental sense-organs. Here stands the tactile part of the organ, an exact copy of every feature seen in the corresponding part of a segmental sense-organ; and below and behind, but in continuity with the tactile portion, lies the mass of visual cells. The common nerve runs up in front of the visual cells, dwindling gradually in size as its fibres pass to the cells, and at length it is lost in the tactile cells. The main features of this eye have been known to me for about two years, but it did not seem best to hasten the communication of the facts before giving the whole subject careful study. The sense-hairs were first clearly demonstrated in *Nephelis*, and next in both the young and adult of *Clepsine.* The nerves supplying the eyes and sense-organs of the head arise in *Branchelliopsis* and *Clepsine* from the five sub-œsophageal ganglia.

12. In *Hirudo*, the visual cells are symmetrically placed around the *axial* nerve fibres, and no tactile cells are developed; in *Clepsine* and *Hæmenteria*, the visual cells are developed only on the posterior side of the nerve, while the tactile cells are grouped above and in front. In *Nephelis* the nerve is again axial; in *Branchelliopsis* it is eccentric, as in *Clepsine*, and there are comparatively few visual cells.

13. Both the eyes and the segmental sense-organs develop as local thickenings of the epidermis. At first the cells are alike in form, size, and structure. About the time the pigment begins to appear, the two sorts of sense-cells begin to show a difference in size, and an indistinct boundary line appears between them.

14. The *metameric* arrangement of the sense-organs of the *Hirudinea* is a matter of more importance than the latest writer on the subject, Mr. Apàthy, appears to realize. The limits of this paper do not permit me to review the arguments which this young naturalist has entombed in a *preliminary* report of about eighty pages (portentous dimensions !). I am compelled to remark, however, that this author has not been sufficiently careful in presenting the views of others. As one out of many instances that might be cited, the following is characteristic. I am rep-

resented as having made the supremely ridiculous mistake of taking the wart-like protuberances found on many species of *Clepsine* for sense-organs. In *C. marginata* — to cite one more case — I reported *four* anal ganglia. My statement was made with reference to a single species, and is perfectly accurate; but Mr. A. charges me with an error, because, forsooth, my statement is not true for *all* leaches. This is the style of criticism indulged in throughout this preliminary monograph. What I have called visual cells are put down, *ex cathedra*, for "fat-cells," "gland-cells," etc. Charity and necessity alike commend us in taking immediate leave of such oracular wisdom. It is to be hoped that before that impending final monograph is launched, our author will have discovered the unregenerate source of his present afflatus.

15. The key to the analytical study of the external form is to be found in the metameric disposition of the sense-organs. Of course internal structure is to be taken into account, and a fair critic would hardly have fallen into the mistake of supposing that I had neglected this side of the subject. I have had considerable opportunity to learn the practical value of this key for systematic purposes, and the longer I use it the more indispensable it proves. The terminal somites are of the highest importance for specific diagnosis, and their annular composition, which offers so much of theoretical interest, cannot be deciphered without the aid of the segmental sense-organs. What clearer demonstration of all this could be desired than has already been furnished in the case of the ten-eyed *Hirudinea?* I am now prepared to show that the same holds true of both fresh-water and marine *Rhyncobdellidæ*, although the application of the method is, as a rule, more difficult here than in the *Gnathobdellidæ*. The number of ventral ganglia is generally supposed to be the same for all the different species, genera, families, and so on for the entire class. While we may be sure that the number of somites represented in the rings does not exceed the number of ganglia, is it not perfectly clear that the latter cannot serve as a guide in determining the *annular limits* of somites, particularly at the ends of the body? Then it must be remembered that the number of ganglia in the cephalic group has never been satisfactorily determined, and even the number

in the caudal group has been variously estimated at six, seven, and eight.

16. The importance of the segmental character of the sense-organs is not to be measured by its usefulness in systematic determinations. Leydig showed long ago, in *Hirudo*, how the same nerve supplies successive sets of eyes. How, then, could the ganglia or nerves of the so-called brain be made to reveal the metameric character of the eyes? And how could the important serial homology of the eyes ever have been determined except through the discovery of their relations to sense-organs known to have a metameric arrangement? It is by virtue of this arrangement that I have succeeded in getting such a complete and convincing picture of the origin and history of the leech eye. Segmental sense-organs are found in other annelids and in vertebrates, but nowhere is the transition from lower to higher sense-organs so perfectly illustrated as in the leech. *Branchelliopsis*, *Clepsine* and *Hirudo* reveal all the intermediate steps, beginning with the purely tactile organ; then advancing to the compound organ, in which a few of the cells have been modified to serve the purpose of vision, while the rest have retained their primitive character; and finally, culminating after a long series of progressive encroachments, — the visual elements increasing gradually at the expense of the tactile, — in an organ in which the original function has been entirely suppressed and a new one substituted for it. Here is a chapter in the evolution of sense-organs so perfectly preserved in all its details as to leave no room for scepticism.

17. Without entering into the discussion of the point, I desire to repeat here the suggestion made on another occasion, that the segmental sense-organs of the leech are identical with the lateral-line organs of vertebrates. I do not venture to express such an opinion without having duly reflected on the objections that might be raised. Having spent considerable time in the study of the lateral-line organs in the larval stages of amphibia and marine fishes, and having followed closely the work of my colleague on *Amia*, *Lepidosteus*, and various teleostei, I know, at first hand, where the difficulties lie, and I do not think I underestimate their importance.

18. Perhaps it will not be venturing too far on speculative ground if, in this connection, another suggestion be offered;

namely, *that the segmental sense-organs of annelids have formed the starting-point for the development of the organs of special sense in the higher animals, not excepting even the eyes of vertebrates.* The evidence is rapidly growing stronger in favor of the origin of the olfactory and auditory organs from lateral-line organs; and the gustatory organs are certainly destined to fall into the same line. Mr. Allis' observations show how lateral-line organs may travel through gill-slits, and the mode of growth of the surface bulbs shows how they may spread to new areas. In regard to the vertebrate eye, we can never expect, of course, to determine its identity with lateral-line organs by such direct evidence as is available in tracing the origin of the leech eye. Assuming that vertebrates and annelids have had common ancestors with segmental sense-organs, the fact that such organs have been converted into eyes in at least one large group of annelids, raises the suspicion that nature may have practised the same economy in all branches from the common stock. And when we find strong grounds for thinking that the lateral-line organs have served as the point of departure for the formation of gustatory, olfactory, and auditory organs, our suspicion in regard to the eyes no longer appears incredible. I am not at all unmindful of what might now appear to be an almost insurmountable objection to regarding the vertebrate eye as a segmental organ. As one of my laboratory colleagues is soon to bring some new facts to bear on this subject, and as further discussion might lead to the expression of views that have certainly been corroborated by his observations, I drop the question for the present. I would, however, mention one observation of mine with reference to the eye of *Necturus.* The basis for the eye is already discernible as a circular area — after treatment with osmic acid followed by Merkel's fluid — long before the closure of the medullary folds of the brain, at a stage corresponding closely with Goette's Fig. 12, Pl. III., of *Bombinator igneus.*

But we have an *unpaired* vertebrate eye, of recent discovery, but possibly of very ancient origin. How is it possible to apply the hypothesis of segmental derivation here? As segmental sense-organs are always *paired,* it is not easy to account for the origin of an azygous organ from them except through the fusion of at least one pair. We are not able to point to many indications of a double origin, but the two vesicles in *Petromyzon* (Ahlborn, Beard), and the double pineal stalk of *Varanus giganteus* (Spencer), are facts that certainly favor such a view. Moreover, the position of the organ is such that we must suppose it to be derived from two sources, namely, the lateral (sutural) edges of the medullary plate. The fusion of segmental sense-organs has nothing improbable in it, as can be shown by more than one example from the *Hirudinea*. On the other hand, the origin of organs by division, although claimed by a number of authors of high repute, has not a single verified fact in its favor. I am quite confident that such a process does not underlie the multiplication of lateral-line organs, and I have found nothing of the kind in the development of the segmental sense-organs of the *Hirudinea*.

The origin of the pineal eye from the lateral eyes, as held by Beard, is open to more serious objections. In the first place, it is difficult to believe that this organ is of later origin than the lateral eyes; and in the second place, the idea that the entire optic vesicles (before and during the closure of the neural plate) represented retinal epithelium does not appear probable.

Professor Cope has recently brought some new paleontological evidence to bear on this question, and suggests that the lateral eyes may have arisen from the pineal eye. The condition represented in *Mycterops* is not claimed to necessitate such a view, and there is another interpretation which seems to me admissible, and more in accordance with what we know of the genesis of sense-organs. If the whole median orifice is not to be regarded as a parietal foramen, and if its lateral portions are really orbits as pointed out by Professor Cope, then there seems to be nothing in the way of interpreting the pair of orifices in the plate that divides the orbits as parietal foramina, if the possibility of the double origin of the pineal eye be conceded. Beard has already called attention to the possible existence of a parietal foramen in a corresponding position in *Asterolepis ornatus*.

Leydig's interpretation of the pineal eye is the only one that approaches my view, but it does not carry the origin directly back to invertebrate segmental sense-organs. It must be remembered, however, that Leydig[1] identifies the lateral-line

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[1] Since the above was written, Professor Leydig has published a paper, in which he contends that the pineal organ is not an eye nor a sense-organ of any kind, but a

organs with the sense-organs of the annelids. If an authority of Professor Leydig's standing can be presumed to stand in need of instruction on the differences that divide cerebral from peripheral sense-organs, it is not of course to be expected that my suggestion will meet with a less patronizing reception. These differences have been insisted on so often that they have become common property, and it indicates no small measure of audacity in a critic to assume the role of instructor in regard to them. Take what are now incontestable facts in the phylogeny of annelid and arthropod sense-organs, and add to them the evidences in favor of the common derivation of the vertebrate organs of special sense, and is it not enough to awaken a very strong suspicion that the visual organs of vertebrates will not be able much longer to hold the position of isolation so long conceded to them?

In the study of this question the following points seem to me of first importance: 1. Vertebrate sense-organs must be assumed to be derived from invertebrate sense-organs, and the history of the latter must furnish clues to the genesis of the former. 2. In the development of special senses, visual cells have made the widest departure from the primitive tactile cells. As the derivation of visual cells from cells of the tactile order is now, as I maintain, clearly established by the facts announced in this paper, it follows that structural and functional differences in sensory organs cannot be accepted as proof of diversity of origin. 3. The medullary plate of the vertebrate is undoubtedly an enormous extension of the ancestral invertebrate plate. 4. Sense-organs lying originally outside the neural plate have probably, in consequence of this extension in width, been brought within the medullary area. 5. The ancestral segmental sense-organs were not limited to a single pair of lateral lines, but to several paired lines symmetrically placed on the dorso-lateral and ventro-lateral surface.

19. The *caudal ganglia* are *seven* in number, with perhaps a rudimentary eighth. Sometimes from *two* to *four* ganglia in front of the caudal group are approximated, and the group thus formed constitutes the anal ganglia. In several American species of *Clepsine*, however, no such group exists, all the

lymph-sac. This startling announcement is evidently based on extended and careful observations, and it will make it necessary to re-examine the whole ground.

ganglia standing at regular intervals apart. There are generally *seven* pairs of distinct spinal nerves arising from the caudal ganglia, and sometimes eight.

20. The postoral (infra-pharyngeal) ganglia represent five somites, as can be shown in *Clepsine parasitica* and *Branchelliopsis.* Whether one or more somites are represented in the pre-oral (supra-pharyngeal) ganglia, I am not prepared to say. As there are always twenty-one ganglia between the pharyngeal and caudal groups, we have *thirty-three somites represented in the ventral chain* (exclusive of the pre-oral ganglia).

21. A careful analysis of the annular composition of the body of *Clepsine* has enabled me to find just *twenty-six* somites in front of the caudal sucker. Adding seven for the sucker, we have thirty-three, which makes the number of somites determined by the external rings agree precisely with the number of ganglia in the ventral chain.

22. The assertion by Mr. Apàthy that there are *six* caudal ganglia lacks *one* of being true; and his statement that there are always three anal ganglia would hit the mark in very few cases indeed. Mr. A. boldly asserts that there are *six* somites represented in the pharyngeal ganglia. This author does not appear to be aware that the nice balance which he strikes between the head and the tail of a leech is open to any serious objection. For the present I pursue the criticism no further.

23. The nervous system of *Branchelliopsis* presents one feature of exceptional interest. This leech possesses veritable *spinal ganglia.* These ganglia are lodged in the anterior (*sensory*) of the two spinal nerves of each somite, at a short distance from the ventral cord. The two nerves issue side by side, but diverge after passing the ganglia of the ventral cord, and then are re-united by a commissure, at the level of the spinal ganglion. Passing the spinal ganglion, the nerves at once subdivide into several branches. One of the main sensory branches runs outward in the anterior wall of the segmental sinus, while another large branch (motor ?) runs in the dorsal and posterior wall of the sinus. The pre-sinal branch divides just before reaching the longitudinal muscles, into three branches, the smallest of which appears to end in the muscles, while the two remaining pass on, one to the anterior, the other to the posterior side of the lateral heart, and eventually end in segmental sense-organs.

24. A pair of *colossal axial nerve-cells* are found between every two consecutive ganglia in the ventral cord of *Branchelliopsis.* The nuclei are very large, and placed about midway between the ganglia. The cells stretch from ganglion to ganglion, but do not pass these limits. Between the brain and the caudal ganglia there are twenty-two pairs, and in both these groups of ganglia the same cells probably occur, for a nucleus, resembling in general appearance the nuclei of the axial cells, is found imbedded close to the root of each nerve. These axial cells undoubtedly correspond to the neurochord cells of other annelids, and probably to the colossal nerve-fibres of *Amphioxus,* Müller's fibres in *Petromyzon,* and Manthner's fibres in *Teleostei.* Faivre's intermediate nerve terminates here in the manner described by Hermann for *Hirudo,* and has nothing whatever to do with the axial cells. Hermann's "*median ganglion-cells*" are also found in this leech.

25. In *Clepsine chelydræ,* the spinal nerves issue from the ventral cord as *three* distinct roots. The anterior, smaller root unites with the middle root, at the lateral edge of the ganglia, and the two then pass on as one nerve, corresponding to the anterior nerve of other leeches.

26. The agreement in form and structure between *Piscicolaria* and the Japanese *Branchelliopsis,* is remarkable, for it is much closer than that between the fresh-water *Piscicola* of Europe and marine leeches. Each has *three* rings to the somite, *five* pairs of testes, and *eleven* pairs of nephridia. The testes and nephridia are in corresponding somites in the two forms. I have not thus far succeeded in finding segmental sense-organs in *Piscicolaria,* but fresh material may bring them to light.

27. The nephridial organs of *Branchelliopsis* resemble those of *Clepsine.* Each pair appears to be entirely distinct, and thus to present conditions quite unlike the nephridial net-work described by Bourne in *Pontobdella* and *Branchellion.* For each pair of organs there is a pair of funnels and a pair of external pores. The funnel lies in a diverticulum from the posterior wall of the segmental sinus, in the angle formed by the junction of the segmental with the lateral sinus. A vertical plane cutting a pair of funnels would divide the first ring of the somite into two unequal parts, the posterior of which would be the smaller. A horizontal plane would cut the ventral wall of the

lateral hearts and the dorsal sides of the testes. Its position is thus a little behind the nephridial pore, which opens on the ventral surface a little below the lateral heart, in the anterior half of the first ring.

28. There are four longitudinal vessels and as many sinuses, one dorsal, one ventral, and two lateral. The dorsal vessel is inclosed for the greater part of its length in the dorsal sinus; the ventral vessel lies mostly outside the ventral sinus; the lateral vessels lie just above the lateral sinuses, and run parallel with them. In the post-clitellar region, a pair of branchial vessels are given off in each somite from the lateral vessels. Each branchial vessel divides into two branches, after passing through the muscular strata of the body, one of which passes forward to meet a posterior branch coming from the preceding branchial vessel, while the other passes backward to meet an anterior branch coming from the succeeding branchial vessel. The two branches do not actually meet, but rather each enters separately the base of the auricular chamber of the heart, where the two inflowing currents mingle and ascend to pass through a wide common opening into the main chamber. This opening is on the dorso-lateral face of the chamber, while the efferent opening lies on the ventro-median surface, and leads into the branchial sinus, which opens in turn into the lateral sinus, opposite the junction of the latter with the segmental sinus. The four sinal ostia thus brought together are guarded by peculiar pluriramous muscles. The dorso-ventral sinus communicates with the testicular sinus, and passes into the segmental sinus just before the latter unites with the lateral sinus. The connections between the vessels and sinuses at the ends of the body have not yet been completely traced.

29. All the *Hirudinea* may be derived from a form in which the somite consists of *three* rings. The 5-ring type of *Nephelis* and *Hirudo* has been derived, not from a 6-ring or 12-ring type, but from a 3-ring type, by the acquisition of two new rings. The position of the nephridial pores in the posterior edge of the last ring of the somite, can be accounted for more readily as the result of shifting than of a loss of rings. How three rings can become 4, 5, 6, or 12, I can promise to make clear in an early paper.

30. Copulation in Clepsine is never direct, *i.e.*, by union of

the sexual pores. The spermatozoa are transmitted in spermatophores, which are planted on any part of the exterior, preferably on the back. The gradual contraction of the sperm-case forces the contents through the skin in a steady stream that can be seen under a magnifying power of 20 diameters. By means of sections, I have traced the spermatozoa from the place of entrance to within a few millimetres of the ovaries. The same mode of copulation occurs in Nephelis, and in Peripatus (Sedgwick).

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Dec. 25, 1888.

SEGMENTAL SENSE-ORGANS OF ARTHROPODS.

WILLIAM PATTEN.

The cephalic lobes of Acilius are composed of three segments, each of which contains a segment of the brain, optic ganglion, and optic plate, the latter bearing two pairs of segmental sense-organs, or eyes. That these characters are common to all insects is very probable since the larvæ of many Coleoptera, Neuroptera, and Lepidoptera agree with those of Acilius in having six pairs of ocelli and three optic ganglia, while in the adult the ganglion of the convex eye is generally composed of three lobes probably derived from three independent ganglia.

The segmental nature of the eyes is more clearly seen in the embryos of Scorpions, Spiders, and Limulus, where it can be shown that they are serially homologous, with one or more pairs of sense-organs on each segment of the thorax.

In Scorpions, whose cephalic lobes are composed of three segments similar to those of Acilius, the ganglionic invaginations of the first segment, which has no eyes, unite to form a transverse furrow that is soon converted into a closed sac, the walls of which are formed by the first segment of the optic plate, optic ganglion, and brain.

The second ganglionic invagination is at first like that of Acilius; but the optic plate itself is soon infolded, forming the outer wall of the ganglionic sac, the inner wall being the optic ganglion. The two cavities finally unite in the median line, and the median eyes appear as a pair of thickenings on the inverted optic plates. A small group of upright cells soon appears on the posterior edge of each eye, and pushing its way over the inverted cells, gives rise to the permanent retina. The primitive retinophoræ are finally converted into the irregular pigment cells, filling the inner portion of the eye, some of which Lankester supposed to be of mesodermic origin. A thin part of the inner wall of the ganglionic sac, belonging neither to the optic plate nor the optic ganglion, forms the capsule of the eye.

The ganglionic invagination of the third segment is not as extensive as the preceding ones, and the optic plate which bears the lateral eyes is not involved in the infolding. If the cephalic lobes of Scorpions could be stretched out, the eyes would lie, as in Acilius, on the thickened outer edge of each segment. This thickened edge is represented in the post-oral region by the pleuræ of the thoracic segments, each of which bears two large sense-organs, close together near the outer edge of the base of the legs. It is clear that the eyes are serially homologous with these thoracic sense-organs. The latter contain a cavity, shaped like the bowl and stalk of a goblet, lined with striated cuticula similar to that found at an early stage over the eyes of Acilius.

In Spiders the structure of the cephalic lobes is the same as those of Scorpions. The two anterior median eyes belong to the second segment, and are homologous with the median eyes of Scorpions, the development being the same in both cases.

The three remaining pairs belong to the third segment, and are homologous with the lateral eyes of Scorpions. They are invaginated to form optic cups in the same way as those of Acilius. The retina is apparently cut into two separate layers by the tapetum; but the tapetum is really pierced by regularly arranged holes, through each of which passes a pair of retinophoræ. Above the narrow openings, each cell expands into an oblong body containing two rods like those of Acilius. Beyond the rods the cell terminates in a short, rounded swelling, containing the primary nucleus of the retinophora. The secondary nucleus lies at the opposite extremity, where the cell is continuous with a bundle of nerve fibres. The segmental sense-organs at the base of the legs are smaller than in Scorpions and easily overlooked.

In Limulus the cephalic lobes are composed of three highly modified segments, the first and second being invaginated to form two sacs. An evagination of that part of each sac formed by the optic plate then gives rise to a tube, at the end of which is formed an eye. A pair of these tubes from the first segment unites with a similar pair from the second to form the stalk of the median eye, the eye itself being formed by the union of the four eyes at the ends of these tubes. The two posterior eyes are therefore homologous with the median eyes of Scorpions and Spiders.

Before the segments just described are invaginated, the optic plate extends backward, almost the whole length of the body, as a thickened ridge which in every thoracic segment gives rise to a large sense-organ. On the median edge of the plate is formed a segmentally deepened furrow that gives rise to a longitudinal cord of ganglion cells. The three optic ganglia are segmental thickenings of this cord. The convex eye arises from three small sense-organs near the third thoracic segment, its nerve being derived from a part of the lateral cord of ganglion cells. The sense-organ of the third cephalic segment developed into a pigmented body connected by a nerve with the ganglion of the convex eyes. The remaining sense-organs soon disappear. That of the fourth thoracic segment is very large, and has been erroneously described as giving rise to the convex eyes.

The ventral cord and brain of Arthropods is at first composed entirely of minute sense-organs, which in Scorpions have the same structure as the segmental ones at the base of the legs.

On the lateral edge of each ganglion of the ventral cord of Scorpions are two of these sense-organs, conspicuous on account of their size and dark color. In each segment of the brain are similar but still larger ones. All these sense-organs are converted into the ganglion cells of the brain and ventral cord.

The above-mentioned facts and others will be fully discussed and illustrated in one of the following numbers of this Journal.

MILWAUKEE, Feb. 19.