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BIOLOGICAL BULLETIN.

SOME RELATIONS BETWEEN NERVOUS TISSUE AND GLANDULAR TISSUE IN THE TUNICATA.

MAYNARD M. METCALF.

It is well known that in the ascidians the definitive brain and the neural gland are both derived from the same region — the trunk region of the central nerve tube of the tadpole. The ganglion is derived from one wall of this tube, and the gland is derived from the opposite wall. Six years ago I pointed out that the ganglion of *Salpa* is homologous with both the ganglion and the neural gland of ascidians; the dorsal part of the *Salpa* ganglion corresponding to the ascidian brain, and its ventral part corresponding to the ascidian neural gland.[1] That is, a certain portion of the embryonic nervous system in ascidians becomes transformed into the neural gland, while in *Salpa* the corresponding region does not suffer this change, but remains as part of the definitive brain, its cells functioning as gland cells in the adult. I have recently found in the ascidians an interesting series of diverse conditions as to the origin of the gangliated nerve which runs down in the median line of the partition between pharynx and cloaca.

In this region, the dorsal raphe, one finds a large blood sinus, a muscle (either single or double), a gangliated nerve cord (the rapheal nerve), and frequently a prolongation from the neural

[1] "The Eyes and Sub-Neural Gland of Salpa," *Memoirs from the Biological Laboratory of the Johns Hopkins University.* Vol. ii, Part iv. 1893.

gland, which I have called the rapheal duct. In different species the rapheal nerve may arise from the cellular cortex of the brain, from the neural gland, or from a mass of cells formed by the fusion of the brain and the gland. The five accompanying diagrams show some of the conditions found.

In *Cynthia papillosa*, Fig. 1, the rapheal nerve arises from the cellular cortex of the brain. Alongside it in the raphe is found the unusually large rapheal duct, which has extended down from near the posterior end of the epineural gland. The rapheal duct and rapheal nerve are wholly distinct.

In *Distaplia magnilarva*, Fig. 2, there is no rapheal duct. The brain and neural gland are united posteriorly. The rapheal nerve arises from the cortex of the brain, a little behind the point of fusion of the brain with the gland.

In *Amaroecium constellatum*, Fig. 3, we find a rudimentary rapheal duct starting back from the gland, but it looses its lumen before going far, and then its cells become united with the cells of the brain to form a common mass of cells whose origin, whether from the brain or the gland, we are unable to determine. From this common mass of cells the *ganglion cells* of the rapheal nerve are derived, its *fibers* coming from the right posterior siphonal nerve.

In *Ascidia atra*, Fig. 4, we have a similar origin for the fibers of the rapheal nerve, but find an interesting difference in the derivation of its ganglion cells. A cord of cells pushes out from the dorsal surface of the brain, near its posterior end, and, after running back a short distance, unites with a backward prolongation of the gland, which runs up to meet it. The prolongation of the gland is evidently the rapheal duct. The two cords fuse immediately, the duct loosing its lumen. The single cord of cells thus formed runs back some distance and then bends down to accompany the fibers of the rapheal nerve. Its cells soon become loosely arranged among these nerve fibers and are clearly the ganglion cells of the rapheal nerve.

In *Phallusia mammillata*, Fig. 5, these organs are exactly similar, except that the prolongation from the dorsal surface of the ganglion does not unite with the rapheal duct, but bends forward, soon ending blindly. In this species, then, the ganglion

cells of the rapheal nerve are derived solely from the rapheal duct, which is a prolongation from the neural gland.

The ganglion cells of the rapheal nerve in *Phallusia* have therefore had a roundabout history. Certain cells of the larval nerve tube were pushed out to form the neural gland. A portion of these gland cells extended backward until they came in contact with the fibers of the rapheal nerve.[1] Here they lose their regular arrangement and become the ganglion cells of the nerve. There is no evidence that these particular cells, even though a part of the gland, were ever functional as glandular cells. The corresponding cells, however, in many other species are functional gland cells. (Compare *Cynthia papillosa* above.)

The facts referred to in this paper show a peculiarly intimate relation between glandular tissue and nervous tissue in the *Tunicata*, hardly to be paralleled elsewhere in the animal kingdom.

The Marine Biological Laboratory,
Woods Holl, Mass.,
July 20, 1899.

[1] This is based upon the assumption that the rapheal duct arises as a down-growth from the definitive gland rather than by the metamorphosis *in situ* of the trunk portion of the nerve tube of the tadpole. The rapheal nerve in *Salpa* and probably in ascidians arises as a down-growth from the brain. It is probable that the rapheal duct arises in a similar way as a down-growth from the definitive gland.

EXPLANATION OF FIGURES.

Reference Letters.

a.s.n. = anterior siphonal nerve.
d. = duct from neural gland to ciliated funnel.
f.r.n. = fibers of rapheal nerve.
g.c. = cord of ganglion cells.
gg. = ganglion (brain).
gl. = neural gland.
g.r.n. = ganglion cells of rapheal nerve.
p.s.n. = posterior siphonal nerve.
r.d. = rapheal duct.
r.n. = rapheal nerve.

The figures are diagrammatic parasagittal sections of the ganglion and neural gland, a little to the right of the median plane. In Figs. 4 and 5 the rapheal duct, which in reality lies on the right surface of the ganglion, is shown, although in reality it lies much to the right of the plane of the rest of the section.

FIG. 1. Cynthia papillosa.
FIG. 2. Distaplia magnilarva.
FIG. 3. Amaroecium constellatum.
FIG. 4. Ascidia atra.
FIG. 5. Phallusia mammillata.

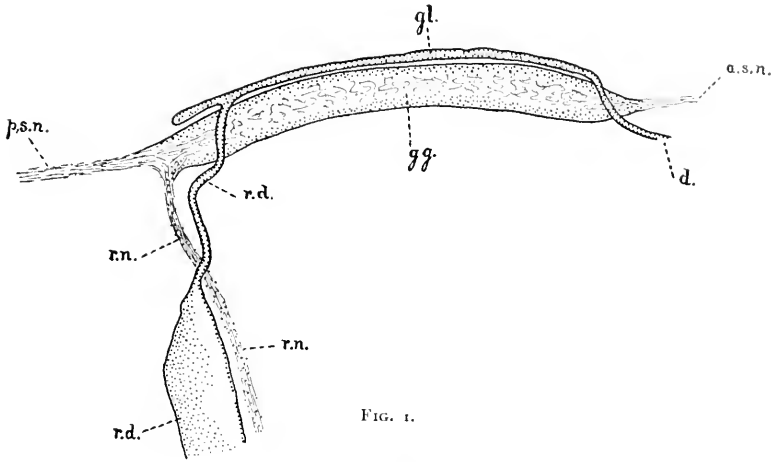


FIG. 1.

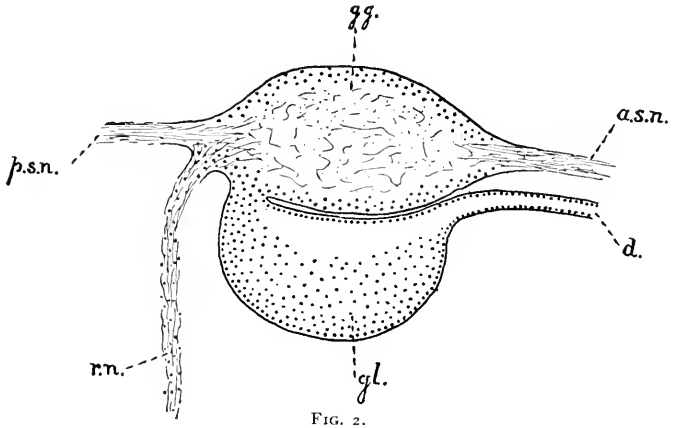


FIG. 2.

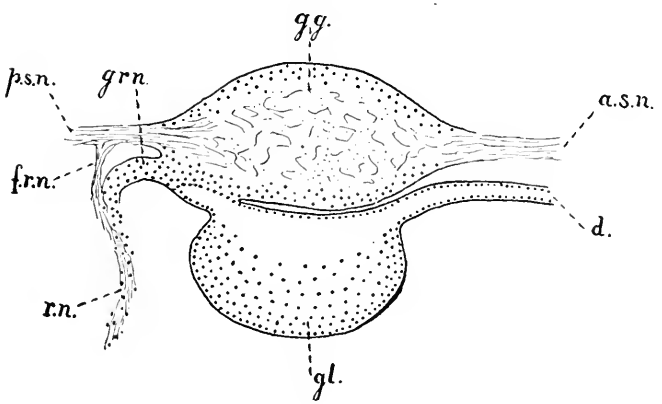


FIG. 3.

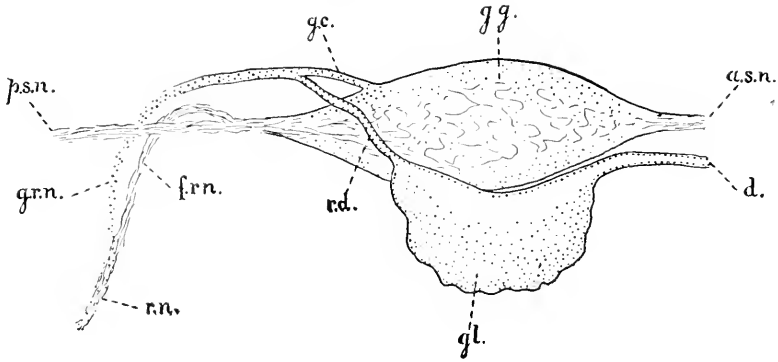


FIG. 4.

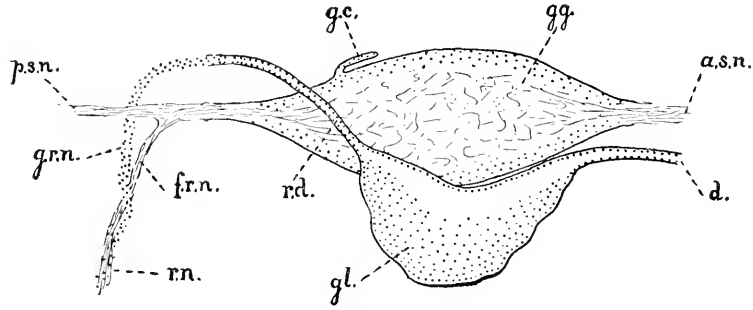


FIG. 5.

REGENERATION OF TISSUE COMPOSED OF PARTS OF TWO SPECIES.

T. H. MORGAN.

Born's experiments in grafting together tadpoles of different species of frogs have demonstrated that each part, whether large or small, retains the characteristics of the species to which it belongs. During the development of an animal, formed by the union of parts of two species, the tissues do not influence each other, but each develops its own specific peculiarities.

Joest has shown that when parts of two different species of earthworms are grafted together each part retains its specific characters. He has further shown that if, after grafting, a portion of one of the parts is cut off, the new part that is regenerated is like the part from which it immediately arises, and is not influenced by the part belonging to the other species, even when the latter is very large, and the former (that from which the new part arises) is very small.

Many experiments have been made with plants in which different species have been grafted together, and the subsequent growth of the two parts studied. Vöchting, who has given a detailed account of these experiments and has made others himself, has shown that in general no influence of a specific character is transmitted from one part to the other, although in certain cases[1] the parts do have some influence on each other.

The following experiments were made, not so much to determine whether the tissues of one component of a graft influence the kind of regeneration of the other, since this point seemed fairly settled by Joest and by Harrison, but I hoped to find out if new tissue, made up of cells derived from parts of two species, showed any mixing of the specific characters of the two species.

[1] Particularly in those cases where annual and biennial varieties are grafted together.

It seemed possible, at least, that new tissue, composed of cells derived from two species, might show the influence of its dual origin.

Harrison[1] has shown that the tails of young tadpoles may be interchanged even when two species are used, and that later the ectoderm of the body of the larger component grows out over the base of the grafted tail, slipping over the region where the tail has been grafted on, as shown in Fig. 1. If two species be used, and then, after the tail has grown to the stage shown in this figure, the tail be cut off just distal to the point of union, as shown in Fig. 2 by the vertical line, there will be present at the exposed end two kinds of tissue — the ectoderm, which is the same as that covering the body of the tadpole, and the inner tissue, composed of muscles, connective tissue, pig-

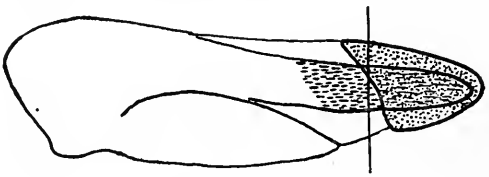


FIG. 1. (After Harrison.)

ment cells, notochord and nerve cord, that belong to the grafted tail. Under these circumstances the new tail that regenerates will be made up of parts of two species. Harrison carried out an experiment of this sort. He writes[2] in regard to the result: "The tail of a larva of *R. virescens* was replaced by the tail of a larva of *R. palustris*, in the manner described above. Forty-eight hours later, at which time the sketch was made (see Fig. 1), the tail was amputated. The epidermis from the virescens body had then pushed out considerably over the root of the tail, so that in cutting, almost all of the grafted epidermis (stippled in the figure) was removed. But a considerable portion of the underlying organs of the transplanted piece (shaded in the figure) remained, and it was from this component that regeneration took place in all the tissues, with the exception of part of the epidermis. The newly grown tail was

[1] Harrison, R. G., "The Growth and Regeneration of the Tail of the Frog Larva," *Roux's Archiv.* Vol. vii, 1898. [2] Page 473. Case 13.

of normal form, and, as far as could be observed, it had the characteristics of the species of the grafted stump (palustris) and not those of the body (virescens). This was seen in the character of the pigmentation, and especially in the absence of the large black blotches along the side of the tail, which are found constantly in the regenerated appendages of *R. virescens*. In spite of the insignificant size of the grafted stump, as compared with the whole body, and in spite of the fact that the nourishment conveyed to the growing appendage is brought there in blood, which is largely derived from the body, the tissues maintain their specific characters.[1]"

By using two species in which there is a marked difference in the pigmentation of the ectoderm and also some distinctive difference in the color of the pigment cells in the mesoderm, I hoped to be able to determine more definitely the character of the new part, and further, by observing the tissues of the two species, where they are regenerating side by side, to see if they mutually influence each other. The problem is somewhat different from the one Harrison examined, since I was less concerned with the influence of the major component on the new regenerating part than with the possibility of a mutual influence of the new cells on each other. Harrison has shown, with some degree of probability, that the former influence is not shown in the new part, but the latter problem is not specially considered.

I have found it possible to graft together two such differently pigmented tadpoles as *Rana* (*temporaria*) *sylvatica* and *R. palustris*. The former breeds earlier, but the development will be retarded several weeks if the dishes in which the tadpoles are placed be put on ice in an ice chest. It is better to let the tadpoles develop as far as the stage when the tail-knob is just about to appear, since at this stage they withstand better

[1] "I had hoped to obtain more definite evidence concerning the influences which regulate regeneration, from experiments carried out along these lines. But, owing to unfortunate circumstances, most of the larvae of this series died. Besides, all regenerated tails deviate somewhat from the normal type, especially as regards pigmentation, which fact would bring in a considerable element of uncertainty, and in the tail I have not been able to find any other characters which could with safety be considered diagnostic of either species."

the effect of the ice-cold water. If segmenting eggs or the early gastrula stages be put on ice they are killed after several days, although the latter stages withstand the cold longer than the former. The young tadpoles do not seem to be in the least injured, and may even slowly continue to develop, but at so slow a rate that after three weeks the tail had grown only a very little. Since in this locality the eggs of *R. palustris* can be obtained in great abundance for a period of at least two weeks, I have had plenty of material of both species.

The tadpoles were operated upon at the time when they had reached the age shown in Harrison's Fig. 2. They were still in the jelly membranes. Muscular movements of the body had scarcely begun at this time. The tadpoles were held in place by small pieces of aluminium wire. Silver wire used by Born and by Harrison would probably be better, since it is heavier.

The young tadpole of *R. sylvatica* is very black, the color being due to the deeply pigmented ectoderm and to some extent to pigment in the mesoderm. The young tadpole of *R. palustris* is much lighter in color. The ectoderm contains a yellowish pigment, and the pigment cells of the mesoderm are lighter in color than those of the other species. After grafting together parts of these two species, the difference in color of the two parts is so marked that it can be easily seen with the naked eye. Under the microscope one can tell readily whether an individual cell in the ectoderm belongs to the one or to the other species. In later stages, when the ectoderm has become clearer, the two kinds of cells can no longer be distinguished without a microscope. The core of the tail of *R. sylvatica* is much darker than that of *R. palustris*, and the line of union of the two can be seen with the unaided eye.

As the tadpole grows larger, it will be found that the ectoderm of the smaller component grows less rapidly than the rest of the tail, and as a result the ectoderm of the larger component extends over the base of the grafted tail, as Harrison has stated (Figs. 2 and 3). The tadpoles were allowed to grow for about ten days, or somewhat longer,[1] and then the tail was cut off in various ways.

[1] It would have been better to have cut the tail off sooner, since the difference in the ectoderm of the two species is less marked in later stages.

Experiment I. — The tail of *R. palustris* had been grafted upon the body of *R. sylvatica*. The tadpole appeared at the time of the second operation, as shown in Fig. 2 *A* (April 25). The dark ectoderm of the major component — *R. sylvatica* — had grown out over the base of the tail of the smaller com-

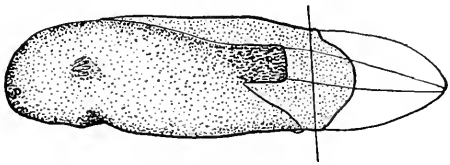


FIG. 2 *A*.

ponent (*R. palustris*). The region of union of the inner tissue can be seen where the dark and the light parts meet. The tail was then cut off, as shown by the vertical line in the figure. In consequence, there was left exposed at the cut end of the tail

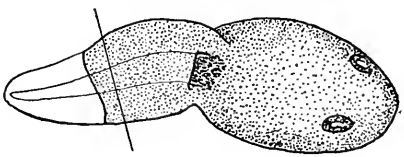


FIG. 2 *B*.

the inner tissues derived from *R. palustris*, and the outer from *R. sylvatica*. A new tail began to regenerate, and during all of its subsequent development the new tail was made up of ectoderm exactly like that of the major component, and of inner

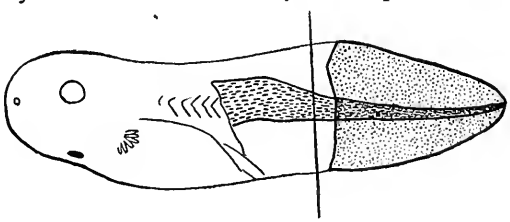


FIG. 3.

tissue whose pigment cells resembled those of the minor component. In other words, both inner and outer tissues regenerated their kind and showed no commingling of characters.

Experiment II. — In this experiment the major component was *R. palustris* and the minor *R. sylvatica*. After the new

tail had reached the stage shown in Fig. 3, it was cut off as indicated by the vertical line. There was left exposed at the cut end the light-colored ectoderm of the major component and the inner tissues of the minor component. The new tail that developed had light ectoderm on the surface and a dark interior. Each part regenerated its specific tissue and was uninfluenced by the developing tissue of the other species.

Two points present themselves for consideration. If the tail of an ordinary tadpole be cut off and subsequently develop, does the regenerated tail show the specific characters of the normal tail or is it different? I have examined the regenerated tails of both species and find that both the ectoderm and the mesodermal pigment cells are like those of a normal tail. It is, however, not very uncommon, both in regenerated tails of normal tadpoles and also in grafted tadpoles, to find the mesodermal pigment cells imperfectly developed, and in such cases the specific character of the cells is not obvious; but in all cases in which the pigment cells are well developed, the specific character is readily seen, especially in the cells lying along the central part of the tail. It should be stated, however, that I have occasionally found isolated cells whose character was doubtful, but the large majority of cells are unquestionably like those of the tissue from which the new tail arises. The second question is whether the ectoderm forms new cells over the new part, or does the old ectoderm simply extend out over the new part? There is the appearance in the regenerating tail of the formation of a new ectoderm at the tip of the new tail, where the cells are more crowded together and smaller than over the base of the tail. It is not improbable that in addition to this new ectoderm the old ectoderm extends also over a part of the new tail.

Experiment III. — In several cases the tail was cut off obliquely, in much the same way as in Harrison's experiment. Owing to the difference in pigmentation of the two kinds of ectoderm, I could follow the subsequent history of each and determine whether, along their line of contact, and in the region where new cells are developing, the specific characters of the cells are altered.

As shown in Fig. 4, the tail of a tadpole, in which the major component is *R. palustris* and the minor *R. sylvatica*, was cut off obliquely, leaving a small amount of the dark ectoderm of *R. sylvatica* on the upper side. The inner cells at the cut edge all belonged to *R. sylvatica*. When the new tail developed, it showed along its upper part the dark ectoderm of *R. sylvatica*, that had developed from the small piece left at the time of the

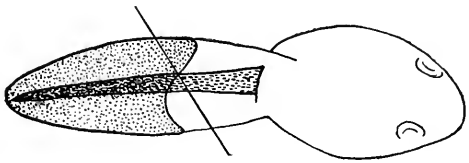


FIG. 4.

operation. The area covered by the dark ectoderm was greater than that left after the tail was cut off, but it cannot be stated how much of this increase is due to the cells becoming flatter and how much to new cells formed at the free edge.

In another similar experiment, in which, however, the major component was the dark species, *R. sylvatica*, and the minor the paler species, *R. palustris*, the tail was cut off (April 27), as shown in Fig. 5. A large area of light ectoderm was left on the dorsal surface of the tail, and only a small amount of the

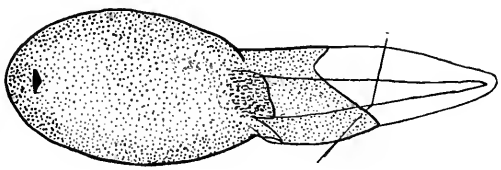


FIG. 5.

black ectoderm came to the edge of the lower part. On May 10, when the new tail was fairly well developed, it was found to have its upper surface covered by light-colored ectoderm, and its lower by dark ectoderm, while the interior mesodermal pigment cells were like those of *R. palustris*. Each tissue had regenerated its like, and the light ectoderm of the minor component showed no influence of the other, dark ectoderm, even along the line of contact where new cells were developing.

In addition to these experiments I have records of four others similar to Experiment I (Fig. 2, *A*, *B*); three others similar to Experiment II (Fig. 3); and four others in which the tail was cut off obliquely, leaving both kinds of ectoderm at the cut edge. In all cases the specific character of the new tissue was like that of the old tissue from which it arose.

At first the difference in the ectoderm of the two species is very marked, but as the tadpoles get older the ectoderm seems to flatten and become more transparent, so that in these tadpoles it is difficult to distinguish between the two kinds of ectoderm. But if the tadpoles are examined every day one can detect differences in the two kinds of ectoderm for a longer period than could be done by casual observations alone. Wherever the ectoderm has not spread out, particularly at the tip of the tail, the dark pigmented cells of *R. sylvatica* and the yellowish cells of *R. palustris* can be readily detected. The pigment cells in the mesoderm assume their characteristic arrangement during the older stages, and as the ectoderm becomes more transparent, the cells can be easily seen in the living tadpoles. The tadpoles were all kept under the same condition, so that the effect of light on the pigment cells would be approximately the same in all experiments.

Unfortunately the differences in pigmentation are the only specific characters that can be made out readily in these tadpoles, but I think there can be little doubt that if the cells retain their characteristic pigmentation they also retain their other peculiarities.

We may conclude with some degree of probability that during regeneration in a region where the cells have been derived from two different species, each kind of new cell retains the character of the cells from which it is derived, and the specific characters of the cells of one species are not transmitted to the cells of the other species, although the developing cells in the new tissue may be in actual contact.

DINOPHILUS GARDINERI (*Sp. Nov.*).

ANNE MOORE.

Preliminary Note.

A new species of *Dinophilus* was found in the summer of 1897, by Dr. E. G. Gardiner, at Woods Holl. The pool in which it is found is an artificial one, 12 by 14 feet, dug about eight years ago to obtain the peat in the marsh. Sea water does not flow into it, but when the tide is unusually high it percolates in through the sand. The salinity of the water is therefore subject to great variation, for a run of low tides results in condensation through evaporation, while heavy rains dilute it. In May, 1898 and 1899, *Dinophilus* was found by Dr. Gardiner in abundance upon green algae floating on the surface of the water. In June, 1898, he kindly brought the animal to my notice and I began work upon it. At that time it was not abundant, and by July 16 had entirely disappeared. In 1899 only two specimens were seen after June 28. Both years the disappearance was coincident with a rainstorm, so that it is quite possible that the influx of fresh water may account for it. Other observers (Hallez,[1] Weldon,[2] Harmer[3]) have noted the periodical disappearance of *Dinophilus*. Weldon attributes it to the disintegration of the female, consequent upon the setting free of the ova, but Schimkewitsch[4] maintains that eggs may be laid several times during the year, and that the female lives for some time after depositing them. He found special ducts present for carrying the eggs to the exterior, so that there

[1] Hallez, P., *Contributions à l'Histoire Naturelle des Turbellaires*. Lille, 1879, p. 155. (D. metameroides.)

[2] Weldon, W. F. R., "On Dinophilus gigas," *Quart. Journ. Micr. Sci.* Vol. xxvii. 1887.

[3] Harmer, S. F., "Notes on the Anatomy of Dinophilus," p. 109, *Journ. Mar. Biol. Ass. of United Kingdoms*. New Series. Vol. ii, October, 1899.

[4] Schimkewitsch, W., "Zur Kenntnis des Baues und der Entwicklung des Dinophilus vom Wei Ben Meere," *Zeit. für wiss. Zool.* Bd. lix. 1895.

is no necessity for disintegration to set them free. Of the disappearance of the animal, and a possible explanation of it, I will speak later.

This species of *Dinophilus*, which I take pleasure in calling *D. Gardineri*, differs in certain features from those species which have been noted by other observers. It is easily recognized without a lens, for its bright orange-red pigment makes a sharp contrast with the green algae upon which it is found. The average length of the form is about 1 mm., but under a dissecting lens the highly colored intestine, with its characteristic stomach portion, and the red kidney-shaped eyes, are noticeable features. The body is about three times as long as it is broad, the proportions varying, of course, with extension or contraction; it is somewhat flattened dorso-ventrally, and when fully extended tapers toward the posterior end. It consists of six definite segments, exclusive of head and tail, distinctly visible in young individuals in a state of extension (Fig. 2). Neither young nor old individuals show segmentation when contracted, and old ones show it only when making a turn, not when moving rapidly in full extension. The head is rounded in front and bears the eyes on its dorsal surface (Fig. 1). The mouth is situated on the ventral surface posterior to the eyes at, or just anterior to, the union of the head with the first body segment. The small unsegmented tail approximates the length of a body segment. It is considerably narrower than the body and tapers to a point. The anus is situated dorsally to its base. Owing to the scarcity of material, I did not ascertain to my satisfaction the arrangement of the cilia, but as nearly as I could determine the animal is com-

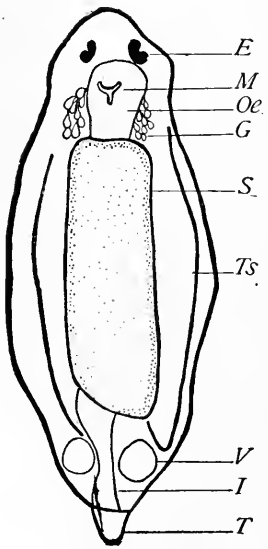


FIG. 1.

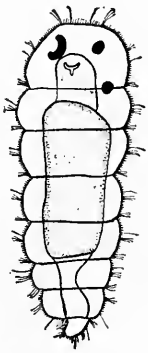


FIG. 2.

pletely ciliated, and, in addition, each segment shows laterally two tufts of long cilia and a strong bristle anteriorly placed. These probably indicate the presence of two rings of cilia on each segment. The head bears two tufts of long cilia in front, and the tail bears several bristles. These are probably of a sensory nature.

No sexual dimorphism is present; it is impossible to distinguish the sex of young individuals. In mature females the paired ovaries are strongly colored and may be clearly seen.

This species differs from *D. gyrociliatus* (*apatris*) and *D. metameroides* in its lack of sexual dimorphism; in the number of segments and in the arrangement of cilia it differs from *D. gigas* (7 segments), *D. taeniatus* (5 segments), *D. pygmaeus* (5 segments), and *D. simplex* (4 segments); in the arrangement of cilia and in the possession of an unsegmented tail it differs from *D. vorticoides* (*caudatus*).

The bilobed or crescentic shape of the eyes of *Dinophilus* often looks as if they were on the way to becoming double, as is the case with some *Turbellaria*. I have found two specimens in which the right eye was made up of two spheres completely separated from each other. In one case they lay close together; in the other, one sphere was in the normal position, the other in the next segment (Fig. 2).

In explanation of the disappearance of *Dinophilus*, alluded to above, I have to offer an observation of a stage in its life history which to my knowledge has not been noted before. On June 27, 1899, in my search for specimens I came across capsules imbedded in the tangle of algae. Through the thin transparent walls I could distinctly see the characteristic form, color, and eyes of *Dinophilus*. In addition to the capsules, eight specimens were found on the same day. These were put by themselves in a shallow glass dish containing salt water and some algae, and were watered from day to day. At the end of a week only five specimens were seen; on searching for the other three, three capsules were found. I then realized that these capsules really represented an encysted stage of *Dinophilus*. The five remaining specimens were transferred to a fresh dish of clear water. Four of them disintegrated;

the fifth formed a cyst. Every stage of the process was watched. The animal became perfectly quiet, and a clear secretion was given off. After a time, probably from a sense of discomfort, it moved away from this secretion, leaving behind it an impression of its form. These impressions had been seen before, but it was not known to what they were due. After moving, the animal continued to give off the secretion, and at the end of the next day the capsule was completed, the whole process taking three days. The other individuals began to secrete in the same way, but in one case the animal was disturbed and the process stopped, and in the others they were attacked by protozoa, causing disintegration. The largest cyst that was found measured .5 mm., the smallest .13 mm. This decrease in size might easily account for their being overlooked, but in addition to this it was found that after keeping the cyst for a time the color faded out so that it became practically unrecognizable.

It is quite probable that this cyst is formed through the activity of numerous gland cells in the skin. Many observers have noted these glands, but no one has suggested an adequate function for them.

The affinities of *Dinophilus* and its systematic position make it a peculiarly interesting form, and I hope in a more favorable year to obtain sufficient material to complete my work upon it.

THE MARINE BIOLOGICAL LABORATORY,
WOODS HOLL, AUG. 6, 1899.

Squamula thoracalis not broadened mesad and caudad. Wings not rilled.[1]

b. *Muscinae ariciaeformes.* — Front narrow in the male, broad in the female. Squamula thoracalis not broadened mesad and caudad. Wings in the most recent forms (geologically speaking, the "youngest") rilled.

c. *Muscinae muscaeformes.* — Front as in b. Squamula thoracalis broadened out mesad and caudad as far as the edge of the scutellum. Wings rilled. Apical cross-vein present.

Girschner's family *Anthomyidae* includes, in the first two groups, the *Anthomyidae* and part of the *Muscidae* (sens. strict.) of other authors. The genera belonging to the former have been made the subject of a recent paper by Mr. Paul Stein in the *Berl. Ent. Zeit.*, Vol. XLII, pp. 151–288, 1897. This paper covers the *Coenosiinae*;[2] the *Muscinae coenosiaeformes;* and the *Muscinae ariciaeformes*, except the genera *Myospila*, *Muscina*, *Clinopera*, *Hemichlora*, *Stomoxys*, and *Haematobia*. In these genera the fourth longitudinal vein is bent up, near its apical end, towards the third, and the arista is either pectinate or long plumose. They may be separated from one another as follows:

1. Proboscis long, slender, horny, adapted for piercing . . . 2
   Proboscis not so constructed, provided at the tip with fleshy labellae 3
2. Palpi much shorter than the proboscis, arista pectinate *Stomoxys* Geoffroy
   Palpi nearly as long as the proboscis, arista pectinate, sometimes also with a few hairs below . . . . . *Haematobia* Desvoidy
3. Arista pectinate . . . . . *Hemichlora* v. d. Wulp
   Arista plumose 4
4. Sternopleural macrochaetae 2 : 2; eyes hairy . *Myospila* Rondan
   Sternopleural macrochaetae 1 : 2; eyes not hairy 5
5. First longitudinal vein ends far beyond the middle of the costa. One or more well-developed pairs of anterior acrostichal bristles *Muscina* Desvoidy
   First longitudinal vein ends before the middle of the costa. No anterior acrostichal macrochaetae . . . *Clinopera* v. d. Wulp

[1] These rills are very fine grooves in the surface of the wing which run in a sort of radiate manner toward the border. They are very numerous. A rilled wing denotes a higher stage of development, a more recent form, than an unrilled wing.

[2] Girschner's *Coenosiinae* includes a few genera which are commonly considered as members of the Acalyptrate family *Scatomyzidae;* these genera are not considered by Mr. Stein.

SOME MUSCINAE OF NORTH AMERICA.

GARRY DE N. HOUGH, M.D.

GIRSCHNER divides the *Muscidea* into two series — *Calyptratae* and *Acalyptratae*. The former he divides into two families, one of which is the *Anthomyidae*. Hypopleural bristles lacking. If three sternopleural bristles are present, they always have the arrangement 1 : 2 (*i.e.*, one in front and two behind). Ventral membrane usually present. Elbow of fourth longitudinal vein (if there is any) without an appendix.

This family Girschner divides into three groups :

1. *Coenosiinae*. — Fifth ventral segment of the male heart-shaped or split in the median line from the caudal border to a point beyond the middle. Fourth longitudinal vein straight. Abdomen usually elongate. Sternopleural bristles present. Squamulae separated from one another by an interspace that is broad to the very bottom ; squamula thoracalis never broadened towards the scutellum.

2. *Muscinae*. — Fifth ventral segment of the male with its caudal border straight or moderately concave (lunulate), at any rate not split beyond the middle, except in *Lispe*, where it is three-pronged. Fourth longitudinal vein straight or more or less bent up toward the third in the form of an apical cross-vein. Abdomen usually short or long oval. Sternopleural bristles present. Squamulae not separated from one another, in contact at their attached borders ; angle between them narrow and acute.

3. *Gastrophilinae*. — Sternopleural bristles absent. Fourth vein straight. Costal vein reaching only to or a little beyond the third vein. Squamulae but little developed, separated from one another by a projecting angle.

The *Muscinae* are divided into three sections :

a. *Muscinae coenosiaeformes*. — Front broad in both sexes.

Stomoxys. — I have seen but one American species of this genus, which is the well-known "Stable Fly," *S. calcitrans* L. (Fig. 1, wing and chaetotaxy), very common both in Europe and this country. Of the species mentioned in Osten-Sacken's *Catalog*, *dira* Desv. and *inimica* Desv. are varieties of *calcitrans; occidentis* Walk. and *parasita* Fabr. are expressly stated to have plumose antennae, and must therefore belong to some other genus. As to *S. cybira* Walk., Walker himself questions its position in this genus. *S. calcitrans* L. is a brownish gray fly; its thorax has three rather broad, whitish stripes; on each border

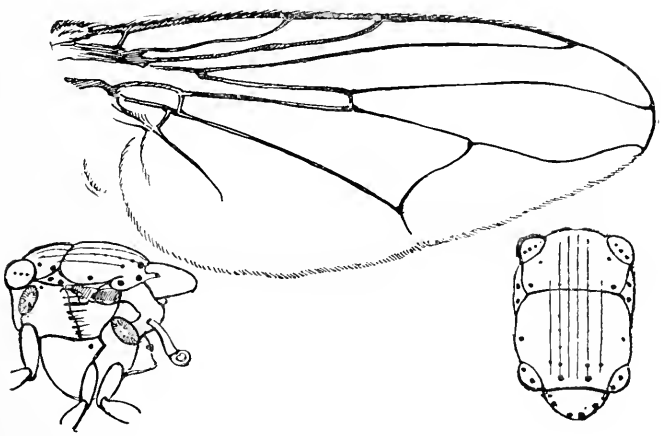


Fig. 1.

of the middle stripe and on the mesal borders of the lateral stripes is a blackish brown line; abdomen yellowish brown; on the second, third, and fourth segments are three brown spots which may be faint or even absent; wings hyaline or tinged with brown at base and along the costa. It has seemed to me that specimens taken on the borders of woods are more likely to have the brownish wings. Antennae brown; palpi yellowish brown; legs blackish brown, with yellowish or reddish knees.

Haematobia. — Two American species are known: *H. serrata* Desv. (Fig. 2 *a*), the "Horn Fly," an unpleasant importation from southern Europe, and *H. alcis.* Snow (Fig. 2 *b*), found by Professor Dyche in the cranberry swamps of northern Minnesota.

The two species are easily separated by the following points: hind tarsi of male serrate in *serrata*, not so in *alcis;* palpi black in *serrata*, yellow in *alcis;* pile of bucca black in *alcis*, yellow in *serrata;* at cephalo-dorsal angle of mesopleura *alcis*

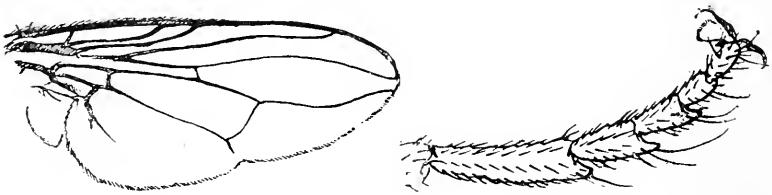
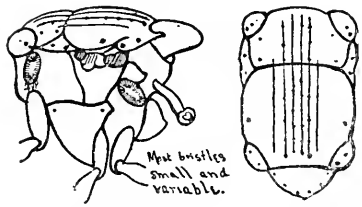


FIG. 2 *a*.



has a large macrochaeta curved dorsad; *serrata* has no macrochaeta at this point; at the cephalo-ventral angle of the mesopleura (protecting the prostigma) *alcis* has two small bristles; *serrata* has a tuft of golden yellow hairs; *serrata* has much longer and denser pile on the dorsum of the thorax. Other color differences are pointed out by Professor Snow in connection with his description of *alcis* in *Can. Ent.*, April, 1891. I am much indebted to the Entomological Department of Kansas University for a pair of specimens of *H. alcis* which have enabled me to ascertain the important differences in the chaetotaxy of the mesopleurae above mentioned.

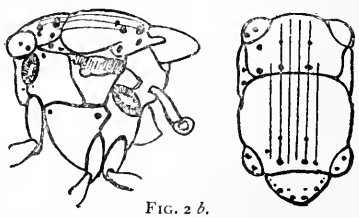


FIG. 2 *b*.

Hemichlora. — Only known species and type of genus *H. vittigera* Bigot, Mexico. Professor Williston, in his *Manual of North American Diptera*, p. 143, suggests parenthetically that this may be the *Idia viridis* of Wiedemann (*Auss. Zweif.*, Vol. II, pp. 354, 11). I quite agree with this suggestion for the following reasons. Meigen founded the genus *Idia* in 1826, and in his characterization (*Syst. Beschr. Eur. Zweif.*, Vol. V, p. 9) the only distinguishing character is the pectinate arista. To this Wiedemann (*loc. cit.*, p. 347) adds: face prolonged forwards

below and entirely without hair. Wiedemann's description of *Idia viridis* is based on one poorly preserved and greasy specimen and reads: "With black antennae, everywhere bronzy green, with hyaline wings and blackish legs. Face and front rusty brown, the green color dark, tending toward emerald green." *Hemichlora* has the pectinate arista, a slightly prominent oral margin, and is in part of a metallic blue color. A metallic blue color may vary to metallic green. Certainly *Hemichlora vittigera* comes nearer to the description of *Idia viridis* than any other known North American Muscid. No other *Idia* has been described from North America, and only the original specimen of *I. viridis* is known.

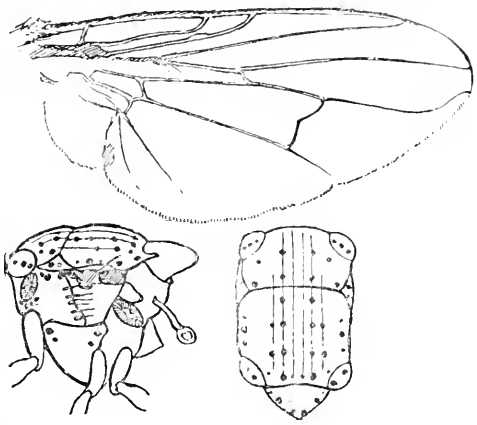


Fig. 3.

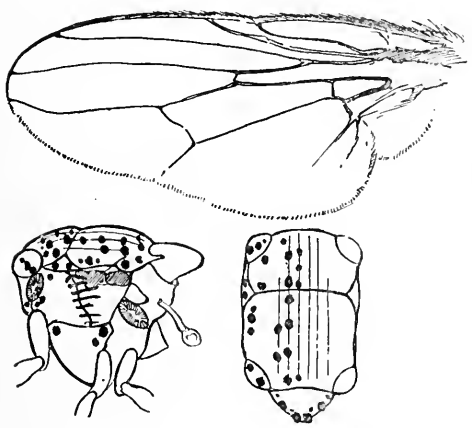


Fig. 4.

Myospila.—There is but one known North American species, *M. meditabunda* Fabr. (Fig. 3). It is common to Europe and America. Many of our specimens have the pubescence of the eyes very short; in the females sometimes it is very difficult to make out with an amplification of twenty diameters. No other difference am I able to find between European and American specimens. It seems to me very probable that *Cyrtoneura quadrisetosa* Thomson (*Eugen. Resa*, p. 549) is one of those

specimens whose eyes are almost bare. I have seen such specimens from California.

Muscina. — Until within a few years our species of *Muscina* have been referred to *Cyrtoneura*. Such authorities as van der Wulp and Williston are of the opinion that *Cyrtoneura* is a badly conceived genus and that the name should be dropped, the species formerly referred to it being divided among the genera *Muscina*, *Clinopera*, *Hemichlora*, and *Morellia*. Similarly, *Cyrtoneurina* should be dropped as a generic name, its species being distributed among some of the genera just mentioned. Following van der Wulp's views in cases where the species are unknown to me, the following are the known North American species of *Muscina: stabulans* Fall., *assimilis* Fall., *mexicana* Macq., *pallidicornis* Bigot, *parilis* Gigl.-Tos, *vecta* Gigl.-Tos, *linea* v. d. W., *tripuncata* v. d. W., *aurantiaca* nov. sp., and *texana* nov. sp. The species that I know may be separated by this table:

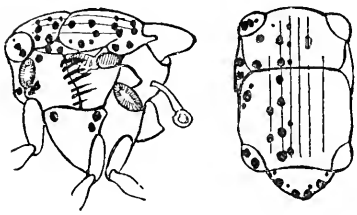
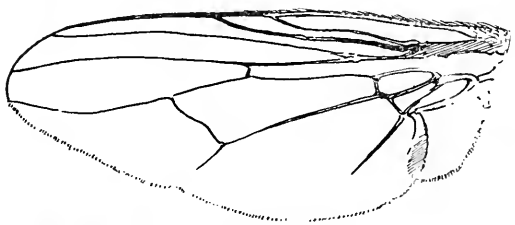


Fig. 5.



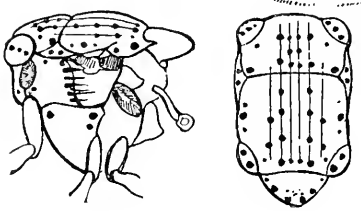


Fig. 6.

1. Legs wholly or partly yellow; palpi yellow 3
2. Legs wholly black 4
3. Antennae brown; three pairs acrostichal bristles cephalad the transverse suture; prostigma brown; humeri concolorous with thorax . . . *stabulans* Fall. (Fig. 4)

Antennae pale yellow; one pair acrostichals cephalad the suture; prostigma whitish yellow; humeri not concolorous with thorax *texana* nov. sp. (Fig. 7)

4. Palpi and antennae . . . . . *assimilis* Fall. (Fig. 5)
Palpi and antennae orange yellow . *aurantiaca* nov. sp. (Fig. 6)

M. aurantiaca nov. sp. — Male and female; several specimens collected by Mr. G. R. Pilate at Tifton, Ga. General appearance like that of *stabulans*, *assimilis*, and *pabulorum*, *i.e.*, with gray-striped thorax and abdomen with variable spots. Chaetotaxy like stabulans, etc.

M. texana nov. sp. — Two males, Texas. Agrees very closely with Giglio-Tos's descriptions of *M. parilis* and *M. vecta*, from which its rather broad front, with the series of transfrontal

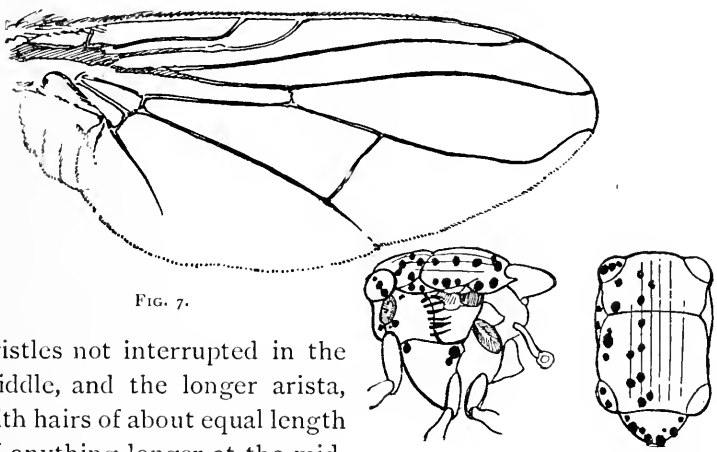


Fig. 7.

bristles not interrupted in the middle, and the longer arista, with hairs of about equal length (if anything longer at the middle of the arista than at the base), and much more scattered than in *vecta* and *parilis*, clearly separate it. The same characters separate it from *M. linca* v. d. W. I separate it from *tripunctata* v. d. W. because of the striking appearance of the prostigma, which I think Mr. van der Wulp would hardly have failed to note had it been present in his specimens.

Clinopera (Fig. 8, *C. inuber* G.-Tos). — Mr. van der Wulp describes in *Biologia Centrali Americana* seven species, and refers to this genus *Cyrtoneurina uber* G.-Tos, *inuber* G.-Tos, *gluto* G.-Tos, and *pellex* G.-Tos. All these species are Mexican. He also refers *Cyrtoneura anthomydea* Bigot to *Clinopera*. It seems to me that there is nothing in Bigot's description that does not apply to *Muscina assimilis* Fall., specimens of which

from the Rocky Mountains (the source of Bigot's specimen) are in my collection.

Muscinae Muscaeformes.

1. Middle tibia with a prominent macrochaeta on its flexor surface . 2
   (The male of some European Mesembrinae has no such macrochaeta, but its middle tibiae are elongate and on their flexor surface thickly hairy.)
   Middle tibiae without such a prominent macrochaeta . . 3
2. Sternopleural macrochaetae 1 : 2 ; elbow of fourth vein forming a rounded angle ; no orbital macrochaetae, but the geno-vertical plate uniformly beset with minute bristly hairs ; transfrontal macrochaetae small and weak, often difficult to see . . . *Pseudopyrellia* Girschner.

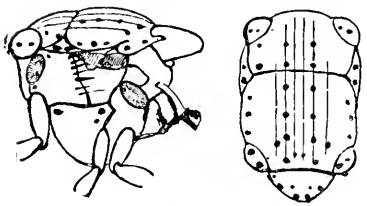


Fig. 8.

   Sternopleural macrochaetae 1 : 3 ; first longitudinal vein ending in the costa at about the middle of the wing ; small cross-vein about opposite the end of the first longitudinal ; elbow of fourth longitudinal not forming an angle but a gentle curve convex toward the hind border of the wing forming an apical cross-vein which is longer than the terminal portion of the fourth vein before its curvature . . . *Pyrellia* Desvoidy
   Sternopleural macrochaetae varying, 1 : 3, 1 : 2, 0 : 1 ; if (rarely) 1 : 1 then the anterior notably the smaller ; first longitudinal vein ending in the costa far beyond the middle of the wing ; small cross-vein a long distance basad to the end of the first longitudinal ; fourth longitudinal sweeping in a broad curve, convex toward hind border of wing, towards the third, thus forming an apical cross-vein, which, however, in our species, is not longer than the terminal portion of the fourth vein before its curvature . . . . . *Mesembrina* Macquart
3. Bend of fourth longitudinal forming a rounded angle. Outline of arista as a whole fan-shaped. Sternopleural macrochaetae 1 : 2. *Musca* Linnaeus
   Bend of fourth longitudinal not forming an angle at all, but a gentle curve 4
4. Antennae separated at their base by a distinct ridge ; sternopleural macrochaetae 0 : 2 ; eyes very distinctly hairy *Graphomyia* Desvoidy
   Antennae not thus separated ; sternopleural macrochaetae 1 : 2 ; eyes not distinctly hairy 5
5. Arista naked . . . *Synthesiomyia* Brauer and Bergenstamm
   Arista plumose . . . . . *Morellia* Desvoidy

Pseudopyrellia (Fig. 9). — Our only known species is *P. cornicina* Fabr. I consider *Lucilia carolinensis* Desv., *L. compar* Desv., and *L. Heraea* Walk., as synonyms.

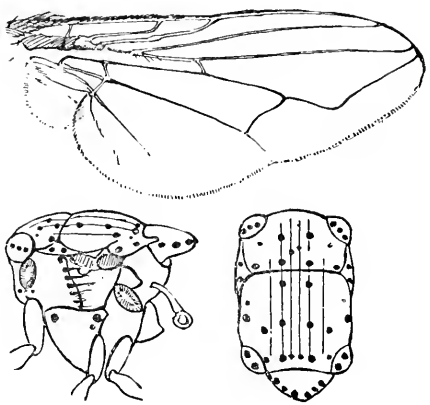


Fig. 9.

Pyrellia (Fig. 10). — The only North American species that I have seen is *P. cyanicolor* Zett. The specimens agree perfectly with the description and with European specimens from Prof. G. Strobl and others. *P. setosa* Lw. is a synonym; I have compared the types in the Agassiz Museum with my American and European specimens. Occasionally one finds a specimen which is of a rather bright metallic green instead of the usual dark steely blue, but I can find no structural or other color differences. *Musca occidentis* Walk., *Dipt. Saund*, p. 347, is probably this same species.

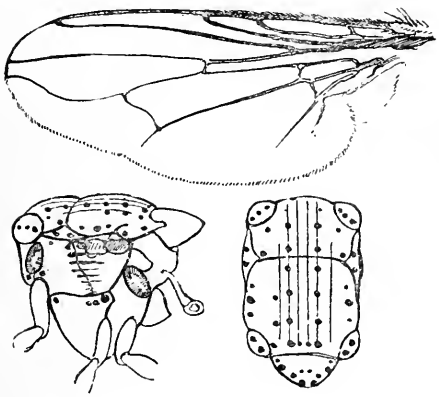


Fig. 10.

P. cadaverina L. may be distinguished from *cyanicolor* by the entire absence of any trace of hoary coating on the thorax even at the cephalic border, while *cyanicolor* has three broad hoary stripes, a median and two humeral, which are specially distinct at the cephalic border.

Mesembrina. — There is but one known North American species, which we must call *M. latreillii* Desv. (Fig. 11) because no other species is known. Desvoidy says: "Tout à fait semblable au *M. meridiana;* un peu plus petite; antennes brunes; la face est d'un argenté brillant sur les côtés." Now

the species is by no means just like *M. meridiana* (Fig. 12); it does not average smaller than that species; the antennae vary in color from yellow to brown; the sides of the face are, however, silvery. The species agrees perfectly with the description of

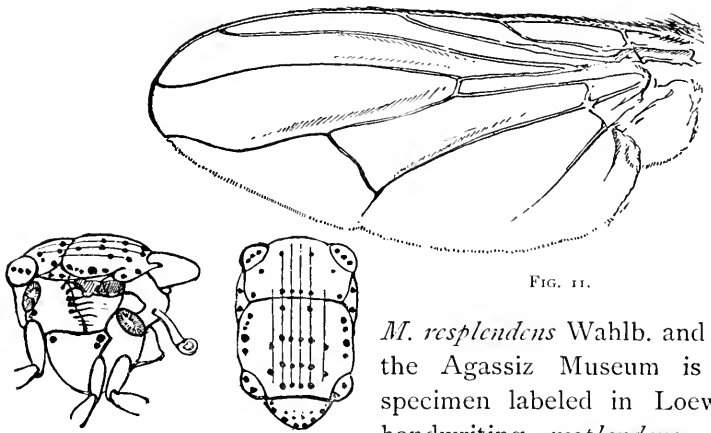


Fig. 11.

M. resplendens Wahlb. and in the Agassiz Museum is a specimen labeled in Loew's handwriting *resplendens*. I think there can be no doubt of the synonymy. Mt. Washington, N. H.; North Mt., Pa.; Seattle, Wash.; Dakota. For comparison I introduce here Fig. 13, *M. mystacea L.* If the truth could ever be known, it is highly probable that *M.*

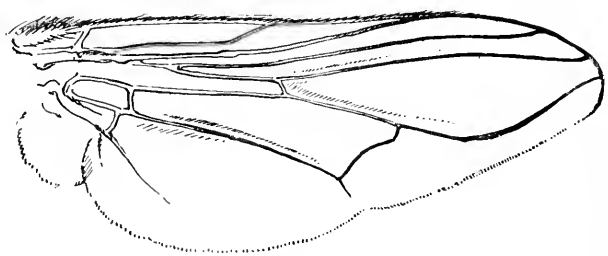


Fig. 12.

pallida Say would be found to be an *Oestrophasia* very near or identical with *O. punctata* Coq.

M. anomala Jaennicke is evidently not a *Mesembrina* at all. Professor Brauer suggests that it belongs near *Spilogaster*.

Musca. — *M. domestica* L. (Fig. 14) is very common. Walker says that *M. corvina* Fabr. occurs in Nova Scotia. The front of *corvina* is very narrow in the male, that of the male *domes-*

tica is about one-fourth as wide as the head; the frontal vitta of the female *corvina* is of uniform width throughout, while that of the female *domestica* is narrow near the antennae and broadens out very considerably towards the vertex. Specimens from

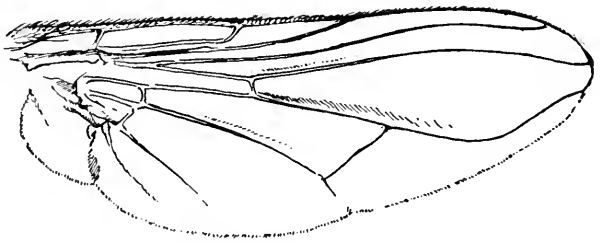


FIG. 13.

Jamaica, agreeing with Macquart's description of *M. basilaris*, are certainly *M. domestica*.

Graphomyia (Fig. 15). — Our single species does not differ structurally and has but insignificant color differences from *G.*

FIG. 14.

maculata Scop., with which I identify it. *G. americana* Desv. is the same species.

Synthesiomyia. — *S. brasiliana* BB. occurs in Florida and in Georgia (Fig. 16). It is the only species of the genus.

Morellia. — *M. micans* Macq. (Fig. 17) is very common all over the United States. Bluish black; thorax with three broad

hoary stripes; last abdominal segment of female brown with hoary coating. Macquart described the female only; the male resembles the female in color (except that the last abdominal segment has much less of a brown color) and has the following structural features which are characteristic: a beard of long hairs on the mesal border of the hind tarsi and a fringe of short, fine hairs on the anterior surface of the middle tibiae not far from the extensor border.

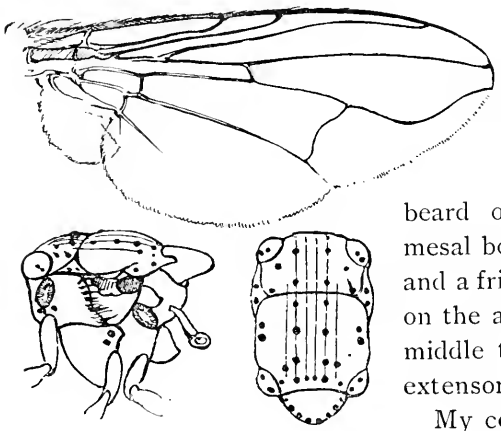


FIG. 15.

My collection contains also two species of *Morellia* from Mexico and Jamaica. One is rather variable, the variations corresponding to the descriptions of *Musca violacea* (Fig. 18) Fabr., *Pyrellia maculipennata* Macq., *P. specialis* Walk., *P. sus-*

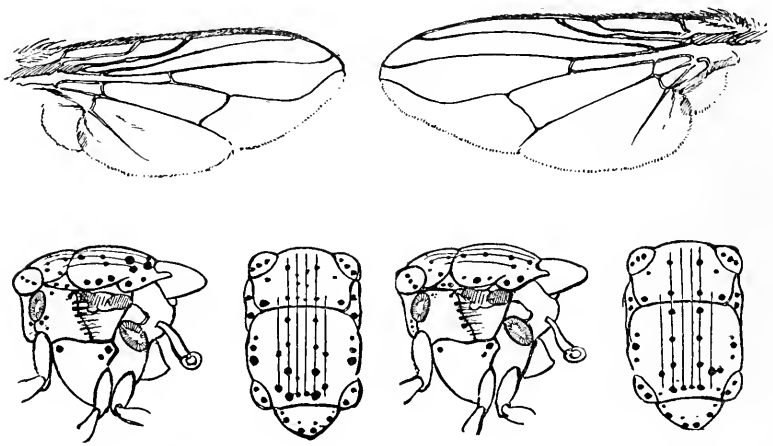


FIG. 16.

FIG. 17.

picax Walk., *P. basalis* Walk., *P. centralis* Lw. (types compared and found to agree), and *P. iris* Bigot. Fabricius's name has priority. The male has on the anterior surface of

the middle tibia, near the extensor border, a series of bristles extending from base to apex; the basal half of the series are very tiny but stout as compared with their length, real little spines; at about the middle of the series the form changes gradually to that of a delicate and moderately long bristle. This arrangement is very like that of the European *M. hortorum* Fall. My specimens of this species are from Jamaica, C. W. Johnson, and from Mexico, O. W. Barrett.

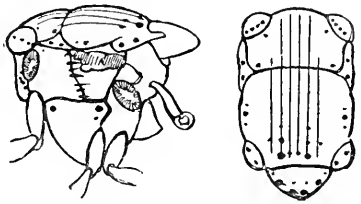


FIG. 18.

The other species agrees with the descriptions of *Pyrellia scapulata* Bigot (Fig. 19) and *P. flora* Bigot. The middle tibia of the male has some noteworthy structures. On the anterior surface at the base is a tubercle about 0.3 mm. (one-seventh the length of the tibia) long and half as broad, its long diameter parallel to that of the tibia. On this tubercle is a row of six or eight very short thick spines, and in some specimens a second row, flexad the first, of about four similar but much smaller spines, can be made out. From the apical end of the tubercle the principal row is prolonged as a series of about equal and equidistant, much more delicate spines, as far as the apex of the tibia. Just at the junction of the posterior and flexor surfaces there are three large bristles; one is at the junction of the basal and middle thirds, the second at the middle of the tibia, the third at the junction of the middle and apical thirds. My specimens of this species are from Jamaica, collected by C. W. Johnson. The name *scapulata* has priority.

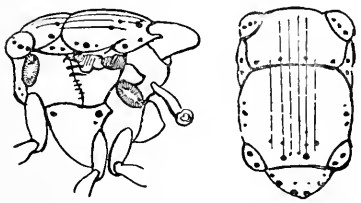


FIG. 19.

Catalogue of Muscinae Mentioned in this Paper but not Referred to in Osten-Sacken's Catalogue.

Haematobia serrata Desv., Myod., 389, 3.

Haematobia alcis Snow, *Can. Ent.*, April, 1891. Vol. xxiii, pp. 87–91.

Hemichlora vittigera Bigot, van der Wulp, Biol. Cent.-Amer. Vol. ii, p. 304.

Cyrtoneura Bigot, Bull. Soc. Zoöl. Fr., p. 613, male. 1887.

Cyrtoneurina Gigl.-Tos, Mem. R. Accad. Sci. Torino. Ser. 2, vol. xlv (sep.), p. 13, female.

Muscina assimilis Fall.

Musca assimilis Fall., Dipt. Suec., Musc., 56, 41. 1820.

Musca caesia Meigen, Syst. Beschr. Vol. v, p. 76, 43. 1826.

Muscina concolor Desv. (?), Myodaires, p. 408, 5. 1830.

Muscina fungivora Desv., *loc. cit.*, p. 408, 6.

Cyrtoneura aperta Macq., Dipt. du Nord de Fr., 11, 4. 1834.

Musca borealis Zett., Ins. Lapp., p. 660, 28. 1838–40.

Cyrtoneura caesia Meig., Syst. Beschr. Vol. vii, p. 309, 5. 1838.

Cyrtoneura aperta Macq., Meigen, *loc. cit.* Vol. vii, p. 309, 14. 1838.

Cyrtoneura caesia Meig., Zetterstedt, Dipt. Scand. Vol. iv, p. 1351, 5. 1845.

Cyrtoneura assimilis Fall., Zett., Dipt. Scand. Vol. iv, p. 1351, 6. 1845.

Cyrtoneura caesia Meig., Schiner, Fauna Austr. Vol. i, p. 597. 1862.

Cyrtoneura assimilis Fall., Schiner, *loc. cit.*, p. 598. 1862.

Cyrtoneura assimilis Fall., Rondani, Dipt. Ital. Prod. Vol. v, pp. 214 and 216. 1862.

Cyrtoneura assimilis Fall., Strobl, Dipt. Steiermark. Vol. ii, p. 76. 1894.

Muscina pallidicornis Bigot, van der Wulp, *loc. cit.*, p. 311.

Cyrtoneura pallidicornis Bigot, Bull. Soc. Zoöl. Fr. Vol. xii, p. 614. 1887.

Muscina parilis Gigl.-Tos, van der Wulp, *loc. cit.*, p. 311.

Cyrtoneurina parilis Gigl.-Tos, *loc. cit.*, p. 14, No. 154.

Muscina vecta Gigl.-Tos, van der Wulp, *loc. cit.*, p. 311.

Cyrtoneurina vecta Gigl.-Tos, *loc. cit.*, p. 14, No. 155.

Muscina linea v. d. W., *loc. cit.*, p. 304.

Muscina trilineata v. d. W., *loc. cit.*, p. 305.

Muscina texana nov. sp.

Muscina aurantiaca nov. sp.

Clinopera. Mr. van der Wulp's species are described in Biol. Cent.-Amer., Dipt. Vol. ii, pp. 305–310. He includes *C. uber* Gigl.-Tos and

inuber Gigl.-Tos in his table, p. 306, and makes some remarks on them, pp. 307 and 308. On p. 311 he refers *Cyrtoneurina gluto* Gigl.-Tos and *pellex* Gigl.-Tos to *Clinopera*. All these species of Giglio-Tos were described as *Cyrtoneurinae* in Mem. R. Accad. Sci. Torino, ser. 2, vol. xlv (sep.), pp. 14–17. *Cyrtoneura anthomydea* Bigot, Bull. Soc. Zoöl. Fr., vol. xii, p. 614 (1887), is referred by Gigl.-Tos, *loc. cit.*, p. 15, to *Cyrtoneurina*, and by van der Wulp, *loc. cit.*, p. 311, to *Clinopera*.

Pyrellia cyanicolor Zett., Dipt. Scand. Vol. iv, p. 1323, 4.

Pyrellia serena Meig., Rondani, Dipt. Ital. Prod. Vol. v, p. 203.

Pyrellia cyanicolor Zett., Strobl, Dipt. Steiermark. Vol. ii, p. 73.

Pyrellia setosa Loew, Centuriae. viii, 63.

Synthesiomyia brasiliana BB. Brauer and Bergenstamm, Vorarb. z. Monog. Musc. Schiz. Vol. iii, pp. 96 and 110.

Morellia violacea Fabr.

Musca violacea Fabr., Syst. Antl., p. 288, No. 25; Wied., Auss. Zweif. Vol ii, p. 409, 43.

Cyrtoneura violacea Fabr., Brauer and Bergenstamm, *loc. cit.*

Pyrellia maculipennata Macq., Dipt. Exot. Supp. 4, 252, 12.

Cyrtoneura maculipennata Macq., Townsend, Ann. New York Acad., p. 33. 1892.

Pyrellia iris Bigot, Ann. Soc. Ent. Fr., p. 36, female. 1878.

Pyrellia centralis Loew, Centuriae. viii, 62.

Morellia scapulata Bigot.

Pyrellia scapulata Bigot, *loc. cit.*, p. 35, female. Mexico.

Pyrellia flora Bigot, *loc. cit.* Male. Haiti.

EXPERIMENTAL STUDIES UPON HYDROMEDUSAE.

C. W. HARGITT.

Syracuse University, Syracuse, N.Y.

In connection with previous work on regeneration the problem of animal grafting was repeatedly suggested by many phenomena associated with that work, and during the summer of 1898 a series of experiments was undertaken at the Marine Biological Laboratory and carried on through the months of July and August.

It is a pleasure in this connection to acknowledge many courtesies extended by the director, Prof. C. O. Whitman, and valuable suggestions from Dr. Jacques Loeb, during the progress of the work. The following paper aims simply to present a résumé of methods and results, deferring speculative considerations which might be suggested by any of the phenomena involved.

I. *Material.*

This was restricted to two sorts of organisms, Hydroids and Medusae. Of Hydroids an almost unlimited amount and of many genera and species were available and easily obtained from the waters about the docks of the U. S. Fish Commission, from the rocks and fucus in the harbor and adjacent waters. It was obtained fresh every morning and experiments were made only upon it within a few hours. The genera used in the experiments were Eudendrium, Pennaria, Parypha, and a few of the Campanularidae.

Of Medusae only one species was available in sufficient abundance and size for experimentation, namely, *Gonionemus vertens*, a Medusa occurring in considerable numbers in the "eel pond," a small body of water adjacent to the laboratory and communicating with the waters of the harbor by a very

narrow inlet. As this Medusa endures artificial conditions with considerable ease for days and even weeks, it lends itself readily to such experiments. Its size also, varying from 2 or 3 mm. to as many cm., is also a factor of convenience, though a larger species would prove desirable in some operations. Its activity during at least three months also facilitates extended experiments.

II. *Methods.*

In grafting the Hydroids, the stems were cut into fragments varying from 5 to 10 mm. in length, and usually taken from the younger and fresher portions of the stem. Successful unions were made from older portions but in much smaller proportions, and requiring much longer time. The hydranths were excised, since the motion of the body and tentacles would invariably disturb the contact of the specimens. Having prepared suitable sections, they were brought into contact in watch-glasses, or small petri dishes, of perfectly fresh sea water, and retained in position by small bits of lead shaved freshly from thin sheets. Bits of platinum wire would have been better, though it was not available at the time, and little appreciable difficulty was had with the lead. The water was changed on the specimens daily.

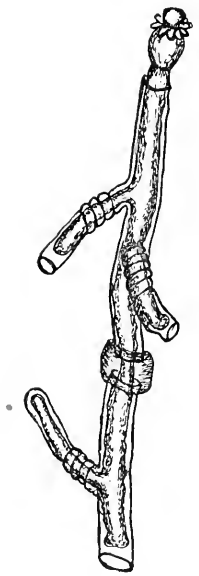


FIG. 1.

With the Medusae the task was a much more difficult one, for while the power of spontaneous movement had been largely eliminated by emarginating the bell and thus removing the marginal nerve ring, and thus the centers of spontaneity, the contractility had not been destroyed, and for a time great difficulty was found in retaining the parts in even contact. And in this connection I desire to correct a partial error in my previous paper on "Regeneration,"[1] where I had failed to recognize the paralyzing effects of such emargination, a fact due to failure

[1] *Zoölogical Bulletin*, I, p. 29.

to remove sufficient of the margin. If the least portion was left, or even a portion quite near the margin, automaticity was retained, but by removing carefully and completely some 2 or 3 mm. of the bell-margin I was able to confirm quite fully the experiment of Romanes[1] on Scyphomedusae.

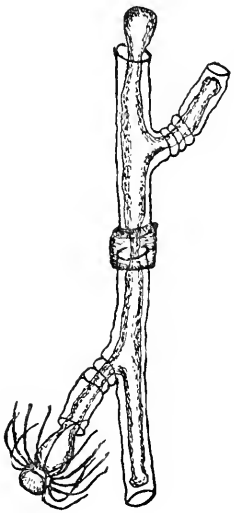


Fig. 2.

After various expedients had failed, resort was had to bits of rather fine shoemaker's bristles, cut into proper lengths. These were thrust through the gelatinous portions of the Medusae in such directions as would serve to fairly secure the desired contact of the surfaces to be united. An inspection of the several figures will give the best idea of how this was secured. *Cf.* Figs. 8 and 9. But at best the method was only partially successful. It may be mentioned in this connection that one of the difficulties attending these experiments was the danger of deleterious contamination involved in the whole of the operations from Bacteria and parasitic Infusoria invading the water and impeding or destroying the experiments. This was much more noticeable in experiments on Medusae than on Hydroids, a fact due in part, certainly, to the promptness with which the latter reacted in regeneration of tissues as compared with the former. Notwithstanding, it is rather remarkable that so small a proportion in either case suffered, since no *special* pains were taken in the way of critically guarding against contamination beyond the more ordinary provisions of clean glassware and instruments. To maintain a fairly equable temperature during unusually hot days, the covered vessels containing the specimens were set under the running water taps of the laboratory.

[1] Jellyfishes, etc., p. 27 *et seq.*

III. *Grafting.*

Hydroids. — The work upon Hydroids was restricted chiefly to species of Eudendrium, Pennaria, and Parypha, though a few experiments were tried upon Campanularians. Upon the latter the results were almost entirely *negative*, though for this no apparent cause was ascertained. The experiments were not of sufficient numbers, nor of sufficiently varied conditions, to warrant any conclusions as to the incapacity of these to regenerate or coalesce. Time was not adequate to extend the attention to this group which might have resulted more favorably. Again, the relatively small size of the members of this group available was a further embarrassment to successful experimentation. However, neither of these is offered as sufficient account of the negative character of the experiments. Indeed, the work of Davenport ('94) on Obelia is strongly affirmative, at least so far as regeneration is concerned.

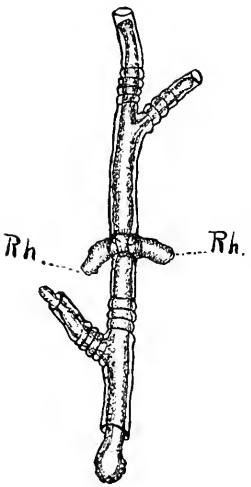


Fig. 3.

Experiments upon species of the genera named were specially successful. While of course in all such work a large number of failures must result, yet when the difficulties of manipulation and the artificial conditions necessary are considered, this is not strange.

While no mathematical estimates were made as to the ratio of successful experiments, I think it may be safely said that at least 20 per cent of all were successful. It need hardly be pointed out that results varied materially in both the time necessary, and the degree of perfection, in the coalescences. This will be noted in detail in connection with the several experiments described.

A comparison of the several figures will perhaps indicate in general better than words the methods and results. *Cf.* Figs. 1–6.

The union between sections of the same species was usually quite perfect within from eighteen to thirty-six hours. A

delicate sheath of perisarc secreted over the ends was the first indication of special activity and regeneration. This usually occurred at any wounded point. It became specially marked at the points of contact of the grafted specimens. The first effect of the sectioning of the specimens preparatory to their being placed in contact was a pronounced contraction of the coenosarc within the tubular perisarc, and the closure of the cut ends of the enteric cavity. This was usually, however, soon followed by an outgrowth till the coenosarc of the two specimens came into contact, when the secretion of the extra perisarc proceeded as a joint operation, though sometimes by a single one, if its activity and response were the more prompt. *Cf.* Figs. 1 and 2.

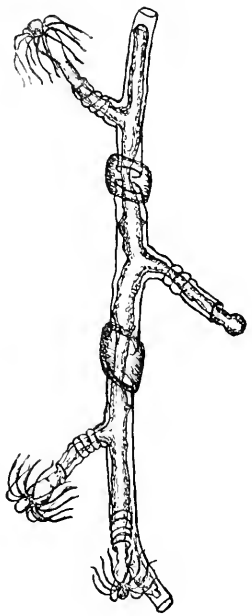


Fig. 4.

Following this the contact of the two became more intimate, the healed ends united with each other, fusion being followed by the absorption of the terminal portions and the consequent confluence of the enteric channels and their contents.

In the experiments no apparent difference was noticeable as to anything like polarity, the parts uniting orally, aborally, or otherwise, with equal freedom and promptness. With species of Eudendrium and Pennaria this was demonstrated with absolute certainty, the directions of the branches making any mistaking impossible. *Cf.* Figs. 2–4.

In these species the sexes are distinct, and experiments in grafting specimens of the opposite sexes were quite as prompt and perfect as otherwise. There would seem, therefore, to be not only no definite differences of polarity as seems to be the case in Hydra, but no sexual difference in so far as regenerative or coalescence capacity is concerned. It remains to note results as to grafting different species. With none of these are the distinctions sufficiently clear to warrant positive con-

clusions. Of Pennaria, only one species was available, and the same was true of Parypha. Of the species of Eudendrium there have been several indicated, but their distinctness is to my mind open to serious doubt.

FIG. 5.

If the distinctness of Agassiz's species of *E. dispar* and *ramosum* is to be maintained, then the grafting of these has been as clearly established as that of the different sexes. It would not be strange should closely allied, though definitely distinct, species be found to coalesce in these organisms, for such has been long known among plants, and shown for animals by the recent experiments of Born ('96), Crampton ('97), Harrison ('98), and others. But so far as I am aware it has not hitherto been demonstrated for the Hydroids; indeed, most of such efforts have been negative in results.

As to the coalescence between specimens of different genera, the experiments seem to be conclusive and wholly negative. Out of a considerable series, while there were indications of temporary union, in no case did it become conclusively permanent. The most favorable indications were upon Eudendrium and Pennaria, Hydroids of very similar size, structure, and habit; but after repeated experiments under different conditions the results were as already indicated. In Fig. 6 it will be noted that the usual secretion of perisarc at the points of contact has been deposited, and apparently by the coöperation of both sections; still at no time were there evidences of organic union of the coenosarc, and later this was distinctly withdrawn, and the sections continued an independent existence, each producing new hydranths, though in the case of Eudendrium they continued rudimentary in the specimen figured.

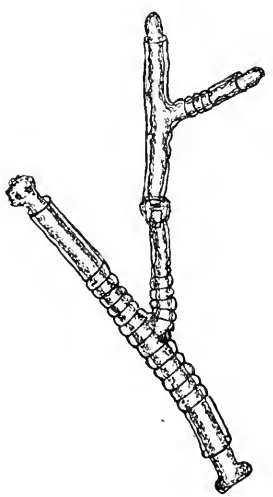


FIG. 6.

IV. *Medusae.*

Experiments upon Medusae were restricted to *Gonionemus vertens*, being the only species available in sufficient numbers, and capable of adaptation to the artificial condition necessitated by the nature of the work. This Medusa is found in great numbers, though only in a limited locality adjacent to the Marine Laboratory, and lives readily for several days, or even weeks, in table aquaria, if reasonable precautions be taken to keep the water fresh and supply suitable food.

While the experiments were quite extensive and various, aiming at first to ascertain the trend of resultants, no attempt will be made in this connection to describe them in any con-

FIG. 7.

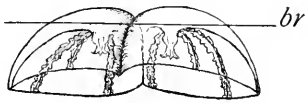


FIG. 8.

siderable detail, but rather to call attention to a few of the more conspicuous of them, and to indicate something of their probable significance.

Fig. 7 will afford a good idea of the general features of the Medusa with the entire margin of the bell and its organs excised, preparatory to any contact experiments.

In Fig. 8 are shown two Medusae from which portions have been removed, the larger part of each being brought into contact and retained by the bristle, *br.*, passing through the body. In some instances two or three bristles were passed through in different planes, thus giving greater stability of contact.

Parts of various sizes and from different regions were similarly grafted, and with usually similar results. The time required for union differed greatly in experiments conducted under exactly the same conditions and care. In some cases complete union had taken place within twenty-four hours, while in others it only occurred after several days. It should be noted, however, that when once coalescence had begun it usually went forward with comparatively great rapidity.

In Fig. 9 is shown the coalescence of two Medusae by their oval margins. This was usually the most easily performed of any of the experiments upon the Medusae, and union was rather more prompt if any difference was noticeable. As will be seen from the figure, fusion was not entire in this case, a small mouth-like opening remaining on one side through which aëration of the interior was made possible, and by means of which by contraction the united individuals were able to move about in the water. It should be noted in this connection that upon stimulation coördinated movements were produced, and in a few instances even apparently spontaneous movements were clearly recognized. I have said that this action was *apparently* spontaneous. It is not impossible, of course, that some extraneous stimulus might have been involved, but, if so, it was wholly beyond any ordinary physical detection, and was distinctly recognized by several persons to whom it was pointed out.

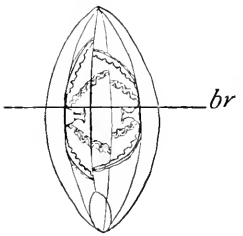


FIG. 9.

In these experiments, in a few cases, the specimens united completely throughout the entire margin, but with the result that the specimen died within a comparatively short time, presumably from inability to secure aëration of the portions where metabolism was most active and aëration most imperative.

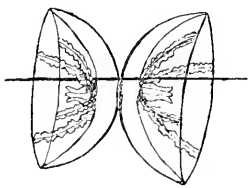


FIG. 10.

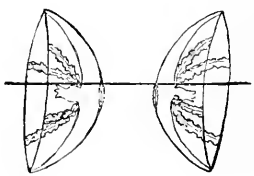


FIG. 11.

Figs. 10 and 11 show a method of aboral grafting made upon a considerable number of specimens, but uniformly without permanent success. As will be noted in Fig. 11, the points of contact were slightly scarified, or in some cases portions excised with sharp scissors, in order to favor coalescence of

the surfaces, but after a few hours the specimens would almost invariably have drawn apart by some sort of creeping movements, probably aided in part by the prehensile character of the manubrium, and usually one or both finally extracting the bristle entirely. I am not able to suggest any satisfactory explanation of the negative character of this experiment. Whether regenerative tissue is wanting on this area, or whether some intrinsic repugnance to such fusion be the cause or occasion, or whether some cause wholly undetected was present, seems a matter of doubt. There would seem to be no *a priori* reason why this particular experiment should not find as ready a response as those already described. The inverted position could hardly be assigned, for specimens in similarly inverted aspects readily united by the margins, as indicated in Fig. 12.

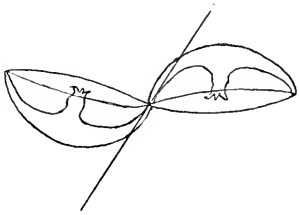


FIG. 12.

In Figs. 13–16 is shown a phenomenon which appeared in connection with the series of experiments quite incidentally, and of which I shall undertake no particular explanation, and yet which is one of the most novel and interesting of the entire series.

FIG. 13.

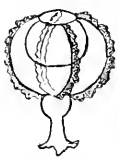


FIG. 14.

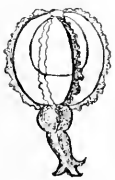


FIG. 15.

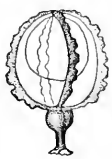


FIG. 16.

In certain aboral grafts, similar to those already described in Fig. 10, a single specimen was found with the bell somewhat evaginated, as in Fig. 13. During the following days, July 27 and 28, it passed successively through the phases represented in Figs. 14, 15, and 16, becoming permanently united in the completely evaginated form of Fig. 16, in which condition it continued to live and even take particles of food, though it showed no evidences of growth, beyond a distension of the gastric pouch due to the engulfed food. Finally, on August 3 the specimen died during the very sultry night, and was found the

following morning in a partially disintegrated condition, a result due in part to the unusual temperature, and perhaps in part to overfeeding.

A series of experiments were undertaken by which to secure, if possible, by artificial means other inversions of a similar sort, and though various expedients were adopted by which to facilitate such, they gave no permanent results.

The phenomenon of eversion in the Medusae of Obelia and other Hydroids in their young or newly discharged condition is quite well known, but it continues for a brief time only, and with no disposition toward permanence so far as I have known.

Of course the classical experiments of Trembley (**1744**), Nussbaum ('**87**, etc.), and others upon Hydra are too well known for special comment, and at first sight might be thought to be analogous to that now under consideration ; but a moment's reflection will suffice to show that it is only so in a very general way. For example, there is no inversion of the relative position of ectoderm and endoderm, since the lining of the bell, outer surface of the manubrium, etc., is ectodermal. The enclosed cavity of the everted specimen served no new function in its changed condition, nor did the outer layer in its new relations. That any change in the histological characters would be induced may therefore be considered very unlikely since the change of relative position, while considerable, is yet not such as would necessitate any change of function. Nevertheless the fact is an interesting one, and apparently quite unique. At one time, just about the completion of union of the inverted margins, a decided papilla-like bud appeared at the aboral area which presented some resemblance to a second manubrium, but this soon after was absorbed entirely, and was probably only the elevation due to the approximation of the margins preparatory to final union.

V. *Regeneration and Heteromorphosis.*

In connection with the foregoing experiments occasion was taken to repeat some of my earlier experiments on regeneration and to extend them somewhat. At an earlier point in

this paper I have indicated an error in the former paper, as to the paralysis of the Medusa following the complete removal of the marginal portion of the bell. I desire, moreover, to express more definitely than appears in the earlier paper, though it was clearly implied at several points, the fact that in all those experiments there does not appear to be any actual increase of mass, or growth of the body as a whole, but that in all the regenerative activity it was evidently at the expense of other portions of the body proper. This would naturally follow in most cases, since in producing a new manubrium, or new tentacles, or in the grafting experiments, the animal was practically incapacitated for obtaining food, and under the artificial conditions of the experiment could hardly have been sufficiently fed to make evident any growth. In many cases a very evident decrease in size was apparent in the progress of the experiment. Indeed, in many cases manubrium, velum, tentacles, etc., continued to live for weeks accompanied by a gradual decrease in the body mass, till it finally became wholly consumed, after which the organs gradually disintegrated.

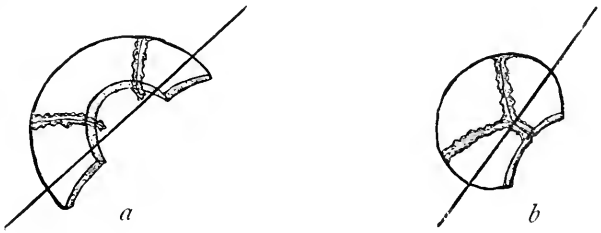


FIG. 17.

In all essentials the later experiments confirm those earlier made. Further attempts were made to put specimens under such conditions as would render difficult any mere contraction or approximation of the surfaces. Figs. 17 and 18 will show two out of a considerable number and variety of the experiments. In these the portions of the body were set in their relative positions by bristles in such a way that only continued contractions of considerable vigor would be able to change them. But within forty-eight hours the results indicated in the several figures had taken place, the stereotype form of body assumed,

and without indication of specific regenerative growth and absolutely no hint at heteromorphism in the slightest way.

Figs. 19 and 20 show experiments designed to further test the regeneration of the manubrium. The operation of removing the organ was made on August 4. As will be seen in the case of Fig. 19, about three-quarters of the animal were excised, leaving one chymiferous canal fairly complete, and a mere remnant of a second, the whole of the manubrium hav-

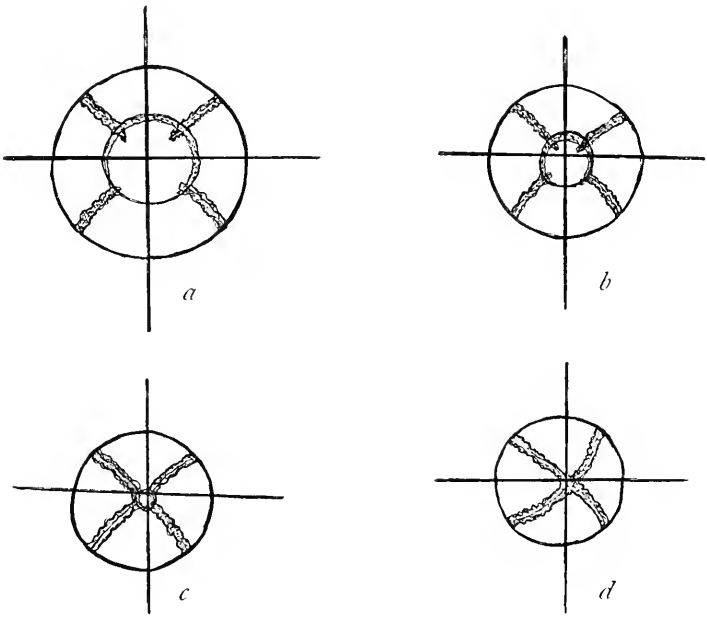


FIG. 18.

ing been removed, as indicated by the line of the cut, *a-b*. In Fig. 20 a wedge-shaped piece, about one-fourth the body mass, including the manubrium, one entire canal and the central portions of the other three, as indicated, was excised.

On August 5 the cut margins in each case had approximated each other and were evidently uniting. On August 7 the union was complete and the Medusae were swimming quite freely and naturally. On August 9 the first indications of a new manubrium were apparent, and in approximately the normal position. Its color and texture clearly indicated its forma-

tion as a new outgrowth, there being only the slightest traces of pigment present. The growth was quite gradual, and not until about August 14 had it become fully formed and functional.

In each case there had also been regenerated additional radial canals, as indicated in the figures. These appeared in connection with the lines of union, and were not at first

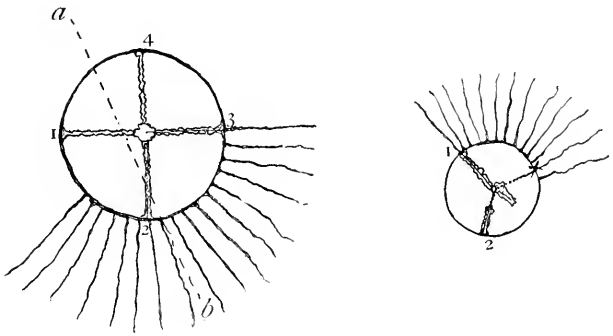


FIG. 19.

suspected as canals. Later the deposition of pigment along their course pointed strongly to the conclusion that they were canals, though whether yet functional I am not able to say.

In none of my experiments has there been any clear confirmation of the results and conclusions of Bickford ('94) that in Hydroid regeneration the polyp, tentacles, etc., are produced

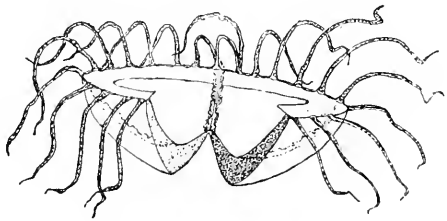


FIG. 20.

simply by a "transformation of the tissues of the stem"—that is, that the tentacles are formed by a sort of longitudinal cleavage of the coenosarc, and a remolding of it directly, without any tissue changes. In cases where there is only a recasting of a portion of the body into the *form* of the original, as in the case of a Medusa divided into sections, where each

part assumes the typical shape of the whole, being only different in *size*, this is of course clear. But from an inspection of Fig. 1 it will be evident that the tentacles are regenerated by a process of budding and growth exactly as in Hydra. The same was even more evident in the regeneration of tentacles, manubria, etc., in the Medusae. In every case they originate as minute buds, and become functional only after a considerable period of growth.

Whether additional tissue is formed from "*a few undifferentiated cells*," a sort of reserve embryonic tissue, may indeed be doubtful. Still, that there is *growth* in the ordinary histogenic sense must be evident in these cases as truly as in that of the regeneration of the tail or limb of the newt. And, indeed, it hardly seems to be more than a verbal quibble whether it be by one or *both* processes. For in either case it simply implies the presence in these organisms of cells or tissues possessing the capacity, shared in common with embryonic or undifferentiated tissues, of reparation.

VI. *Historical.*

Experimental work on the Hydrozoa may be said to date from the classical researches of Trembley, published in 1744, upon species of Hydra. He divided specimens into pieces of various sizes and shapes, and from various portions of the body, securing entire polyps from each.

He turned polyps inside out and had them live and thrive for months. He also grafted portions of one upon another with equal facility and success.

These researches were later repeated by Baker, who, while confirming some of Trembley's experiments, was not able to do so for all of them. Similar results were had by Rösel von Rosenhoff in 1755, who in addition claimed to have secured entire polyps from fragments of tentacles.

In 1878 Engelmann again repeated Trembley's experiments, and with results very similar to those of von Rosenhoff.

Marshall in 1882 was not able to secure successful grafting or eversion, but regeneration of polyps from portions of ten-

tacles, the body of the tentacle becoming the body of the polyp, and in turn forming new tentacles.

Nussbaum in 1887 and 1890 successfully everted specimens and described the process by which the body layers righted themselves. He secured no regeneration from detached tentacles.

Ischikawa in 1889 experimented upon eversion of Hydras successfully and described the process by which the layers readjusted themselves, differing in some respects from the account of Nussbaum.

In 1895 and 1898 Wetzel grafted specimens and secured union between portions of same species; but while bits of a different polarity united, the distinctness of polarity was only exceptionally modified. He secured only temporary unions of portions of different species.

Miss Peebles in 1897 undertook the determination of the smallest portions of Hydra capable of regeneration.

Rand in 1898 worked out interesting results on the "Regulation" of regeneration in Hydra.

Comparatively little has been done of an experimental nature upon Hydroids.

Loeb in 1891 carried on an extensive series of experiments on regeneration and heteromorphosis among Hydroids, chiefly of the genera Antennularia, Eudendrium, and Tubularia, with the object of determining as far as possible the external conditions and causes which affect life and growth. Light and gravitation were shown to have a profound influence in determining many of the phenomena.

In 1892 Miss Bickford conducted experiments on *Tubularia tenella*, confirming in many points the work of Loeb.

Davenport in 1894 conducted regenerative experiments upon *Obelia commisuralis*, with a view to determining the distribution of generative or embryonic tissue in various regions of the Hydroid.

The contribution of the present writer to the general subject in 1897 has already been cited.

Driesch in 1897 reviewed the work of Loeb and Bickford on Tubularia.

Summary and Conclusions.

1. Tubularian Hydroids readily react to experiments directed toward regeneration or grafting.

2. They exhibit in most cases striking illustrations of heteromorphosis.

3. They show no marked polarity, readily coalescing in either oral or aboral relations.

4. They show no sex differentiation of tissues limiting the process of grafting.

5. Closely allied species may be intergrafted.

6. Different genera have not been successfully grafted.

7. Hydromedusae respond to regenerative and grafting experiments with almost equal readiness.

8. No definite aboral grafting of Medusae has been successfully made.

9. Medusae show throughout a sharp polar orientation.

10. No heteromorphic results have been shown among Medusae.

SYRACUSE UNIVERSITY, June, 1899.

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BIBLIOGRAPHY AND PUBLICATION.

Zoölogical Bibliography and Publication. — Second Report of the Committee, consisting of Sir W. H. Flower (*Chairman*), Professor W. A. Herdman, Mr. W. E. Hoyle, Dr. P. L. Sclater, Mr. Adam Sedgwick, Dr. D. Sharp, Mr. C. D. Sherborn, Rev. T. R. R. Stebbing, Professor W. F. R. Weldon, *and* Mr. F. A. Bather (*Secretary*).

The Committee wishes to state clearly that it has no wish, even if it had the authority, to lay down laws for zoölogists or for publishing bodies and editors. It is, however, plain that many are grateful for some guidance, and the Committee hopes that it may serve as a medium for conveying to those who need it the general opinion of the experienced. There are also difficulties which, though they appear to some insuperable, may possibly be surmounted in ways that have been communicated to the Committee.

> (1) 'That each part of a serial publication should have the date of actual publication, as near as may be, printed on the wrapper, and, when possible, on the last sheet sent to press.'

Five correspondents do not see the use of this, thinking that the date on the wrapper is enough, and that in the case of annual publications the date of the year suffices. The Committee would point out that wrappers are constantly lost in binding, and that periodicals are often broken up by specialists or secondhand booksellers, the consequent loss of date causing much trouble to workers of a later day. To avoid this, the Cincinnati Society of Natural History would add the date at the head of each paper, while *Natural Science* prints the month and year across every page opening. Some societies, *e.g.*, the Philadelphia Academy, issue a certificate of dates at the end of the volume. The Liverpool Biological Society 'put at the head of each paper the date when it is read, and are willing to add the date when it is printed off'; neither of these dates are necessary, and they may be misleading. In most cases the actual day of publication is immaterial, especially in cases where no new species are described, but at least the month should always be given, and the Committee does not see that there need be any difficulty in doing

this. If some unforeseen delay does occur, the date can always be rectified with a date stamp.

> (2) 'That authors' separate copies should be issued with the original pagination and plate numbers clearly indicated on each page and plate, and with a reference to the original place of publication.'

The Committee believes this to be a most important recommendation, and its view is supported by all the zoölogists consulted. Nevertheless, many leading publications continue to issue authors' copies repaged, and often without reference to volume number, date, or even the name of the periodical. The remedy is so simple that the Committee urgently appeals for its universal application.

> (3) 'That authors' separate copies should not be distributed privately before the paper has been published in the regular manner.'

It is a curious fact that on this question editors take a different line to working zoölogists. All the latter who have discussed the matter agree with the Committee as to the extreme inconvenience caused by the general custom. Among the editors, however, nine (*i.e.*, nearly one-quarter) protest against the present recommendation. The objectors represent small societies which publish at lengthy intervals, and their reasons are: that it is not fair to an author to prevent him from receiving his separate copies for perhaps a year; that it is not to the advantage of science that work should thus be delayed; that a society which did this would receive fewer contributions and lose its members. In brief, the argument is: 'We are too poor to publish properly; therefore we must allow authors to publish improperly.' This form of argument suggests an easy remedy, and one that, on the informal suggestion of the Committee, has already been put into practice by the Liverpool Biological Society and by the R. Physical Society of Edinburgh. The remedy is this:

In cases where a volume or part can only appear at long intervals, each author that requires separate copies of his paper for private distribution before its publication in the volume or part should be permitted them only on this condition — that, for every month before the probable issue of the volume, a certain number of copies — say five — should be placed by him in the hands of the society or its accredited publisher, in order that they may be offered for sale to the public at a fixed price. Further, that the society, for its part, should announce the publication, with price and

agent, of their papers to some recognized office, or to some such paper as the Zoologischer Anzeiger. The details of expense must be settled between the author and the society.

(4) 'That it is desirable to express the subject of one's paper in its title, while keeping the title as concise as possible.'

It is satisfactory to find no objections raised to this recommendation, since there is no doubt that there is room for much improvement in this direction. Such phrases as 'Further contributions towards our knowledge of the . . . ,' or 'Einige Beobachtungen über . . . ,' or 'Essai d'une Monographie du genre . . . ,' might well be dispensed with as superfluous. The ornithologist who, in 1895, published a book with a title of ninety-one words would seem to have forgotten the functions of a preface.

On the other hand, it is pointed out that certain periodicals, such as the *Bulletin de la Société Entomologique de France* and the *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin*, publish communications without any title, to the constant confusion of naturalists. The Committee begs to urge the reform of this practice, in which it can see no advantage.

(5) 'That new species should be properly diagnosed, and figured when possible.'

The only comment on this is the proposed omission of the words 'when possible.' With this the Committee sympathize, but wish to avoid all appearance of laying down a law that would constantly be broken.

(6) 'That new names should not be proposed in irrelevant footnotes or anonymous paragraphs.'

Naturally nobody supports such actions as are here objected to, but since some have doubted the possibility of the latter, it is as well to state that the suggestion was based on an actual case occurring in the Report of a well-known International Congress. The proposal of a new name, without diagnosis, in a footnote to a student's text-book, or in a short review of a work by another author, is a by no means rare occurrence. The Committee believes that such practices are calculated to throw nomenclature into confusion rather than to advance science.

(7) 'That references to previous publications should be made fully and correctly if possible, in accordance with one of the recognized sets of rules for quotation, such as that recently adopted by the French Zoölogical Society.'

Dr. Paul Mayer, of Naples, writes : 'Most authors are extremely idle in making good lists of literature themselves, and even oppose my correcting them according to our rules. There ought to be some training in this at our Universities.' This is confirmed by one or two other editors, but not all have the energy of Dr. Mayer. Some, indeed, oppose the word 'fully' on the ground that it leads to waste of time and space. The Committee would explain that the reference to a particular set of rules was intended merely as a guide to those who have not had the training that Dr. Mayer would like to see; they would also point out, in the words of the editor of the Cincinnati Society of Natural History, that 'what may be intelligible to the specialist is very puzzling to the general student.' Nowadays, when so many zoölogists work with the aid of authors' separate copies, it is an enormous convenience to them to have the title of the paper at least indicated, and not merely the volume, date, and pagination given. The Committee, therefore, cannot agree that this suggestion involves a waste of time.

Communications with reference to this Report should be addressed to F. A. Bather, Natural History Museum, Cromwell Rd., London.

Volume I.] *January, 1900.* [*No. 2.*

BIOLOGICAL BULLETIN.

THE EARLY STAGES IN THE DEVELOPMENT OF THE HYPOPHYSIS OF AMIA CALVA.

J. M. PRATHER.[1]

THE results of my work on Amia do not agree with the common assumption that the pituitary body is always of epiblastic origin. This disagreement has led me to an examination of the literature on the subject to see if there is sufficient unity of opinion among recent investigators to warrant such a general conclusion. As a result it is found that a diversity of opinion still prevails, and that it is unsafe to predict its origin in any class of vertebrates.

A brief classification of the various views and their respective advocates is of interest in this connection: K. E. von Baer ('28), Huschke ('54), and F. Schmidt ('62) believed the hypophysis to be a modified part of the brain. Reichert ('40) and His ('68) claimed that it is derived from the end of the chorda. Reichert ('61) and Rathke ('61) believed it to be derived from the pia mater, each having changed his earlier view. Dursy ('68) maintained that it is of threefold origin — from the foregut, the chorda, and the brain.

The above represent the earlier but now generally discarded hypotheses. The more modern views, some of which were also held by the older anatomists, may be grouped as follows:

1. *That the hypophysis is of hypoblastic origin,* as held by

[1] This study was undertaken at the suggestion of Dr. A. C. Eycleshymer and completed under his direction in the Department of Anatomy and Histology in the University of Chicago during the summer of 1899.

Rathke ('38), Luschke ('60), Kölliker ('61), Miklucho-Maclay ('70), W. Müller ('71), His ('75), Hatschek ('81), Dohrn ('81), Owen ('82), Balfour and Parker ('82).

It should be emphasized that, in general, this was claimed for the particular form investigated, but not claimed to hold true for all vertebrates.

2. *That the hypophysis is of epiblastic origin*, as claimed by Goette ('72), Balfour ('74), Mihalkovics ('74), Kölliker ('76), Cattie ('81), Julin ('81), Dohrn ('82), Kraushaar ('83), Johnson and Sheldon ('86), Orr ('87), Scott ('87), Kupffer ('90), Lundborg ('94), Dean ('96), Haller ('96), Braem (98), Minot ('98).

It should be added that the majority of these observers not only claimed the hypophysis to be of epiblastic origin in the particular form examined, but also believed this to hold good for the Vertebrata.

3. *That the hypophysis is partially of hypoblastic and partially of epiblastic origin*, as positively maintained by Kupffer ('93), Valenti ('95), and Nussbaum ('96), and considered probable by Hoffmann ('85), Orr ('87), and Gaupp ('93).

The researches made by the above-named writers show that the organ varies so much in its development and structure in the different forms that generalizations should be made with extreme caution, until more extended and precise observations have been made.

While its development has been more or less carefully traced in animals representing nearly every group of vertebrates, I find that the Ganoids have received but little attention. Kupffer has described and figured its earliest stages in *Acipenser sturio*. This author finds such an unusual mode of development that it seems possible that he has misinterpreted certain structures connected with the development of the sucking discs, for, as the sequel will show, at a certain stage in their formation in Amia these discs present appearances very similar to those regarded by him as the beginnings of the hypophysis. A fuller discussion is reserved for a later page.

Balfour and Parker have figured some of its early stages in *Lepidosteus osseus*, but have given no adequate description of its origin. Judging from their figures and few

remarks, its early history is in most respects quite similar to that in Amia.

Dean has figured a very early and a very late stage in its formation in *Amia calva*. No description is given of these stages, but the generalizations made therefrom seem, in the light of my researches, to be somewhat questionable, and to them I shall later recur.

Concerning the observations by Professor Minot I know nothing further than the simple statement in *Science*, Feb. 18, 1898, that he had confirmed and extended the results of B. Haller. As Haller's extensive observations did not embrace the Ganoids, I infer that this statement does not pertain to Minot's investigations upon Amia.

With these facts before us it will be seen that a detailed account of the development of the hypophysis in the last mentioned form will not be superfluous.

The sections for this study were placed at my disposal by Dr. Eycleshymer, and consist of series of sagittal, horizontal, and transverse sections of the embryo and larva, in many successive stages of development, up to and including the thirty-fifth day after fertilization. All ages given in the following descriptions are reckoned from the time of fertilization.

Many examinations were made with the oil-immersion and all the drawings have been made with the aid of the camera lucida. The literature consulted, and that to which reference has been made, consists for the most part of papers enumerated by Kupffer[1] and Haller.[2] Since a very complete bibliography is given by each of these authors it would be superfluous to duplicate them in the present paper.

Description of Stages.

The earliest stage in the formation of the hypophysis, clearly recognizable as such, is found in an embryo a few hours before

[1] Kupffer, C. von, "Die Entwicklung des Kopfes von Acipenser Sturio an Medianschnitten untersucht." München und Leipzig. 1893. "Die Deutung des Hirnanhanges," *Sitzungsber. d. Gesell. f. Morph. u. Phys. in München.* Jahrg. 1894.

[2] Haller, B., "Untersuchungen über die Hypophyse und die Infundibularorgane," *Morph. Jahrb.* 1897.

hatching, as shown in Figs. 2 and 3. In order to show the relations of position which the various organs bear to one another prior to the differentiation of the hypophysis, I figure a median sagittal section of an embryo surrounding about 245° of the circumference of the yolk, corresponding to an age of about 148 hours (Fig. 1). At this stage the foregut (*fg.*) is seen to have formed as far back as the posterior limit of the third primary vesicle (*hb.*), where the endoderm forming its wall is reflexed upon itself and passes forwards again over the surface of the yolk (*y.*). By tracing the foregut through the successive sections of the series, we find it to be a very broad cavity compressed dorso-ventrally until its upper and lower walls are in close apposition in the region immediately under the base of the first primary vesicle, which rests directly upon its dorsal wall. Its walls are slightly separated both anterior and posterior to this region. In the median plane, as shown by the figure, the cavity can be traced forwards to a point somewhat anterior to the front wall of the brain (*br.*). From its anterior end a diverticulum may be traced on either side in front of the brain, nearly to the dorsal median plane. These endodermal diverticula later become transformed into the larval adhesive organ, as has recently been shown. The endodermic layer increases in thickness anteriorly until a maximum thickness is attained in the adhesive organ just mentioned. The walls of the endoderm cells cannot be distinguished, owing to the great amount of yolk material found in them.

The ectoderm at the anterior end is invaginated in two places. The upper invagination (*o.*) is merely a depression within the adhesive organ which is developing beneath the ectoderm by diverticula from the foregut, as just described, pushing the ectoderm outwards in the form of a circular ridge (*ao.*) around the snout. The lower invagination is the involution for the stomodaeum (*st.*), and has already pushed inwards nearly to the endoderm surrounding the foregut. This invagination is on a lower plane than the foregut and is directed distinctly downwards, making a small angle with that plane.

The large cavity (*c.*) between the brain and the epiblast in front is for the most part filled by the developing adhesive

organ. But surrounding this may be seen mesodermal cells which form a strand running downwards between the stomodaeum and foregut and connecting with those forming the heart (*h.*) below. The chorda extends no further forwards than the posterior margin of the hind brain. The brain is not as clearly delimited from the ectoderm above as the figure indicates. The first primary vesicle (*fv.*) is evaginated at its base both in front and behind, giving rise to the recessus opticus (*ro.*) and the infundibulum (*in.*) respectively. The base of this vesicle is arched considerably and conforms closely to the dorsal wall of the foregut.

In an embryo about 160 hours old (Fig. 2) marked changes may be noted in all the organs described in the preceding stage. The adhesive organ has broken through the ectoderm, forming a semicircular row of sucking cups on either side of the snout. The section, not being exactly vertical, passes through one of these cups (*sc.*) on the dorsal side. The space between this organ and the brain is now filled with mesoblastic cells (*ms.*). The stomodaeal invagination has deepened a little, owing to the development of the sucking disc over and in front of it. By the vertical growth of the brain the anterior end of the alimentary canal has been pushed downwards to a level with the mouth fold, so that the ectoderm lining the stomodaeum is in close contact with the endoderm forming the wall of the foregut. The oral plate (*op.*) thus formed is on the point of breaking through, and the point of fusion of the endoderm roofing the gut with the ectodermal roof of the stomodaeum is scarcely recognizable. There is no fold of the ectoderm comparable to "Rathke's pocket" discernible, nor is there an endodermal fold comparable to "Seesel's pocket." The ectoderm immediately over the stomodaeum is much thickened and composed of large cells of irregular shape loosely aggregated.

Fig. 3, an enlarged portion of the same section, will show that this ectodermal layer (*ec.*) terminates rather abruptly at the point of junction (*pf.*) with the endoderm (*en.*), at which point the cells are seen suddenly to become smaller. While they are somewhat disconnected in this region, they soon become arranged into three definite layers running back under the ante-

rior part of the thalamencephalon as far as the posterior limit of the optic chiasma (*oc.*). Here, immediately under the central part of the thalamencephalon (*lpo.*), the hypoblastic cells may be seen to have assumed a different shape and size, and the number of layers to have increased. From roundish or ovoid cells they become long, spindle-shaped, much smaller, and arranged in crescent-shaped layers about six in number and fitting one within another, so that the whole mass of cells over a region about 180 μ in length is nested in this peculiar manner. This is the first trace of the hypophysis (*hy.*) recognizable. Back of this differentiation the cells of the endoderm are again of the same rounded or ovoid shape as in front and arranged in two layers. Thus, I repeat, there can be detected no fold or overgrowth of ectoderm to give rise to the hypophysis nor evagination of the endoderm. Its cells are differentiated *in situ* apparently by longitudinal division of the cells constituting the roof of the foregut.

The chorda at this stage extends forwards under the hind brain to near the tip of the infundibular fold, which has greatly enlarged. The base of the thalamencephalon has elongated and is now a single layer of cells (*lpo.*) posterior to the chiasma, resting closely upon the dorsal wall of the foregut.

In a larva early in the eighth day, shortly after hatching, a sagittal section (Fig. 4) shows the oral plate broken in the center. But sections of the series on either side show the membrane or its remnants still intact, stretching across the oral cavity from a point near the tip of the now forming lower jaw to a point (*op.*) on the dorsal side of the cavity just forwards of the anterior limit of the thalamencephalon where it rests upon the dorsal wall of the foregut. It is thus seen that the position of the membrane relative to surrounding parts has not changed from the preceding stage. The floor of the foregut, however, has dropped down in the anterior part, making a rather deep cavity (*fg.*) immediately below the thalamencephalon and behind the oral plate. The dimensions of the thalamencephalon have increased vertically and decreased antero-posteriorly. The infundibular fold has apparently widened, but not deepened. The optic chiasma has greatly thickened, while the base of the

brain remains one cell in thickness and rests flatly upon the dorsal wall of the gut and the hypophysis. The sucking disc (*sc.*) is relatively at its largest size. The cavity between it and the brain is filled with a denser aggregation of mesoblastic cells than in the previous stage.

Fig. 5 shows the base of the brain and the hypophysis of the same section more highly magnified. The hypophysis now measures 150 μ in length and 28 μ in thickness. This apparent shortening may be due to the uncertainty of the limits of the organ in the previous stage, or to individual variations in the two larvae. That peculiar nesting of the cells in the hypophysis, as described above, will be seen to continue, but the cells are now perceptibly larger, while the epithelial cells (*em.*) forming the roof of the mouth beneath the hypophysis have again attained the size and shape of those with which they are continuous in front and behind. The basal layers of endoderm, however, still seem to be dividing, adding new layers to the base of the hypophysis by proliferation. The roof of the mouth is now three layers deep both before and behind the hypophysis.

A transverse section (Fig. 6) of a larva about eight days old, through the posterior part of the hypophysis and the infundibulum, shows that the organ is at this stage convex on the dorsal side in a transverse plane, fitting into a concavity in the base of the infundibulum lying closely upon it. An examination of the successive sections forwards and backwards from this shows that the upward convexity gradually diminishes forwards, but more abruptly backwards. This figure, in connection with the figures of longitudinal sections of larvae both older and younger, shows that the organ is now approximately lenticular in shape. In transverse, as in longitudinal sections, that characteristic nesting of the cells differentiated to form the hypophysis is found to prevail, a basin-shaped stratum of lenticular cells formed from the deeper layers of the endoderm, with other similar strata, each successively smaller, fitting into the previous ones, until we get a nest of seven or eight basins, while the hollow of the upper basin is filled to a rounded fullness with cells of a more nearly uniform diameter, rounded or

polygonal, and with no evident order of arrangement. This fact is strikingly evident, that the limits of the organ, both longitudinally and transversely, mark very accurately the borders of the area over which the brain is in such close contact with the hypoblast.

The mouth cavity posterior to the oral plate is now rather shallow but very wide. Just over the oral epithelium roofing the mouth, on either side of the hypophysis and the infundibulum, the internal carotid arteries (*v.*) are forming, while dorsal to these, in the folds formed between the infundibular lobe and the thalamocoele above, may be seen two other large cavities (*v'*), the cavities of the preoral somites.

A sagittal section of a larva about nine days old (Fig. 7) shows the base of the thalamencephalon (*fv.*) to be a single layer of columnar cells where it rests on the hypophysis, but thickened in front for the chiasma and likewise behind in the infundibular region, which has grown larger. The end of the chorda approaches very near to the infundibulum, but remains separated therefrom by mesoblastic cells, which may be seen to grow in between the brain and mouth roof to the limits of the hypophysis at either end. The lower jaw is relatively further back, its tip now lying under the anterior end of the hypophysis. The epithelium of the mouth is continuous beneath the hypophysis, but the basal layer of endoderm appears to continue to divide, adding new cells to the hypophysis by proliferation. The marked difference between the shape and arrangement of the cells in the upper and lower portions of the organ may be noticed still. At the posterior end the body is distinctly separated from the mother layer, while at the anterior end its cells take on more and more the character of the mother layer as we go forwards. The organ measures in this plane 196 μ in length by 41 μ in thickness.

A transverse section of a slightly older stage (Fig. 8), during the tenth day, shows an oval-shaped organ 130 μ in breadth by 64 μ in thickness. It is clearly separated from the endoderm at either side, so that it seems to be wholly differentiated, but still lying in a depression in the endoderm caused by the transformation of the cells of this layer into cells of the hypophysis.

The characteristic stratification on the ventral side and the irregular grouping of the cells above are still pronounced. Very nearly in the center, between these lower strata and the cells above, is a nearly spherical cavity (*l.*) about 16 μ in diameter, the first lumen that has been recognized. This lumen is not a longitudinal slit, as it is found only in this section; and since it is enveloped by no distinct membrane, and the cells have no definite arrangement about it, it has the appearance of an intercellular space. The mesoderm (*ms.*) is seen to grow between the brain and the mouth up to the sides of the hypophysis, just as at the ends. It would thus appear to be a biconvex body fitting into concavities in the brain above and the endoderm below.

In a larva ten days old, of which Fig. 9 is a sagittal section of the hypophysis and parts adjacent and Fig. 10 a transverse section more highly magnified, the organ has become entirely separated from the mouth roof, which has again become two cells in thickness beneath it. A strand of mesoderm (*ms.*) passes between the hypophysis and mouth roof and is continuous at the sides with the thickened mesoderm differentiating to form the cranial cartilages. An outfold of the infundibular wall at its posterior lower margin, 33 μ by 39 μ internal measurement, is the first stage in the formation of the infundibular gland, or saccus vasculosus (*sv.*). The single layer of cells characterizing the base of the infundibulum and the base of the thalamencephalon is continued into the saccus, but here the cells are columnar, with nuclei at their outer ends, in marked contrast with the cells in the brain wall contiguous. The chorda (*ch.*) runs forwards under the hind brain almost in contact with the roof of the mouth, and its cephalic end (*chh.*) abuts against this infundibular process with a strand of mesoderm between. This mesoderm grows into the space about the hypophysis, and a thin strand of it runs between the organ and the mouth roof below.

The hypophysis now measures in longitudinal section 143 μ by 57 μ, in transverse 136 μ by 66 μ. A lumen may be seen in the center, — an oval cavity with a membrane surrounding. About this lumen the spindle-shaped cells seem to be arranged in a radiate fashion, with long axes pointing towards it.

In a larva about fourteen days old a median sagittal section (Fig. 11) shows marked changes in surrounding parts, with but little change in the hypophysis. The saccus vasculosus has grown until it measures at this stage 120 μ in length, and from 6 μ in width at its point of origin to 27 μ at its widest part. Its tip now touches the base of the hind brain. The columnar cells which characterized it in the preceding stage are yet very noticeable, the transition to the rounder cells of the infundibular wall above being very abrupt, while the transition to the cells of the infundibular base is more gradual. Beneath, the hypophysis rests directly upon a strand of fibrous tissue (*ms.*) continuous before and behind with the perichondrium surrounding the sphenoidal cartilages, which are encroaching from all sides. The membrane roofing the mouth (*em.*) has become widely separated from the hypophysis, and in it dental protuberances and glandular cells have differentiated. The hypophysis has now attained a size of 156 μ by 56 μ, and has several small spherical or lenticular cavities which do not communicate.

A sagittal section of the hypophysis of a larva about the same age is shown in Fig. 12 strongly magnified. It will be seen that a few mesodermal cells have come to lie between the hypophysis and the brain, forming a thin layer separating the two organs. With this interpolation of mesoblastic tissue the lobing of the hypophysis begins, and this continues to increase with age. A large central oval lumen is conspicuous at every stage, while in the section here figured, several smaller lumina are met with as one examines the sections of the series. The principal lumen in this case measures 19 μ by 6 μ, and can be detected in but two sections, showing that its shape is lenticular. The smaller ones are more nearly spherical, and each is found in but a single section. No communication between them can be found. The hypophysis in this larva measures 164 μ in length by 57 μ in thickness. The characteristic radiate arrangement of the cells about the lumina is very noticeable.

Fig. 13 shows the relations of the hypophysis to surrounding parts, at a stage about one day older, in a transverse section through the middle of the organ. The oral epithelium has

further differentiated. The lateral cartilages (*sk.*) of the skull are closely encroaching from the sides, enclosing the internal carotids (*bv*). These cartilages are connected by a strand of the perichondrial membrane which runs beneath the hypophysis. The organ is almost perfectly lenticular in cross-section, measuring 180 μ by 70 μ. A principal lumen is seen in the center, but others are found at other positions in sections in front and back of this one.

In a larva between twenty-two and twenty-six days old, a cross-section (Fig. 14) shows the hypophysis appreciably enlarged, measuring now 220 μ by 75 μ. An irregular but distinct lobing may be seen, more pronounced on the upper than on the lower side. In this way, from a very symmetrical organ in the fifteen-days stage, we get here a marked asymmetry. It is here firmly adherent to the infundibulum, but quite apart from the wall of the cranial cavity. This separation from the base of the cranial cavity may be considered an artificial condition, as succeeding stages invariably show it to be in contact with this wall. The distinct upward bend in the infundibular base, the enlargement and gradual encroachment of the lateral cartilages, and the advancing differentiation of organs in the oral epithelium may be remarked.

The same section of the hypophysis highly magnified (Fig. 15) shows its histological structure to present some interesting features. The large central lumen with its very definite lining membrane is a striking object. It is ovoid, measuring 24 μ by 14 μ. Other spheroidal but smaller lumina are to be found near the tip of the different lobes as they are traced by sections, but communication of these lumina with each other, or with the central lumen, cannot be definitely proved. It seems that communication may be had through very narrow channels representing connected intercellular spaces between rather definite rows of cells and running from the lumina of the lobes towards the central lumen. But apparently these channels are closed before reaching the lumen. Such spaces may be seen in the figure (*sl.*) running out into the lobes to the right and to the left. It will be noticed that the cells maintain a rather definite and orderly arrangement about the central lumen. There is a

row encircling the lumen in a radiate manner, long spindle-shaped in the upper and lateral parts, more rounded below. The other cells appear to have a general tendency to arrange themselves in rows pointing towards the center of the organ, but this arrangement is modified by a secondary tendency to be grouped about the secondary lumina and the longitudinal channels. A marked feature of this and succeeding stages is the indistinctness or total obscurity of the nuclei.

A sagittal section at this stage shows the same peculiar arrangement of cells about the lumina and channels in the separate lobes. And the other characters of the hypophysis are similar to those shown in the cross-section. The anterior sphenoidal cartilage has now advanced to the posterior part of the chiasma nearing the hypophysis, the posterior to a point not far from the posterior point of the saccus, while dense skeletogenous tissue continues to and below the saccus nearly to the hypophysis. The perichondrium, as before, stretches across from one cartilage to the other below the organ. The basilar artery is now well formed, running along the base of the hind brain up into the fold between the hind brain and the primary forebrain. A blood vessel may be seen also just posterior to the hypophysis beneath the point of origin of the saccus. The saccus has enlarged, and in its cavity may be seen abundant granular secretions.

Passing from this stage to a stage between thirty and thirty-five days, a sagittal section (Fig. 16) shows all parts much enlarged. The finger-shaped saccus measures internally 311 μ by 18 μ at its narrow opening into the infundibulum, and 77 μ at its widest part. The granular secretions noticed in the previous stage have increased in amount. While the sphenoidal cartilages have enlarged and strengthened compared with the condition in the previous stage, they have approached very little nearer to the hypophysis; but the connective tissue between the hypophysis and the roof of the mouth has considerably increased. The hypophysis at this stage has attained a size of 359 μ by 96 μ. Increased lobing is not apparent from the figure, but the series shows a great increase in the number of lobes and of the lumina in them. The arrangement and char-

acteristics of the cells are not enough different from those described in the preceding stage to call for special remark.

A comparison of sagittal with transverse sections (Fig. 17) demonstrates that in shape the organ retains the general lenticular form acquired early in its formation. It measures now 284 μ in breadth by 88 μ in thickness. The lateral cartilages (*sk.*) have advanced far in towards the hypophysis, so that it may be clearly seen that the organ lies in a distinctive space surrounded by cartilages on all sides — the pituitary fossa. Small bits of connective tissue may be seen between the hypophysis and the brain in the folds of the former, and also in the recesses between the lobes on the under side. The infundibular base is folded more or less in conformity to the lobing of the hypophysis. No evident communication between the cavities nor ducts opening to the exterior have been observed at this, the latest stage studied.

A horizontal section of the hypophysis (Fig. 18) of a larva about 20 mm. in length, thirty days old, shows that the lobing of the organ is principally around the edge ; that its general shape is circular in this plane, lenticular as a solid ; that a cavity may be found near the end of each well-formed lobe, which may possibly communicate with the central lumen by a very narrow indistinctly defined channel ; that the cells are, in general, arranged in a double row around each lobe, the space between the rows constituting the channel mentioned ; that the cells are arranged radially about the lumina. The section figured is not exactly in a horizontal plane, but dips a little posteriorly and to the right, so that the lobes mostly appear to be on the anterior side, but are in reality of approximately the same number in each half. The organ is here seen to be enclosed in the sella turcica, which is far advanced in its formation. The infundibulum fits closely upon its upper surface, the projections of the one fitting roughly into the depressions of the other. No blood vessels can at this stage be seen entering the organ, nor nervous tissue be found connecting it with the brain. It seems not to have become glandular as yet.

SUMMARY.

In distinction from an epiblastic origin, as found in most forms, my observations lead me to believe that the hypophysis is of hypoblastic origin in Amia.

Prior to the differentiation of the hypophysis the foregut extends far forwards; by diverticula the hypoblast reaches even the dorsal side of the head in front of the brain. At this time the stomodaeal involution is below the front end of the foregut. The diverticula later sever their connection with the foregut and are metamorphosed into the larval adhesive organ. The hypoblast unites with the epiblast on the last day before hatching, seventh day, forming the oral plate at a point forwards of the anterior limit of the brain.

There is no indication of an overgrowth of epiblast between the brain and the foregut, nor is there an invagination from the stomodaeum to give rise to the pituitary body. Neither does an outfold from the hypoblast occur to form it. Its first stage is found near the close of the embryonic period, about 160 hours, as a local differentiation of hypoblastic cells in the dorsal wall of the mesenteron, immediately under the thalamencephalon where the base of the brain is in close contact with the hypoblast. The intimate fusion of the base of the first primary vesicle with the hypoblast, from a time long before the stomodaeum has united with the foregut until after the hypophysis has become well differentiated, seems to me to preclude the possibility of any epiblastic tissue entering into its composition, and leads me to think that its origin is probably due to a mechanical cause. This region of fusion is far back of the oral plate, which remains intact for several hours after the differentiation of the hypophysis has begun.

The growth of the hypophysis is at first apparently due more to the enlargement of the cells first differentiated to form it than to the addition or multiplication of cells. It appears to remain in genetic connection with the mother layer until about the tenth day, when it becomes wholly delimited therefrom by an ingrowth of mesoblastic tissue between it and the mouth roof.

During this early period there is a distinct stratification in the arrangement of cells in its lower portion, as if formed in successive strata by proliferation from the mother layer. This stratification is not apparent in the upper part of the organ, and is no longer seen in the lower part after the ninth day.

The first lumen is formed about the ninth day, from which time on an increasing number of lumina is to be found as the organ develops. A lumen appears near the end of each lobe. These lumina are oval or spherical cavities, and definite channels of communication have not been observed, though indications that such channels are forming are found in the arrangement of the cells about the longitudinal axes of the lobes. The cells have a tendency to arrange themselves radially about the lumina.

The organ is almost perfectly lens-shaped until about the fifteenth day, when the formation of lobes begins with the interpolation of mesoblastic cells between the hypophysis and the brain. The number of lobes multiplies from this time on till the thirty-fifth day, beyond which stage observations have not been made. The lobes form chiefly around the periphery of the lenticular body.

The organ is thus, at this stage, a spongy body with isolated cavities, rather than a complex of glandular tubules which so frequently characterize it. The nuclei of the cells become indistinct or wholly disappear by the twenty-second day. This may indicate a glandular modification, but no evident glandular secretions have been detected. No duct nor external opening of cavities has been observed.

No arteries or blood vessels are to be found in it at the latest stage examined. Neither have nerve fibers been seen connecting it with the brain.

The cranial cartilages developing from the mesoblast increase in size and strength from about the tenth day, until at the thirty-fifth day they closely surround the organ on all sides, forming the pituitary fossa, in which the organ lies in close contact with the infundibulum on the dorsal side, but separated from the mouth by a fibrous strand of connective tissue on the ventral.

The saccus vasculosus begins to form about the tenth day and steadily enlarges, until at the thirty-fifth day it forms a process of the infundibulum in the shape of a glove-finger, extending directly backwards under the base of the medulla and parallel with the base of the cranium.

This is very nearly its position in the adult brain as figured by Allis.[1] At no stage, therefore, is it in close association with the hypophysis, which connection is found to be true in so many cases. Abundant granular secretions are found in it at the twenty-second-day stage, and these increase in amount thereafter.

General Remarks.

The course of development of the hypophysis in Amia as described in the preceding pages, when compared with the descriptions given by other observers, both in Amia and other Ganoids, will be seen to present some striking peculiarities.

Dean[2] says: "The hypophysis is by no means as important an element in the development of the head in Amia as in other Ganoids. Its appearance is late and inconspicuous. It has not been found in stages earlier than that of Fig. O (*hatching time*),[3] and even here its presence is not definite. At the most the position of its lumen can be recognized as the line *HY*, formed by the arrangement of cells immediately below the region of the recessus opticus. These cells are apparently ectodermal, for they are arranged in a continuous line with the cells of the formative epiblast of the dorsal wall of the stomodaeum, but, on the other hand, their ventral limit cannot be distinguished from the entodermal cells roofing the foregut."

In what respect the development of the hypophysis is less important in Amia than in other Ganoids is not clear. In point of size and position its relations are almost exactly the same as in the other Ganoids, so far as the larval stages have been examined. As for its appearance being "late and incon-

[1] Allis, Edward Phelps, "The Cranial Muscles and Cranial and First Spinal Nerves in Amia Calva," *Journ. of Morph.* Vol. xii, No. 3, Pl. XXXVIII. 1897.

[2] "On the Larval Development of Amia Calva," *Zool. Jahrb.*, p. 667. 1896.

[3] Italics are mine.

spicuous," I may say that it arises, as will be shown, at a time intermediate between the time of its first occurrence in the other two forms in which this point has been determined, and it is certainly a conspicuous, I might say, striking differentiation of cells, even in its fundaments, although it may not be a prominent object in point of size or in the distinctness with which its limits may be fixed. The actual time of its appearance I have found to be several hours earlier than the time assigned by Dr. Dean, as a comparison of Fig. 4 with his Fig. O plainly proves. His figure and description indicate a stage nearly the same as my Fig. 4, which is shortly after the time of hatching. Although in his figure the oral plate is still unbroken, the cavity of the foregut posterior to it has noticeably deepened by the dropping downwards of its basal wall, while in the stage I figure the cavity is of about the same depth, and the oral plate is only severed at its middle point, remaining intact at the sides. While in Fig. 4 the cells, which he would call the beginning of the hypophysis, may be said to be "continuous with the cells of the formative epiblast," being in the same plane with them, there is no other evidence of a connection and certainly no ground whatever for considering them derived therefrom, as the enlargement of this section (Fig. 5) makes very clear their differentiation from cells of the hypoblast. But its earliest stage is found (Figs. 2 and 3) some hours previous to this stage, far back of the oral plate and the epiblast, as a well-defined modification of cells of the basal layer of hypoblast where the post-optical lamina of the brain rests closely upon it. Considering the common assumption of embryologists that its origin is from the epiblast, my observations become of interest, since I believe that I have proved beyond question that the hypophysis is of hypoblastic origin, and I do not at present understand how Dean could have considered it otherwise.

Balfour and Parker[1] state in a footnote: "We have not been able to work out the early development of the hypophysis as satisfactorily as we could have wished. . . . Were it not for

[1] "On the Structure and Development of Lepidosteus," *Trans. Roy. Soc.* Pt. ii, p. 379. 1882.

the evidence in other types of its being derived from the epiblast, we should be inclined to regard it as hypoblastic in origin." They speak of it as an invagination of the oral epithelium, without stating whether this invagination is anterior or posterior to the oral plate. Presumably from the previous statement they consider it derived from the roof of the foregut posterior to the oral plate. They figure a transverse section of the anterior part of the head of an embryo on the ninth day after impregnation, showing an invagination from the mouth roof with a thickened, solid, conical process extending upwards into the cranial cavity. This, with the exception of the invagination, is very similar to its condition in cross-sections of Amia late in the seventh day, passing through the anterior end of the organ, as shown in Fig. 6. They also figure transverse sections through the anterior and posterior ends of the hypophysis of an embryo eleven days old, where in front it is still in connection with the oral epithelium, while behind it is constricted from that layer. These sections indicate relations almost exactly the same as transections of the organ in Amia shown in sagittal section (Fig. 7) at an age of not quite nine days. Comparing these few sections of Lepidosteus and the few words of description with the conditions which I find in Amia, it seems that the hypophysis undergoes a nearly parallel series of changes in the two forms from the time of its primary origin to a late larval stage, but that corresponding embryonic stages are met with in Amia from one and a half to three days earlier than in Lepidosteus, and the corresponding larval stages are found earlier and earlier as the animal advances in age. This justifies, so far as the hypophysis is concerned, Dean's statement that "the organogeny of Amia progresses more rapidly than in Lepidosteus."

I find no lumen earlier than the ninth day, when it appears as a single nearly spherical cavity near the center of the organ, rather than a longitudinal slit, as indicated by Dean in Fig. O. Furthermore, as my sections show, the lumen is never a longitudinal slit, even at the late stage of thirty-five days, corresponding to Dean's Fig. Q of a four-weeks-old larva which shows it as such. Instead of a single lumen at this late period,

I find several lumina which apparently do not communicate. Neither do my observations agree with those of Balfour and Parker on Lepidosteus at a corresponding age, where the hypophysis is described as "small, not divided into lobes, and provided with a very small lumen"; whereas in Amia at this period it is much lobed and possesses numerous spherical lumina.

Kupffer (*loc. cit.* p. 59) has described a very early and unusual formation of the hypophysis in *Acipenser sturio*. According to him the organ arises during the second day after fertilization by an invagination of the basal layer of the ectoderm on the dorsal side of the head, in front of the brain, between the yet unclosed neuropore and the sucking disc. This invagination grows downwards and backwards until it comes in contact with the endoderm, and then, before the close of the second day (forty-five hours), by a rupture of this layer, it communicates with the alimentary canal, which communication persists for about twenty-four hours. But before the stomodaeum has formed a connection with the foregut, this union of the hypophysis with the latter has broken off (*i.e.*, by the sixty-fourth hour), and the lower blind end of the tube becomes swollen into a hollow bulb. This bulb gradually enlarges and migrates backwards to a position between the dorsal wall of the gut and the base of the thalamencephalon, while the remaining part of the tube, namely, the stalk, gradually atrophies and has wholly disappeared by the time the embryo is hatched (eighty-seven hours).

Haller has expressed a doubt as to Kupffer's interpretations. This doubt is based upon the indistinctness of the parts observed at this early time. From Kupffer's own words it would seem that the cells were greatly obscured by food-yolk. I give the passage quoted by Haller: "Die Entodermzellen sind noch mit Dotter überladen, die Zellen der Epidermis und des Hirnes schon fast dotterfrei, aber diejenigen Ektodermzellen, die in der Bildung der gleich zu besprechenden Organe (*Hypophysenanlage*, etc., Haller) eingehen, zeigen noch denselben Dottervorrath wie die Elemente des Entoderms und sind daher durch Färbungen von diesen nicht zu unterscheiden. Die Abgren-

zung der einzelnen Theile dieser Region gelang mir erst unter vergleichender Prüfung nahe auf einander folgender älterer Stadien."

I likewise believe that Kupffer has misinterpreted what he saw, but for an entirely different reason from that given by Haller, yet based upon the same passage.

Miss Phelps[1] has recently shown that the "larval adhesive organ" in Amia develops at about the time that Kupffer assigns to the formation of the hypophysis in Acipenser. The adhesive organ begins as a diverticulum from the endoderm anterior to the brain, which later becomes divided into a pair of diverticula whose connection with the endoderm becomes broken off after a time. Acipenser and Lepidosteus each possesses a sucking disc, or adhesive organ, similar to that in Amia and at a corresponding developmental period. It would therefore seem that they should justly be regarded as homologous organs, and, further, we should naturally expect them to have a similar ontogeny. Previous to the observations of Miss Phelps this organ has been assumed to be of ectodermic origin (Dean for Amia, Balfour and Parker for Lepidosteus, and Kupffer for Acipenser).

In my own studies on Amia, as described on a preceding page, I observed these diverticula connecting the foregut with lateral masses of cells lying on either side of the snout and between the anterior end of the brain and the overlying epidermis, filling nearly the whole of this pre-cerebral region. These masses of cells present an appearance exactly like the cells walling the foregut, being laden with much yolk just as Kupffer describes, and could not be distinguished from them. The narrow channels can be traced from the cavity of the foregut upwards through the masses to near the epidermis on the dorsal side where they end blindly. The cells of the epidermis and brain contiguous to these present a very different appearance, due to their freedom from yolk.

I was at a loss to account for these canals connecting the enteric cavity with organs on the dorsal side of the head, until

[1] "On the Development of the Larval Adhesive Organ in Amia." Abstract in *Science*. March 10, 1899.

I saw the account of the development of the adhesive organ by Miss Phelps. I at once concluded that I had not only confirmed her discovery, but had also found wherein Kupffer has probably erred in his interpretation of the structures which he believed to be connected with the development of the hypophysis, but which to my mind have an entirely different meaning. The statement by Kupffer, that the cells overladen with yolk going to form the hypophysis are not to be distinguished from the elements of the endoderm, receives its explanation in the fact that they are endodermal cells growing out from the foregut by evagination. The canal which, according to Kupffer, connects the foregut with the dorsal ectoderm is nothing else, in the opinion of the writer, than this median diverticulum from the foregut, or possibly one of the lateral diverticula resulting from it, running up through the adhesive organ to the point of closure of the neuropore. A slightly oblique dorso-ventral section through this region in Amia during the sixth day of development would show strikingly similar appearances to those figured and described by Kupffer in Acipenser.

As a phylogenetic interpretation of the singular development of the hypophysis in Acipenser, Kupffer holds that we here have traces of the ancestral mouth which opened above the sucking disc and in front of the brain. Its origin from the stomodaeal roof as found in most vertebrates, he claims, is a secondary condition due to a migration downwards from its original position, compelled by the great development of the fore brain in these forms and the concomitant degeneration of the adhesive discs, whose remnants, he thinks, are still to be found in the fold between "Rathke's pocket" and the oral plate.

This explanation fails to account for its origin in Amia and Lepidosteus, in which the sucking disc is still large and functional, and whose fore brain is little different from that found in Acipenser; and yet in them the hypophysis arises at a point far back of the sucking disc and under the brain.

It may be considered highly probable that the hypophysis is

endodermic in origin in Lepidosteus as well as in Amia, and I venture the prediction that a further study of Acipenser will demonstrate the same for that form. The foregut extends far forwards in each of the Ganoids in which its development has been studied, and the writer believes that in all these it arises from the endoderm. A study of the figures of the head parts in those animals in which the hypophysis is undoubtedly of ectodermal origin shows that in them the foregut stops short of the infundibulum, while in some, at least, of those forms in which its origin is questionable — ectodermic or endodermic — the foregut and stomodaeum meet at an intermediate point, directly under the base of the thalamencephalon. These facts lead me to suggest that mechanical factors, acting at the point of fusion of the brain base to the oral roof, may play an important part in determining its development from this or that layer.

If my observations be confirmed, that the hypophysis in Amia is derived from the hypoblast, will this fact strengthen Kupffer's hypothesis that it represents a degenerated "paleostome," or will it rather revive the old theory of Dohrn, that it represents a portion of a canal connecting the alimentary tract with an exterior dorsal opening through the thalamencephalon and the epiphysis and accordingly believed to be homologous with the invertebrate pharynx? I find nothing in its structure or its relations, other than its point of origin, which can be interpreted as evidence in support of either hypothesis. I have given what I believe to be the facts, but must leave their interpretation to the maturer judgment that will come from the more complete and extended observations of the future.

HULL ANATOMICAL LABORATORY,
September 22, 1899.

ABBREVIATIONS.

A. anterior.
ao. outfold of ectoderm caused by the developing adhesive organ.
br. wall of brain.
bv. blood vessels.
c. cavity occupied by adhesive organ in its young stages.
ch. chorda.
chh. cephalic end of the chorda.
ec. ectoderm.
egm. egg membrane.
em. epithelium of mouth.
en. endoderm.
ep. epiphysis.
fg. foregut.
fv. first primary vesicle of brain.
h. position of heart.
hb. third primary vesicle of brain.
hy. hypophysis.
in. infundibulum.
l. lumen of hypophysis.
lpo. lamina postoptica.
ls. crystalline lens.
m. mouth cavity.
mb. mesencephalon.
ms. mesoderm.
o. involution of ectoderm between the sucking discs.
oc. optic chiasma.
op. oral plate.
ov. optic vesicle.
P. posterior.
pf. point of fusion of ectoderm with endoderm.
ro. recessus opticus.
s. strand of fibrous tissue continuous with the perichondrium.
sc. sucking cup.
sk. skeletal cartilages.
sl. cleft between rows of cells.
st. stomodaeum.
sv. saccus vasculosus or infundibular gland.
v. internal carotid artery.
v'. head cavities.
y. yolk.

EXPLANATION OF FIGURES.

FIG. 1. Median sagittal section of the anterior portion of an embryo surrounding about 245° of the egg's circumference. About 148 hours. × 60.

FIG. 2. Median sagittal section of the anterior portion of an embryo a few hours before hatching time. About 160 hours. × 60.

FIG. 3. The base of the thalamencephalon, the foregut, and the stomodaeum of the same section under stronger magnification. × 190.

FIG. 4. Median sagittal section through the anterior portion of a larva soon after hatching, early in the eighth day. × 60.

FIG. 5. The roof of the mouth and the hypophysis of the same section more highly magnified. × 190.

FIG. 6. Transverse section through the brain and hypophysis of a larva about eight days old. × 60.

FIG. 7. Median sagittal section through the hypophysis and base of the thalamencephalon of a larva nearly nine days old. × 190.

FIG. 8. Transverse section through the hypophysis and base of the infundibulum of a larva during the tenth day. × 190.

FIG. 9. Median sagittal section through the hypophysis and infundibulum of a larva ten days old. × 60.

FIG. 10. Transverse section of the hypophysis and base of the infundibulum of a larva ten days old. × 190.

FIG. 11. Median sagittal section through the hypophysis and infundibulum of a larva fourteen days old. × 60.

FIG. 12. Median sagittal section through the hypophysis and adjacent parts of a larva about the same age as the preceding. × 190.

FIG. 13. Transverse section of the hypophysis and infundibulum of a larva about fifteen days old. × 60.

FIG. 14. Transverse section through the hypophysis and infundibulum of a larva between twenty-two and twenty-six days old. × 60.

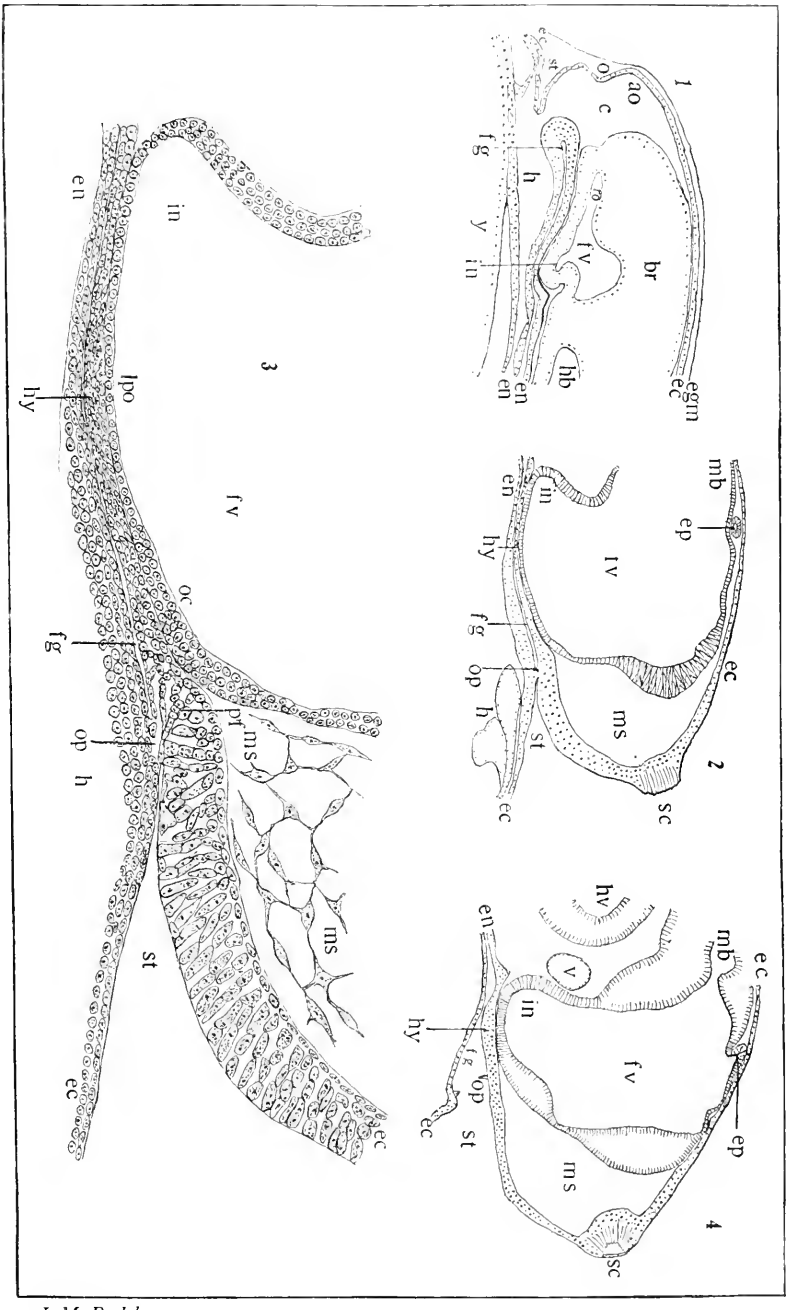
FIG. 15. The hypophysis of the same section more highly magnified. × 215.

FIG. 16. Median sagittal section through the hypophysis and infundibulum of a larva between thirty and thirty-five days old. × 60.

FIG. 17. Transverse section through the hypophysis and infundibulum of a larva of the same age as the preceding. × 60.

FIG. 18. A nearly horizontal section through the hypophysis of a larva about thirty days old. × 105.

Plate 1.



J. M. P. del.

Plate II.

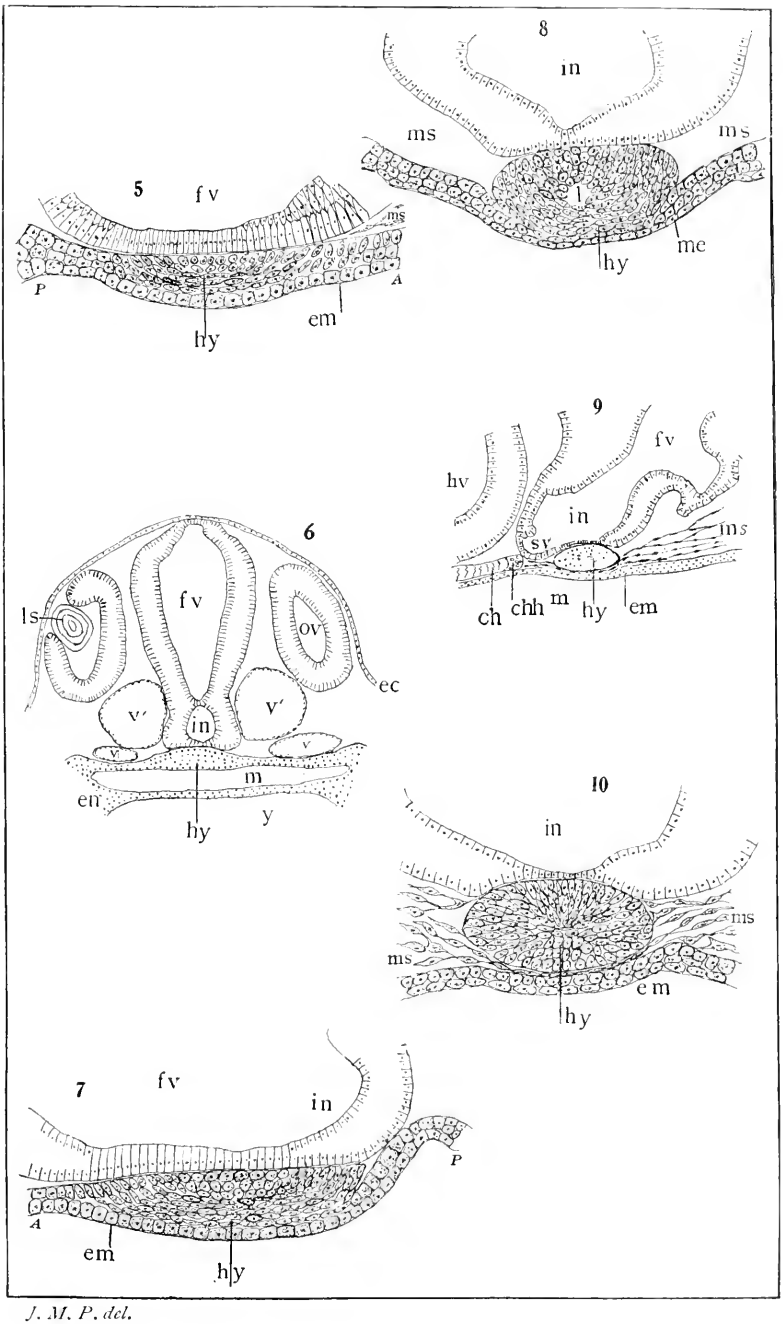


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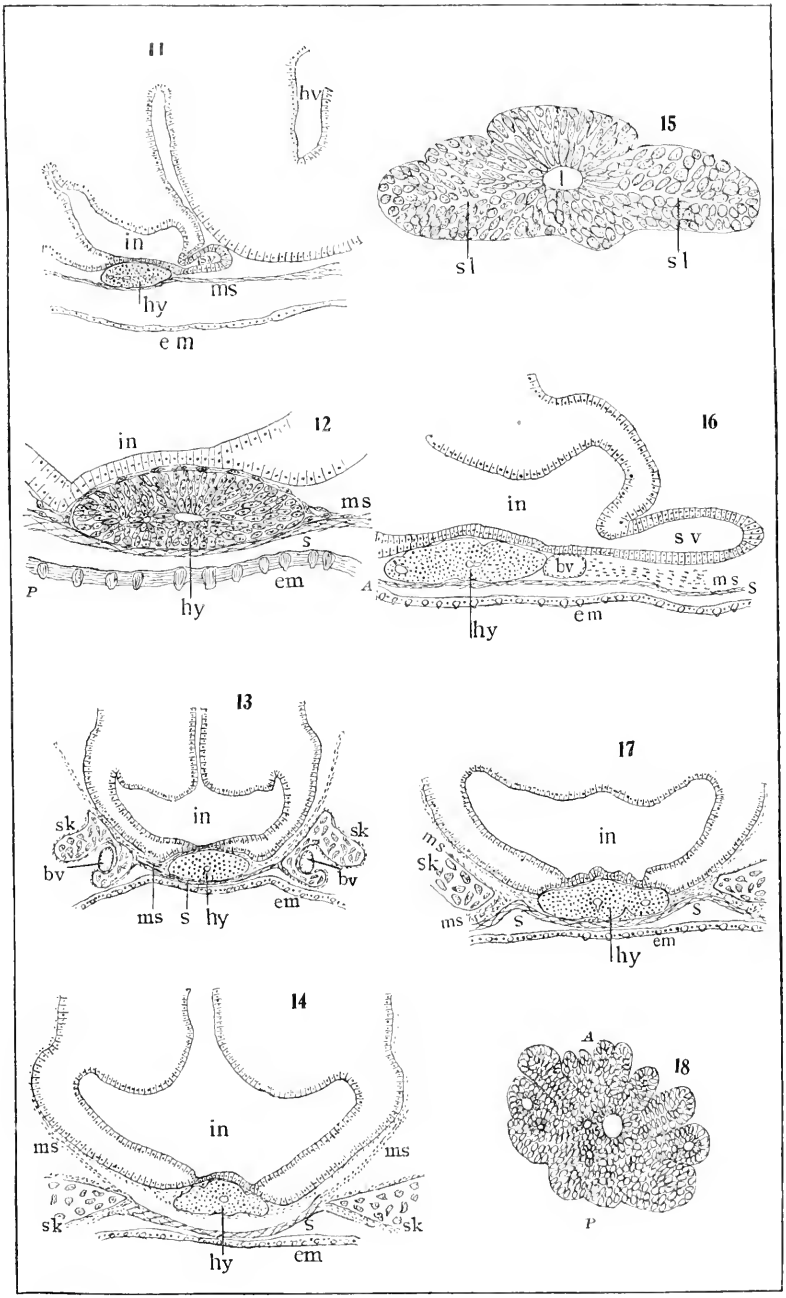
Plate III.



J. M. P. del.

AN EXTRAORDINARY NEW MARITIME FLY.

VERNON L. KELLOGG.

THERE have been established recently two new[1] families of flies, to which I have to add a third. In the case of two of these three new families the members show great divergence from the usual dipterous condition. The three genera of Wandolleck's new family, Stethopathidae, are wingless and are without halteres. The thorax is greatly reduced and the compound eyes are feebly developed. The mouth-parts are of the general sort possessed by the Nematocera, *i.e.*, a short lip-like labium without pseudo-tracheae, a distinct labrum, and a hypopharynx, but no mandibles nor maxillar lobes. Coquillet's new family, the Stenoxenidae, established for a single female fly, presents no such extraordinary characters as the Stethopathidae. "The shape and structure of the head, body, and legs, and the unusual development of the first antennal joint appear to indicate its nearest approach to the genus Ceratopogon of the family Chironomidae; but the venation as well as the general appearance of the insect is very different from anything now located in that family" (Coquillet).

There has come into my hands a number of specimens, 153 in all, of a fly which must prove of unusual interest to zoölogists and entomologists, both because of its peculiar habitat and of its extraordinary structural condition. This new fly can certainly not be ascribed to any known dipterous family; its affinities can only be determined in the most general way. I feel constrained to establish for it a new family, which may be called the Eretmopteridae.

The 153 specimens of the new form, 139 males and 13 females, and 1 female pupa, were collected on Dec. 27, 1898,

[1] Wandolleck, Bruno, "Die Stethopathidae, eine neue Dipteren-Familie," *Zool. Jahrb.* Bd. xi, pp. 412–441, Pls. XXV and XXVI. 1898.

Coquillet, D. W., "A New Dipterous Family Related to the Chironomidae," *Ent. News.* Vol. x, pp. 60 and 61 (figure). March, 1899.

by Mr. J. C. Brown, a student assistant in my laboratory, at Point Lobos, a rocky point on the Pacific Coast near Monterey, California. The flies, of which there were many ("thousands," says Mr. Brown), were resting or running on the surface of the ocean water of tide pools and had a tendency to gather in large numbers in "patches" and in "ball-like masses" on the water. None were seen below the surface, nor were any seen flying. They moved about on the surface of the water very rapidly. In the last week of March, 1899, I visited Point Lobos and searched carefully for the fly, examining the same tide pools on which

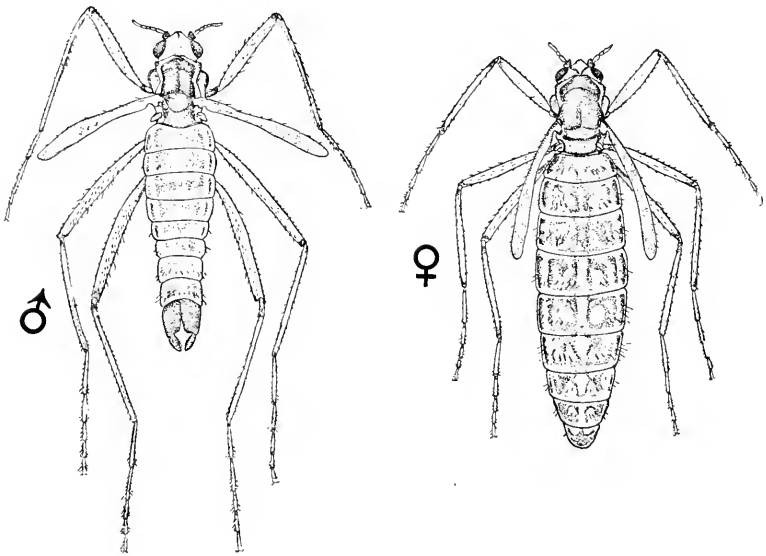


FIG. 1.—*Eretmoptera browni*; male and female.

Mr. Brown found his specimens; but no flies were to be found, nor were there any dipterous larvae or pupae in these pools. Mr. Brown also searched again in July and August without finding more specimens. So we have as yet no knowledge of the eggs and larvae, nor of the course of the life history of the fly.

The new form may be named and described as follows:

Eretmoptera browni nov. gen. et sp.—Male (Fig. 1). Length 2 mm. Head slightly broader than thorax; eyes widely separated, very small, very convex, hairy, and with rather large

facets; ocelli absent; antennae (Fig. 3, *ant.*) short, length 3 mm., 6-segmented, the basal segment wide and globose, the sixth segment longest, the second next, the third and fifth about equal, the fourth shortest, with a few short strong hairs on each segment, and the surface everywhere with a fine stiff pubescence. The mouth-parts are of simple nematocerous type, short, and with distinct labrum-epipharynx, maxillae, hypopharynx, and labium, mandibles absent; labrum-epipharynx (Fig. 2,

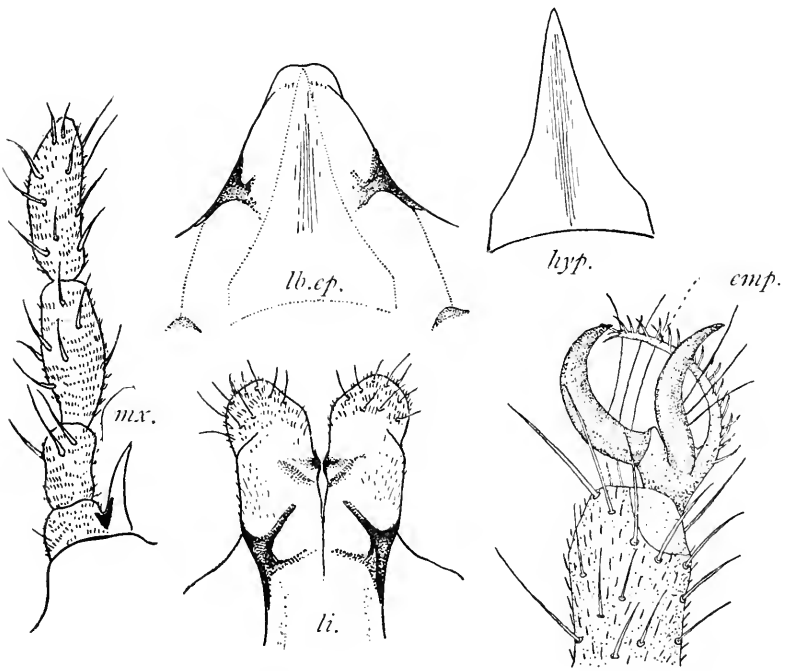


FIG. 2.—*Eretmoptera browni*: *mx.*, maxilla of male; *lb.ep.*, labrum-epipharynx of male; *li.*, labium of male; *hyp.*, hypopharynx of male; *emp.*, empodium of male.

lb.ep.) short, broadly triangular, with obtusely rounded tip; maxillae (Fig. 2, *mx.*) with short, weak, tapering, pointed lobe, and 4-segmented palpi, 3 mm. long; the palpi with last two segments longest and equal, and all the segments provided like the antennae with a few short stray hairs and a fine stiff pubescence; hypopharynx (Fig. 2, *hyp.*) elongate, triangular, as long as the labrum-epipharynx, but narrower and more acute; labium (Fig. 2, *li.*) short, lip-like, with free paraglossae, without pseudo-

tracheae. The face is whitish, with a median longitudinal dark line, and the antennary fossae with dark margins; the basal segment of the antenna is rather dark, the other segments pale. Thorax without bristles, dark above, pale beneath. Legs long and slender, whitish with blackish joints; middle and hind legs longest and equal, front legs only a little shorter; average measurement of middle leg, femur 1 mm., tibia 1 mm., tarsus 1 mm.; tarsus 5-segmented, segment 1 as long as segments 2, 3, and 4 together; segment 5 slightly longer than segment 4; tibiae of all legs with single apical spur; tarsal claws strongly curved, thickened at base, and with a few (three ?) delicate spines on basal half; no pulvilli; empodium (Fig. 2, *emp.*) rather long, curving, filiform, and plumose or pectinate for its whole length. Wings narrow, strap-like, extending only to fourth abdominal segment, length .75 mm., and wholly without veins; whitish, somewhat wrinkled, and finely spinulose. These strange veinless wings are not specially thin or delicate, but, on the contrary, are rather thickened, the costal margin being especially thickened and perhaps folded. The halteres (Fig. 3, *h.*), or the structures which occupy the usual position of halteres, are not of the usual pedicel and knob type common among Diptera, but are minute, lobe-, or scale-like processes, appearing like rudiments of metathoracic wings; like the mesothoracic wings, they are rather thickened and are finely spinulose; they are widest at base and taper to a rounded tip; they average .08 mm. in length. Abdomen of nine segments, tapering gradually posteriorly; mottled gray and blackish above, lighter below, palest laterally; a few scattered, small, wholly inconspicuous hairs, the body appearing glabrous; external genitalia consisting of a pair of large, conspicuous, strong, articulated claspers (Fig. 3, *cl.*), which are covered with a pubescence.

Female (Fig. 1). — Length 2.5 mm., thus being one-fourth longer than the male; this extra length is all in the abdomen, which is markedly larger in every way than the abdomen of the male. The head and thorax are narrower than the robust abdomen, which is sub-cylindrical, tapering only slightly posteriorly. Eyes as in male very small, very widely separated, and hairy. Antennae (Fig. 3, *ant.*) only 4-segmented. Mouth-parts

essentially as in male, with, however, appreciable differences in shape; the labrum-epipharynx is narrower at base, and is more pointed apically; the labium with paraglossae separated farther back and slightly narrower. The reduced wings and halteres like those of male, the wings, length .85 mm., slightly longer. The abdomen consists of nine segments mottled blackish, with conspicuous white sutural spaces, caused by the distention of the abdomen. The external genitalia are inconspicuous. There is a short emarginate dorsal plate with rounded tips and a pair of small lateral processes. There appears to be no extrusible ovipositor.

Pupa of Female. — Among the many specimens collected by Mr. Brown, I find a single female pupa. This specimen throws the only light upon the condition of the immature life of the fly that we yet have. The pupa is of that simple unprotected, unmodified type characteristic of those flies, like the Cecidomyidae and Mycetophilidae, whose pupae are protected by lying enclosed in plant tissue. There are no projecting breathing tubes like those of the aquatic pupae, and it would seem that the pupa was quite unfit for an aquatic life. And yet Mr. Brown took this pupa with the imagines from the surface of a tide pool. There is a puzzle here. The pupa may be described as follows: Length 2.5 mm. (as large as adult female). Immediately recognizable as pupa of the female from the similarity in size, shape, and markings. Abdomen just as in adult both as regards size, shape, color, and markings. The antennae, legs, and wings are folded on the lateral and ventral aspects of the anterior part of the body and extend backwards only to (hardly reaching) the posterior margin of the second abdominal segment. There are no external tracheal gills or elongated spiracles (breathing tubes). There are no bristles nor special clinging organs. The pupa is of a very simple, unmodified, unprotected type.

The "extraordinary" features of the external structure of the fly are the condition of the wings and halteres. The condition of the antennae and the empodium is also unusual. The reduction of the wings and loss of flight are accompanied by a reduction of the halteres, the flight-directing (?) organs. The

halteres being not wholly obsolete, but existing still in rudimentary condition, are especially suggestive in their likeness to rudimentary wings. The general affinities of the fly are shown by the character of the mouth-parts (and pupa) to be with the simpler nematocerous families. The habitat is unusual, but of course not unique. The discovery of the conditions of life of the immature stages may, however, give the matter of habi-

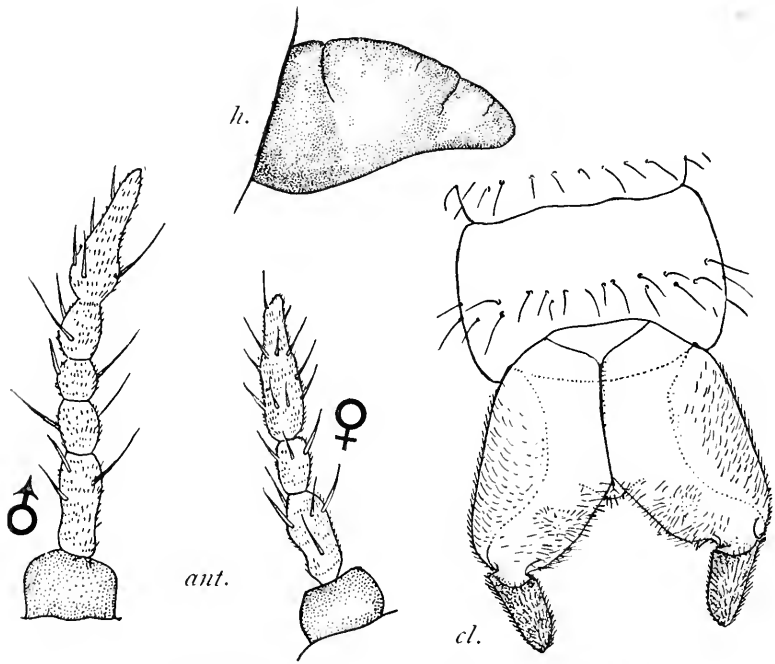


FIG. 3. — *Eretmoptera browni*: *ant.*, antennae of male and female; *h.*, balancer of male; *cl.*, claspers of male.

tat a very great interest. The fact that the imagines are unable to fly is to be remembered in connection with their presence on the tide pools. Are the thickened strap-like reduced wings used in locomotion at all?

Other tide-pool flies are known. Various winged forms are common at the verge of the water and must become accustomed to occasional watery overwhelmings. Wheeler[1] has

[1] Wheeler, W. M., "A Genus of Maritime Dolichopodidae New to America," *Proc. Cal. Acad. Sci.*, 3d series. Vol. i, pp. 145–152, Pl. IV. 1897.

described three species of Dolichopodidae which he found "flitting about in the spray of the breakers among the sea-weeds on the rocks below high-water mark." Eaton, and later Verrall,[1] describe certain flies from the Kerguelen Islands which live on the verge of the tide. One of these forms, *Halirytus amphibius*, assigned to the Chironomidae, has 6-segmented antennae and rudimentary wings "reaching to the apex of the first abdominal segment." But it has but 2-segmented palpi, and the halteres are of the usual form. It was found "walking upon the surface of puddles and tide pools." And many of the flies were undoubtedly occasionally submerged at high tide, although none was seen under water.

STANFORD UNIVERSITY, CALIFORNIA.

[1] Verrall, in *Phil. Trans. Royal Soc.* Vol. clxxxvi, p. 247, Pl. XIV, Fig. 6. London, 1879.

ON THE VARIATION IN THE POSITION OF THE STOLON IN AUTOLYTUS.

P. CALVIN MENSCH.

In the investigation of the variation in the position of the region of stolonization in bud-forming syllidians, observations were made upon four of the most abundant forms occurring along the Atlantic coast.

Three of these forms — Autolytus cornutus, Autolytus varians, and Proceraea ornata — may be found in abundance at Woods Holl in the summer months, during which time also the phenomenon of budding is most active. The fourth, Proceraea tardigrada, occurs in almost equal abundance at Beaufort, N. C. Of these A. cornutus, P. ornata, and P. tardigrada are solitary stolon-bearing, and invariably cast off the first stolon before a trace of a second stolon appears, while A. varians belongs to the chain-forming variety and may bear as many as eight stolons in various stages of development attached to the adult individual or so-called parent stock.

The greatest number of variations were observed in the chain-bearing form A. varians. The range in the position of the chain stolon in this species is from segment 19 to 58. The largest percentage of individuals were found to bear the chain on or between segments 30 and 38; a smaller percentage on or between segments 39 and 48, and an equal number between segments 25 and 29; fewer between segments 19 and 24, and a very few between segments 50 and 58.

In 155 individuals examined the following results were tabulated. (The upper numerals indicate the number of the segment to which the chain of stolons is attached; the lower, the number of individuals.)

A	Seg.	30	31	32	33	34	35	36	37	38
	Ind.	16	5	19	4	20	10	5	14	13

B	Seg.	25	26	29	39	40	41	45	48
	Ind.	5	4	9	9	6	4	2	3
C	Seg.	19	21	24	52	58			
	Ind.	1	1	2	2	1			

From this it will be noted that the position of the chain occurs most frequently on some segment in Table *A*, varying between segments 30 and 38, with a decided preponderance in favor of segments 34, 32, and 30, respectively. In other words, the greatest number of individuals have parent stocks of medium length, with from 30 to 38 segments; and the position of the chain on parent stocks of fewer or more numerous segments than this range occurs less frequently as the number of segments becomes less or greater.

Within the range in which the chain has been found to occur most frequently, it will also be noticed that several segments (31, 33, 36) bear the chain much less often than others, so that the chain-bearing phenomenon would appear to be confined more particularly to certain ones of the segments in this range (30, 32, 34, 37, 38).

In observing the sex of the individuals tabulated, it was noted that by far the greater majority of the specimens with the chain attached to the thirtieth segment or anterior thereto bore female stolons, while those with a great number of segments invariably bore male stolons. In this lot of specimens examined no individuals with female stolons were found with a parent stock of more than 41 segments, while those of 19, 21, and 24 segments all bore female stolons. On the other hand, those of 45 and more segments all bore male chains. Bearing in mind that the first stolon of the series in the chain is formed by the separation of a number of segments from the posterior part of the parent stock, this condition might possibly be due to the fact that the female stolons always consist of a far greater number of segments than do the male, and hence in the process of forming the first stolon leave a more reduced parent stock; while in the process of forming the first male stolon fewer segments would be required, and hence a longer parent stock left back.

In P. ornata and P. tardigrada variations in the position of

the stolon are of comparatively infrequent occurrence. The position of the stolon is very constantly on the thirteenth segment. In more than 200 specimens of P. ornata examined, not more than nine were found in which the stolon was attached to any other than the thirteenth segment; of these, six were found to bear the stolon on the fourteenth segment, while in three it was borne on the twelfth segment. In a single instance I have found the stolon as far forward as the eleventh segment. In all cases the variation was among individuals which bore male stolons.

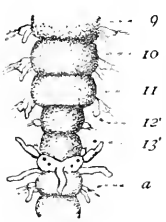
P. tardigrada shows even less variation than P. ornata. In 55 individuals examined, not a single case of variation was observed. Out of 110 individuals examined, Andrews (*Proc. U. S. Nat. Mus.*, Vol. XIV) obtained three specimens with the bud attached to the fourteenth segment.

Variations in the position of the stolon in the two species of Proceraea would accordingly be confined almost exclusively to occurrences of the position of the stolon either immediately anterior or posterior to a fixed segment, the posterior position being the most frequent form of variation.

In A. cornutus variations in the position of the bud are of still less frequent occurrence. Out of 178 specimens examined at a time when the forms were most abundant, not a single case of variation was observed. I have, however, found specimens in which the stolon was attached to the twelfth segment, but, as compared with Proceraea, such occurrences are very rare.

A further proof of the more constant occurrence of the bud on the thirteenth segment in this species is the fact that in individuals in which mutilation or severance of segments anterior to the region of budding has occurred, in the subsequent regeneration of new segments, the bud will not, as I have observed in Proceraea, develop its head from the tissues of the most anterior regenerated segment, but will first of all regenerate the lost segments of the parent stock, and following these produce the bud. The accompanying figure represents a specimen in which all the segments of the parent stock posterior to the eleventh were amputated and have been replaced by a series of new segments. The bud, instead of taking its origin in the

plane of new tissue formation, *i.e.*, on the twelfth segment, has followed the law of budding in this species and developed its head from the tissues of the fourteenth segment, and thus added two segments to the parent stock. The addition of new tissue to the parent stock, after amputation of one or two of its posterior segments, I have never been able to find in Proceraea, and so far as I have been able to carry my observations, I am convinced that such a condition does not take place, but that instead, wherever new segments are formed following amputation, the head takes its origin from the tissues of the first new segment formed.



9, 10, 11, old segments of parent stock; *12', 13',* regenerated segments of parent stock; *a,* stolon with developing head.

From these observations it would appear, therefore, that by far the greatest variation occurs in the chain-bearing form of Autolytus. The great range in the position of the chain, and hence the amount of variation, is modified by a condition to which I have already referred in a previous paper (*Journal of Morphology*, Vol. XVI, No. 2). I have there shown that in this species, in the region in which new segments are being formed (region of proliferation), not all the newly formed segments are pushed back for the formation of new stolons, but that occasionally some of these segments become segments of the parent stock, and thus considerably increase its length. In this way I endeavor to account for the great length (40–58 segments) of the parent stock in the stouter and more developed specimens—a length which I have shown does not exist in the younger and more slender forms. This being the case, the true range of variation would have to be sought in such specimens only which are in the act of forming a first stolon by the separation of the posterior segments of the parent stock. Of such individuals I have found specimens sufficient to give a range from segment 19 to as high as segment 38. Thus while variation here, as identical with the mode of variation in the species investigated, does not present so wide a range as indicated in the tabulation, nevertheless it shows a far greater range and is of much more frequent occurrence in chain-forming

than in the solitary stolon forms. In marked contrast to the variations in A. varians is the constancy in the position of the bud in A. cornutus, where new segments even are formed for the maintenance of a fixed position of budding.

URSINUS COLLEGE, COLLEGEVILLE, PA.,
Nov. 16, 1899.

GORDIACEA FROM THE COPE COLLECTION.

THOS. H. MONTGOMERY, Jr.

At his death Prof. Edward D. Cope left to the Philadelphia Academy of Natural Sciences, among other alcoholic collections, a few specimens of Gordiacea. Among them is a new species, while the others are interesting from the standpoint of geographical distribution.

1. *Gordius aquaticus* (Linn). One ♂ from Haines Falls, Catskills, New York, U. S. A. This specimen is a typical one of this species, and is particularly interesting as coming from such an eastern locality of the United States; previous specimens I have described only from Mexico and California, while all others of the species seen by me from the eastern part of the continent belonged to the following subspecies:

2. *G. aquaticus robustus* (Leidy). Three ♂♂ from Austin, Texas, the first record from this State.

3. *Paragordius varius* (Leidy). One ♂ from the same locality.

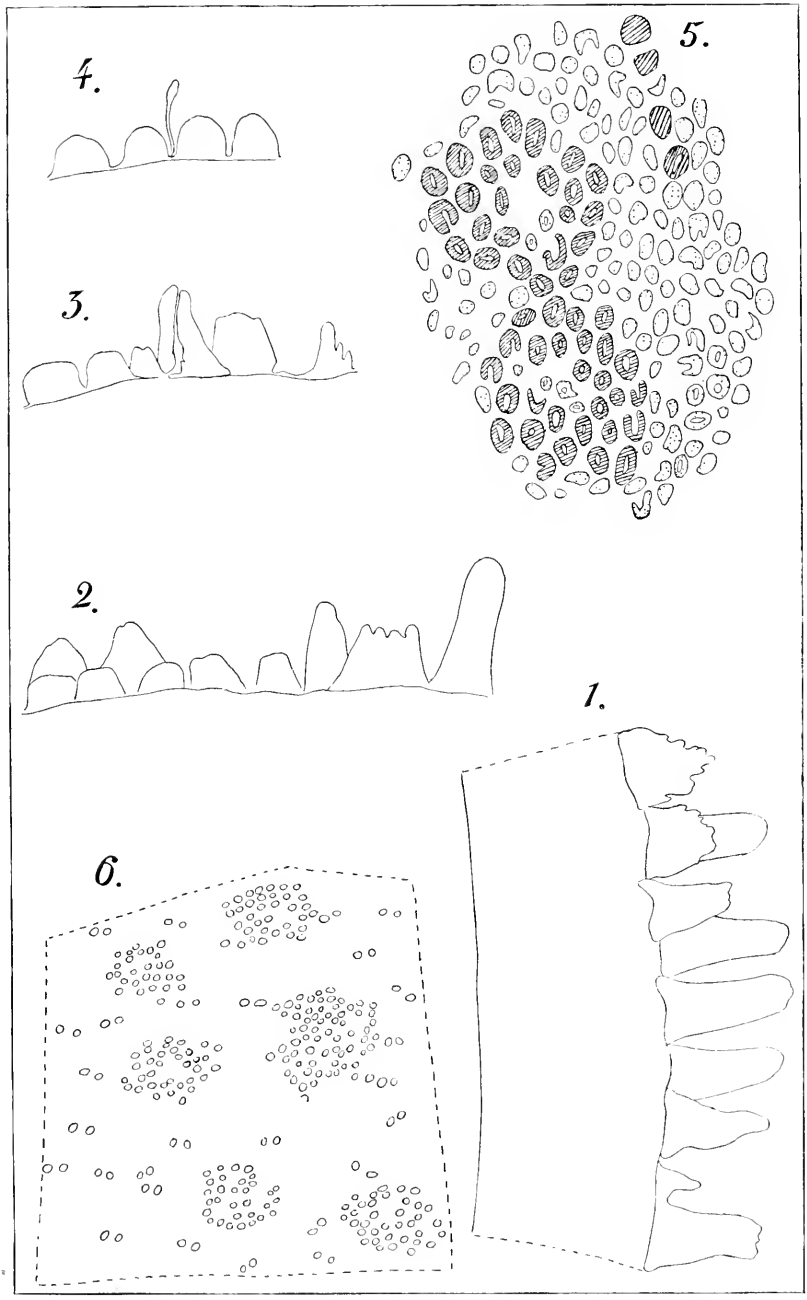
4. *Chordodes occidentalis* (Montg.). One ♂ from Texas, taken from the abdomen of a large grasshopper.

5. *C. Cameranonis*, n. sp. One ♂ from the West Coast, "Mazatlan or Panama." This type is in the collection of the Philadelphia Academy of Natural Sciences.

Form. — Body dorso-ventrally flattened, with slight median grooves. Anterior third of the body gradually tapering to a point, but the extreme end of the head truncated. Posterior end also attenuated, but less so than head; rounded terminally. A post-cloacal ventral groove is in the males of most species of the genus.

Cuticle. — Three main kinds of cuticular processes may be distinguished:

(1) The most abundant are low tubercles, which, on surface view (Fig. 5), appear more or less rounded or oval in outline, less frequently notched at one side, or sickle-shaped. While on



Figs. 1–4, portions of transverse sections of the cuticle, the cuticular processes shown only in outline; in Fig. 1 the outline of the fibrous cuticle is shown. (Zeiss homog. 1 mm. $\frac{1}{12}$, oc. 2.) Fig. 5, surface view of a portion of the cuticle, showing both tubercles and papillae (the latter darker) (Oc. 4, obj. C.) Fig. 6, surface view of the cuticle, seen in water, to show only the arrangement of the groups of papillae, the tubercles not being shown. (Obj. A, oc. 4.)

surface view they appear to be more or less clearly separated from one another, on cross-section they are seen to be connected at their bases. On section (Figs. 2–4) most of them appear of a conical or rounded conical outline, with rounded or flattened smooth summits; but in some the summits are notched or toothed, and this is especially the case with those tubercles found on the margins of the papillar groups next to be described.

(2) Papillae, which on surface view of the cuticle (Fig. 5) appear darker than the tubercles just described, owing to their greater height. On the surface of the cuticle they are arranged in groups of two kinds (Fig. 6, where only these groups of papillae are shown, and none of the tubercles; and Fig. 5, where both tubercles and papillae are shown): (*a*) In larger groups consisting of from about twenty-five to fifty papillae (usually about forty) each; and (*b*) in pairs, the pairs being much more numerous than the larger groups. The line joining the two papillae of a pair lies in the transverse axis of the body, and not infrequently two or three pairs of papillae may lie in such close juxtaposition as to form transverse rows of four or six papillae each. In the larger groups of papillae the center of each group is occupied by papillae of less height than those on the periphery, or is devoid of papillae. These papillae may be readily recognized on surface view, in addition to their dark coloring, by the clearer central portion, which is often narrow and slit-like (Fig. 5).

Transverse sections of the cuticle (Figs. 1–4) show these papillae in two forms. First, there are long, comparatively slender, finger-shaped papillae, with smooth outlines and rounded summits; some of these attain a height nearly equal to the transverse diameter of the underlying fibrous portion of the cuticle. And, secondly, there are papillae of greater diameter at the base, but less height, which lie among the former kind, and may be distinguished by the irregular notching and tuberculation of their summits and sides. The clear central portion of these papillae seen on surface view is shown on cross-section to be a clear axial core running the whole length of the papilla and representing possibly a pore canal.

On none of these papillae have I been able to find terminal

hairs, such as are so frequently found in the larger papillae of many species of the genus; no hairs were to be seen on the cuticle on surface view examined in water and in balsam, nor yet on cross-sections examined with the one-twelfth immersion lens of Zeiss.

(3) Hyaline, club-shaped, delicate processes scattered sparingly over the cuticle (Fig. 4).

Color. — Black, head rufous-brown.

Dimensions. — Length, 425 mm.; greatest diameter, 2 mm. The structure of the genital organs showed this specimen to be sexually mature.

Comparisons. — This appears to be a well-marked species. In the arrangement of the papillae it bears some resemblance to *C. festae* Camerano, but differs from the latter in having no fine hairs ("corti e fini prolungamenti trasparenti") on the summits of the papillae and also in having no large, transparent, recurved hooks on the surface of the cuticle (*cf.* Camerano, "Monografia dei Gordii," *Accad. Real. Sci. di Torino*, 1897, p. 386, Taf. III, Fig. 38).

It is a pleasure to me to name this species in honor of Prof. Lorenzo Camerano, of Turin, who has given such an able systematic monograph of the group.

Biological School,
University of Pennsylvania, Philadelphia,
December 11, 1899.

A PRELIMINARY ACCOUNT OF THE SPERMATOGENESIS OF BATRACHOSEPS ATTENUATUS, POLYMORPHOUS SPERMATOGONIA, AUXOCYTES AND SPERMATOCYTES.

GUSTAV EISEN, PH.D.

INTRODUCTORY.

THIS paper is a preliminary report of my investigations on the spermatogenesis of *Batrachoseps attenuatus*. The memoir will be published in the *Journal of Morphology*, Vol. XVII, No. 1. As, however, some considerable time must elapse before the paper can be published, it has been deemed proper to publish this short extract covering a few of the more important points.

Batrachoseps is adult in the months of June and July, and is at this time difficult to find, as it is then estivating deep below the surface. The testes were fixed by my iridium-chloride method and sectioned in paraffin. The stain used was the iron haematoxylin, according to Benda, and after-staining with congo. The sections were studied with Zeiss Apochromate, 2 mm. Ap. l. 40. The light used was the incandescent gas-light passing through the achromatic filter described lately in the *Zeitschrift f. wiss. Microscopie*, Bd. XIV, p. 444.

The figures illustrating this paper are entirely diagrammatic. No special effort has been made to insert the correct number of chromioles in the chromosomes; and the author's want of skill in preparing this kind of drawing will account for many other discrepancies.

CONSTITUENTS OF THE CELL.

The following general division of the structures of the cells of the testes is proposed: Cytosome, Caryosome, and Archo-

some. This division is in accordance with the one proposed in my paper on the plasmocytes in the blood of *Batrachoseps*.[1]

The cytosome comprises all that part of the cell situated exterior to the nucleus except the archosome. The cytosome contains the following distinct structures: cytoplasm proper, plasmosphere, hyalosphere, granosphere, metaplasmic secretions, cytoplasmic membrane, and cell wall. None of these

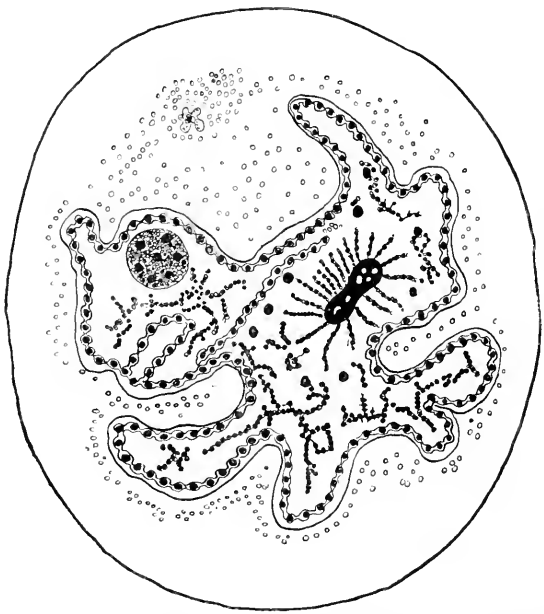


FIG. 1. — A polymorphous spermatogonium in the "perfect resting stage." The form of the nucleus allows the most perfect metabolism. Numerous chromioles are connected by a thread of chromoplasma. A network of linosomes is partially indicated, the individual granules being connected by Linopodia. A large chromoplast with endochromatic granules. Eight parachromatic granules. A single archosome in the cytoplasm, the latter only partially indicated by small open circles. A single large linoplast, with seven endonucleolar granules.

structures are in any way intimately connected with the archosome. The three spheres mentioned above surround each other, like three concentric shells, at the time when the cell is in partial resting stage; but at a later stage, or as soon as the prophase is entered, these spheres break up and scatter in the cytoplasm proper. Each one of the spheres constitutes an independent structure, and they are not developed one from the other.

[1] *Proc. Cal. Acad. Sci.*, 3d Ser., Zoöl. Vol. i, No. 1.

The plasmosphere is the outermost sphere; the granosphere is the innermost one. The plasmosphere is the first one to break up into minor parts. These arrange themselves in the equatorial of the cell and serve as material for the mantle fibers

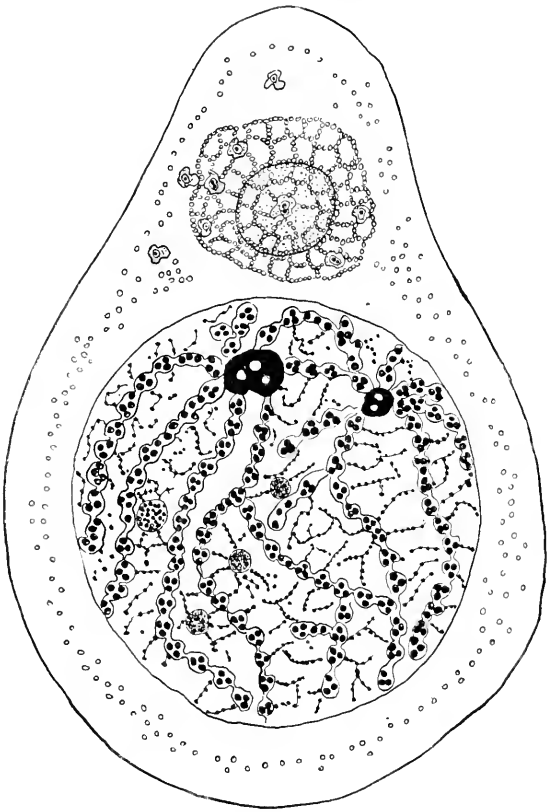


FIG. 2. — Auxocyte in the "imperfect resting stage," showing the formation of leaders consisting of round chromioles surrounded by a film of chromoplasm. The leaders start from two chromoplasts of unequal size, both containing endochromatic granules. The leaders are connected by a linosomic network. Four linoplasts. In the cytoplasm are seen the two spheres, the inner one, the granosphere, containing the archosome. There are eight accessory archosomes, some in the plasmosphere, others in the cytoplasm. The two spheres are of a foam-like structure. The cytoplasm is only partially indicated.

and for the new cell wall which is formed when the two daughter-cells separate.

The granosphere remains longer, but when it breaks up it furnishes material for the fibers of the central spindle. It also constitutes the main dwelling place of the archosome.

The archosome, or centrosomal structures, consists of three distinct parts, situated one interior to the other. These three parts constitute one single organized and individualized body — the archosome. The most interior part is the centriole; this centriole is surrounded by a thin layer or zone — the somosphere. The somosphere is surrounded by a generally non-staining zone — the centrosphere. There are one or more centrioles.

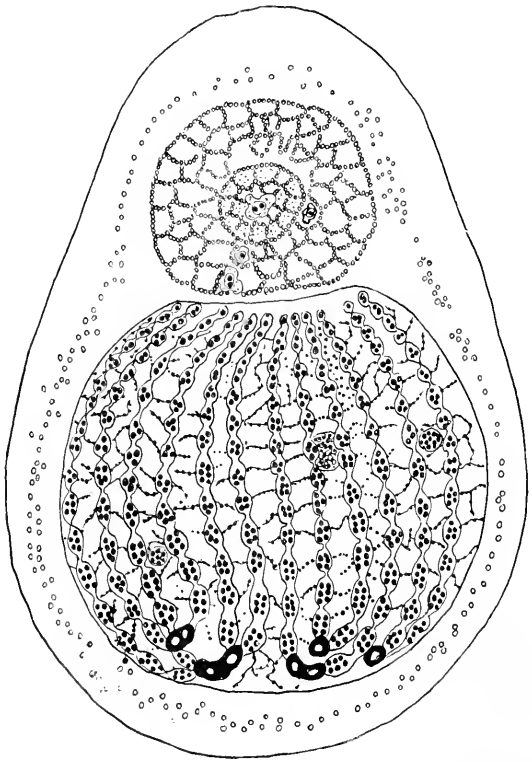


FIG. 3. — An auxocyte in the "bouquet stage." There are twelve leaders starting from five chromoplasts. The leaders consist of chromomeres containing chromioles suspended in a film of chromoplasm. The spheres are of a foam-like structure. There are three accessory archosomes and one archosome with two centrioles. The open space between the inner granosphere and the outer plasmosphere represents the hyalosphere. The cytoplasm is only partially indicated.

Both the somosphere and the centrosphere are amoeboid, especially the centrosphere. The latter constitutes the organ of locomotion of the archosome. There are besides the archosome several accessory archosomes. The function of the

archosome is to conduct the development and evolution of the fibers of the mitotic figures. The function of the accessory archosomes is to conduct the formation of the contractile fibers and perhaps furnish material for their construction. They also conduct the "fiber cones."

The location of the archosome is variable; it is sometimes situated in the granosphere, but is at other times found outside

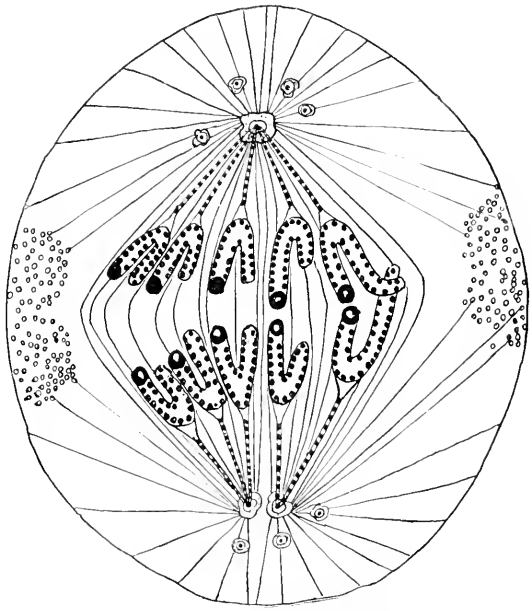


FIG. 4. — An auxocyte in the beginning of the anaphase. Only a few of the chromosomes are indicated. At each pole there are one and two archosomes and three and four accessory archosomes. The chromosomes contain chromioles suspended in chromoplasm. At the apex of each chromosome there is seen a chromoplast with endochromatic granules. To the right and left in the cell are seen agglomerations of plasmosphere indicating the position of the new cell wall, which is to separate the two daughter-cells. The chromosomes are seen to be connected with the chromiole by contractile fibers, the latter consisting of granules enclosed in a common sheath. The spindle fibers as well as the polar fibers start from the centrosphere.

of it. The accessory archosomes are of the same structure as the archosome, and one of the former may assume the function of the latter.

The accessory archosomes, if too numerous, are expelled from the cell, and then become paracellular bodies. Similarly, parts of the spheres are also expelled from the cell.

The nucleus contains the following more or less distinct

parts: chromioles, chromomeres, chromosomes, chromoplasts, linoplasts, linin, chromoplasm, endochromatic granules, and parachromatic granules.

Chromioles. — These are the most minute of the visible organized and individualized primary structures of the nucleus, and are the most important constituents of the chromosomes, probably being the carriers of heredity. They appear as minute globules, staining darker than the other parts of the nucleus except the chromoplasts. The chromioles are of a certain size and number in every species of nucleus and in every perfect chromosome. They are, as a rule, arranged in a regular manner in the chromosomes and in the chromomeres. During the absolute resting stage of the cell the chromioles are situated free in the nucleus, connected only by tiny filaments of linin and chromoplasm; while during the mitotic stages they are grouped into chromomeres, and these again into chromosomes. With absolute resting stage is indicated only absolute rest from "mitotic work." During this stage active metabolism is carried on.

There are thirty-six chromioles in every perfect chromosome, and these are divided among six chromomeres, each chromomere containing six chromioles. The chromioles are surrounded by a connective, apparently homogenous substance — the chromoplasm. The chromoplasm thus constitutes the greatest bulk of the chromosome.

The chromomeres are small aggregations of chromioles from three to six in number, according to the stage of development of the nucleus. The chromosomes in the polymorphous nuclei are twenty-four in number, but in the other testes cells there are only twelve. Each perfect chromosome contains six chromomeres.

In the resting stage of the polymorphous spermatogonia we find in the nucleus one or more large dark-staining bodies — the chromoplasts (net-knots). These chromoplasts are particular and most important organs of the nucleus. Their function is to attract the chromioles and to arrange them first into leaders, and later, through certain changes of the leaders, into chromosomes. The chromoplasts finally divide up into as many parts as there are chromosomes, one part adhering to each chromo-

some through its entire existence. The chromoplasts are characterized by one or more highly refractive endochromatic granules, which probably serve as nourishment for the chromi-

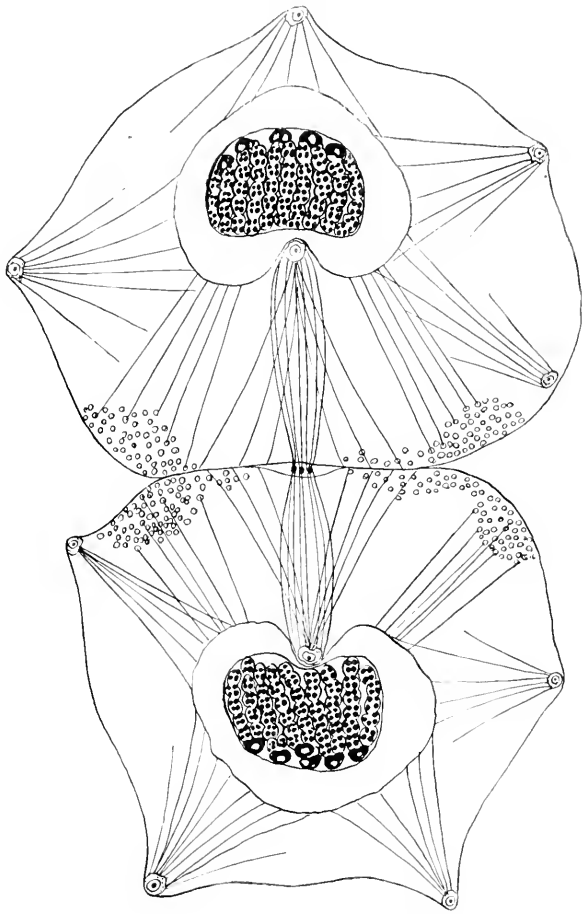


Fig. 5. — Two daughter-cells of an auxocyte connected by a spindle bridge. There are eight accessory archosomes at the apex of as many fiber cones. Two archosomes are connected by a central spindle. In the latter is seen a mid-body consisting of three condensation granules. The chromosomes are being regenerated, and the chromoplasts appear at the angle of the chromosomes instead of at the apex, as in the last cell stage. In one nucleus are seen five, in the other six chromoplasts with endochromatic granules. Between the true nuclear membrane and the false membrane is an open space caused by the false membrane being pulled away by the fiber cones.

oles. The chromoplasts serve as landmarks by which the position of the chromosomes can be ascertained with great accuracy.

The linin consists of minute granules — linosomes — arranged in a more or less regular network, which latter at certain times supports the elements of the chromosomes. The true nucleoli or linoplasts are principally agglomerations of linosomes, and serve as storage reservoirs for the linin network.

The nuclear membrane is formed apparently from linin and not from cytoplasm proper. During the anaphase a false nuclear membrane is formed from cytoplasm proper, but this membrane is again dissolved as soon as the object for which it is formed is accomplished.

Spindles and Spindle Fibers.

The following varieties may be segregated: mantle fibers, polar fibers, central spindle fibers, contractile fibers, retractile fibers, and fiber cones. All these fibers originate only in connection with an archosome. The contractile fibers alone are directly connected with the centriole of the archosome. All the other fibers and rays emanate from the outer margin of the centrosphere of the archosome, but do not penetrate into this sphere, and accordingly are not connected with the centrioles or the somosphere. The material for the mantle fibers is furnished from the granules and the secretions of the plasmosphere; while the material for the central spindle is furnished by the granules and secretions of the granosphere.

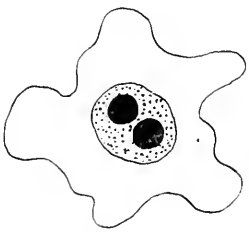


FIG. 6. — An archosome consisting of an outer centrosphere, an inner somosphere, with two centrioles.

The contractile fibers are those which connect the chromosomes with the archosome. They are from the beginning of a different structure from any of the other fibers, being beaded and highly contractile. Their structure strongly recalls that of muscle fiber.

The fiber cones are particular structures, so far not met with in any other cells. They consist of bundles of fibers held together at one point by an accessory archosome, while the distal ends of the fibers are attached to the false nuclear membrane

formed around the nucleus at the time of the anaphase. The archosome moves away and carries with it the fibers, which pull away the false nuclear membrane, thus causing a vacuole to form around the nucleus. The object of all this is probably to enable the nucleus to develop without the interference of surrounding structures. These fiber cones are frequently very numerous, as many as seventeen having been counted in a single cell. They are of large size and cause the cell membrane to be pushed out.[1]

The spindle bridge, which connects two or more cells, consists of the remnant of the central spindle. As the spindle bridge exists only in cells which commence the same phase of mitosis at the same time, it is probable that the purpose of the spindle bridge is to time or regulate the commencement of this mitosis. The mid-body of the spindle bridge serves probably as a storage reservoir for the cytoplasm of the spindle bridge.

Varieties of Cells.

The testes of *Batrachoseps* contain four distinct varieties of cells, as follows : polymorphous spermatogonia, auxocytes, spermatocytes, and spermatids. These originate one from the other in the order mentioned above. Of these varieties there are one or more generations. They are characterized as follows :

Polymorphous Spermatogonia. — These possess a perfect resting stage in which the nucleus is polymorphous as regards form, being greatly indentated and folded during the perfect resting stage. The nucleus during this stage contains neither chromosomes nor chromomeres, the chromioles being scattered about and not connected with the chromoplasts. These cells give rise to several generations of cells of the same nature, with the exception that there is no perfect resting stage like the one in the mother-cell, and that consequently the nucleus is not folded, but perfectly even, round, or oblong. The mitosis of the poly-

[1] Fiber cones of similar appearance, but of a different nature, have been described by botanists from the pollen cells of higher plants. These cones, however, do not possess archosomes.

morphous spermatogonia and their offspring is through twenty-four chromosomes and somatic division. The last generation of these cells gives rise to the auxocytes.

The auxocytes are characterized as follows: They possess a bouquet stage; they are the first cells with twelve chromosomes; their mitosis is heterotypic and by equation; they pos-

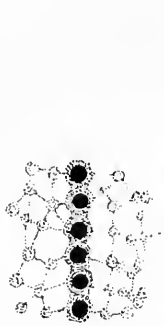


FIG. 7.

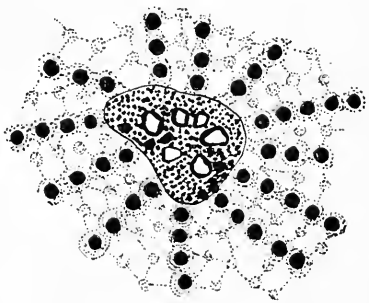


FIG. 8.

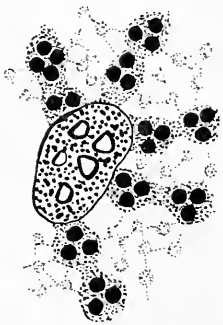


FIG. 9.

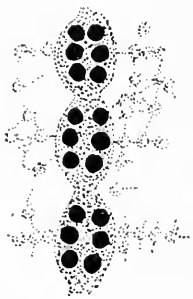


FIG. 10.

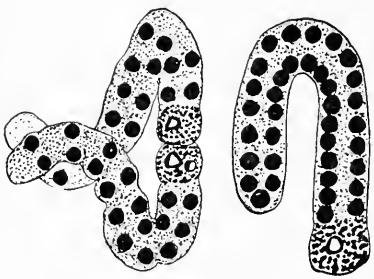


FIG. 11.

FIG. 12.

FIG. 13.

FIGS. 7–13 represent a broken series of leaders illustrating the formation of the leader and the chromosome.

FIG. 7. — Isolated row of chromioles surrounded by chromoplasm and suspended in a network of linosomes.

FIG. 8. — Chromoplast with twelve leaders of chromioles. From the imperfect resting stage of the polymorphous spermatogonium.

FIG. 9. — Chromoplast with five leaders. Each leader is made up of chromomeres, and each chromomere consists of three or more chromioles surrounded by chromoplasm. A network of linosomes between the chromomeres.

FIG. 10. — Three chromomeres, each with six chromioles surrounded by a chromoplasm and suspended in a network of linosomes.

FIG. 11. — A pretzel chromosome containing chromioles and two chromoplasts with endochromatic granules.

FIG. 12. — A chromosome from the metaphase. It contains thirty-six chromioles and a terminal chromoplast with an endochromatic granule.

FIG. 13. — Part of a chromosome from the spermatocyte.

sess no perfect resting stage, the chromioles being arranged into leaders and always connected with the chromoplasts; there is but one generation; the daughter-cells are the spermatocytes; and they have numerous fiber cones at the end of the anaphase.

The spermatocytes are characterized as follows: They have numerous fiber cones in the beginning of the mitosis, homotypic mitosis with twelve chromosomes and with equation division; no bouquet stage and no perfect resting stage; but one generation; the daughter-cells are the spermatids which give rise to the spermatozoa through direct development and growth; and the chromosomes are *I*-shaped.

The Mitosis.

The mitosis is the result of two distinct and separate processes which, for the greater part, run parallel and independent of each other, but which meet at certain nodes in order to

Fig. 14.—A diagrammatic representation of the structure of the granosphere. The dotted globules are cytoplasmic granules, and between them are seen metaplasmic secretions represented by small open rings. The globules are connected by Linopodia, and form a foam structure, partly a network.

accomplish certain objects jointly. These processes are the chromosomic process and the radiosomic process.

The radiosomic process is presided over by the archosome and the accessory archosomes, and consists in the development and evolution of the various fibers and the central spindle, in the evolution of the spheres, and the dissolution of the nuclear membrane. To this process belong also the development and dissolution of the false nuclear membrane and the reabsorption of the fibers.

The chromosomic process is presided over by the chromo-

plasts, and consists in the development and evolution of the leaders out of chromoplasm and the chromioles, the formation of the latter into chromomeres and chromosomes, and the multiplication of the chromioles and their proper distribution in the chromosomes. The two processes coöperate in the separation and equation of the chromosomes, which coöperation commences with the dissolution of the nuclear membrane. To the chromosomic process belongs also the movement of the chromoplasts in the umbrella-shaped and confluent nucleus at the end of the anaphase. With this process the archosomes have nothing to do, as it is accomplished before the nuclear membrane is dissolved by the mantle fibers.

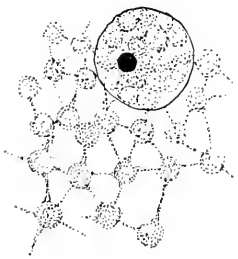


Fig. 15. — A diagrammatic representation of the structure of linosomes and the linoplast. The individual linin granules are connected by means of Linopodia. The linoplast contains linosomes as well as an endonucleolar body.

The radiosomic process commences with the dispersion of the spheres. The plasmosphere is dispersed first, and its granules are arranged in the equatorial of the cell, there to furnish material for the new cell walls. The central spindle fibers are then formed out of material furnished by the granosphere, which is in this way entirely used up. The nuclear membrane is dissolved by the mantle fibers and not by the central spindle fibers. The contractile fibers are formed after the central spindle fibers have reached considerable size.

The chromosomic process begins with the formation of leaders out of chromioles and chromoplasm. The chromioles aggregate into chromomeres, and, later on, a certain number of these form chromosomes. Their formation is shortly as follows: The leaders to the number of twelve are connected with the chromoplasts, and by contraction and a certain arrangement assume the bouquet stage. The leaders then split lengthwise, the two forks being held together by a fragment of the chromoplasts. The chromoplast divides into as many parts as there are to be chromosomes, but each part is always attached to a leader. Next, the two halves of the leader spread apart and twist around each other and thus form a pretzel-shaped chromosome. By this time the nuclear membrane is dissolved and

the pretzel-shaped chromosomes are placed on the central spindle, where they are taken hold of by the contractile fibers, which attach themselves to the prongs halfway between the

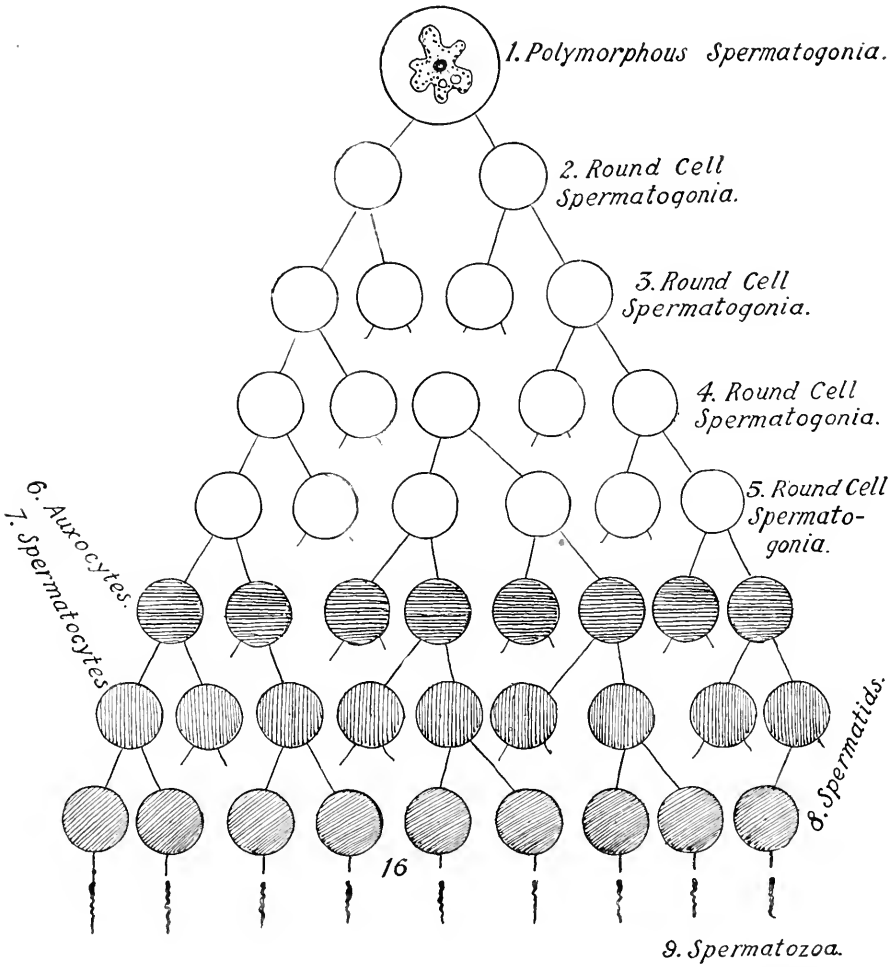


FIG. 16. — Diagram of the cell generations in *Batrachoseps* testes; 1, polymorphous spermatogonia; 2 to 5, four generations of round cell spermatogonia; 6, auxocytes; 7, spermatocytes; 8, spermatids; 9, spermatozoa.

chromoplasts and the free end. Each half is then pulled away and the chromosome is formed by an equation and not by a reduction. In the new chromosome the fragment of chromo-

plast is attached to one of the ends. This process is the one that takes place in the auxocytes.

The next step is the formation of a confluent umbrella stage or ring-like nucleus. The object of this form is to allow the chromoplasts to change their place. When the nucleus is reorganized in the spermatocyte the chromoplasts are found to be situated not at the end of each chromosome, but at the angle of the fork. This change of position could not take place except through the medium of an umbrella-shaped nucleus. During this stage the chromioles are also doubled. The nucleus now passes through a stage of growth which is facilitated through the large vacuole which is formed around the nucleus with the aid of the fiber cones and the accessory archosomes.

In the spermatocyte the central spindle is frequently formed from two opposite fiber cones left over from the last mitosis. The chromosomes of the spermatocytes are *V*-shaped before mitosis. They are divided longitudinally in the way usual in the homotypic mitosis, and by equation, not by reduction. During the prophases of the radiosomic mitosis the superfluous archosomes are expelled from the cell and remain for some time as paracellular bodies between the cells.

PERMANENCY AND NATURE OF THE CELL STRUCTURES.

The cytosome proper contains no permanent structures of any kind. The plasmosphere, hyalosphere, granosphere, the various kinds of fibers, as well as the central spindle, are all ephemeral structures which are developed by rearrangement of preëxisting granula, and which again disperse when their function is over. The granula contained in the cytosome is at least of four different kinds, and everything points to the conclusion that one kind of granula is never converted into any other kind. In other words, the granula of the granosphere is not evolved from the granula of the plasmosphere, etc., but both are independent and individualized primary structures as compared with the secondary ones of spheres and fibers. For the principal granula of the cell the following terminology is proposed : cytosomes, plasmosomes, hyalosomes, somosomes, granosomes, and linosomes, the latter being of nuclear origin.

If we turn to the nucleus, we find similarly that the chromomeres, the chromosomes, and the leaders are also ephemeral and secondary structures which form and disperse, the chromioles alone being the permanent individualities of the chromosomic structures. The nucleus then contains the following permanent granula: linosomes, the chromoplasmic granula, the chromioles, and the granula composing the chromoplasts. The permanent structures of the cell are the centrioles, the chromioles, and the chromoplasts. As regards the primary parts of these last-mentioned structures we are yet in doubt, but there is every reason to believe that these structures are of a highly complicated nature.

Similarly the fibrillar and alveolar structures of the protoplasm are only secondary, ephemeral, and temporary. With proper optical means we see that the alveole, as well as the reticulum, is built up of granules. These granules adhere to each other by means of minute projections or arms, for which I have proposed the name of Linopodia. The ultimate visible structure of the protoplasm is thus a granule, capable of projecting and retracting Linopodia.

For a fuller explanation and demonstration of these facts I must refer to the larger paper now in the hands of the publisher of the *Journal of Morphology*.

Biological Laboratory,
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San Francisco, California.

ERRATUM.

In No. 1, p. 1, 13th line, last word, read *ganglion* in place of "*gland.*"

Volume I.] *May, 1900.* [*No. 3.*

BIOLOGICAL BULLETIN.

THE EARLY CLEAVAGE AND FORMATION OF THE MESODERM OF SERPULORBIS SQUAMIGERUS CARPENTER.

S. J. HOLMES.

THE material upon which the present paper is based was collected at San Pedro, Cal., in the summer of 1895. Work upon it was carried on for a time during the winter of 1895–96, under Prof. C. O. Whitman, at the University of Chicago; but as the series of stages the material afforded proved incomplete, the subject was laid aside in the hope that, at some future time, when new material could be collected, the gaps might be filled. Since it is improbable that an opportunity of remedying this defect will soon present itself, and as the development of this form shows several interesting points of comparison as regards the formation of the mesoderm with what has recently been found to obtain in other mollusks and certain annelids, it was thought best to publish the present account. The development of Vermetus, a genus from which Serpulorbis is somewhat doubtfully distinct, has been studied by Salensky[1] in considerable detail. According to Salensky, mesoblastic pole cells do not appear, and the mesoderm in Vermetus arises at a comparatively late period of development by a proliferation from the ectoderm in the region of the blastopore. With this conclusion my own observations do not agree, as certain stages that were found afford very clear evidence that the mesoderm arises

[1] *Archives de Biologie.* I, vi, 1887.

from the posterior macromere *D*, as has been found in so many other cases among mollusks and annelids.

Serpulorbis squamigerus is a common mollusk on the coast of southern California. The shell early loses all traces of its originally spiral form, and becomes bent and twisted in a very irregular way. Many individuals are often found tangled together, resembling a group of worm tubes, and forming masses of considerable size. The eggs are deposited in elongated capsules attached by one end a short distance within the mouth of the shell. In addition to the eggs the capsules contain numerous small cells, probably follicular, which doubtless serve to nourish the developing embryos. A large number of the eggs in each capsule fail to develop normally, and sooner or later break up into masses of isolated blastomeres. The cleavage of such eggs is irregular, sometimes from the start, but often the irregularity appears only after the egg has developed for some time in an apparently normal manner. As this departure from the typical path of development occurs at different stages in different eggs, it is not always easy to distinguish the normal from the abnormal process of cleavage.

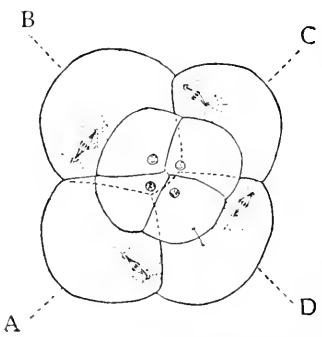

FIG. 1. — Eight-cell stage, seen from the animal pole. The dexiotropic origin of the first quartette of micromeres is indicated, and the spindles in the angles of the macromeres show that the next division will be laeotropic.

The first two cleavages are total and equal, giving rise to a four-cell stage of the usual molluscan type, in which two cells meet in a cross furrow at the vegetal pole. The next cleavage, which results in the formation of the first generation, or quartette, of micromeres, is dexiotropic. The micromeres are rather small, as is the rule in molluscan eggs, in which, as in the present case, there is a large amount of yolk. At the next cleavage the second quartette of micromeres are given off from the macromeres in a laeotropic direction. The spindles appear at one angle of the macromeres, but before the next division the nuclei wander through the cell so that the spindles next

appear at the opposite angle. The same migration is repeated in an opposite direction in preparation for the next ensuing division. The appearance of the second quartette is soon followed by a laeotropic division of the cells of the first. A dexiotropic cleavage of the second quartette next appears, and at about the same time the macromeres bud off the third quartette in a right-handed spiral, completing the separation of the ectoderm from the entoderm. The twenty micromeres composing the ectoderm are all transparent and devoid of yolk. While they form about one-half the surface of the egg, they

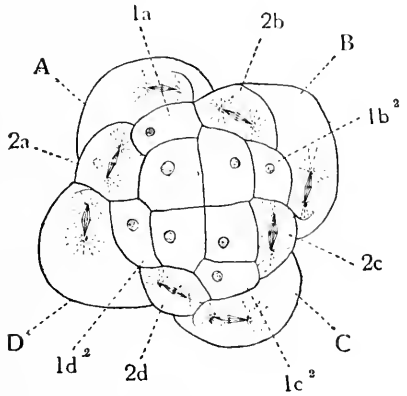

FIG. 2.

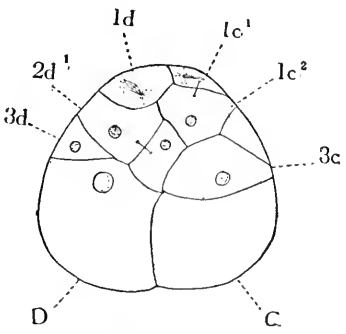

FIG. 3.

FIG. 2. — Sixteen to twenty-four cell stage from the animal pole, showing the origin of the third quartette and the dexiotropic cleavage of the second. The first quartette has divided, producing the four "trochoblasts."

FIG. 3. — Lateral view of the twenty-four cell stage. A cleavage is taking place in the apical cells.

form much less than half its bulk, as their thickness is not nearly so great as that of the large yolk-laden entomeres. The conclusion drawn by Salensky, that in Vermetus there are four quartettes of micromeres produced, is doubtless erroneous. The cleavage of the first quartette of ectomeres was probably overlooked, and the outer products of this division regarded as having had a separate origin from the macromeres. A comparison of Salensky's figures with the cleavage of Serpulorbis renders this interpretation probable. Besides, there are strong reasons for doubting that four generations of ectomeres are ever produced among the gasteropods, as I have attempted to show elsewhere.

The next cleavage occurs in the macromere *D*, and results in the formation of a yolk-laden cell, lying obliquely above the larger stem cell in such a way as to indicate that the division was laeotropic. This cell corresponds exactly as regards its time and mode of origin with the primary mesoblast cell of other mollusks. The corresponding division of the other three macromeres to form the remainder of the fourth quartette does not occur until a considerably later period. These divisions do not give rise to ectomeres, but to large yolk-laden entomeres, the cells of the fourth quartette being somewhat larger, if anything, than those at the vegetal pole.

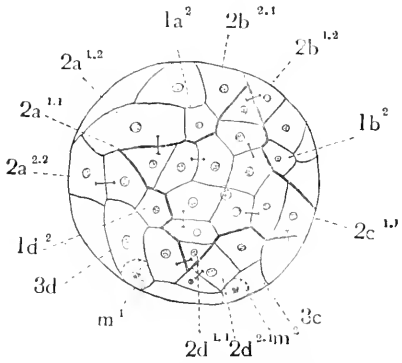

FIG. 4. — Forty-eight-cell stage, seen from the animal pole. The outline of the cross is marked with a heavier line. A dexiotropic twist is apparent in the arms of the cross. The small mesoblast cells are shown in dotted lines on the posterior side of the egg.

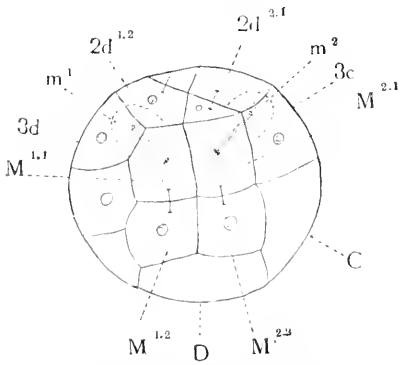

FIG. 5. — Posterior side of the same egg, showing the four derivatives of 4*d*, the upper pair budding off the mesomeres, m^1 and m^2, into the interior of the egg.

About the time the primary mesoblast cell is given off the four apical cells of the first quartette divide in a dexiotropic direction, the outer products of the division forming the basal cells of the arms of the cross. Up to this time the cleavages of Serpulorbis agree, point for point, with those of Crepidula, Lymnaea, Limax, Planorbis, and Physa, with the exception that the divisions in the latter two genera are reversed. A comparison of the forty-eight-cell stage, shown in Figs. 4 and 5, indicates that the following divisions have taken place: The four upper cells of the second quartette have divided in a laeotropic direction, giving rise to the cells $2a^{1.1}$, $2b^{1.1}$, etc., which

form the tip cells of the arms of the cross. The four tip cells are smaller than the others, as in Crepidula and Planorbis. A cleavage of the four lower cells of the second quartette has taken place, likewise in a laeotropic direction. The second quartette now contains sixteen cells in four groups of four cells each. These cells bear exactly the same relations to each other, to the arms of the cross, and to the adjacent cells of the other quartettes, that they do in Crepidula, Planorbis, and several other forms at the corresponding stage of development. There can be no doubt, therefore, of their derivation, though their actual divisions were not all observed. The large entomeres, *A*, *B*, and *C*, have divided laeotropically, completing the formation of the fourth quartette. In place of the mesoblast cell 4 *D* there is a group of four cells, an upper pair containing little yolk, and a lower pair of about the same size in which the yolk is abundant. The origin of these cells was not followed, but there can be little doubt that they all owe their origin to the mesoblastic pole cell. They occupy the same area that was occupied by the pole cell. The cap of ectodermic cells is radially symmetrical, and contains no cells of sufficient size to have given rise to such large cells as the upper pair of the four without altering very materially the symmetrical relations shown in the figure. Besides, nothing corresponding to such a division is seen in other forms. In all probability these cells arose first by a horizontal division of the mesoblast cell, such as occurs in a large number of forms, and then by a division of the two daughter-cells in a plane at right angles to the previous one. At this period the egg contains a regular cap of ectodermic cells, four entomeres at the vegetal pole, three entomeres, 4 *a*, 4 *b*, and 4 *c* of the fourth quartette, and the group of four cells above described, in place of the remaining cell of the fourth quartette, 4 *d*. A comparison with the corresponding stage in the egg of Crepidula, as shown in Fig. 31 of Conklin's paper,[1] shows that the cells of the ectodermic cap correspond point for point, and also *that the four cells we have derived from 4 d are represented in Crepidula by four cells of subequal size having the same origin and position.* The fourth quartette is formed a

[1] *Journ. Morph.* Vol. xiii. 1897.

little later in Crepidula than the stage shown in Fig. 31, otherwise the two eggs are practically identical. The four cells in Serpulorbis are all on the surface of the egg and are not overlapped so much by the ectomeres as in Crepidula. The upper pair in Fig. 4 is shown in process of division. Each cell buds off a small cell into the interior of the egg, the spindles diverging anteriorly. At about the same period an almost exactly similar division occurs in Crepidula, the upper pair of cells budding off a small cell into the interior of the egg in very nearly the same direction. At a somewhat later stage in Serpulorbis, shown in Fig. 6, I have found two pairs of small cells lying entirely within the cleavage cavity which probably represent the descendants of the single pair whose origin has just been described. The parallelism with Crepidula extends also to this division as the corresponding pair of small cells in that form divides at about the same period. This is as far as the cleavage of these cells was carried. These results were worked out before Conklin's paper appeared, and as I did not follow the further history of these cells, as Conklin has succeeded in doing in Crepidula, it seemed uncertain what interpretation of them should be made. It seemed improbable that all of 4 *d* should form the mesoblast, as it was supposed to do in several forms. The four large cells showed no signs of passing into the interior of the egg, and it is probable that, after the mesoderm is separated from the upper pair, they enter into the formation of the entoderm, as in Crepidula.

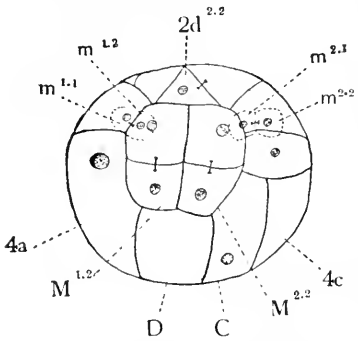

FIG. 6.—View of the posterior side of an egg in a somewhat later stage. There are seen two pairs of mesomeres in the cleavage cavity.

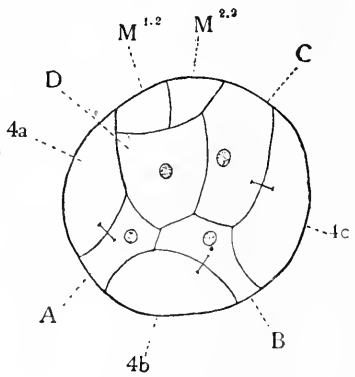

FIG. 7.—Vegetal pole of the same egg shown in Fig. 5.

Recent researches render it probable that the cell 4 *d* is not typically a purely mesoblastic cell. As Conklin has pointed out, the divisions of 4 *d* in Umbrella are strikingly like those in Crepidula, and strongly indicate, as Conklin maintains, that this cell contains both mesoderm and entoderm. The same cell in Cyclas was held by Stauffacher[1] to produce both mesoderm and entoderm. In Unio, Lillie[2] found that the pole cells budded off small cells at the surface before giving rise to the mesoblastic bands, and among annelids similar phenomena have been observed by Mead[3] in Amphitrite, by Wilson[4] in Nereis and Aricia, and by Treadwell[5] in Podarke. In Planorbis[6] I have found that a minute cell is budded off from each of the pole cells before they divide to form the mesoblastic bands. It has been suggested by Wilson that these minute cells correspond to the small entomeres found in Nereis, but they are budded off in a different direction and lie in the cleavage cavity instead of on the surface. This does not prove, however, that they are not homologous with entodermic cells, as a slight change in the direction of division of the pole cells would bring them in the wall of the blastula. And as they are probably not functional they may represent the last vestige of the entodermic portion of the mesentomeres.

[1] *Jen. Zeit.* Bd. xxviii. 1893.
[2] *Journ. Morph.* Vol. x. 1895.
[3] *Journ. Morph.* Vol. xiii. 1897.
[4] *Ann. N. Y. Acad. Sci.* Vol. xi. 1898.
[5] *Biological Lectures*, delivered at Woods Holl, Session of 1898, 1899.
[6] *Zoöl. Bull.* Vol. i. 1897.

NEW SPECIES OF HYGROCELEUTHUS AND DOLICHOPUS, WITH REMARKS ON HYGROCELEUTHUS.[1]

AXEL LEONARD MELANDER AND CHARLES THOMAS BRUES.

THE recognition of two new species of *Hygroceleuthus* and a study of both sexes of the other American species of this genus, and of another species which has been hitherto placed in *Dolichopus*, have shown the necessity of revising this genus. Hitherto but little attention has been paid to the females, which are very difficult to separate, whereas the males present very evident characters and are easily identified.

Previous to 1868 only one species of *Hygroceleuthus* was known from North America, and three others from the rest of the world. Since then North America has produced at least eight species, making it the richest country known in species of this genus.

Hygroceleuthus and *Dolichopus* are very closely allied, their separation being effected by male characters alone. These two genera form a group distinct from other *Dolichopodidae* by the presence of a number of bristles on the upper surface of the hind metatarsi. They have in common also the first joint of the antennae hairy above, third joint short, its arista dorsal, and hypopygium free.

The so-called distinction between the two genera is to be found in the length of the face which, in the typical males of *Hygroceleuthus*, is lengthened and attains the lower corner of the eye. Subordinate to this and even less constant are the lengthened antennae, deep incision in the hind margin of the wing, and broadened wings. In the three typical species of *Hygroceleuthus*, which have tarsal ornamentation, this occurs on the middle legs. In *Dolichopus* there is no species with the

[1] *Contributions from the Zoölogical Laboratory of the University of Texas*, under the direction of W. M. Wheeler, *No. 1.*

middle legs similarly ornamented if we except *plumipes*. For this reason and because it shows a tendency toward the lengthened face of *Hygroceleuthus*, we have included *plumipes* in the present paper. But as this species shows strong *Dolichopus* characters in the short, stout antennae and slight costal thickening, it cannot be placed satisfactorily in either genus as they have been defined. On the other hand, the European *Hygroceleuthus diadema* merges with *Dolichopus* on account of its shortened antennae.

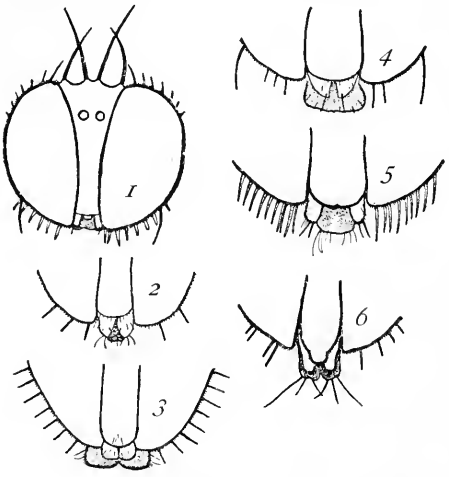

FIG. 1.—Showing length of face: 1, *Dolichopus comatus*, male; 2, *Hygroceleuthus plumipes*, male; 3, *Hygroceleuthus Wheelerii*, male; 4, *Hygroceleuthus amnicola*, female; 5, *Hygroceleuthus afflictus*, male; 6, *Hygroceleuthus latipes*, male.

The original definition of *Hygroceleuthus* included a deep incision in the hind margin of the wing and broadened wings. From these characters *Aldrichii* and *Wheelerii* deviate very decidedly.

Latipes, the only North American *Hygroceleuthus* which Loew saw, possessed no characters at variance with the typical species. It was because of limited material that Loew felt justified in constructing this genus. Like other genera founded on secondary sexual characters alone, such as *Rhagoneura* and *Spathochira* of this same group, *Hygroceleuthus* has been found invalid as the number of species increased.

From the foregoing it seems advisable that *Hygroceleuthus* be no longer retained with generic value, but may be kept as an expression for a group of the genus *Dolichopus*.

Of the previously described species of *Hygroceleuthus*, one has failed to be recognized, *lamellicornis* Thom., if indeed this be a species of *Hygroceleuthus*. The type was a female from California, but the description omitted the important points.

We have examined types of all the species except *latipes, plumipes, crenatus, afflictus,* and *ciliatus.* The specimens studied in the preparation of this paper are in the collection of Dr. Wm. M. Wheeler, who kindly placed his collection at our disposal.

Although the name *ciliatus* has been previously used by Walker,[1] Aldrich's *ciliatus* may remain, as Walker's species is too poorly characterized to admit of its recognition.

Males.

Middle tarsi ornamented 2
Middle tarsi plain 5
2. Antennae largely black . . . . . *Aldrichii* Wheeler
First joint of antennae yellow 3
3. Middle tarsi strongly compressed . . . . . *latipes* Loew
Middle tarsi not compressed, first joint feathered laterally . . 4
4. Middle tibia twice length of femur . . . *Wheelerii*, sp. nov.
Middle tibia not elongated, slender . . . . *plumipes* Scop.
5. Cilia of tegulae yellow 6
Cilia of tegulae mostly black 8
6. Second abdominal segment laterally with a tuft of yellow hairs *afflictus* O. S.
Abdomen without such tuft 7
7. Face yellowish white . . . . . *crenatus* O. S.
Face silvery . . . . . *idahoensis* Aldrich
8. Arista bare . . . . . *ciliatus* Aldrich
Arista densely pubescent 9
9. Front coxae yellow, postocular cilia in part yellow *consanguineus* Wheeler
Coxae black, postocular cilia wholly black . . var. *propinquus*

Females.

First joint of antennae yellow 2
First joint of antennae in great part black 4
2. Species about 6 mm. first joint of middle tarsus yellow at base . 3
Species about 4 mm. Middle tarsi wholly black . . *plumipes* Scop.
3. Hind tibiae wholly yellow, vertex green . . . *latipes* Loew
Hind tibiae black at tip, vertex violet . . . *latipes* var. *cognatus*
4. Tip of hind tibiae black, or, if yellow, the wings narrow . . 5
Hind tibiae wholly yellow 6

[1] *List of Diptera in Collection of British Museum*, pt. iii, p. 661.

5. Front femora with the basal two-thirds infuscated *amnicola* sp. nov.
   Front femora wholly yellow . . . . . *Aldrichii* Wheeler
6. Arista with slight pubescence; wings usually with a stump-vein at the bend of the fourth vein 7
   Arista bare 8
7. Second joint of hind tarsi yellow at base; legs yellow; smaller species *crenatus* O. S.
   Second joint of hind tarsi black; legs darker; larger species *consanguineus* Wheeler
8. Tegular cilia wholly black, somewhat robust . . . *ciliatus* Aldrich
   Tegular cilia yellow at sides 9
9. Wings yellowish anteriorly, coxae yellow . . . *afflictus* O. S.
   Wings hyaline, coxae darker . . . . *idahoensis* Aldrich

Hygroceleuthus Wheelerii, sp. nov.

Male. Length 5 mm.; length of wing 4 mm. Shining metallic cupreous green. Proboscis piceous. Face covered with a thick dust, silvery on lower half, becoming golden towards antennae. Antennae yellow, first two joints wholly so, the third black on upper surface and outer half. First joint hairy above, and with a slight swelling on inner surface to meet the other antenna; second joint tipped with a fringe of black hairs, becoming stouter and longer on underside, nearly one-half the length of first joint when viewed from above. Third joint somewhat longer than the first, bearing dorsally a stout arista with very short pubescence. Vertex metallic violet. Postocular cilia delicate, black above and light yellow below. Thorax bright grassy green, becoming cupreous at sides and with a faint indication of the two narrow approximated median brown lines. Abdomen green, with silvery dust at sides and beneath. Posterior margins of segments becoming cupreous and margined with piceous. Hypopygium green, almost piceous, overlaid with a grayish dust. Lamellae pale, with a distinct narrow dark border and a black fringe. Internal appendages yellow. Sides of thorax glaucous; shining green when viewed from behind. Fore coxae yellow, hairy on whole anterior face and with a few bristles at tip. Middle and hind coxae yellow with outer face glaucous at basal two-thirds. Trochanters, femora, and tibiae yellow. Middle tibiae very long and thin, the proportion of femur to tibia of the middle leg being 20 to 39. Hind tibiae not incrassate, nor with smooth space on inner surface. Anterior tarsi black from tip of first joint, middle and hind tarsi black. Middle

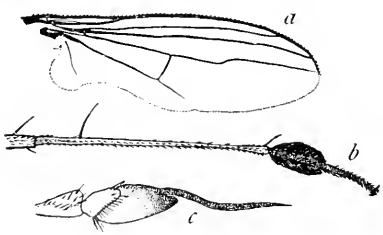

FIG. 2.—*H. Wheelerii*: *a*, wing of male; *b*, middle leg; *c*, antenna.

tarsi short, first joint broadly feathered laterally. Wings narrow, hyaline, distinctly yellowish towards costa. The usual costal swelling at tip of first vein is slight. Almost no incision at tip of fifth vein. The anal angle of wing is produced into a large distinct lobe. Veins dark. Bend in fourth vein regular. Halteres and tegulae yellow, the tegular cilia long and black.

One male specimen taken by Dr. Wm. M. Wheeler in a cranberry bog at Woods Holl, Mass., July 13, 1899.

This very distinct species is readily recognized by its lengthened middle tibiae. Aside from this the following are more or less characteristic: the reduced costal swelling and incision of the wing as well as the pronounced anal lobe; the peculiar lateral ornamentation of the middle tarsi, which are unusually short; the violet front; the light-colored antennae and finely pubescent arista; and the yellow hind tibiae.

Hygroceleuthus plumipes Scopoli.

Male. Length 3.5–4.5 mm. Length of wing 3.5–4 mm. Face yellow pollinose. Antennae yellow, third joint black at tip. First joint with a slightly prominent projection on its inner side. Arista slightly pubescent. Front metallic green. Thorax without distinct dusted bands. Abdomen

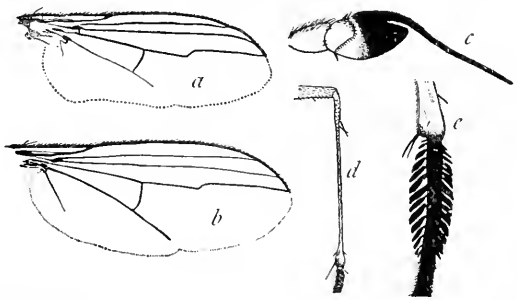

FIG. 3. — *H. plumipes*: *a*, male wing; *b*, female wing; *c*, antenna; *d*, middle tibia; *e*, middle metatarsus, male.

metallic green above and distinctly bronzed toward the apex; white dusted at the sides and covered throughout with short black hairs. Lamellae of hypopygium narrowly bordered with fuscous. Pleurae metallic green, covered with white dust. Coxae of same color as the pleurae, except the anterior ones, which are yellow and covered with black hairs on the anterior and inner surfaces, bearing also a few black bristles at their tips. Femora yellow. Tibiae yellow, the middle pair slightly, and the posterior pair distinctly tipped with black. Middle tibiae flat, very slender except at extreme

base and apex, which are normal in form. The flat sides each with a wide, shallow, piceous groove extending along the entire length of the tibia. Tarsi black, except basal two-thirds of anterior pair. Middle tarsi with the first joint longer than the two following and broadly feathered laterally. Wings narrow, the anterior and posterior margins subparallel, nearly hyaline. Swelling at tip of humeral vein slight, incision at tip of fifth vein slight. Tegulae with long black cilia.

Female. Length 3.5–4.5 mm. Length of wing 3.5–4 mm. Face broader, gray, greenish in certain lights and darker below. Middle tibiae and tarsi of the usual form. Anal lobe of wing more rounded than in the male, and the costa not thickened.

Twenty-three specimens examined. Sixteen males and six females, from Rabbit Ear Pass 10,000 feet, and North Park, 9000 feet, Colorado. Also one male specimen from Vancouver Island, collected by Mr. C. Livingston.

This species is readily distinguished by the peculiarly formed middle tibia and tarsus of the male. The female may be separated from *latipes* by its smaller size and wholly black middle tarsi, and from all the other species by the entirely yellow first antennal joint.

The distribution of this species is most interesting. It is one of the three species of *Dolichopus* which are common to Europe and North America. It is mostly a boreal species, being found in great numbers throughout Northern Europe, from Cape North to Switzerland. In America it was noticed by Loew from Alaska. Where *plumipes* extends toward the south it is limited to high altitudes, as witnessed in Switzerland and Colorado.

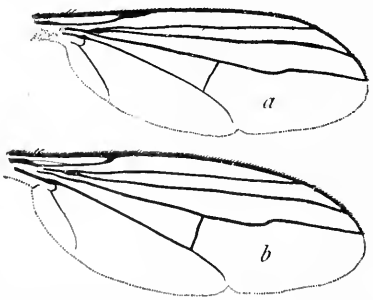

FIG. 4. — *H. latipes*: *a*, male; *b*, female.

Hygroceleuthus latipes Loew.

Male. Length 5–7 mm., of wing 4.5–6.5 mm. Face silvery, yellowish above. First joint of antennae yellow, at most slightly darkened above, long. Arista pubescent. Vertex generally green. About 6 to 8 of the supraocular cilia black, the remainder pale. Abdomen with posterior margins of the segments cupreous. Lamellae of hypopygium white with narrow black border and fringe. Anterior coxae yellow, hairy on distal

portion in front. Femora and tibiae yellow. Middle tarsi compressed, ornamentation dorsal on last four joints. Wings thickened at tip of first vein and incised at fifth. Tegula cilia black, a few yellow inside.

Female. Face silvery, broader. Antennae shorter, first joint hairy above, sometimes infuscated above. Vertex green. Abdomen more cupreous, and anterior and middle tarsi slightly lighter than in the male. Posterior femora with two macrochaetae near tip on outer side. Wing incision not very deep.

This species has a greater distribution than any of the other species, except *plumipes*. It has been taken at various places in the Northern States from Connecticut to Idaho. This is the commonest species, and, aside from *Wheelerii*, the only species yet found east of the Dakotas.

Latipes, var.? *cognatus*. Two specimens vary from the type as follows and may possibly represent another species. Posterior tibiae black at tip and hind tarsi totally black. Vertex violet. Posterior femora each with only one macrochaeta on outer side near apex. One female from Woods Holl, Mass., July 19, 1899, and another female from Pullman, Ill., August 7, 1897.

Hygroceleuthus Aldrichii Wheeler.

Male. Length 4–5 mm. Face with silvery white dust below, ochreous above. Antennae black, first and second joints yellow below on mesial surface. Arista moderately pubescent. Front green. Postocular cilia white on lower two-thirds, black above. Lamellae of hypopygium yellow with black border and fringe of delicate black hairs. Anterior coxae yellow, others dark. Second, third, and fourth joints of middle tarsi distinctly compressed and fringed with stout black hairs. Anal angle of wing bilobed, costal thickening prominent and incision at tip of fifth vein slight. Tegulae with long black cilia.

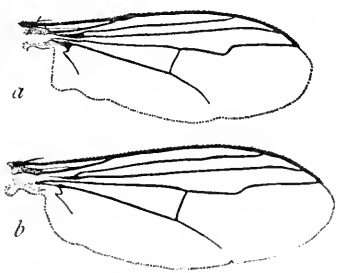

FIG. 5.—*H. Aldrichii*: *a*, male; *b*, female.

Female. Length 4–5.5 mm. Face grayish-yellow. First joint of antennae almost entirely black. Tip of hind tibiae usually black. Incision at tip of fifth vein slight. Anal angle not bilobed, and tarsi but very slightly compressed.

Numerous specimens examined, males and females. From Idaho, Wyoming, and Colorado.

The peculiar anal lobe of the male wing easily identifies this species. The female is not so easily distinguished, but can be recognized by the characters given above.

Hygroceleuthus amnicola, sp. nov.

Female. Length 4.5 mm., of wing 4.5 mm. Of a bright metallic green with cupreous reflections. Palpi light yellow with black hairs. Face evenly overlaid with golden dust. Antennae black with lower half of first and second joints yellow. The difference in color is sharply marked. First joint hairy above, with a rather large yellow projection from inner side. Second joint tipped with a fringe of black hairs which are longer below. Front metallic brassy green. Upper half of the postocular cilia black, lower pale. Thorax shining green, not much dusted in front, disc somewhat cupreous; the two narrow approximated lines are left green. Sides of thorax glaucous, becoming more piceous in all the coxae. Front coxae with black hairs on whole anterior face. Middle and hind femora yellow; fore femora black for nearly proximal two-thirds. All the tibiae yellow, infuscated at tip; the darkening especially prominent on the hind legs. Front tarsi black from tip of first joint; middle tarsi with first and second joints yellow, their tips black, remaining joints black; hind tarsi black from base of first joint. Wings long and narrow, greatly prolonged beyond tip of fourth vein; the fourth vein with a very strong bend and continued obliquely forward. Halteres and tegulae yellow, the cilia of the latter long and black.

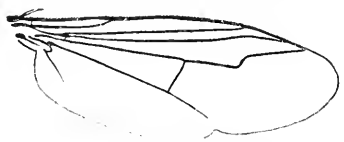

FIG. 6. — *H. amnicola*: wing of female.

One specimen, Colorado, Grizzly Creek, North Park; collected by Mr. C. F. Baker.

Although this species is represented by a single female specimen, it is so distinct that there is no hesitancy about its position. The wings reach further beyond the fourth vein; the angle of the fourth vein is more nearly rectangular; the coxae are darker and the femora blacker than in any other female *Hygroceleuthus*.

Amnicola differs from *Aldrichii* thus: middle tarsi are not compressed and are largely yellow; the front femora and coxae are much darker; the wings are hyaline and more extended beyond the veins, and the fourth vein is more sharply bent.

Hygroceleuthus crenatus O. S.

Male. Length 5–6 mm. Face yellowish-white. Antennae with the two basal joints black, except a yellow protuberance on the inner side of each. Arista densely pubescent. Postocular cilia black on upper third, yellow below. Anterior coxae yellow, with a black stripe outwardly. Femora and tibiae yellow; the hind tibiae incrassate, with a shallow, broad, brownish groove on the inner side. Anterior and middle tibiae infuscated toward the tips. Hind tarsi black except base of first joint. Lamellae of hypopygium nearly white, margined with black at the tips. Wings very broad, narrowed to the base. Costa moderately thickened, incision at tip of fifth vein moderate. Cilia of tegulae yellow, delicate, sometimes with a few black hairs intermixed.

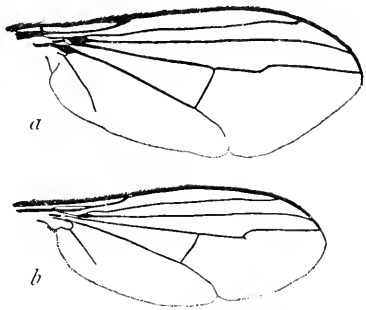

FIG. 7. — *H. crenatus: a*, male; *b*, female.

Female. Length 5–6 mm. Face uniform gray. First joint of antennae in great part black. Arista black, slightly pubescent. Hind tibiae wholly yellow, the hind tarsi with the second joint yellow at the base. Wings with a distinct incision at tip of fifth vein. A stump-vein projecting from the bend of the fourth vein, sometimes abbreviated.

Numerous male and female specimens examined from California, Washington, Wyoming, Idaho, and Vancouver Island.

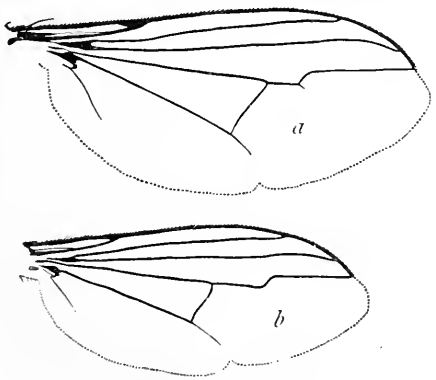

FIG. 8. — *H. consanguineus: a*, male; *b*, female.

Hygroceleuthus consanguineus Wheeler.

Male. Length 5.5–6.5 mm., of wing 4.5–5.5 mm. Upper two-thirds of face more opaque than lower third, generally with two broad vertical bands on upper two-thirds. Antennae black, in small part yellow below, and on mesial surface of first and second joints. First joint with smooth swelling inside. Arista thick, densely pubescent. Postocular cilia black, becoming thick and flat below; upper infraorbital cilia bright orange, lower black. Lamellae of hypopygium

piceous with suffused black border. Legs yellow, black from tip of first tarsal joint. Hind tibiae incrassate slightly. Distal portion of fourth vein with abrupt angle and with stump-vein. Cilia of tegulae black.

Female. Somewhat smaller and with relatively longer wings. Stump-vein at angle of fourth longitudinal present. Tegular cilia black. Fore coxae with black hairs in front. The dilation of first antennal joint is less prominent. The lower postocular cilia are also parti-colored but less flattened than in the male.

This species was described from a large number of specimens collected in July, 1896, near Monterey, Cal.

Consanguineus, var. *propinquus*. Several interesting specimens received from Mr. C. Livingston, from Corfield, Vancouver Island, vary from the typical *consanguineus* as follows:

Darker. All the coxae piceous; femora piceous beneath near base. Postocular cilia black, none of the orange-colored cilia of the typical *consanguineus* present, not so many of the infraocular cilia flattened. Lamellae of hypopygium darker.

Hygroceleuthus afflictus O. S.

Male. Length 6–6.5 mm. Face white, silvery. Antennae with yellow expansion on inner side of first joint; second joint with only a vestige of yellow on the inner side. Pubescence of arista sparse but robust. Vertex green. Postocular cilia black above for a long distance, descending nearly to the middle of the eye; below light yellow. Second abdominal segment bearing on each side near the middle a tuft of long yellow hairs, directed backward and reaching to the middle of the fourth segment. Third segment with a very small similar tuft. Hind tibiae incrassate, with a broad shallow groove on the inner side. Costal thickening and incision at fifth vein of wing distinct.

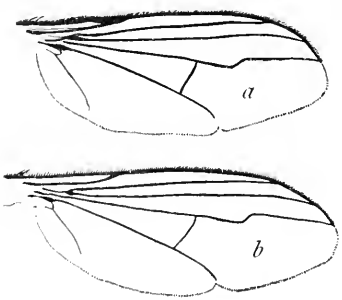

FIG. 9. — *H. afflictus*: *a*, male; *b*, female.

Female. Length 5.5–6.5 mm. Face gray, with a greenish tinge on the lower part and slightly ochreous near the base of the antennae. Antennae dark, first and second joints in great part black. Arista bare. Abdomen without any tufts of yellow hair. Anterior coxae yellow, sometimes with a small posterior stripe dark. Hind tibiae completely yellow. Wings yellowish anteriorly, costa not thickened, notch at tip of fifth vein very pronounced. Tegular cilia black, yellow at the sides.

Numerous males and females examined from Arizona, Monterey County, Cal., and Wyoming. It was described from San Rafael, Cal., and is recorded also from Washington.

The male of this species is very easily known by the presence of the tufts of yellow hair upon the second abdominal segment.

Hygroceleuthus ciliatus Aldrich.

Male. Length 4–5.5 mm. Face yellowish-white. Front green. Antennae black, except lower half of first and second joints. Arista bare. Postocular cilia black on upper third, below nearly white. Sides of first abdominal segment with a few white hairs. Tips of hind tibiae blackish. Tarsi simple, black from tip of first joint. Wings narrow, hyaline, costa not thickened at tip of first longitudinal. Indention at tip of fifth vein slight. Tegulae with long black cilia.

Female. Length 4–5.5 mm. Face yellowish-gray. Arista of antennae bare. Hind tibiae wholly yellow. First joint of hind tarsi lighter at base. Tegular cilia black. Wings with a distinct incision at tip of fifth vein.

Numerous specimens examined from South Dakota and Wyoming.

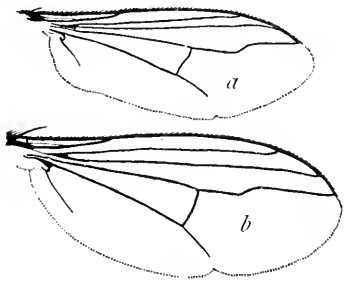

FIG. 10.—*H. ciliatus: a*, male; *b*, female.

Hygroceleuthus idahoensis Aldrich.

Male. Length 5.2 mm., of wing 4.8 mm. Face silvery. Antennae black, not large but with swollen yellow protuberance on inner side; second joint slightly yellow on inner side; arista rather stout. Vertex blue-green. Lamellae of hypopygium small, white, with rather wide black margin. Anterior coxae yellow with a dark green stripe on outer face, and with a few hairs on lower part. Hind tibiae incrassate with a longitudinal depression. Tarsi black from tip of first joint. Costa thickened for a long distance, the incision in hind margin slight. Tegular cilia pale, not large.

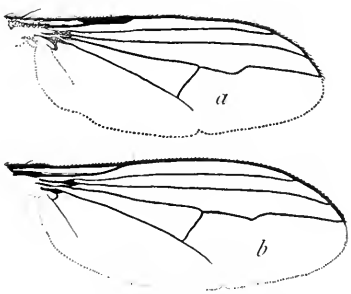

FIG. 11.—*H. idahoensis: a*, male; *b*, female.

Female. Face broader, darker than in the male. Anterior coxae more hairy. Wings less yellow anteriorly, costa not thickened. Tegular cilia larger, black with a slight admixture of pale ones.

Moscow, Idaho. September. The original collection numbered about seventy-five specimens.

List of the Species of the Group Hygroceleuthus.

plumipes Scopoli, 1763. *Ent. Carn.*, 334.
latipes Loew, 1861. *Neue Beitraege*, Fasc. viii., 5.
? *lamellicornis* Thomson, 1868. *Eugenies Resa*, 511.
crenatus Osten Sacken, 1877. *Western Diptera*, 312.
afflictus Osten Sacken, 1877. *Western Diptera*, 313.
ciliatus Aldrich, 1893. *Kan. Univ. Quart.*, 25.
idahoensis Aldrich, 1894. *Kan. Univ. Quart.*, 154.
Aldrichii Wheeler, 1899. *Proc. Cal. Acad. Sci.*, 3.
consanguineus Wheeler, 1899. *Proc. Cal. Acad. Sci.*, 5.
Wheelerii Melander and Brues, *sp. nov.*
amnicola Melander and Brues, *sp. nov.*

Dolichopus.

The following notes and descriptions were made from specimens belonging to Dr. Wm. M. Wheeler, who has not only given us his entire collection to work over, but has also tendered us much aid and advice.

The appended list is given in the hope that it may prove useful, as it contains many new localities. It is interesting to note that so many of Loew's species have been again recognized.

Dimorphism has not been noticed in the genus *Dolichopus* as yet, but a most interesting case of what may turn out to be such is to be found in the species *Henshawi* and *marginatus*. Of the more specific characters these two species possess in common the following: antennae similarly colored, vertex violet, fore coxae with dark hairs, hind tibiae with similar dark glabrous stripes, similar wing neuration, and the yellow hind femora of the male ciliated with black hairs, in which character they differ from all other dolichopodes. On the other hand, the males seem evidently distinct as follows:

Henshawi. Face generally yellow; postocular cilia darker yellow; fore tibiae incrassated at tip; fore tarsi ornamented and banded; hind tibiae not evidently darkened towards tip

except a large black blotch on inner side; lamellae of hypopygium fringed with comparatively short hairs.

Marginatus. Face gray; all the legs plain; front tarsi gradually darker toward tip; hind tibiae more infuscated at apex; lamellae fringed with numerous longer hairs.

The females of these species cannot be separated. They agree rather with *marginatus* in the color of the postocular cilia and of the legs. The males, evidently so distinct, were taken, together with the females, in the same netful at Woods Holl, Mass., by Dr. Wheeler. *Marginatus* is the commoner form. In all were taken from July 14 to August 9, 1899, forty-eight females, thirteen male *Henshawi*, and nineteen male *marginatus*.

Dolichopus partitus, sp. nov.

Femora chiefly black, cilia of inferior orbit black, wings infuscated, coxae wholly black.

Male. Length 5–5.5 mm., of wing the same. Dark green with metallic lustre. Proboscis and palpi black. Face rather wide, short, concave beneath the antenna, and with a pronounced transverse ridge at its lower fourth, below this convex. Face covered with light brown pollen, except a small spot at each side of the ridge. Antennae totally black; the first joint with short bristles above; the bristles about the apex of the second joint much longer below. Third joint short, ovate, obtusely pointed at tip; arista black, pubescent. Front dark violaceous green. Postocular cilia totally black. Thorax above, dark green, with a median longitudinal dark cupreous band. Scutellum of same color as thorax. Abdomen metallic green, lighter than thorax. Surface covered with short black hairs, more sparse towards base; very slightly covered with whitish dust. Hypopygium almost black, shining with two patches of black hair on dorsal side near the base; internal appendages ferruginous. Lamellae yellow, of usual size, with a black border. Between the white center and black border is a ferruginous band. The border is very much jagged at apex and furnished with strong bristles, becoming more slender towards base. Pleurae greenish-black, covered with whitish dust; coxae black. Legs black, except femora and tibiae just at their articulation, the four anterior tibiae and the base of the first joint of four anterior tarsi. Posterior femora not ciliated. Wings infuscated about cross-vein and at apex between costa and third vein. The

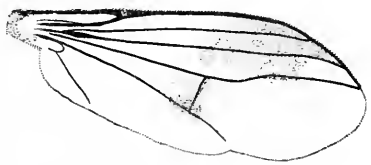

FIG. 12. — *D. partitus:* male wing.

latter spot reaches only to the second longitudinal in one specimen. Veins black; costa with an elongate swelling at the junction of the humeral vein; notch at tip of fifth vein distinct. Tegulae and halteres light yellow, the former with long black cilia.

Described from two male specimens collected in North Park, Colorado.

This species is related to *Johnsoni* Aldrich, but may be distinguished by its wide face, totally black coxae, spotted wings, and violaceous front.

Dolichopus paluster, sp. nov.

Bluish-green; antennae totally black; infraocular cilia black; tegular cilia black; legs including coxae black; tarsi not ornamented; hind femora ciliated in male.

Male. Length 5–5.5 mm. Wing 4.5–5 mm. Shining bluish-green. Proboscis and palpi piceous. Face moderately wide, between three and four times as long as the width at the middle, covered with brownish-yellow pollen, not at all silvery. Vertex dark blue-green. Postocular cilia all black. Antennae totally black; first joint with but few bristles above, those about the apex of the second joint very long below. Third joint oval, obtuse at apex. Arista black, pubescent, about twice as long as the antenna. Dorsum of thorax dark green, tinged with blue. In some specimens there is a median stripe, more blue and shining. Scutellum of the same color as thorax, fringed with short light-brown hairs. Abdomen green, distinctly bluish in many specimens, and very shining, sharply compressed towards apex and somewhat inflated near the base; destitute of light dust. Hypopygium black, shining, slightly ochreous-dusted near the base, and bearing a bunch of black hairs basally. Lamellae oval, slightly angulated inwardly, nearly white, with a sharply defined black border, fringed with black bristles which are more delicate basally. Internal appendages dark ferruginous. Pleurae black, white dusted, those of the prothorax green like the dorsum. Legs, including coxae, wholly black, fore coxae white dusted, and with short black hairs. Anterior tarsi not ornamented, about one-fourth longer than the tibiae; middle tarsi but slightly longer than tibiae. Hind femora ciliated on apical half with black hairs, the longest hairs not longer than the width of the femur at the point of their insertion. Posterior tibiae somewhat thickened. Wings grayish; veins black; costa but slightly thickened at tip of first longitudinal; fourth vein not sharply bent, approximated with the third vein at tip. Incision at tip of fifth vein slight. Tegulae and halteres yellow, tegular cilia black.

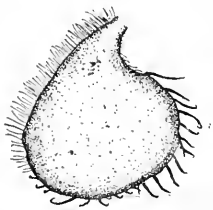

FIG. 13.—*D. paluster*: male lamella.

Female. Size same. More coppery than the male, especially on the sides of the thorax and abdomen. Face dark yellowish-gray; slightly more than twice as long as wide. Posterior femora not ciliated below, hind tibiae not thickened. The wings are brownish, darker anteriorly between the costa and second longitudinal; the veins black, very narrowly margined with brown. Otherwise like the male.

Described from five male and four female specimens, collected by Dr. Wm. M. Wheeler, in Monterey County, Cal., during July, 1896.

This species is most closely related to *corax* Osten Sacken, from which it differs as follows: lamellae nearly white, bordered with black; fore tarsi male plain. In *corax* the front tarsi are ornamented and the lamellae are nearly black, yellowish-brown in the middle only.

Dolichopus intentus, sp. nov.

Femora largely black; tibiae pale; cilia of inferior orbit dark; tegular cilia dark; wings hyaline; lamellae of hypopygium small, dusky; antennae black, third joint long, pointed, with subapical arista.

Male. Length 4 mm., of wing 3.5 mm. Dark bronzed green dusted. Proboscis dirty yellow, palpi piceous. Face thickly covered with silvery dust, except a small median spot immediately below antennae. Antennae black; first and second joints subequal; first two joints more or less shining, densely clothed with appressed short pubescence; third joint more opaque, the pubescence closer. First joint bristly; second joint with a terminal fringe of bristles which become longer beneath; third joint longer than first and second together. Arista subterminal, shorter than third antennal joint. Front violet, metallic, slightly bronze dusted. Post-ocular cilia black. Thorax and abdomen greenish-bronze above, becoming piceous dusted below. Hypopygium piceous dusted, shining inwardly. Internal appendages dark; lamellae small, fuscous without a distinct darker border, fringed with hairs only. Legs plain, dark, with usual bristles. Front coxae somewhat lighter than pleurae, yet silvery. Femora piceous except the yellow tip; hind femora with two ante-apical bristles. Fore and

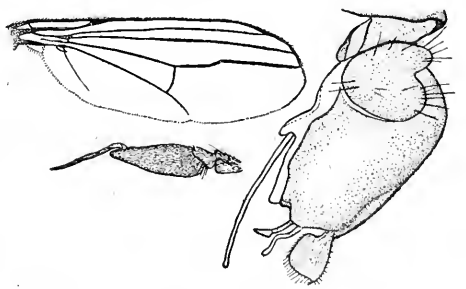

FIG. 14. — *D. intentus*: male wing, antenna and hypopygium.

middle tibiae yellow; hind tibiae black at tip, slightly swollen along middle, but without a smooth space internally. Wings subquadrate, hyaline, third and fourth veins subparallel at tip. Wings with costa at tip of first vein thickened and without an obvious notch at terminus of fifth vein; anal angle rounded. Tegulae and halteres yellow. Tegular cilia black.

One specimen, collected by Dr. Wm. M. Wheeler at Chicago, Ill., dated May 8, 1896.

This species is allied to *laticornis* Loew, and *incongruus* Wheeler, but is at once distinct in the structure of the antennae.

In his table of *Dolichopus*,[1] Mr. Aldrich commits *incongruus* to the section with the femora yellow. The type specimen has dark legs. Division 5 of his table may be thus altered:

5. Third joint of antennae large 5*a*
   Third joint as usual, tegular cilia black 6
5*a*. Tegular cilia yellow; hind tibiae dark on whole under surface
   incongruus Wheeler
   Tibiae of hind legs infuscated towards tip 5*b*
5*b*. Tegular cilia generally yellow; lamellae of hypopygium clear
   laticornis Loew
   Tegular cilia black; lamellae of hypopygium dusky
   intentus nov.

Dolichopus calainus, sp. nov.

Femora chiefly black, cilia of inferior orbit pale, middle tibiae black, femora yellow only at extreme tip, hind femora not ciliated, legs wholly black.

Male. Length 5 mm., of wing 4.5 mm. Bright metallic blue with greenish reflections. Proboscis and palpi piceous. Face of usual length and rather narrow; light gray below, ochreous and darker above. Antennae totally black, third joint ovate, obtusely pointed at tip. Arista black, moderately pubescent, nearly twice as long as the antenna and inserted about the middle of the third joint. First joint but slightly bristly above, more strongly so toward the tip. Front bright blue with a decided greenish tinge. Postocular cilia black above, below the middle light. Just before the lower corner of the eye they are suddenly somewhat longer and placed very close together, forming a sort of brush. Dorsum of thorax and scutellum deep shining blue, greenish only at extreme sides and in front. Abdomen much compressed toward the apex; shining bluish-green, whitish dusted on the sides below and covered with black hairs, which grow longer toward the apex of the abdomen. Hypopygium piceous, with several conspicuous

[1] *Kan. Univ. Quart.* Vol. ii., No. 1, p. 2.

patches of black hairs; internal appendages light brown. Lamellae small, strongly infuscated, lighter at middle; with a narrow black border which is much wider on the lower corner; fringed with black bristles which are slender, especially on the upper edge. Pleurae very dark green, grayish dusted. All the coxae black. The anterior ones silvery in front and covered with short black hairs. Legs black, slightly whitish dusted. The anterior tibiae dark brown on the inner side. All the femora at extreme tip, the tibiae at extreme base and the first joint of anterior and middle tarsi at extreme base, yellow. Wings hyaline, the veins black. Costa with a knot-like swelling at junction of humeral vein. Tegulae and halteres yellow, the former with long black cilia.

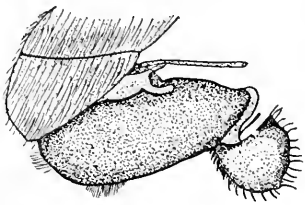

FIG. 15.—*D. calainus:* hypopygium.

Described from one male specimen collected by Dr. Wm. M. Wheeler in Chicago, May 8, 1896.

This species is related to *myosota* O. S., but may be distinguished by the lamellae of the hypopygium, which are larger, darker, wider, and distinctly angulate below.

Dolichopus enigma, sp. nov.

Dark green, shining; wings brownish in front; tegular cilia black; cilia of inferior orbit pale; femora black, hind pair of male not ciliated; fore tibiae brownish-yellow; lamellae of hypopygium subrectangular.

Male. Length 4 mm., of wing 3.5 mm. Bright green, not very shining. Proboscis and palpi piceous. Face rather wide, covered with dense silvery dust, brownish in certain lights. Antennae totally black, sericeous, but little hairy above. First joint long, second and third taken together, about twice the length of first. Arista less than twice as long as antenna, black, but little pubescent. Front dark green, not very shining. Postocular cilia black above and pale below. Dorsum of thorax and scutellum bright green, somewhat cupreous in front. Abdomen dark green, bronzed, not so bright as thorax; covered with black hairs throughout and white dusted on sides and below. Incisures between segments black. Hypopygium

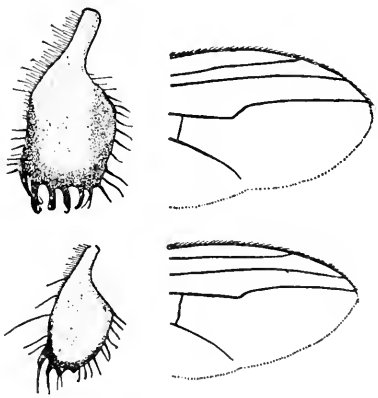

FIG. 16.—*D. enigma*, male; *D. ovatus*, male.

black, basal portion opaque, white dusted, with two patches of black hair dorsally ; towards the apex very shining. Internal appendages ferruginous. Lamellae subrectangular, dirty, translucent, white, with brown border, wider at apex, where it is jagged and bristly. Pleurae very dark green, opaque, white dusted. Legs, including coxae, totally black, except the anterior tibiae above and the base of anterior tarsi, which are more or less yellow above. femora indistinctly tipped with brownish-yellow. Tarsi not ornamented, hind tarsi with the usual bristles. Wings grayish, tinged with brown in front and along the veins ; costa with a short swelling in the angle which it makes with the first vein ; bend in the fourth vein not very abrupt ; second and third veins much approximated except at tip ; no distinct incision at tip of fifth vein. Tegulae and halteres yellow ; tegular cilia black.

One male, North Park, Colorado, over 9000 feet, collected during July.

This is closely related to *ovatus* Loew, but is distinct by the much larger subrectangular lamellae, costa with a swelling, second and third veins more approximated, and wings brownish in front.

Dolichopus agronomus, sp. nov.

Femora chiefly black, cilia of inferior orbit pale, middle tibiae yellow, first joint of hind tarsi with few bristles, hind femora ciliated with short hairs.

Male. Length 3.5 mm., of wing 3 mm. Dark metallic green. Proboscis and palpi piceous. Face very long, densely covered with bright silvery pollen, which continues past the antennae as far as the frontal bristles. Above the antennae it is greenish-white and not so dense. Antennae long, totally black, the first two joints short, the third large and broad, elongated ovate and rather sharply pointed. Arista black, pubescent, a little longer than the antenna. Postocular cilia black above, pure white below. Thorax bluish-green, covered with very fine white dust. A median shining stripe is not at all dusted. Abdomen very strongly compressed toward apex, dark green, white dusted, especially along the sides. The extreme basal and apical margins of the segments more or less free from the dust. Entire abdomen covered with short black hairs. Hypopygium black, shining, covered at base with white dust. Internal appendages light yellow. Lamellae nearly white with an indistinct narrow blackish border ; elongate oval. Each lamella nearly bilaterally symmetrical, but little angulate inwardly and beset with the usual bristles. Pleurae greenish-black, dusted with gray. Coxae of same color as the pleurae, all tipped with yellow, the

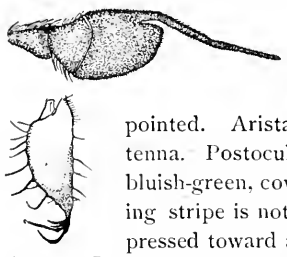

Fig. 17.—*D. agronomus*: male antenna and lamella.

anterior ones silvery in front. Femora brownish-black, tipped with yellow. Anterior and middle tibiae yellow, the anterior ones lighter. Posterior tibiae and tarsi deep black, the former yellow at extreme base. Anterior and middle tarsi blackened from the tip of first joint. Wings oval, much narrowed toward the base, hyaline, the veins dark brown. Costal swelling and incision at tip of fifth vein not well marked. Tegulae and halteres yellow. Tegular cilia yellow, with a couple of strong black ones intermixed.

Described from one male specimen, collected by Dr. Garry deN. Hough, at New Bedford, Mass., June 8.

From *convergens* it differs by the vertex being white pollinose, as well as the face. Also the hind femora are ciliated with short hairs; the hind tibiae are totally black; the lamellae of the hypopygium are oval, and the third and fourth veins of the wing converge less strongly.

From *albiciliatus* it differs by the smaller size; longer third antennal joint, and the black hind tibiae. Moreover, the ciliation of the hind femora of the male is shorter; the lamellae are not broad and rounded, and are much lighter in color.

From *xanthocnemus* it can be readily distinguished by the shorter ciliation of the hind femora and the black hind tibiae.

This is a very peculiar species and superficially resembles the species of the group *Hygroceleuthus*, although it is otherwise quite different.

Dolichopus pernix, sp. nov.

Green; face whitish; antennae black, arista plain; infraocular cilia white; tegular cilia black; feet yellow, including fore coxae, tip of hind tibiae conspicuously black; last two joints of male fore tarsi moderately enlarged, black; fourth longitudinal vein not broken.

Male. Length 4.75 mm., of wing 4.5 mm. Green, shining. Proboscis piceous, palpi yellow. Face narrow, silvery white, flavescent towards antennae. Antennae wide, black, first joint dark brown below; joints subequal; second and third together ovate; third obtusely pointed; arista dorsal, sericeous, longer than antenna, inserted at middle of third joint. Vertex shining green. Postocular cilia except upper five white. Thoracic dorsum green, more or less shining, towards front and sides brassy. Abdomen shining green, sparsely silvery dusted above, becoming thickly at sides and below, cupreous towards tip. Hypopygium piceous, dusted, greenish towards base, shining on inner surface. Lamellae elongate,

FIG. 18. — *D. pernix:* male antenna and tip of fore tarsus.

light yellow, narrowly margined with black, fringed with dark hairs, inner and apical angle prolonged into several long filaments. Pleurae glaucous, in different parts green, cupreous or piceous, according to angle of vision. Middle and hind coxae piceous, glaucous. Fore coxae yellow, piceous and dusted basally on posterior face; front surface besides the strong apical bristles with fine dark hairs which are supplanted by lighter ones on proximal portion. Legs yellow except apex of hind tibiae, hind tarsi, and last two joints of front tarsi. The middle and front tarsi increase in density of color from tip of first joint. Hind femora not ciliated, with a subterminal bristle. Hind tibiae not glabrous inwardly. Front tarsi slender, as are the tibiae, nearly twice the length of the tibiae; first joint longest, a little shorter than two following; second and third subequal, fourth shortest, fourth and fifth together about equal to third; fourth and fifth joints flattened. Empodia distinct, yellowish. Wings long, hyaline; costa with a small tubercle at juncture of first vein; third vein converging towards fourth; bend in fourth vein slight; at tip of fifth vein a broad, shallow sinus; anal portion moderately prominent. Tegulae and halteres yellow, the former with long black cilia.

One male taken by Mr. Clermont Livingston at Corfield, Vancouver Island, May 21, 1896.

Though closely related to *discifer*, it appears quite distinct. The more evident points of difference are these:

Pernix: First antennal joint not red beneath; arista inserted near middle of third joint of antenna; numerous dark hairs on anterior face of fore coxae; tip of hind tibiae evidently black for some distance; fourth tarsal joint flattened, black; wings not evidently narrowed at base.

Discifer: First antennal joint reddish on under side; arista beyond middle of third antennal joint; front coxae with white hairs (dark hairs on inner side of female, only); hind tibiae dark at only extreme tip and less on outer side; fifth tarsal joint only black; wings rather narrowed towards base.

The proportion of the tarsi to the tibiae is also different, as is also the comparative length of the tarsal joints.

Dolichopus pantomimus, sp. nov.

Green; face narrow, light brown; antennae black with simple arista; cilia of inferior orbit pale; cilia of tegulae black; feet yellow, including front coxae and excepting tip of hind tibiae and tarsi, not ornamented in the male excepting femoral brush; fourth vein not broken.

Male. Length 4 mm., of wing 3 mm. Bright metallic green, somewhat brassy. Proboscis piceous, palpi ferruginous at tip with few dark hairs. Face very narrow, with eyes almost contiguous at middle, thickly overlaid with ferruginous dust, shining. Antennae black, sericeous, not noticeably bristly; second joint closely applied to the third; first joint equal to second on inner side; third joint long, pointed, equal to first two together. Arista finely pubescent, arising from middle of upper surface of second and third joints taken together. Vertex green, shining. Infraocular cilia white. Thorax with dorsum bright green, cupreous anterior to wing insertion, dusted in front; with an indication of two brown median longitudinal lines in front. Abdomen dorsally bright green, cupreous tinged; the posterior margins of segments blackened. Hypopygium wholly piceous, somewhat shining, and finely sericeous. Lamellae in length equal to antennae, white translucent, with a jagged, moderately wide black apical border, and closely fringed with black hairs at tip. Pleurae, sides of abdomen, and base of posterior fore coxae dark green, glaucous. Fore coxae wholly yellow, rather sparsely beset with pale hair, besides the apical bristles. Legs plain, yellow; hind femora with an ante-apical bristle and ciliated below with not long yellow hairs; hind tibiae stouter than the others, and with a long glabrous streak on hind surface, black at tip for one-seventh its length; hind tarsi entirely black, anterior pairs darker towards tip, but not black. Empodia very small, silvery. Wings narrow, tinged somewhat dark gray; costa, at tip of first vein, with an evident knot; fourth longitudinal vein not broken; hind margin entire at tip of fifth vein; anal angle rather strong.

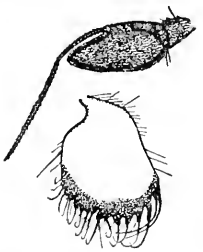

FIG. 19. — *D. pantomimus*: male antenna and lamella.

A single male from New Bedford, Mass., collected May 30, by Dr. Garry deN. Hough.

Related to Loew's *melanocerus*, but differs in the smaller size, color of the hairs of the fore coxae, which are not black at base, anterior tarsi not black, and the narrowed darker face.

Dolichopus renidescens, sp. nov.

Green; shining; face broad, light brown, antennae black, with a plain arista; vertex violet; cilia of inferior orbit white, of tegulae black; legs yellow, except tips of the tarsi and hind legs from outer portion of hind tibiae, not ornamented except the ciliation of hind femora; fourth vein not broken.

Length 4.5–5 mm., of wing the same. Bright green, shining, darker on thoracic dorsum, almost bluish. Proboscis piceous, palpi brunneous. Face

broad. Antennae dull black, sericeous, short, with slender, dark, sericeous arista, once and a half the length of the antenna; third joint a little shorter than the first two together, broadly oval, rounded but obtusely pointed at apex; second joint with circlet of hairs. Front violet. Upper seven of postocular cilia black, rest pale yellow. Thoracic dorsum bluish-green, brilliantly shining except for indications of longitudinal dusted rows; scutellum and ante-scutellar region purer green. Abdomen shining green, with brassy tinge, lightly dusted. Pleurae glaucous on a green foundation. Middle and hind coxae, except tip, and extreme base of fore coxae of same color as pleurae. Front coxae with black pubescence on anterior face. Legs largely yellow, the hind femora with two ante-apical bristles; fore and middle legs dark from tip of first tarsal joint; hind tarsi black, hind tibiae infuscated at tip. Wings hyaline, normal, a slight sinus at tip of fifth longitudinal. Tegulae yellow with rather long black cilia. Halteres yellow.

FIG. 20. — *D. renidescens*: male wing and lamella.

Male. Face ferruginous. Hypopygium piceous with brassy green tinge; sericeous below, shining inwardly; internal appendages yellow. Lamellae clavate, broad, white translucent, rather broadly margined with black at extremity, apex jagged and fringed with rather long, slender, nearly straight, black hairs. Hind tibiae with a long, narrow glabrous streak, more evident near tip, on hind face. Anal angle of wing full; costa thickened at junction with humeral vein.

Female. Face with gray dust. First antennal joint a little longer than in male. Hind tibiae not glabrous, the apical infuscation not evident. Anal angle of wing rounded; costa not thickened.

Two males and one female from North Park, Colorado, collected at an altitude of over 9000 feet during July.

The shorter antennae, broader face, violet front, more extended margination of hypopygial lamellae, and the closer ciliation with brown hairs of the hind femora which possess two ante-apical bristles, distinguish this species from *melanocerus* Loew.

Dolichopus apheles, sp. nov.

Green; face ochraceous; antennae black, with a simple arista; infra-orbital cilia white; tegular cilia black; feet plain, yellow, except tips of hind femora and tibiae black; hind tarsi black; fore coxae yellow with dark hairs; fourth longitudinal vein not broken.

Male. Length 5 mm., of wing 4 mm. Not so brightly colored as in most species, largely green. Proboscis piceous, palpi roseous yellow. Face

ochraceous. Antennae sericeous, black, except underside of first joint, which is indistinctly reddish, very like those of a female *Hygroceleuthus;* first joint longer than second, short, hairy above ; second with a crown of black bristles ; third short, deep, subtriangular. Arista sericeous. Vertex blue green in certain lights, violet in others, somewhat shining. Infraocular cilia pale ; six of the supraocular cilia black. Thorax dull, bluish on dorsum ; posterior declivity and scutellum shining green. Abdomen shining green dorsally, cupreous toward apex, transverse margins of segments piceous. Hypopygium piceous with greenish tint, shining, and not sericeous on inner face ; lamellae rounded, rather short, white translucent, with a narrow, black, apical border, jagged and fringed with black hairs. Pleurae glaucous, as are the middle and hind coxae, except tips. Front coxae yellow with a basal glaucous-piceous spot on the outer side ; front surface with a coating of short black hairs, besides apical bristles. Legs yellow, entirely unornamented ; the darker places are : hind tarsi and outer fourth of hind tibiae black, tip of hind femora more evidently on upper surface black ; the infuscation of fore and middle tarsi begins at middle of first joint. Hind femora with a single ante-apical bristle and not ciliated beneath ; hind tibiae with no evidently glabrous space. Wings normal, rather dusky anteriorly ; without costal thickening at tip of first vein ; fourth vein unbroken, beyond bend gradually converging with third, but almost subparallel with it ; no indention in posterior margin ; anal angle full. Tegulae and halteres yellow, tegular cilia black, rather short and stout.

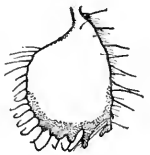

FIG. 21. — *D. apheles:* male lamella.

One male collected by Dr. Wm. M. Wheeler near Milwaukee, Wis., June 28, 1895.

This unique species is allied nearest to those species grouped about *melanocerus* Loew and *incisuralis* Loew.

The addition of the last four species has necessitated the following modification of Divisions 52 to 56 of Professor Aldrich's table.[1]

52.	Front legs of male ornamented	2
	Front legs plain	3
2.	Fourth joint of fore tarsi of male not flat . . .	*discifer* Stan.
	Fourth joint of fore tarsi of male flat, black . .	*pernix* sp. nov.
3.	Antennae wholly black ; hind femora of male ciliated . . .	4
	First antennal joint lighter below	6
4.	Front coxae with light hairs	*pantomimus* sp. nov.
	Front coxae with dark hairs in front	5

[1] *Kan. Univ. Quart.* Vol. ii, No. 1, p. 5.

5. Face rather narrow; front green . . . *melanocerus* Loew
   Face broad; front violet . . . . . *renidescens* sp. nov.
6. Femora of hind legs of male ciliated, not blackened . . . 7
   Male hind femora not ciliated, black at tip . *apheles* sp. nov.
7. Front coxae with black pubescence 8
   Front coxae with white pubescence . . . *platyprosopus* Loew
8. Bristles of hind tibiae long . . . . . *setosus* Loew
   Bristles of hind tibiae normal . . . . *incisuralis* Loew

56. *praeustus*, etc.

Dolichopus amphericus, sp. nov.

Light green; antennae yellow, except third joint and tip of second; fore tarsi ornamented; femora yellow; postocular cilia pale below; tegular cilia black, hind tibiae not black at tip.

Male. Length 6.5–7 mm., of wing 5.5–6 mm. Light coppery green with much white dust. Proboscis piceous, palpi testaceous. Face of medium width, about four times as long as broad, thickly covered with brilliant yellow dust. Front shining green. Antennae rather elongate; first joint yellow, with many short black hairs above; second joint yellow at base, becoming black at apex; third joint black, sericeous, obtusely

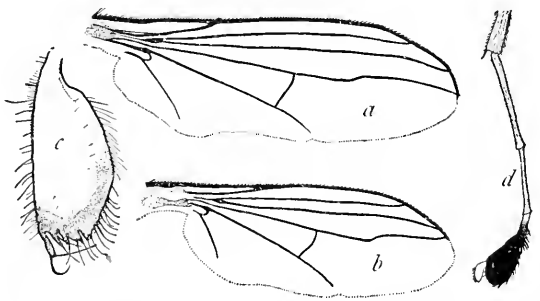

FIG. 22.—*a*, *D. amphericus*, male wing; *b*, *D. coloradensis*, male wing; *c*, *D. amphericus*, lamella; *d*, *D. amphericus*, male fore tarsus.

pointed at apex. Arista less than twice as long as antenna, very distinctly pubescent. Postocular cilia black above and light yellow on lower three-fourths. Thorax light green, coppery on the disc; slightly opaque by the presence of light yellow dust. Dorsally there is a deep coppery longitudinal stripe. Abdomen shining green, white dusted. The white dust is so thick as to obscure the ground color on the lower part of the sides. Incisures coppery. Hypopygium black, shining, except at base, where it is white dusted. Near the base bearing a large patch of black hair. Internal appendages ferruginous; lamellae very pale yellow, with a wide, sharp border of black at apex, where they are bristly and deeply toothed. Outer tooth bearing at its tip a strong, curved bristle. Pleurae greenish-black,

white dusted. Fore coxae yellow with white pubescence in front, at apex and inwardly with black hairs. Middle and hind coxae of same color as the pleurae, yellow only at extreme tip. The middle pair with white hairs in front. Legs yellow. Fore tarsi ornamented; the first two joints long and slender, first about once and a half the length of the second; third less than one-half the length of the first, much enlarged at apex, where it is infuscated; fourth joint small, shorter than the third, flattened, velvety black; fifth oval, about one-half as long as the first, broadly compressed, deep black and fringed on anterior edge with black hairs; empodia silvery white. Middle tarsi infuscated from tip of first joint. Hind femora not ciliated; hind tibiae wholly yellow with a dorsal, apical, glabrous stripe; hind tarsi wholly black. Tegulae and halteres yellow; tegular cilia black. Wings narrow, nearly hyaline, slightly brownish in front; costa with no noticeable swelling; fourth vein not broken; distinctly lobed at tip of sixth vein.

Female. Length 5.5–6.5 mm., of wing 6.25–6.75 mm. Face yellowish-gray. Front tarsi plain, infuscated from tip of first joint, the second and third joints lighter at base, giving the tarsus a somewhat banded appearance. Wings darker and longer than in the male; only a faint indication of the preanal lobe.

Two males and three females from Price County, Wis.; collected by Dr. Wm. M. Wheeler.

This species resembles *coloradensis* Aldrich, from which it differs by the larger size, bright yellow face, lighter antennae, brownish wings, and white hair on front face of anterior coxae.

Together with *flagellitenens* Wheeler, *amphericus* possesses greatly enlarged metapleurae which give a winged appearance to the first abdominal segment. The posterior portion of the metapleurae is dull black and pubescent.

The following localities are those of species in the collection of Dr. Wm. M. Wheeler:

Group *Hygroceleuthus.*

latipes Lw. Wisconsin, Illinois.
var. *cognatus*, Illinois, Massachusetts.
Aldrichii Wheeler. Idaho, Wyoming, Colorado.
plumipes Scop. Colorado. Vancouver.
Wheelerii M. *et* B. Massachusetts.
amnicola M. *et* B. Colorado.
crenatus O. S. Vancouver, California, Washington, Wyoming, Idaho.
consanguineus Wheeler. California.
var. *propinquus.* Vancouver Island.
afflictus O. S. Arizona, California, Washington.
ciliatus Ald. Wyoming, South Dakota.
idahoensis Ald. Idaho.

Group *Dolichopus*.

partitus M. *et* B. Colorado.
paluster M. *et* B. California.
laticornis Lw. Wisconsin, Wyoming.
intentus M. *et* B. Illinois.
incongruus Wheeler. Wisconsin.
gratus Lw. Illinois, Wisconsin.
calcaratus Ald. Massachusetts.
detersus Lw. Illinois, Wisconsin.
myosota O. S. California.
calainus M. *et* B. Illinois.
acuminatus Lw. Illinois, Wisconsin.
ovatus Lw. Wisconsin.
enigma M. *et* B. Colorado.
setifer Lw. Wisconsin, Massachusetts.
albiciliatus Lw. Massachusetts, Illinois, Wisconsin.
agronomus M. *et* B. Massachusetts.
xanthocnemus Lw. Vancouver Island.
pachycnemus Lw. Massachusetts.
longimanus Lw. Wisconsin, Massachusetts.
albicoxa Ald. Massachusetts, Illinois.
brevimanus Lw. Massachusetts, New Hampshire.
socius Lw. Massachusetts, New Jersey, Wisconsin.
palaestricus Lw. Illinois, New Hampshire.
splendidus Lw. Ontario, Michigan, Illinois.
splendidulus Lw. Illinois, New Hampshire.
batillifer Lw. Massachusetts.
tonsus Lw. Massachusetts.
tener Lw. Wisconsin.
variabilis Lw. Illinois, Wisconsin.
luticpennis Lw. Vancouver Island.
bifractus Lw. Massachusetts, Illinois, Nebraska.
obcordatus Ald. Wyoming, Idaho.
ramifer Lw. Illinois, Texas, Wyoming.
vittatus Lw. Illinois, Wisconsin.
cuprinus Wied. Illinois, Wisconsin, Wyoming.
longipennis Lw. Vancouver Island.
flagellitenens Wheeler. Illinois, Wisconsin.
comatus Lw. Massachusetts, Illinois, Wisconsin.
pernix M. *et* B. Vancouver Island.
melanocerus Lw. Massachusetts.
pantomimus M. *et* B. Massachusetts.
renidescens M. *et* B. Colorado.
apheles M. *et* B. Wisconsin.
setosus Lw. Massachusetts, Vancouver Island.
gracilis Ald. Wisconsin.
angustatus Ald. Massachusetts.
lobatus Lw. Illinois, Wisconsin, Michigan.
coloradensis Ald. Colorado.
amphericus M. *et* B. Wisconsin.
Henshawi Wheeler. Massachusetts.
marginatus Ald. Massachusetts, New Jersey.
scoparius Lw. Massachusetts, Illinois, Wisconsin.
canaliculatus Thomson. California.
duplicatus Ald. Idaho.
Coquilletti Ald. Idaho, Vancouver Island.
tenuipes Ald. Idaho, California.
occidentalis Ald. Idaho, Vancouver Island.
scapularis Lw. Wisconsin.
germanus Wheeler. Wisconsin, Wyoming.
grandis Ald. California.
sexarticulatus Lw. Illinois, Louisiana.
Willistonii Ald. Kansas.
terminalis Lw. Wisconsin.
sarotes Lw. Wisconsin.

ON THE ORIGIN OF THE SPERM-BLASTOPHORE OF SOME AQUATIC OLIGOCHAETA.

SHINKISHI HATAI.

THE first investigator to discuss the origin of the sperm-blastophore in Oligochaeta was Bloomfield.[1] His work was done mostly on living material, although he supplemented it to some extent by preparations mounted in glycerine. He studied the external features only. Later, Calkins[2] published a detailed account on the same subject, his views being opposed to those of Bloomfield. Both of these writers made their observations upon Lumbricus terricolae. A more complete statement of their respective views will be given on a later page.

In the Limicolae the origin of the sperm-blastophore has not yet been studied, although some work on the structure of Limnodrilus Gotoi[3] and Vermiculus limosus[4] of this group has been published recently. These species are common in Japan. The material used in the present study was fixed in Perenyi's fluid and corrosive sublimate. The stains used were Kleinenberg's haematoxylin, Rawitz's haematoxylin, and borax carmine.

The present article deals only with the formation of the sperm-blastophore. The various stages in its development may be described advantageously in the following order:

1. *Spermatogonia.*—A section of the testis (Fig. 1) shows three stages in the maturation of the spermatogonia, namely: (*a*) The cells at and near the proximal end of the testis are

[1] Bloomfield, E., "On the Development of the Spermatozoa. 1. Lumbricus," *Quart. Journ. Micr. Sci.* Vol. xx. 1880.

[2] Calkins, G. N., "The Spermatogenesis of Lumbricus," *Journ. of Morph.* Vol. xi. 1895.

[3] Hatai, S., "On Limnodrilus Gotoi (n. sp.)," *Annotationes Zoologicae Japonesis.* Vol. iii, Part i, 1899.

[4] Hatai, S., "On Vermiculus limosus," *Annotationes Zoologicae Japonesis.* Vol. ii, Part iv, 1896.

somewhat polygonal, firmly connected, and possess comparatively small nuclei. (*b*) The cells of the central part are larger than the former, becoming gradually spheroid and more loosely connected; the nuclei are larger, and the peritoneal membrane of the testis disappears in this region. (*c*) At the free ends of the testis the cells present completely spherical forms, and are so loosely connected that they may be easily detached. The spermatogonia have conspicuous nuclei. Each fully matured spermatogonium has one large nucleus, and is not multinucleate, as in Lumbricus (Calkins).

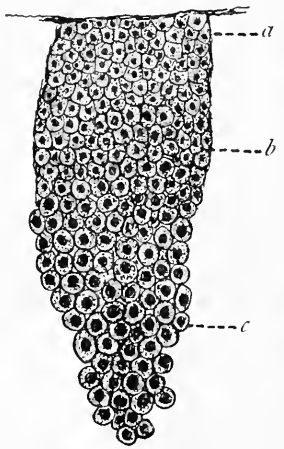

Fig. 1.


Fig. 2.

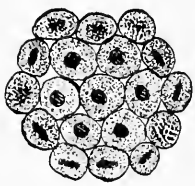
Fig 3.

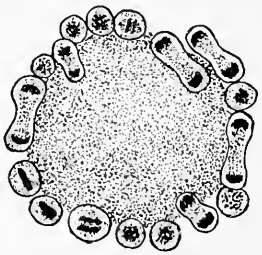
Fig. 4.

2. *Spermatocyte* (Figs. 2, 3). — The primordial germ-cells, or spermatogonia, when fully matured drop from the testis; sometimes one or two, but usually many at the same time, afterwards swelling up gradually. When they are first detached from the testis, no changes are noticeable, but with the beginning of cell division the following nuclear changes are observed: The nucleus of each cell in the outer layer moves inward toward the center of the cluster, as shown in Fig. 2. Each nuclear membrane disappears, while the chromosomes become distributed evenly throughout the nucleus. Soon the chromosomes collect in the equatorial plane (Fig. 3) and undergo division by the usual method of karyokinesis (Fig. 4). The spermatid arises after two or more such divisions. The cells at the central part show no signs of change, but remain in the resting stage.

Usually, after the peripheral cells have divided, the central cells become granular and appear homogeneous; the nuclei and cell membranes can no longer be distinguished (Fig. 5). In other words, the central cells degenerate at this period and become transformed into a cushion for the spermatozoa. This cushion is called the "sperm-blastophore" by Bloomfield.

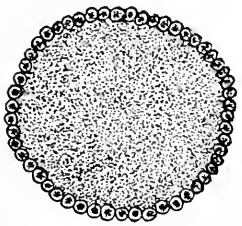

FIG. 5.

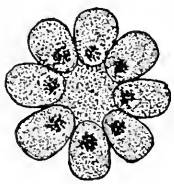

FIG. 6.

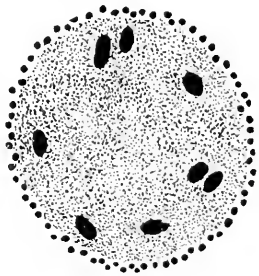

FIG. 7.

(Occasionally this transformation of the central cells occurs previous to the division of the peripheral cells, Fig. 6). The daughter-cells produced by the several divisions of the spermatocyte become half the size of the mother-cells, and retain this size throughout the stages of formation of the spermatozoan. These half-sized cells are the spermatids.

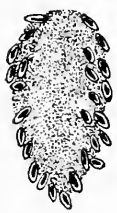

FIG. 8.

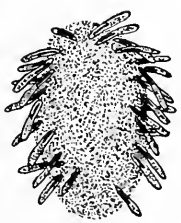

FIG. 9.

FIG. 10.

FIG. 11.

3. *Spermatids.*—The spermatids encircle the blastophore (Fig. 5), which changes to a spherical form and becomes more conspicuous than in the former stage. The spermatids now undergo repeated cell division, producing an enormous number of new spermatids (Fig. 7), which gradually elongate (Figs. 8, 9), and finally become tailed spermatozoa (Figs. 10, 11). The

tails of the spermatozoa all turn in one direction, as depicted in Figs. 10, 11. While these changes of the spermatids are in progress, the blastophore itself changes its form from spheroid to oblong and sometimes becomes spindle-shaped (Fig. 12).

As shown above, the central cells of the original cluster degenerate to form the sperm-blastophore, which appears as a homogeneous substance. It should be here stated that cases have been observed in which several nuclei were scattered through the homogeneous substance of the blastophore, but rarely a complete cell, as shown in Fig. 13. The question arises as to the origin of these nuclei or cells. It seems reasonable to suppose that they are simply belated portions which have not yet been transformed into the homogeneous mass. Fig. 7 shows a condition in which only the nuclei remain. At no time during the formation of the blastophore has a proliferation of the central cells been observed.

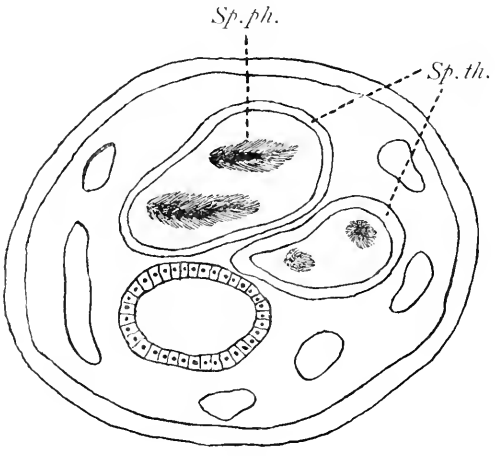

FIG. 12.

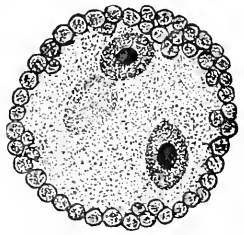
FIG. 13.

The spermatophore becomes slightly modified in passing from the sperm-sac to the spermatheca, as shown in Figs. 12, 14, 15. It is to be noticed that the tails of the spermatozoa turn spirally; this being a secondarily acquired character occasioned by its passage through the sperm-duct. Following these changes, the sperm-blastophore becomes more or less spindle-shaped; it also decreases in size. In the cross-section of a spermatophore a central canal is generally to be seen, as represented in Fig. 15. The blastophores are at first com-

paratively large (Figs. 8–11); they gradually decrease, and finally disappear, as shown in Fig. 15. It would appear, therefore, that the blastophore is produced by the degeneration of the central cells, and that it not only acts as a cushion, affording a means for conveying the spermatozoa, but also serves as nourishment for them.

Bloomfield's principal results, as briefly summarized by Calkins, are as follows:

"1. The early germ-cell is not entirely used in the formation of spermatozoa; a central part remains passive, and serves to carry the developing spermatic cells. This central part is called the sperm-blastophore, and may or may not be nucleated.

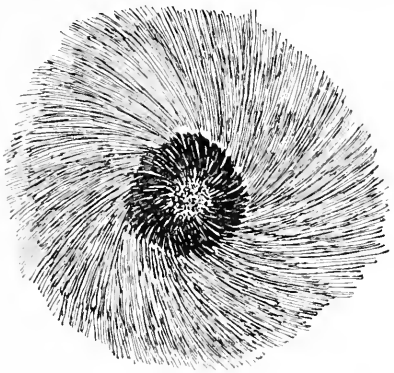

FIG. 14.

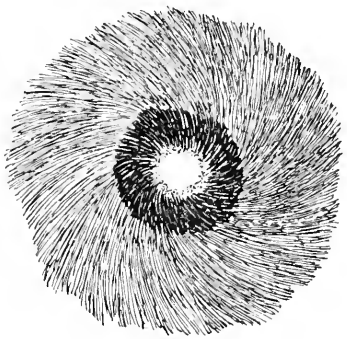

FIG. 15.

2. The sperm-blastophores increase by division while in the testis, and disappear, probably by atrophy, after the spermatozoa leave it.

3. The blastophore corresponds to the nucleated supporting cells (Sertoli's cells) of the frog and salamander.

4. The large nucleus of the early sperm-cell divides many times to form secondary nuclei, which stand out around the central mass, or blastophore, of the generating spheroid with very little protoplasm clothing them. These nuclei become the rod-like heads of the spermatozoa.

5. The protoplasm collects in a small cup, or knob-like mass, at the distal end of the developing cell, and from this grows out the long vibratile tail of the spermatozoan. (This 'mass' must be the archoplasm of the spermatid.)"

Calkins summarized his own results as follows:

"1. A multinucleated cell is formed in the testis; this represents a group of the earliest spermatic cells or spermatogonia. Each spermatogonium gives rise to several spermatozoa.

2. The nuclei arrange themselves around the periphery of the multinucleate cell; cytoplasmic cleavages then ensue between the nuclei, as in the centrolecithal egg. The cleavage grooves deepen until the nuclei are separated from the central mass of cytoplasm by mere filaments.

3. The residual mass of cytoplasm thus formed (the blastophore) is not nucleated, and cannot be compared with a Sertoli's cell in function, form, or mode of origin. It finally disappears. The blastophore furnishes perhaps the chief source of food supply for the parasites — monocysts — which live in the seminal vesicles. A possible explanation of the function of the blastophore is that of superfluous nutritive cytoplasm, the vital protoplasm having gathered around the nuclei."

Thus it will be seen that Bloomfield and Calkins hold very different views regarding the blastophore. The former considers it as having a nutritive or feeding function. It carries developed spermatozoa, and is to be regarded as the homologue of Sertoli's cell. The latter maintains that the blastophore is merely an excess of cytoplasm and not a true cell; therefore it cannot be homologous with the Sertoli cell.

The question as to the structure and function of the blastophore in Lumbricus can be decided only when we learn its true origin. In the present work on the two new species of Limicolae, it appears that the blastophore originates through the degeneration of certain of the primordial germ-cells which lie at the centers of the clusters of spermatogonia given off from the testes.

It serves not only for carrying developed spermatozoa, but for their nourishment as well. Thus it arises from *definite cells*, and, as Bloomfield has suggested, may be compared to the *Sertoli's cell*.

HULL ANATOMICAL LABORATORY,
UNIVERSITY OF CHICAGO.

PECULIAR TRACHEAL DILATATIONS IN BITTACOMORPHA CLAVIPES FABR.[1]

CHARLES THOMAS BRUES.

BITTACOMORPHA is a member of a very aberrant group of *Tipulidae*. In connection with two other genera it has been separated from the *Tipulidae* and considered as a distinct family. Of the genus *Bittacomorpha* only two species are known, both from North America. The species upon which these remarks are based is the commoner and more widely distributed form. It occurs from the New England states westward to the Pacific coast and has been taken as far south as Florida by Osten Sacken. In the northern states it is double brooded, and the imagines are seen during May and September, although much more commonly in the spring. The other species (*Sackenii*), which was described by Von Roeder in 1890,[2] is much more limited in its distribution and is recorded only from Nevada.

The common species (Fig. 3) is of the very slender form so characteristic of the *Tipulidae*. Its appearance is remarkable, however, on account of the peculiar black and white banding and the great inflation of the metatarsi of all the legs. The preparatory stages of a European species of the closely allied genus *Ptychoptera* have long been known, but it was only very recently that the larva and pupa of *Bittacomorpha clavipes* were discovered and figured by Hart.[3] The larva, like that of *Ptychoptera*, is aquatic, living among the submerged brushwood and sticks, which it resembles in color and external appearance. It is in this instar that we find the first peculiar modification of the tracheal system. The larva is furnished with an elon-

[1] *Contributions from the Zoölogical Laboratory of the University of Texas*, under the direction of Wm. M. Wheeler, *No. 3*.

[2] *Wiener Ent. Zeitung*. Heft 8, p. 230.

[3] *Bull. Illinois State Lab. Nat. Hist.* Vol. iv, p. 193.

gated breathing tube, produced by the excessive lengthening of the posterior end of the abdomen (Fig. 1). This formation is not peculiar to this species, as it occurs elsewhere, even in insects in nowise related, as in *Eristalis* among the *Syrphidae*. In the pupa we find a respiratory tube present, but in this instar its insertion is exactly reversed; it proceeds from the head. Although only one tube is functionally developed, it is one of a pair which has lengthened at the expense of its fellow (Fig. 2). Moreover, it is not always the same tube which is developed. Hart mentions that twenty-seven pupae had the right tube elongated as against three in which the left tube functioned. In one anomalous case both were developed, but unequally, their combined length being equal to that of the long one in normal pupae. This unequal length of the tubes is characteristic also of *Ptychoptera*.

Up to the present time it has not been known that the imago also possesses a remarkable modification of the tracheal system. In this stage, however, it is to be found in the legs.

In both sexes the metatarsi are very much enlarged and quite conspicuous on account of their great color contrast. The second and third tarsal joints are also somewhat enlarged, but not nearly to so great an extent.

In order to study the tracheal system of the legs they were decolorized in chlorine water and mounted whole or split into halves. Some specimens were treated also with potassium hydroxide, which successfully separated the delicate tracheae from the integument. Legs were also sectioned in paraffin to show the disposition of the internal parts.

In the basal part of the legs the tracheal tube is of the ordinary form and size. It begins to enlarge just before the middle of the femur, and before it has reached the tip is equal to seven-eighths the diameter of the femur. At this point the taenidia extend entirely around the tube, although faint in some places. The whole tibia is completely filled up by the trachea, which is striated on each side for only about one-fifteenth of its circumference. In the enlarged metatarsus the trachea is enormously distended and almost completely fills the cavity of this joint as well as that of the second and third

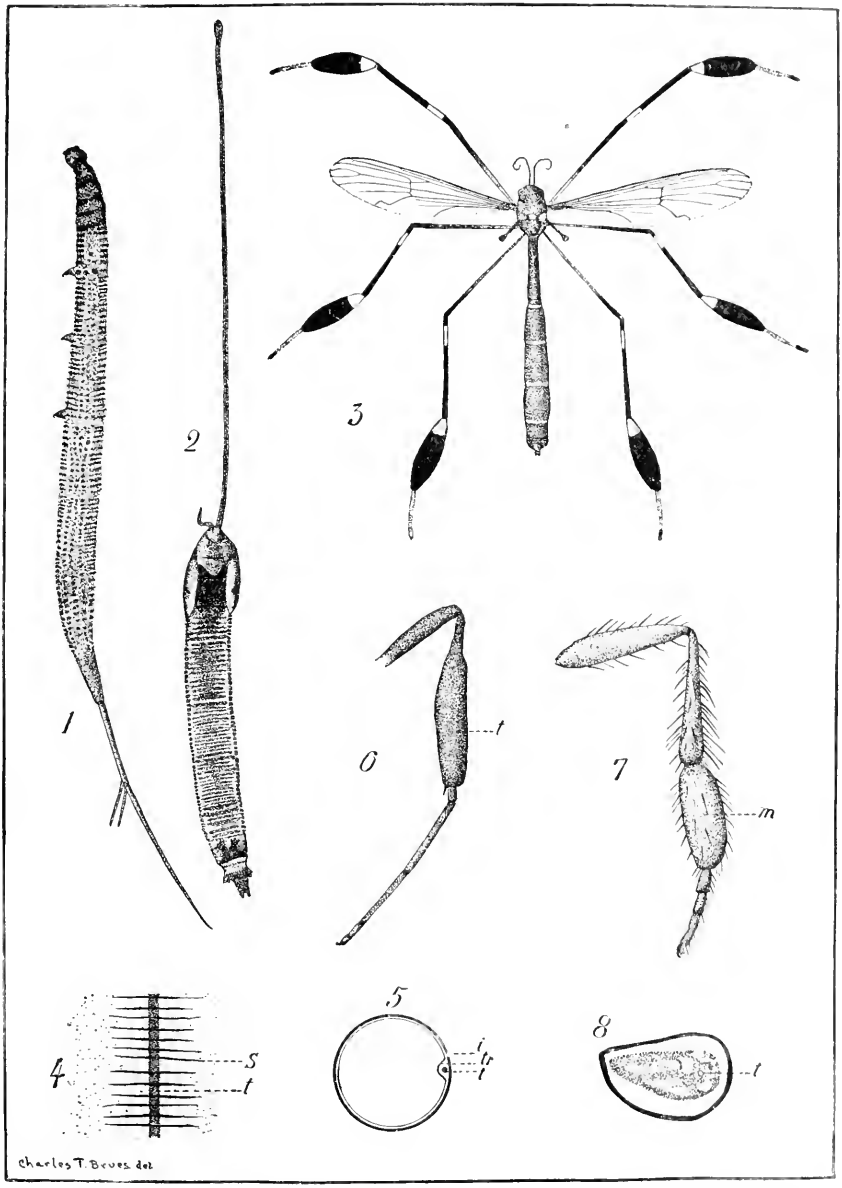

Fig. 1. Larva of *Bittacomorpha clavipes* (after Hart). — Fig. 2. Pupa of *Bittacomorpha clavipes* (after Hart). — Fig. 3. *Bittacomorpha clavipes*, in the position which it assumes when flying. — Fig. 4. Portion of tracheal wall of metatarsus of *Bittacomorpha*, showing position of tendon; *s*, taenidial striation; *t*, tendon. — Fig. 5. Diagrammatic cross-section of metatarsus of *Bittacomorpha*; *t*, tendon; *i*, chitin integument; *tr*, tracheal wall. — Fig. 6. Hind leg of *Pelecinus polyturator*, ♀; *t*, tibia. — Fig. 7. Foreleg of *Hilara trivittata*, ♂; *m*, metatarsus. — Fig. 8. Cross-section of metatarsus of *Hilara trivittata*, ♂; *t*, trachea.

joints of the tarsus. The wall of the trachea lies closely applied to the exoskeleton of the metatarsus, except for a very short distance on one side of the leg, where it is semicircularly bent inward to leave space for the claw tendon which lies in the tubular space thus formed (Fig. 5). Here as in the tibia the taenidia are visible on only about one-fifteenth of the circumference on each side.

The walls of the trachea are here not entirely destitute of taenidia, as is the case with the air vesicles which appear in the body cavities of many active insects. The striations have remained on that part of the tracheal wall which encloses the tendon (Fig. 4). At the point where the tendon passes, the taenidia are thickened and quite robust, but on each side they gradually become weak and fade out entirely. An exactly symmetrical formation of the taenidia is present on the side opposite to the tendon. It is evident that the thickenings on the tendon side may have been retained in order to strengthen the tube at this point, but there is apparently no reason for the anomalous thickening on the opposide side. In the second and third joints the taenidia lengthen until they extend over one-seventh of the circumference. The trachea seems to stop suddenly here, as I have been unable to trace it further.

There are few insects presenting similar enlargements of the leg joints, if we except those forms such as jumping *Orthoptera* and *Chrysomelidae*, where the increase in size is evidently for the accommodation of the larger muscles. Graber and Lubbock mention enlargements of the trachea in the tibiae of *Orthoptera*, ants and *Termitidae*, serving as auditory or chordotonal organs. In this case the adaptation is very extraordinary, but the dilatation of the trachea is not comparable to that of *Bittacomorpha* in extent. *Bittacomorpha* presents the only case known to me of a considerable tracheal dilatation occurring in the insect leg. In the males of many *Empididae*, and notably species of *Hilara*, e.g., *Hilara trivittata* Lw., the metatarsus of the front leg is greatly enlarged (Fig. 7), but here the cavity is occupied in great part by muscular tissue, the trachea being very slender (Fig. 8). In this species there seems to be no trachea beyond the end of the metatarsus.

In the legs of normal *Tipulidae* (*Pachyrrhina* sp.? and several other species) the trachea occupies a considerable space only in the femur and tibia, where it fills up from one-fourth to one-sixteenth of the cavity. In the tarsus the tracheal tube is very delicate or obsolete.

The female of the peculiar parasitic hymenopteron, *Pelecinus polyturator* Drury, presents an external appearance similar to that of *Bittacomorpha* in the enlarged hind tibia (Fig. 6). Here, however, the chitin of the external wall is thick and heavy, and the trachea is robust, strongly striated, but not at all dilated.

It is the rule in insects, wherever a tracheal dilation occurs, that the taenidia become obsolete, but the thinning of the tracheal wall can nearly always be regarded as a modification for the purpose of offering less resistance to osmosis. This is illustrated by the air vesicles in the bodies of insects, which are generally considered to be reservoirs for storing air to be used during extended muscular exertion. The presence of these immense vesicles in the metatarsi cannot be explained on the same principles, for it is impossible that they should serve as reservoirs for air to be used in respiration, on account of their distance from the body of the insect. It is more probable that they may bear some relation to the insect's method of locomotion. When flying, *Bittacomorpha* uses the wings scarcely at all, relying in great measure upon wind currents for transportation. The legs are exceedingly light, as the exoskeleton is thin and delicate, and encloses practically no tissue which can serve to increase their weight. As they expose a large surface, they offer great resistance to the air without adding appreciably to the insect's weight.

Drifting along thus, their extremely slender bodies and white banded appendages give them a most peculiar, intangible appearance, which is heightened by their extremely slow motion.

When examined in the cabinet, the conspicuous white and black banding of *Bittacomorpha* seems to point toward a case of warning coloration. When they are seen against their natural background, however, all these brilliant contrasts fade away into a perfectly neutral color which causes them to resem-

ble a spider's web or thistle seed drifting along. Indeed, when I first saw them it was hard to believe that they were really alive. *Bittacomorpha* seems to have developed its protective coloration along the same lines as the zebra among the vertebrates; it is rendered invisible not only by the fragmentary distribution of color, but by the neutral gray color produced by the visual blending of the black and white.

From the description of *Bittacomorpha Sackenii* by Von Roeder, it seems that this species does not possess any dilatation of the metatarsi. It would be very interesting to see if there is any abnormal development of the tracheal system in this species, but unfortunately I have been unable to procure specimens. The specimens examined were given to me by Dr. Wm. M. Wheeler, to whom I feel greatly indebted for many kind suggestions.

LAMPREYS IN CAPTIVITY.

ALBERT M. REESE.

HAVING had living lampreys of various ages under observation in the biological laboratory of Johns Hopkins University, I present the following facts as to the ability of these animals to live in a very limited space.

I received, about the middle of May, from Ithaca, N. Y., two lots of lamprey eggs, about six dozen eggs in each lot. They were shipped by express and must have been on the road about twenty to twenty-four hours. They had been shoveled out of the "nest," with about 2 l. of gravel, and put into two tin buckets of 8 l. capacity. The space in the buckets above the gravel was filled with water, and in one of the buckets were some three dozen larval lampreys ranging from 2 cm. to 12 cm. in length. None of these eggs developed, although they were put into running water as soon as they reached the laboratory.

My experience with the small larvae (about 5 mm. in length) was more successful. I obtained one hundred or more of these from a stream at Ithaca, and brought them to Baltimore in two glass jars of 3–4 l. capacity each. A small quantity of gravel was placed in the bottom of each jar for the larvae to bury themselves in, and the water was kept cool by partially emptying the jars from time to time, and refilling them with ice water from the coolers on the train. The journey lasted for about eighteen hours, and all the larvae, except three or four, reached the laboratory in good condition.

The small amount of sediment in the city water proving disastrous to the welfare of the larvae, clear spring water was obtained every few days, and this was kept cool by allowing the jars to stand in larger vessels of running water. Even with this arrangement the deaths averaged one per day, and about the first of August the remaining larvae were killed and

preserved, after having, with difficulty, been kept alive for six weeks.

The older larvae which were received, as has been said, in one of the buckets containing eggs, proved to be very hardy, and five or six of them were kept in a 12 l. aquarium for six months or more without the least difficulty. At the end of this time they were killed, two of them having shortly before (October 20) transformed into the adult Petromyzon branchialis. During their entire captivity they remained completely buried in the sand in the aquarium. A small stream of water was kept running through the aquarium, though a *constant* change of water was not necessary.

In the early part of April, I brought from the herring fisheries at Port Deposit, Md., five large sea lampreys (P. marinus) in two tin buckets, each bucket of about 50 l. capacity. Being nearly a meter in length and about 12 cm. in circumference, the five lampreys were rather crowded in the two buckets, and only four of them survived the three-hour journey to the laboratory. They were put into an aquarium (1.5 m. × .8 m. × 12 cm.) of running water, where they lived comfortably for several weeks, until by accident the wire screen was left off the aquarium, and three of them escaped and were found dead upon the floor. On June 22 the remaining lamprey was killed. It proved to be a female, and 250 cc. of ripe ova were "stripped" from her with ease. Had one of the males been kept alive it seems probable that artificial fertilization could easily have been accomplished.

To sum up, then, it seems (1) that the very small larvae are very delicate and hard to keep in confinement; (2) that the large larvae are unusually hardy; and (3) that the adults are able to live in captivity moderately well.

Johns Hopkins University.

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BIOLOGICAL BULLETIN.

OUR NORTH-AMERICAN ECHIURIDS.

A CONTRIBUTION TO THE HABITS AND GEOGRAPHICAL RANGE OF THE GROUP.

CHAS. B. WILSON.

ONLY four species of Echiurids, representing three of the five known genera, have been reported from the North American coast up to the present time. These are as follows: *Thalassema mellita* Conn was found at Beaufort, Va., living in empty sand-dollar tests, and its structure and morphology were most admirably worked out (2). *Thalassema viridis* Verrill has been reported from nodules of blue clay at a depth of seventy-seven fathoms off Head Harbor, Campobello Island (16). *Bonellia sühmii* Selenka was dredged from deep water off the coast of Nova Scotia and was described and named in the *Challenger Reports* (12).

The fourth species, *Echiurus chrysacanthophorus* Pourtales, has been reported by several authors from various localities on the New England coast. Each of these four was established as a new species by its discoverer and has been found nowhere else. The Bonellia species was based upon a single badly mutilated specimen, *T. viridis*, and the species of Echiurus upon a very limited number of specimens, no one of which in the latter species was perfect, leaving *T. mellita* to stand alone beside the well-known and thoroughly studied European forms.

In the present contribution I am able to add American localities for two of the well-known Old World species, and when

the results of the recent Harriman Alaskan Expedition are published another even better known European form will be found among them.

It is hoped also to clear up the cloud of doubt which has hung about the questionable American *Echiurus chrysacanthophorus*, for the reports on this species have contained so many gross errors and conflicting statements, and so little accurate description, that the determination of the exact species has been impossible.

This has been due to a variety of causes, chief among which may be mentioned two. First, it is essentially a shore species, frequenting muddy shallows where the water is too deep or too roily for the shore collector and not deep enough for dredging. Consequently only a limited number of specimens have been obtained.

Again, so far as known, every one of these was so mutilated in the getting as to render a full description impossible. The part most easily injured is the delicate proboscis. This breaks off upon the slightest provocation, and leaves no scar that can be detected even with a good hand lens.

Hence it is difficult to obtain a specimen with the proboscis intact even under favorable circumstances, and absolutely impossible by dredging. It was this denudition of the proboscis with no resultant scar which led the discoverer of the species, Couthouy, to mistake it for a holothurian, and to describe it as *Holothuria chrysacanthophora* in 1838 (3).

The same mistake was made by Gould in 1841 (5), who says: "This is not unlikely to be *H. forcipata* of Fabricius. Several specimens which I have seen were all taken from fishes' stomachs in a mutilated state. Some of the essential characters, therefore, remain yet undetermined. The surface is light colored and appears to be naked, except that there are several long, flexible, sharp-pointed spines about the mouth[1] of a shining golden yellow. One specimen is five or six inches in length."

Pourtales rectified this mistake in 1851 and located it correctly among the Gephyrea, giving it a name which it has since

[1] Really the anus.

borne, *Echiurus chrysacanthophorus* (8). But he also adds: "I have seen but a single specimen of this species. The one I have before me answers very well to the characters assigned to *Echiurus Gaërtneri* by Quatrefages. It wants likewise the spoon-shaped appendage," *i.e.*, the proboscis (*ibid.*).

But Quatrefages himself admitted in 1865 that the species Gaërtneri was based "upon individuals which had been rolled about by the wind," and he adds: "It is very possible that the appendage was broken off" (10). This proved to have been the case, and in 1880 Greef included the species Gaërtneri as one of the synonyms of *E. Pallasii* Guerin, but he retained the doubtful species chrysacanthophorus (7).

A species of Echiurus has been dredged by Professor Verrill at various points along the New England coast, and has been reported conditionally as *E. chrysacanthophorus*. But Verrill wrote me in 1895 that in all his dredging (over 1000 localities) he had met with this species "in very few instances, and *never*[1] a perfect specimen." Hence he wisely refrained from attempting any detailed description of it, and from any comparison with foreign species.

Finally Shipley, in 1896 (13), and again in 1899 (14), rejects the species altogether as being inadequately described, and the locality, "North Atlantic," which he assigns to *Echiurus Pallasii*, doubtless signifies the Norwegian and Greenland shores, from which it has been reported by other authors.

Such being the condition of affairs, it seems fitting to describe the species accurately, to determine it definitely, and to add a few observations upon its habits which may be of generic interest. This is rendered possible by the fact that it has been the good fortune of the author to obtain a large number of absolutely perfect specimens and to keep some of them under observation in aquaria for several weeks, while others were successfully preserved, — a by no means easy task.

The material was all obtained at Casco Bay, on the Maine coast, during the summers of 1895–98. It is also hoped that the photographs which accompany these notes may prove of assistance in locating the species.

[1] The underscoring is his.

Habits. — This species lives in the mud near and below ordinary low-water mark. It can be best obtained during the few days of each month when the tides run lowest, at which time it can be dug in the same way as the common clam (mya).

It is most abundant in close proximity to mussel beds where the mud is soft and very black with organic matter.

I am aware that this habitat is radically different from that given by Greef and others for *E. Pallasii*, but I find a ready explanation in the fact that sand beaches are the rare exception rather than the rule along the Maine coast, so that the animal has simply accommodated itself to its environment.

Its home is a simple burrow formed by pushing aside the mud. The manner in which this is done was repeatedly observed both in its native haunts and in an aquarium.

If not already in that position, the animal turns until it rests upon its ventral surface. This brings the two large anterior setae in contact with the mud. The proboscis is now turned upward and backward, until it lies along the dorsal surface of the body, with its own ventral surface outermost, but protected somewhat by a rolling in of its edges. The proboscis remains inert in this position and *takes no part whatever in the burrowing*. This is in strong contrast to the active locomotor use of the proboscis described by Rietsch in a specimen of *Bonellia minor* (11). By a series of muscular contractions, which include both the longitudinal and circular muscles of the body walls and the special muscles which move the ventral setae, these latter are thrust forward until they project in front of the body almost horizontally.

At the same time the base of the proboscis is drawn backward and somewhat upward, so that the anterior end of the body becomes wedge or chisel shaped, the ventral surface being flattened and extending farthest forward, with the two setae projecting from its anterior edge. These setae are then turned downward and thrust into the mud as far as possible. Being curved, they furnish an excellent leverage, and the body is drawn toward them by a contraction of the longitudinal muscles.

This contraction passes slowly backward along the body until the posterior end is reached, which is moved forward

thereby half or three-quarters of an inch. The two anal rows of setae now serve to hold it in position, while the anterior end is again thrust forward and downward into the mud, and the ventral setae are fastened in a new position. This process is repeated until the animal finally disappears beneath the surface, leaving a circular opening equal in diameter to the body at its greatest lateral contraction. The whole process is extremely slow, and fully forty minutes are consumed in getting the posterior end of the body out of sight beneath the surface.

The burrow proceeds diagonally downward for ten to eighteen inches, then runs horizontally from six inches to two or three feet, and finally turns vertically upward again toward the surface.

When the animal reaches the surface the anterior end of the body is pushed out far enough to free the proboscis. This is then restored to its normal position and the body is withdrawn again into the burrow.

Spengel notes (15) that each burrow of the species (*E. Pallasii*) observed by him at Nordenay possessed two openings close together and each surrounded by a low wall. But those burrows were made in hard sand, while these are in soft mud, and consequently we should expect to find differences. These burrows at first have two openings, but the original entrance soon fills up through the caving in of its walls and the washing in of mud from the surface. The entire diagonal portion is often filled in this way and is never opened again, leaving this end of the burrow blind. These burrows also, when first formed, have low walls around the openings, caused by the pushing aside of the mud, but they quickly disappear.

The Echiurus assumes a position just below the surface, holding itself in place by the two rows of anal bristles (*cf.* Shipley). The mud then washes into the burrow and forms a plug one to two inches thick, with a small opening about the size of a lead-pencil at the center. Through this opening the proboscis is thrust out in search of food when the tide is in, and is then the only portion of the animal which is visible. It is capable of great extension, as was the proboscis of *B. viridis* described by Eisig, and often reaches a length of five or six inches. The

free end moves about in every direction and carefully searches the surface around the opening. Having found a particle of food, the edges are rolled in ventrally toward each other, if not already in that position, and form a more or less closed tube. The whole ventral surface (which is now the interior of the tube) being ciliated, there is generated a current which quickly carries the food toward the mouth. The proboscis often assumes a similar tubular shape when it is not elongated, as can be seen in Fig. 2, so that the curling inward of the edges is independent of the strong contraction of the circular muscles which produces the extension.

Often also it rolls itself into a tight coil, commencing at the tip and curling over ventrally as though it were grasping some object, but nothing save a few food particles is to be found in it, which are much too small to occasion any such effort.

The proboscis is very sensitive over its entire surface, but especially so on the ciliated ventral portion, and the slightest irritation there results in a quick withdrawal.

As would be inferred, such an appendage is of extreme importance to the animal, and yet it breaks off upon the slightest provocation. Whether such a separation is necessarily fatal or not, and whether the animal possesses the power of regenerating its proboscis, could not be definitely determined.

It hardly seems probable, however, that the animal could live for any length of time without it. But it was found that the proboscis itself was so highly innervated that it retained its vitality, and to a marked degree its sensitiveness also, for a long time after separation, a week or more if kept in fresh sea water. When the tide goes out, though there is always water left in the burrow, the proboscis is withdrawn and all indications point to the conclusion that the animal retreats to the lower part of its burrow.

Like other gephyreans, this species secretes a thick mucus, which lines the burrow walls and penetrates the mud for some distance, giving it greater firmness and solidity.

This mucus, as in so many other cases, oxidizes the iron in the mud, so that the walls of the burrow are a rusty brown color and stand out in sharp contrast to the surrounding black.

Movements and Locomotion. — In life, even when out of its burrow, the creature is constantly altering its outward form by energetic contractions of the skin muscles, as noted by Greef (6). Deep constrictions appear at various places, which move now forward, now backward, that portion of the body just in front of or behind the constriction increasing proportionately in size. The proboscis is also kept in constant motion, coiling up and uncoiling, rolling inward from the edges and unrolling or stretching out to a considerable distance and then being withdrawn. In its burrow the animal cannot turn around, but can move either forward or backward at will and with equal rapidity. This motion is accomplished by a series of wave-like contractions and relaxations in the circular and longitudinal muscles of the body wall, the one alternating with the other, and both together producing a fairly rapid gliding motion. The necessary rigidity is given to that portion of the body wall which for the time being serves as a fulcrum, by the pressure of the liquid in the body cavity, as first noted by Quatrefages (9). Andrews has clearly stated (1) the essential factors in the mechanism of *Sipunculus Gouldii* which bring about such "hydrostatic locomotion," and several authors have described similar motion in other gephyreans.

But no one, so far as known, has suggested any other mode of moving about. Indeed, one of the best recent text-books distinctly states that "the gephyrea are only capable of a very slow creeping motion" (Parker and Haswell, p. 461).

It seems never to have been suggested to any one, the present author included, that this same rhythmic contraction of the body walls would furnish an excellent means for swimming.

Hence it was quite a surprise, on visiting an aquarium after dark during the second summer, to find three or four specimens swimming about in it freely. The body was elongated to twice its ordinary length, while the proboscis was elongated even more in proportion and its edges were rolled downward and inward so as nearly to meet along the median line and form a long narrow tube which seemed to take an active part in the swimming.

The resultant motion was peculiar, being gyratory or cork-

screw-like, the anterior end always moving ahead, but it was perfectly free in any direction and quite rapid.

Besides assisting in locomotion the proboscis also seemed to serve as a steering organ, and its extreme sensitiveness rendered it very effective in avoiding obstacles.

The fact that this swimming took place only at night suggests that these animals are more or less nocturnal in their habits, and it may be that they can move about much more freely than has been hitherto supposed. At all events this is probably the mode of locomotion used at or near the breeding season, and it readily explains the large numbers of specimens which are thrown up on the beach after a storm at such seasons.

This species is well known to the clam-diggers along the coast and is sometimes used for bait in deep-sea fishing, but not often, and is never sought designedly for that purpose.

Determination of Species. — After a careful comparison of the descriptions given by Couthouy and Pourtales with that of *E. Pallasii* by its discoverer and subsequent zoölogists, and with the description which follows, there seems no possible doubt that those authors fell into the same error concerning our American species which trapped Quatrefages on the European form, *viz.*, they described an *Echiurus Pallasii* which had lost its proboscis as a new species. Accordingly *Holothuria chrysacanthophora* Couthouy, 1838, and *Echiurus chrysacanthophorus* Pourtales, 1851, must go to swell the long list of synonyms already appended to *Echiurus Pallasii* Guérin-Méneville.

Echiurus Pallasii Guérin-Méneville. — Synonyms: *Holothuria chrysacanthophora* Couthouy, 1838. *Echiurus chrysacanthophorus* Pourtales, 1851.

External Morphology. — Body like that of all known echiuroids, spindle-shaped, tapering slightly at either end; 10–30 cm.[1] long (including the proboscis, 3–6 cm. long) and 3–6 cm. in diameter at the center (Figs. 1 and 2).

[1] This figure is much larger than that usually given for *E. Pallasii*, but is the result of careful measurement and is good evidence in favor of Shipley's statement (13). "It seems probable that *E. forcipatus* of Reinhardt is identical with *E. Pallasii*, though bigger" (*cf.* p. 175).

Color uniform gray or grayish-yellow, shading into a deep orange on the interior of the proboscis. Entire surface of the body rough from being covered with small blunt papillae, which are unequal in size. The larger ones are more globular and are quite regularly arranged in transverse rows in which the individual papillae are so close together that they touch one another. There are twenty-two or twenty-three of these rows, and between them are scattered the smaller papillae, which are more conical in shape and seldom show any arrangement in rows.

Both kinds of papillae are more sharply defined and nearer together toward the ends of the body. There is also usually a bunching of the papillae around the anterior setae where they are larger than elsewhere on the body.

There is a pair of large, shining yellow, hooked setae, one on either side of the ventral mid-line, 16–20 mm. behind the base of the proboscis. These setae are about 20 mm. long and curve toward the posterior end of the body. They are retractile and can be almost wholly withdrawn into the body cavity. The posterior end of the body is surrounded by two rows of yellow setae, somewhat shorter than the anterior pair and perfectly straight. They also are retractile, and in most preserved specimens are withdrawn into the body cavity. In the animal shown in Fig. 4, however, they were extended to their full length. The rows are quite near together (3–5 mm.) and not more than 4 mm. from the anus, which is central and terminal. These posterior setae incline backward and assist the animal in moving about. The anterior row is made up of eight or nine setae, the posterior one of seven or eight.[1]

Reserve setae are present for both rows and for the ventral pair. The setae alternate in the two rows, but neither row is entire, a space being left on the ventral mid-line.

In the posterior row this space corresponds to the omission of one seta, in the anterior row to the omission of three.

There is a papilla around the base of each seta, much larger than those on the body. The spaces between these basal papil-

[1] The fact that these different numbers may be found in individuals otherwise exactly alike is still further evidence that Reinhardt's species, forcipatus, is not well grounded.

lae and the intervals on the ventral surface, up to within 1 mm. of the mid-line, are filled in with ordinary large papillae.

Proboscis large, 3–6 cm. long and 1–3 cm. wide. It is capable of being extended to 12 cm. with a corresponding diminution of its width. It is cylindrical at the base, but quickly opens into a half tube which is broadened at the tip into a shovel form (Fig. 1). The exterior is a brighter yellow than the body and perfectly smooth. The interior is rich orange and completely ciliated, but in most specimens examined it lacks the longitudinal brown stripes noted by Greef in *E. Pallasii* (6). In several specimens, however, they showed up faintly against the orange background.

The skin also on the interior of the proboscis is thrown up into longitudinal ridges, the intervening furrows between which are darker in color than the ridges themselves (Fig. 3). The mouth opens through the center of the cylindrical base. A well-defined ridge runs outward from the mouth along the dorsal mid-line toward the tip of the proboscis. This ridge is somewhat brighter in color than the rest of the interior, but is completely concealed unless the proboscis is opened. The tip of the proboscis sometimes has a well-marked chocolate-brown edge.

The ventral nerve cord and blood vessel show plainly through the skin (*cf.* Figs. 1 and 2), and when the body is extended the dark-colored intestine can be seen at points where it touches the inner surface of the body walls. The sexes are alike externally, with no appreciable difference in size (*cf.* Figs. 1 and 2).

But when sexually ripe, Greef says that the golden eggs or the white semen in the nephridia show through the body wall enough to distinguish the males from the females (6).

Internal Morphology like that of all echiuroids. The alimentary canal is several times the length of the body and is looped irregularly. It is suspended from the body walls by thin muscular strands instead of a continuous mesentery, and upon the slightest perforation of the body walls it is extruded through the orifice by a violent contraction of the muscles.

This alimentary canal may be divided into three regions or parts, called respectively the fore, mid, and hind gut.

The foregut is very short, and contains a pharynx and oesophagus which are often bright orange in color like the inside of the proboscis. The remainder of the foregut is usually larger in diameter and has been called the crop. The midgut constitutes the bulk of the alimentary canal and is distinguished by a groove lined with vibratile cilia which runs along its dorsal side. Opening into this groove at either end is a collateral intestine, much smaller in diameter than the midgut and seemingly analogous to that in echinoderms.

The hindgut is somewhat larger than the midgut and forms near the anus a cloaca into which open two anal vesicles, one on either side. These are quite long, simple sacs, light brown in color, which vary greatly in length in different individuals (40–70 mm.). They open into the body cavity by ciliated funnels, which are most numerous near the base of the sacs, and one of which is terminal.

Both males and females have two pairs of nephridia, which open on the ventral surface on either side of and close to the nerve cord. The mouths of these nephridia are raised into large papillae on the external surface of the body, and can be plainly seen, the anterior pair just behind the ventral setae, and the second pair 5 or 6 mm. farther back.

At the base of each nephridium on the inner side is a ciliated funnel opening into the body cavity, through which the sexual products enter the nephridium when sufficiently ripe.

They are then discharged through the external papillae into the water. When free from eggs the nephridia are 15–20 mm. long and spindle-shaped, with a diameter of 3–5 mm. at the center. Probably when filled with ripe eggs or sperm they increase proportionately in size.

The *Sexual Products* are doubtless formed, as stated by Greef, from small cells near the posterior end of the ventral nerve cord, which are covered with peritoneum. But reproduction certainly does not take place in this locality (Casco Bay) in July and August, as well as in midwinter, *viz.*, it does not occur twice a year. All my specimens were secured in June to August, and not one of them contained ripe sperms or eggs.

But two specimens were obtained September 4 and placed in an aquarium. One of these, which proved to be a female, was injured in the digging, and while being put into the aquarium some nearly ripe eggs escaped through the rent in her side. These furnished the necessary stimulus for the uninjured male and he soon sent out ripe sperms in large quantity from the nephridia.

This would indicate a breeding season for that locality of September to November.

In the female just mentioned the nephridia were perhaps one-eighth full of eggs; all the rest of the eggs were free in the body cavity. This was the only specimen in which any eggs were found in the nephridia, but they may sometimes be found in the body cavity in June, and probably require a long time for development. When ripe (*i.e.*, those from the receptacles) the eggs are spherical, about 0.3 mm. in diameter and nearly opaque, but until fertilization the large germ nucleus can be plainly seen through the yolk granules.

The spermatozoa have a peculiar bullet-shaped head, a short cylindrical middle piece, and a long, very delicate tail. Their vibratory movements are rapid and very strong, and they retain the power of motion for a long time after being discharged into the water.

Just enough description has been here given to fix the species definitely, but considerable work has already been done on the morphology and histology of the body organs and on the origin of the sexual products, and it is expected that the near future will afford an opportunity for a careful study of the complete life history of this interesting species.

Through the courtesy of Dr. W. R. Coe, of the Sheffield Biological Laboratory at Yale University, I have received specimens of an Echiurus secured by him in Alaska, while on the Harriman Alaskan Expedition during the summer of 1899.

This species was found abundantly at many different localities along the Alaskan coast south of the Peninsula and on adjacent islands, nearly always in rich black mud.

It is of considerable interest to note that it proves to be the same species here described, *viz.*, *Echiurus Pallasii*, and that

its habits, so far as observed, correspond exactly with those just given. Its burrow is horseshoe-shaped, the two ends opening at the surface, and around each is a little mound formed by the pushing aside of the mud. The iron ingredients of the mud in the walls of the burrow are also discolored by the mucus secreted by the animal and show as a rusty brown.

In size the Alaskan specimens surpass those from Casco Bay, and the same shovelful of mud often reveals giants and pigmies of the species side by side. But this is simply in accordance with the general results of the expedition, for gigantic specimens of nearly every native species were found.

The number of setae in the anal rings of four specimens selected at random were counted. In three of these there were eight setae in the anterior ring and seven in the posterior, but in the fourth specimen the numbers were nine and eight respectively.

The fact that specimens from two such widely separated localities agree perfectly in carrying the maximum of size beyond 30 cm. and also in the variation of the number of setae in the anal rings, is a third argument, and quite a strong one, against the validity of the species forcipatus.

There seems to be no discernible connection between the number of the setae in the anal rings and the size of the animal; a small specimen is just as likely to possess the larger number.

On the contrary, there is something of a connection between the size of the individual and the temperature of its environment; in general, the colder the water the larger the average of the species. Such a fact strongly corroborates the statement made by Shipley (14) that "this genus is a denizen of the colder seas," and indicates that an Arctic environment is most congenial to its development.

These two new localities also go far toward rendering this species cosmopolitan. It has already been reported from the North Sea, where it was originally discovered, the English Channel, and the coasts of Norway, Sweden, Denmark, Holland, and Belgium. To these can now be added the American North Atlantic and North Pacific, and it may be expected as

one of the results of further investigation in the Asiatic North Pacific.

Thalassema erythrogrammon Max Müller. — I obtained a specimen of this Thalassema through the kindness of Dr. E. A. Andrews of Johns Hopkins University.

It was taken at Green Turtle Cay, off Great Abaco Island, the Bahamas, in the summer of 1886, and when alive was of a flesh color with reddish longitudinal stripes, the proboscis lighter in color, the papillae whitish. The body was raised into longitudinal ridges between the muscle bundles whose prominence varied with the degree of contraction. The specimen was hardened in Perenyi's fluid, and yet the muscle bands show a decided pink-brown color at the present time and stand out very distinctly, as can be seen in the photograph (Fig. 5).

It was excellently preserved in a normal condition and measures 16 cm. in length (including the proboscis, 3 cm. long) and 2.4 cm. in greatest diameter. Body spindle-shaped, with bluntly rounded ends, and after preservation *not* perceptibly furrowed by the longitudinal muscle bands. Papillae in dense placques at the posterior end of the body; no smooth area in the immediate vicinity of the anus. Longitudinal muscles in sixteen bands about 1.5 mm. wide, with interspaces 4.5–7 mm. wide at the center of the body, except the two bands on either side of the ventral mid-line which are close together.

Proboscis so fleshy as to be nearly a solid cylinder, 1 cm. in diameter at the base, thus bringing the mouth to the extreme ventral surface; less fleshy and not broadened toward the tip.

The two setae were so far withdrawn into the thick skin as to be wholly invisible from the external surface, but could be all the more plainly seen on the interior.

The specimen proved to be a ripe male, and the three pairs of nephridia were enormously swollen and packed with sperm.

They increased in size from in front backward, the respective lengths being 3.2, 4.5, and 8.2 cm. The two posterior pairs were constricted at intervals and looked much like a string of sausages; the anterior pair opened 3 mm. in front of the ventral setae, and all three pairs were furnished with spirally coiled internal openings.

Anal glands 9 cm. long, simple, very thin walled, and *without* visible funnels. Intestine filled with the powdered shells of small lamellibranchs.

The chief interest in this specimen centers in the new locality. It has been reported hitherto only from the Red Sea, the Isle of Bourbon, the Malay Peninsula, and New Guinea, about as far distant as possible from the Bahamas. But it evidently belongs to the West Indian fauna and adds one more to the Atlantic species of this genus. Again, this is one of the species in which the number of muscle bands has been given as invariable and fourteen in number. The occurrence of sixteen bands in the present specimen shows that, like most of the other species, the number varies within narrow limits. The position of the anterior nephridia in front of the anal setae, as in *T. caudex* Lampert, is also worthy of note.

STATE NORMAL SCHOOL,
WESTFIELD, MASS.,
March 8, 1900.

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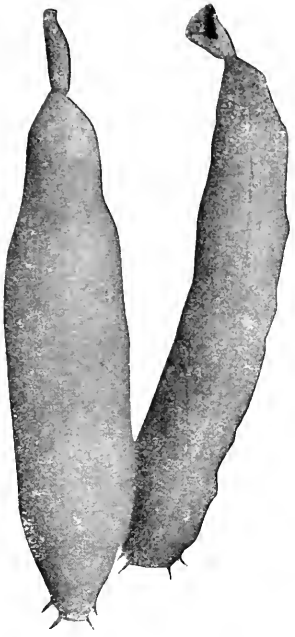

FIG. 1. — A male (right) and female (left) *E. Pallasii* in a normal state of contraction in sea-water. × ½. Photographed from life.

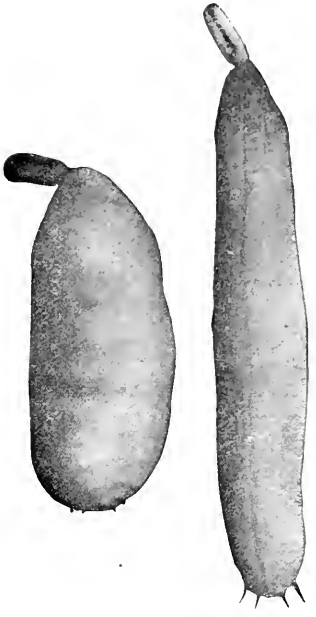

FIG. 2. — The same pair in the same position, but with the female contracted under irritation. × ½. Photographed from life

FIG. 3.— Ventral view of proboscis and anterior body. Photographed from preserved Alaskan specimen. Life size.

FIG. 4. — Anal rows of setae. Photographed from preserved specimen. Life size.

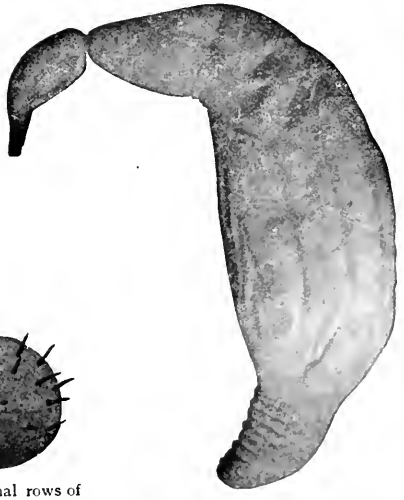

FIG. 5. — *Thalassema erythrogrammon*. Photographed from preserved specimen. ⅔ actual size.

SOME GENERAL FEATURES OF THE METAMORPHOSIS OF THE FLAG WEEVIL MONONYCHUS VULPECULUS FABR.

JAMES G. NEEDHAM.

I HAVE been for some time desirous of studying the development of some beetle which would represent metamorphosis in as complete a condition as is found within the order Coleoptera. Last summer I found an abundance of the flag weevil (*Mononychus vulpeculus* Fabr.) in all stages; and this furnished me the opportunity for which I waited. The larvae of this beetle are little fat grubs, which eat the seeds of the blue flag (*Iris versicolor* Linn.). They are sheltered from first to last within the flag capsule and are very degenerate. They lack eyes, antennae, and legs, as well as wings. They represent a sort of ecological specialization, common among the higher insects, manifest in the adaptation of life to very special situations, and of life history to conditions of transient food supply.

I. *Life History.*

The life history of this long familiar species seems not to have been fully made known.[1] While gathering my material I was not seeking to determine the full life history, but now I find that my collections and notes reveal it pretty completely. Collected material gathered in at intervals of two or three days give data as follows: Eggs were first found June 8. The beetles had just begun to oviposit on the earliest of the flag flowers, first opened that day. Larvae were first found June 29, at which

[1] Dr. John Hamilton published fragmentary notes on its life history in 1894 ("Mononychus vulpeculus and its Parasites," *Entom. News*, vol. v, pp. 287, 288), describing oviposition and the form and feeding habits of the larva, and citing an instance of great destructiveness on the part of two parasites, *Pimpla inquisitor* Say and *P. pterelas* Say.

time but few eggs were hatched. Pupae were first found August 5, and newly transformed imagoes, August 8, two months after egg-laying began.

Examining my collection of several hundred larvae, after the manner of lepidopterists, I find among them three sizes of head, so distinct as to certainly indicate three larval stages. The first, which is of the size attained before hatching, measures in diameter .24–.26 mm., the second .40–.44 mm., and the third .81–.85 mm.

My notes and collection labels together indicate the following life history:

1. An egg stage, lasting about three weeks. The eggs lie at the bottom of punctures made through the wall of the flag ovary by the mother-beetle with her rostrum. The egg is pellucid white, broadly oblong-oval in outline, and measures .38 by .70 mm.

2. A first larval stage, lasting about five days. At the end of this stage an average larva measures 2.2 mm. in length by .4 mm. in greatest diameter.

3. A second larval stage, lasting perhaps ten days (certainly not over two weeks), at the end of which the larva measures 4.60 mm. in length by 1.02 mm. in greatest diameter. Thus far the larva remains slender and quite elongate. During these two stages it traverses the outer face of from three to five seeds, leaving a slowly widening, shallow, brown furrow across their surfaces.

4. A third larval stage, lasting a very little more than two weeks, and divided into two periods:

(*a*) A period of feeding, and extraordinarily rapid growth, lasting hardly more than a week. The greater part of increase in size is attained during this short period. During it the larva is boring through the center of several seeds, feeding on their highly nutritive endosperm. At the end of it the larva measures 6.5 mm. by 2.5 mm.

(*b*) A period of transformation to the pupa.

5. A pupal stage, lasting, apparently, not more than a week, spent within the larval burrow. The pupa is naked and smooth, except for a pair of recurved spines on the tip of the abdomen.

6. A period of adult life, lasting ten or more months. Of this time a month or more is spent (lasting until the bursting of the

flag capsules in autumn) quietly within the larval burrow; eight or more months are spent in hiding in winter quarters; activity only begins with the season of iris flowering, and lasts for about a month. Oviposition continues sparingly after the first week. Except at the beginning of the season, several developmental stages may be taken at the same time, and this fact renders dates of *first observation only* of value as indices of life history.

The more striking features of this life history are:

1. The small number of larval stages, for a representative of this order.[1]

2. The exceedingly rapid growth during the first period of the third larval stage. That an animal which will live a year should attain the greater part of its growth within a week is indeed a striking phenomenon. To be sure, this growth is mainly increase of fat.

3. The long period of adult inactivity, extending through two stretches of warm weather.

The metamorphosis of this beetle is very complete. The segregation of the development life into growth period (period of partial anabolism — fat-making) and differentiation period is very marked. The transformation of the degenerate larva, lacking wings, legs, antennae, eyes, optic lobes, and salivary glands, into the adult with all these parts well developed, is very rapid. There are excellent reasons for believing that these things have been independently acquired in the order Coleoptera. Internal metamorphosis has as yet been studied only in such representatives of this order as, in the larval stages, have legs and antennae and eyes, and undergo a metamorphosis much less rapid and complete. Therefore, it should be important to learn whether this increasing periodicity in life history has produced the same changes here as in other orders, whether disappearance of larval appendages has resulted in the internal development of imaginal discs, whether rapid metamorphosis is accompanied by phagocytosis, etc.

The external signs of internal metamorphic processes begin to

[1] Dr. C. V. Riley found four larval stages in the clover leaf weevil. *Vide*, "The Clover Leaf Beetle Phytonomus punctatus Fabr.," *Rept. U. S. Dept. of Agric.* for 1881, pp. 171–179, Pl. X. The Phytonomus larva is less degenerate.

appear almost as soon as the larva is done feeding. There is a slight loosening of the cuticle, and contraction of the body away from it, especially on the dorsal side of the thoracic segments and of the head. The budding legs and wings, already visible through the transparent skin (Fig. 1), begin to grow and extend downward. The fat at the interior end of the body begins to lose its mottled, slightly grayish appearance, and becomes homogeneous, translucent, slightly yellowish-white.[1]

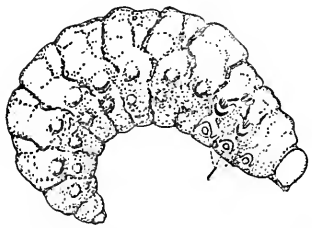

FIG. 1. — Full-grown larva of the flag weevil (*Mononychus vulpeculus* Fabr.). *w*, wing buds, and *l*, leg buds, as seen through the skin.

Then the larval skin is cast, and the pupa appears with all the adult appendages clearly recognizable. After this the progress of internal changes may best be gauged by pigmentation; first, in the eyes, then in the tips of the hind wings, and lastly in the general integument. Some of the corresponding internal phenomena will be discussed under the following headings.

II. *The Hypodermis during Metamorphosis.*

The hypodermis of this weevil is not, so far as observed, destroyed during metamorphosis to be again rebuilt in any part. The cells, however, while maintaining fairly constant relations at their ends, externally with the covering cuticle and internally with the tenuous basement membrane, take on remarkable variety of form and show a fine capacity for shifting, massing, or scattering themselves, previous to the definitive formation of the adult chitin. This might have been anticipated, in view of the exquisite sculpture and ornamentation of the adult beetle. It will be of interest to consider first briefly the origin of the appendage buds ("imaginal discs").

Wings and legs appear at the beginning of the third larval stage, each as a slight thickening of the hypodermis, showing almost from the beginning a slightly concentric arrangement of the elongating cells. Fig. 2, *B*, shows the beginning of a middle

[1] Correspondingly it ceases to be stained black with osmic acid in fixation.

leg. A wing bud would differ only in having the inner surface of the hypodermis free from tracheae, etc.

The striking difference between the behavior of the cells in these buds, and the behavior of hypodermis cells elsewhere (observed, doubtless, by every one who studies sections of insect larvae), I have thought it worth while to emphasize in this figure. Fig. 2, *A*, shows the crumpling which precedes molting everywhere except in these buds. Fig. 2, *B*, is a bud, and shows instead the thickening of the hypodermis and the compression of its cells. Elsewhere the hypodermis stretches as it grows;

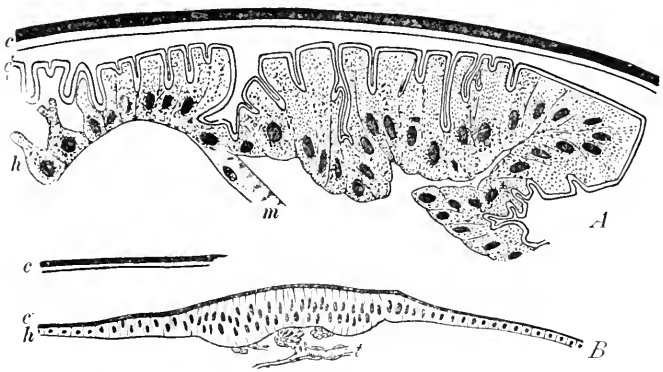

FIG. 2.—Two dispositions of hypodermis. *A*, vertical section of the frons at the end of the second larval stage, showing the crumpling of the hypodermis. *B*, vertical section of the bud of the middle leg at the time of molting at the end of the second larval stage, showing the thickening of the hypodermis, without crumpling. *c*, old chitine; *c'*, new chitine; *m*, developing muscle fiber; *t*, trachea.

the cells separate as they multiply; and that is true also of the hypodermis of the appendages, later, when the time has come for their extension. This we call retarded development, but the physiological explanation of it is still lacking.

There is no invagination of wing and leg buds in this beetle. Even the shallow hypodermal pockets formed about them in the more generalized Coleoptera are absent. The buds do not retreat from the surface. Fig. 1 shows their appearance as seen through the thin integument of the full-grown larva. Fig. 3 is a section of the wing at this time. The inner wall of the projecting shelf of hypodermis below the wing tip is all there is to represent the so-called "peripodal membrane." With

metamorphosis the wing begins to elongate from its apex and soon crowds downward past the shelf; and even before the casting of the last larval skin the general form of the adult elytron with the principal furrows upon its surface will have appeared.[1]

The scales of this weevil are wholly developed during the pupal period. They vary in form from simple sensory hairs as in the antennal club, and slender, lanceolate, sensory scales in the tarsal brushes, to flat, longitudinally fluted, Lepidopter-like scales of yellow and black colors on the dorsal and more exposed surfaces, and delicate, short-plumose, white, or pale yellow scales on the less exposed surfaces. These, one and all, arise from ordinary, single hypodermis cells, after the manner of the development of the scales in the lepidopterous wings, as described by Mayer[2] *et al.*

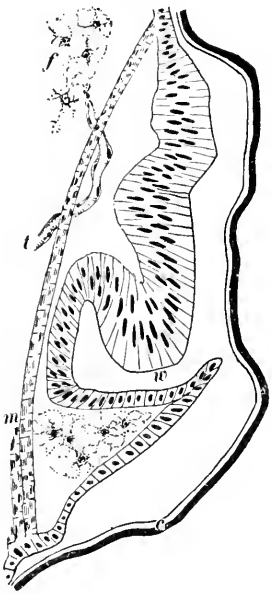

Fig. 3.—Vertical section of the fore wing in a grown larva. *w*, the wing apex; *c*, the loose chitine; *m*, muscle; *t*, trachea; *f*, fat.

First, in early pupal life the cells destined to produce the scales become much larger than their fellows and retreat a little from the surface, so that their nuclei appear at a lower level than the level of the other nuclei. Then each scale mother-cell loses its attachment to the basement membrane, becoming rounded off internally and sometimes acquiring a vacuole, and puts forth a process (the scale that is to be) between the adjacent surface cells (*cf.* Fig. 9). From this process the scale develops, the peculiarities of its own scale kind differentiating rather tardily.[3]

[1] There is no need to recount the wing development, since in all important features it is the same in this beetle as in a Coccinellid of which Professor Comstock and I have hitherto published an account (*Amer. Nat.*, vol. xxxiii, pp. 845–858, 1899).

[2] Mayer, A. G., "The Development of the Wing Scales and their Pigment in Butterflies and Moths," *Bull. Mus. Comp. Zoöl.* Vol. xxix, pp. 209–236, 7 plates, 1896. (Gives bibliography of earlier studies.)

[3] By far the most interesting features of the hypodermis are found in the metamorphosis of the head and the development of the rostrum. These will

III. *The Development of the Legs.*

Aside from a few not very recent accounts of the development of the legs in Diptera, in which the leg buds are deeply invaginated in the larva, Gonin's account of them in the butterfly Pieris remains the only considerable one. And in Pieris there are larval legs, well developed and functional from the first. It

FIG. 4. — Longitudinal section of the middle leg in a grown larva. *f*, fat; *l*, leucocytes; *e*, embryonic cells. (Drawn from a preparation made in my laboratory by Mr. C. Betten.)

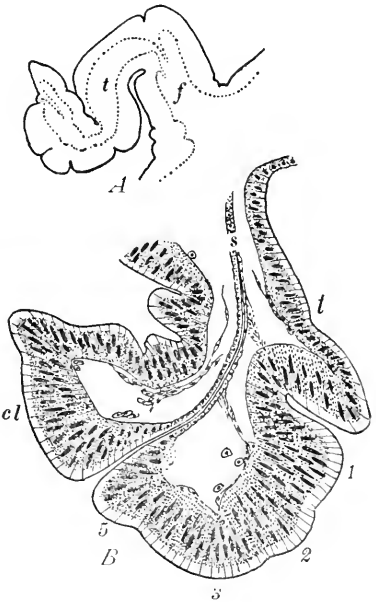

FIG. 5. — The leg of a larva, just before pupation. *A*, the entire leg in outline, and in part in optic section. *B*, a longitudinal section of the tarsus. *f*, femur; *t*, tibia; *1*, *2*, *3*, *5*, tarsal segments; *cl*, claw; *s*, developing tendon.

will be well, therefore, to notice here some points in the development of the legs of this weevil.

We have already called attention to Fig. 2, illustrating their origin. Fig. 4 is a longitudinal section of the leg of a grown larva, such as is shown in Fig. 1. Three principal divisions of the leg are already marked out by two deep constrictions. From the time of the beginning of the metamorphosis the growth of the legs is extremely rapid. Fig. 5, *A*, represents one of them as it appears after stripping off the larval skin just before pupation. (Fig. 8 shows wing and leg together, and in their relations to other parts.) The nine segments of the leg are

constitute the subject of another paper, which is now being prepared by a student in my laboratory.

now clearly recognizable, all save one — the fourth segment of the tarsus, whose size is small in the adult, and whose suppression thus seems to extend back into the ontogeny of the species. Fig. 5, *B*, represents a longitudinal section through the tarsus at the same stage. This shows well the condition of the hypodermis at the time when all is ready for that great extension which accompanies pupation. Here is shown also the development of the strong tendon which protracts the claw, as a hypodermal invagination between segment five of the tarsus and the base of

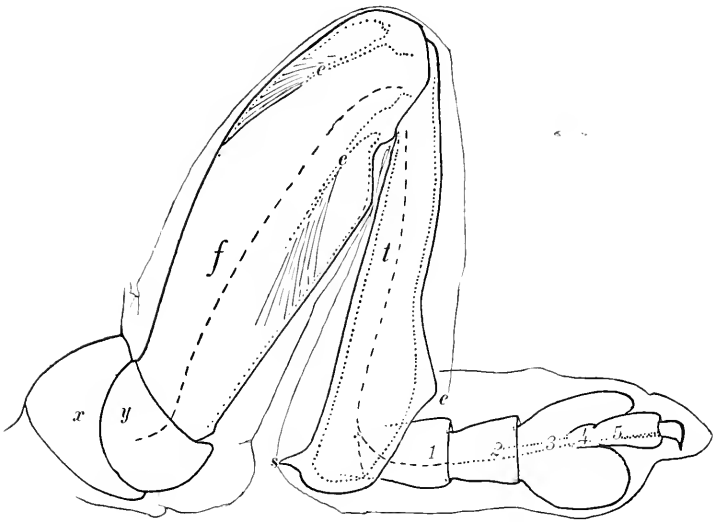

FIG. 6. — Leg of young pupa, within the pupal skin, in part in optic section. *x*, coxa; *y*, trochanter; *f*, femur; *t*, tibia; *c*, corbel; *s*, scrobe; *e*, *e*, developing tendons (flexor and extensor tibiae) and muscles; *1*, *2*, *3*, *4*, *5*, segments of the tarsus.

the claw. At pupation this tendon is drawn out to great length, the hypodermis nuclei move apart, and spend themselves completely in chitine formation. Thus is the tubular ingrowth of soft hypoderm cells transformed into a solid cord of chitine. Muscle cells developing internally at the expense of the fat are from the first intimately associated with these hypoderm cells (*cf.* Fig. 9), and through them become attached later to the tendon. Just after pupation there is a striking similarity in appearance between these tendons growing from the surface into the leg cavity and the tracheae growing from the body cavity into it.

Fig. 6 shows the leg of a young pupa within its sheath. All the leg segments are rapidly assuming their definitive form. The fourth tarsal segment has reached its maximum development; it will be relatively smaller in the adult. The broad, flat, brush-bearing pads of the third tarsal segment are here big bag-like dilatations. Corbel and scrobe are very evident upon the tibia, and the femur and other segments are full of fat, rapidly being metamorphosed into muscle.

Fig. 7, *A*, represents the structure of the tarsus in an old pupa; externally it is practically that of the adult beetle. Fig. 7, *B*, is another section in the same series, passing through one of the lateral pads of the third tarsal segment. It shows a thinner hypodermis above, bearing scattered scales, and a thicker hypodermis below, bearing the dense tarsal brushes. Within are seen disintegrating fat cells, and other growing cells, angular and with large nuclei, which I take to be neuroblasts. Fig. 7, *C*, is from a younger pupa. It shows well the manner of development of the tarsal brush. The mother-cells of its constituent scales settle below the general level of the hypodermis; owing to close crowding, their nuclei take on a cuneate form, and on the inner side of each a minute but distinct vacuole appears. At this age the hypoderm cells generally, as here, reach their basement membrane by long, peaked internal processes. Against this basement membrane here lie heaped embryonic cells, which later differentiate as the above-mentioned neuroblasts. Subse-

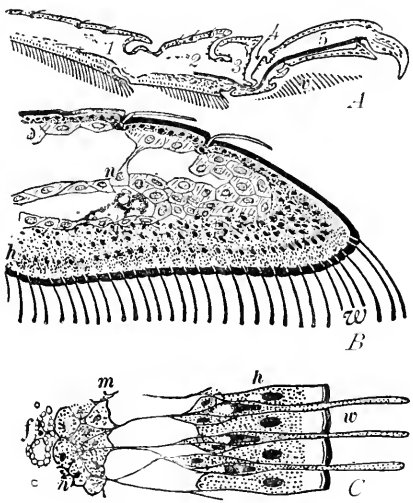

FIG. 7.—The tarsus in the pupal stage. *A*, longitudinal section of the tarsus in an old pupa. *B*, part of another section from the same series passing through one of the brushes of the 3d segment; *w*, the scales constituting the brush; *v*, the edge of one of the brushes belonging to the third segment; the tendon which retracts the claw is drawn in solid black; *n*, neuroblasts. *C*, a bit of a section through the tarsal brush in a young pupa, to show the origin of the scales; *w*, the scales; *h*, hypodermis; *m*, basement membrane; *n*, neuroblasts (undifferentiated); *f*, fat.

quent approximation of hypoderm cells and basement membrane (due, shall we say, to the drawing in of the peaked processes?), together with the loss of distinct cell boundaries in the hypodermis, renders the relation of parts much less clear in the later stages.

The tarsal claw and the tibial scrobe are developed alike from thick projections of hypodermis cells, forming at first a blunt point, which becomes sharp and takes on its characteristic tenacular curvature only when the chitine begins to harden. The corbel, however, being formed not at an angle of the leg, but upon an originally smooth surface, develops differently. There is a dense heaping of the hypoderm cells along what is to be the rim of the *U*-shaped corbel, among which the very large mother-cells of the fringing spines are early differentiated. Within the rim the cells are few, slender, and scattered. Outer (cuticle) and inner (basement membrane) surfaces are at first parallel; but the subsequent settling down of all the hypoderm cells upon their basement membrane leaves, where the few slender cells were within the rim, the proper concavity of the corbel.

IV. *Fat.*

The extraordinary growth taking place during the last larval stage is due almost wholly to the accumulation of fat. This occurring chiefly upon the dorsal side brings about the characteristic curvature of the larva. Hardly has growth been completed, however, before the reverse process sets in; the fat begins to be demolished and used in the construction of new parts. The external appearances accompanying the reduction of the fat have already been described. In sections the appearance is that of local disintegrations of the periphery of certain of the fat masses. Fig. 8 is a section through the middle of the thorax very near the beginning of metamorphosis. At the bases of the budding appendages and immediately above and below the alimentary canal, the fat is disintegrating. The appearance is that of the melting of frost. The fluid *residuum* flows forward into the head and laterally out into wings and legs, bearing along floating islands broken away from the fat masses.

During growth the fat is being stored in undifferentiated mesodermal cells which are free within the body cavity. These cells become greatly distended with the fat globules, which come to fill great interstices in the protoplasm toward the cell periphery. That each nucleus retains its vitality notwithstanding, is shown by its staining reactions, and by its retention of a central mass of protoplasm about itself, from which the peripheral strands that encircle the fat globules proceed. This is certainly not typical fatty degeneration; it seems to me much more properly considered to be partial anabolism, affected by these cells in their rapid elaboration of hydrocarbons during the transient period of abundant food supply. This view is corroborated by their later history. They do not (at least a majority of them do not) die with the dissolution of the fat. Nothing is plainer while one is watching the disintegration of the fat masses than that the nuclei contained therein show none of the usual signs of necrobiosis. Here and there will be seen a nucleus which, together with its enveloping coat of protoplasm, seems to be slipping itself free from its aforetime accumulation of fat. Furthermore, these nuclei thus isolated can be seen associating themselves with the developing muscle rudiments, and, apparently,

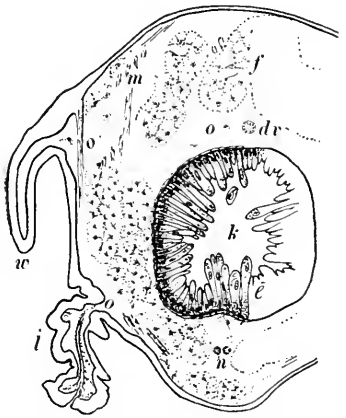

FIG. 8. — Partial cross-section of a larva, nearing pupation. *w*, fore wing; *l*, middle leg; *m*, muscles; *f*, fat; *dv*, dorsal vessel; *k*, alimentary canal; *e*, digestive epithelium, ready for dissolution; *n*, nerve cord; *o*, *o*, *o*, areas of first disintegration of the fat masses.

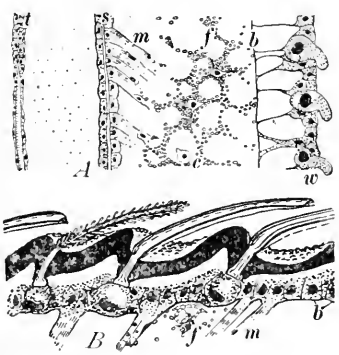

FIG. 9. — The development of scales and of muscle fibers. *A*, a bit of a longitudinal section of the femur of a young pupa; *t*, developing trachea; *s*, developing tendon (flexor tibiae); *m*, developing muscle fibers; *f*, disintegrating fat; *c*, a nucleus belonging to the fat mass isolating itself from the same; *b*, basement membrane; *w*, developing scales, in the midst of ordinary hypodermis. *B*, a bit of the body wall from a newly transformed imago, lettered as in *A*.

themselves becoming the nuclei of new muscle fibers. The single fat globules which they often carry with them and sometimes retain, even after they have become associated with the muscle rudiments, enable one to follow them easily from their former situation into this new one.

There is no destruction of any larval tissue by phagocytes during metamorphosis, but *after the imago stage has been entered upon*, large numbers of phagocytes appear in the midst of the fat along the sides of the abdomen. There are numerous embryonic or undifferentiated cells lying along the sides of the body in the larvae; and these, I believe, begin to penetrate the fat masses toward the end of the pupal stage. Fig. 10 shows the appearance they present in a recently transformed weevil. Up to this time the fat filling the abdomen has not been greatly reduced, except in the anterior end; the change of form in the abdomen in passing from larva to imago is slight as compared with that of other parts. But it is clear that the internal metamorphosis is only well under way when the external is completed. This reserve store of fat is for the completion of the still weak organs of the imago, and for nutrition during the ten long months of inactivity remaining before the flags bloom and feeding begins again.

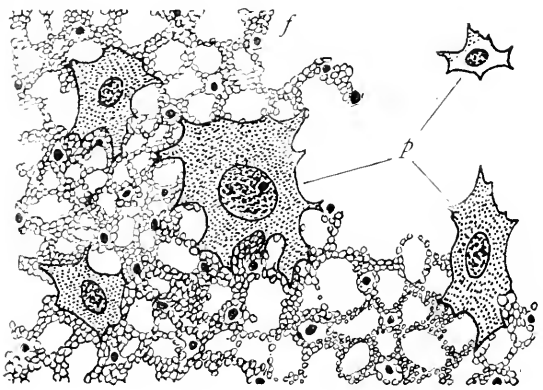

FIG. 10. — Phagocytes attacking the fat; the section is through the abdomen of a recently transformed imago. *p*, phagocytes; *f*, fat. (From a preparation made in my laboratory by Miss Elizabeth Andrews.)

After calling attention to some of the interesting features of post-embryonic development, I would not close this little paper without mentioning the exceptional availability of this species for laboratory study. On a single trip to a favorable flag clump during the latter part of July in this latitude, one may gather in

a little while enough material for studying its entire metamorphosis. This material may be excellently fixed in boiling 70 per cent alcohol, and in all stages preceding the imago the chitine is so thin as to interfere but little with section cutting.

The following conclusions from the foregoing study are believed to be new:

1. In *Mononychus vulpeculus* Fabr. there are three larval stages.

2. The full-grown larva is very degenerate, having only the merest rudiments of antennae, eyes, optic lobes, and salivary glands.

3. The greater part of the increase in size takes place in about a week after entering the third larval stage; it is due mainly to fat accumulation.

4. This brief period of feeding and rapid accumulation of half-assimilated food material is correlated with an extremely long final assimilation period, lasting through months of imaginal life.

5. There is no real invagination of the buds of wings or legs.

6. Many nuclei of fat cells persist after the dissolution of the fat masses, free themselves from these masses, retaining about themselves an investment of protoplasm, associate themselves with developing muscle fibers, and, probably, themselves become the nuclei of new muscle fibers.

7. Phagocytosis, which was observed only in the fat masses along the sides of the abdomen, occurs only after external metamorphosis is complete.

NOTES ON THE PHYSIOLOGY OF REGENERATION OF PARTS IN PLANARIA MACULATA.[1]

C. C. LEMON.

I. *Modes of Regeneration.*

In Planaria maculata there are two methods of inducing regeneration. First, isolated parts of sufficient size taken from any part of the body except the region in front of the eyes will regenerate; and second, partly isolated areas may regenerate, producing compound planarians.

1. *Isolated Parts.* — Randolph,[2] 1897, states that when a worm was cut into eight pieces by cross cuts, seven of them lived, and six of them regenerated all lost parts. The seventh failed to regenerate eyes.

Morgan[3] has shown that there is a limit of size below which regeneration of lost parts will not take place. He also thinks that while the area in front of the eyes, which does not regenerate, is near this lower limit of size, there is another cause, probably that of greater specialization, why it will not regenerate lost organs.

My own observations on regeneration of isolated parts, though limited, for the most part support those of Morgan, as will be seen from the following record of experiments. A worm 10 mm. long and 2 mm. to 3 mm. in width was cut into

[1] The work herein recorded was done in the Laboratory of Experimental Morphology of Michigan University, under the direction of Dr. F. R. Lillie, to whom the writer wishes to express his sincere thanks for assistance and encouragement.

[2] "Observations and Experiments on Regeneration in Planarians," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen.* Bd. v, p. 355. 1897.

[3] "Experimental Studies of the Regeneration of Planaria maculata," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen.* Bd. vii, pp. 365-372. 1898.

eight pieces as nearly equal in size as possible. All pieces regenerated lost parts and became fully developed worms in about ten days at ordinary room temperature. Another worm 5 mm. long and 1 mm. wide was cut into eight pieces. The operation was, however, so delicate that there was not much certainty in obtaining uniform size of the pieces. The larger pieces regenerated the lost organs, while the smaller ones did not. Just what the limit is, was hard to ascertain, as the relation of the piece to the whole could not be accurately determined, on account of its constantly varying shape. Parts which, by the most careful measurements, were shown to be about one-twelfth of the size of the original animal, regenerated and became fully formed planarians, while those of smaller size did not. Experiments on sixteen worms resulted in the same way. The area in front of the eyes did not regenerate in a single case.

2. *Production of Compound Planarians.* — This may be brought about in two ways: (1) Parts separated by cuts made along or near the middle line will generally complete themselves by regeneration without much growth. (2) Even extremely minute strips partly isolated may grow out like buds, and when of sufficient size, develop the characteristic organs of the species.

There is, of course, no line of demarcation between these two ways, which are united by a series of intermediates.

a. *By Regeneration.* — When a worm was split through the middle line of the anterior part of the body, sometimes the partly isolated left half regenerated a new right half and the partly isolated right half a new left half, thus producing a worm with two complete heads (Fig. 1). A similar operation may be performed on the posterior part of the body, resulting in two tails (Fig. 2). The time required for the regeneration of two heads is fifteen to twenty days, varying somewhat according to temperature. The regeneration of double tails occurred in five to ten days.

On Dec. 24, 1898, a large planarian was operated on by splitting the tail, as indicated in Fig. 13, except that the cut did not extend through the pharynx but only to the region

just posterior to it. On Jan. 3, 1899, two fully formed tails had developed. On January 5, the animal divided by fission about 3 mm. in front of the point of union of the two tails. The part possessing the two tails regenerated a new head, producing the animal seen in Fig. 3.

On January 11, the anterior part of the worm was again split posteriorly, this time dividing the pharynx. Five days later, on January 16, the posterior end of the worm again divided off, and subsequently regenerated a new head, as seen in Fig. 4. The third and most anterior part of the original worm was split posteriorly, but the double tails

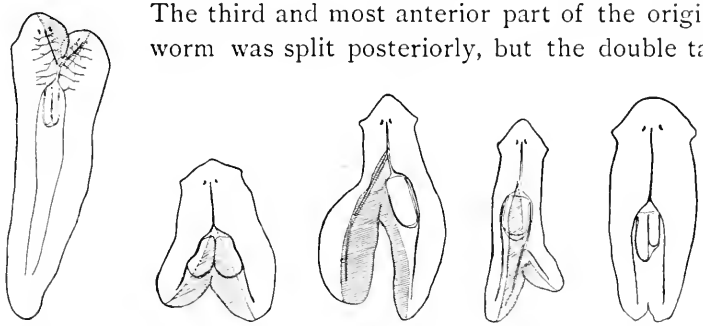

Fig. 1. Fig. 2. Fig. 3. Fig. 4. Fig. 5.

Fig. 1. — A double-headed planarian caused by regeneration after the original head had been split.
Fig. 2. — A planarian with two tails resulting from splitting and regeneration.
Fig. 3. — A planarian which separated from that of Fig. 5 by fission after its tail had been split.
Fig. 4. — This worm also separated from that of Fig. 5 by fission eleven days after Fig. 3.
Fig. 5. — The head end of the worm from which those in Figs. 3 and 4 separated.

could not be produced again, although the operation was performed three times. The only result that could be obtained was a worm with a slightly bifid tail and double pharynx (Fig. 5).

An interesting feature of the experiment with this worm is the way in which the alimentary canal developed in the regenerated parts. The left tail of Fig. 3 is supplied with nutriment by means of a sub-branch which comes off from the anterior branch of the canal, while the original left branch of the canal, which was severed in the operation, has disappeared. On the other hand, the right tail of Fig. 4 receives its nutriment by a sub-branch from the right posterior branch of the canal, which still persists, or is possibly a new formation. This and other problems concerning the anatomy of compound planarians are of interest and should be worked out.

b. *Budding.* — Small strips of tissue from the margin of the body or edge of a cut resemble buds in their capacity for growth and differentiation. These false buds regenerate more rapidly than larger portions of the body. To induce the growth of buds an incision is made, partly severing a very narrow strip (.5 mm.) of tissue, as shown by the lines in Figs. 6 and 10; Fig. 6 *a* indicates the method by which the worms in Figs. 8 and 9 were produced, and Fig. 10 *a* indicates how Figs. 11 and 12 originated.

In Fig. 7 the cut was made as indicated by the dotted line *a*. The bud, which was 4 mm. long, regenerated a new head, with brain, eyes, and cephalic lobes, in fourteen days. This head was developed from tissue in the posterior third of the body. Dalyell,[1] referred to by Randolph, thought that heads could be developed from tissue of the anterior part of the worm only. This idea is wholly disproved by Figs. 7, 11, and 12. At *b*, Fig. 7, is seen a bud one day after being cut.

i. *Growth.* — The bud, not having sufficient muscular strength to right itself against the larger part of the worm, heals without uniting with it, as is the case so often with animals split in the middle line. Growth begins very soon after the operation, being quite perceptible at the end of two days. It occurs in two ways: first, by regenerating new tissue on the cut edge of the bud; and second, by the increase of length, breadth, and thickness of the old tissue.

ii. *Differentiation of New Organs.* — Along with the increase in size the body becomes rounded off on the dorsal surface, and the head becomes broader and thicker in the region of the brain area when the cephalic lobes appear. Finally the eyes and pharynx, where a pharynx is developed, appear almost simultaneously.

In Fig. 8 the bud was formed by partly isolating a narrow strip of tissue from the side of the anterior part of the animal, as indicated by the shaded part *a*. About the time the cephalic lobes appeared, which was twelve days after the operation, the bud began to assert its independence, and was dragged about by the stronger worm with its head extending in a pos-

[1] "Observations and Experiments on Regeneration in Planarians," p. 370.

terior direction. As a result of the tension caused by the pulling, growth took place in the region *a* (Fig. 8), making the position of the posteriorly directed head a permanent and natural one.

In the case of Fig. 9 the bud was produced in the same way, but from day to day as the tension increased a slight cut was made at *a*, and as a result we do not have the head end of the bud directed posteriorly to the main axis of the worm, but nearly at right angles to it. The cutting prevented growth, and hence, when the animal comes to rest, or when relaxed in

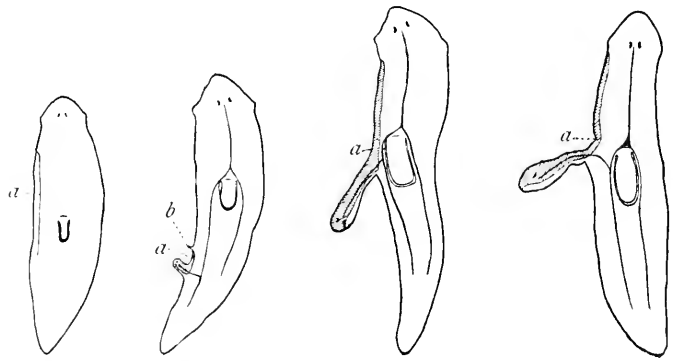

Fig. 6. Fig. 7. Fig. 8. Fig. 9.

Fig. 6. — At *a* is seen the kind of cut which was made to produce buds.
Fig. 7. — A head regenerated from a bud, and a bud, *b*.
Fig. 8. — Pseudoheteromorphosis.
Fig. 9. — Frequent cutting at *a* prevented pseudoheteromorphosis in the worm of this figure.

killing, the bud, instead of remaining in a posteriorly directed position as when in motion, takes a position more nearly the same as that which it originally occupied.

While the bud was developing, the cut edge of the larger part regenerated enough new tissue to replace that which went to produce the bud. Thus we have a well-formed double-headed planarian in the case of Fig. 8. In Fig. 9 the bud failed to develop a left eye. This may be due to the frequently cutting at *a*; otherwise our present knowledge of the case makes it impossible to decide what the cause may be.

iii. *Final Fate of Parts.* — One point was quite noticeable in all the experiments with buds. When the animal had be-

come well formed there was a strong tendency to divide and in this way get rid of the abnormal condition. Ignorance of this fact cost the writer two of his best examples of regeneration; and it was only by diligently watching their development and killing the material at the proper time that the examples for this part of the paper could be obtained.

II. *Heteromorphosis.*

1. *Historical.* — Randolph[1] mentions four cases found by Dalyell in 1811 which are worthy of mention here. The first was a planarian with a bifid tail, between the two branches of which was an erect structure supporting a head. Second, a planarian, upon the side of which incisions had been made, developed a head pointing downward in the direction of the tail. The third and fourth cases consist of two monstrosities, the description of which is quite similar to that of Fig. 11. These were two worms, each of which had another attached to it and lying at right angles to its tail.

Van Duyne[2] gives three figures which he claims prove the possibility of heteromorphosis in the planarian. One, his Fig. 3, represents a worm with two heads on the anterior part of the body, one of which points posteriorly. The second one, his Fig. 4, shows a worm whose body has been split through the tail almost to the head. Between the two tails thus produced two heads have appeared, which, when the tails are widely separated as represented in the figure, point in a posterior direction. And lastly, his Fig. 5 represents a tail pointing in an anterior direction.

Morgan[3] gives one example of apparent heteromorphosis, his Fig. 36. It shows a worm with two heads, which point

[1] "Observations and Experiments on Regeneration in Planarians," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen.* Bd. v, p. 367.

[2] "Ueber Heteromorphosis bei Planarien," Separat-Abdruck aus dem *Archiv für die ges. Physiologie.* Bd. lxiv, Taf. x.

[3] "Experimental Studies of the Regeneration of Planaria maculata," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen.* Bd. vii, p. 381.

in opposite directions when in a relaxed condition, but when expanded form an angle of about 100°.

Morgan[1] has confirmed Spallanzani's discovery of earthworms regenerating a tail in place of a head. Sections of these worms show a ventral cord extending to the new part, that no brain is present, and that the nephrostomes in the new part are turned backward towards the old part.

Loeb,[2] in his investigations to determine the cause of animal forms, produced monstrosities with hydroids in which the oral end was regenerated on the aboral end. Loeb proposed the term "heteromorphosis" for such monstrosities. Heteromorphosis not only includes the regeneration of a head in the place of a tail, but of any organ in any place where in nature one of unequal value would occur, as arms from the hips and legs from the shoulders, etc. Loeb defines heteromorphosis as "the replacement of one organ by another physiologically and morphologically different."

2. *Analysis.* — The term "heteromorphosis" thus includes the entire reversal of axial relations as well as the development of any single organ in place of another. It will be useful to distinguish these as polar heteromorphosis and heteromorphosis of single organs. Examples of the latter are found in various forms, as the regeneration of a tentacle-like organ in place of an eye in crabs, etc. Examples of polar heteromorphosis, on the other hand, with few exceptions, occur only among the Coelenterates.

Cerfontaine,[3] in his "Observations physiologiques sur l'Astroides calycularis," records the regeneration of a crown of tentacles on the base of a severed part of a polyp.

Loeb has found axial heteromorphosis to be quite common among the coelenterates and has been able to produce it in

[1] "A Confirmation of Spallanzani's Discovery of an Earthworm Regenerating a Tail in place of a Head," Abdruck aus dem *Anatomischen Anzeiger*. Bd. xv, pp. 407–410. 1899.

[2] *Untersuchungen zur physiologischen Morphologie der Thiere*. Bd. i, ii. Wurzburg, 1891.

[3] "Notes préliminaires sur l'organisation et le développement de différentes formes d'Anthrozoaides (deuxième communication)," *Bull. de l'Acad. Roy. des Sci., des Lettres et des Beaux-arts de Belgique*. No. 8, Notes v–viii. 1891.

at least the following forms: Tubularia mesembryanthemum, Aglaophemia pluma, Plumularia pinnata, Eudendrium (rasimosum ?), Sertularia (polyzonias ?).

Bickford and Driesch,[1] cited by Morgan, have also shown that in the tubularian hydroids two heads may develop on opposite ends of a piece cut from a stem, especially if the piece be short.

3. *Pseudoheteromorphosis.* — By cutting a narrow strip from any part of the body so as partly to isolate it, a posteriorly directed head may be developed by the reversal of the piece.

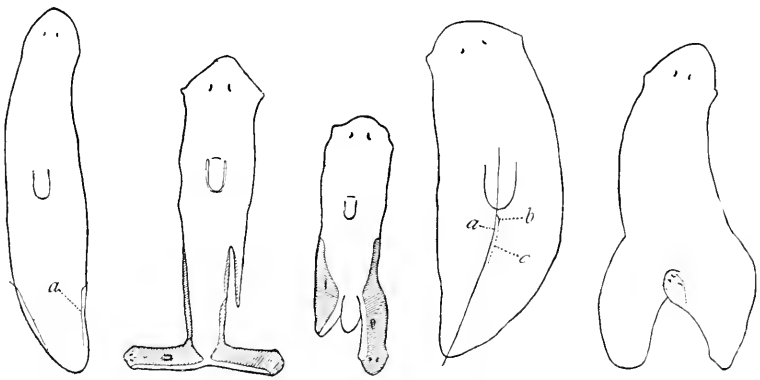

FIG. 10. FIG. 11. FIG. 12. FIG. 13. FIG. 14.

FIG. 10. — The lines *a* show the nature of the cuts which produced heads at right angles to the body.

FIG. 11. — A worm with heads lying at right angles to the main body.

FIG. 12. — Pseudoheteromorphosis.

FIG. 13. — The lines *a*, *b*, and *c* represent the cuts made to induce regeneration of heads in the tail region.

FIG. 14. — A head regenerated on one of the tails.

If by tension and growth this position becomes permanent, forms are produced which, to the casual observer, appear to be marked examples of heteromorphosis. Figs. 8, 12, 15, and 16 possess all the outward appearances of true heteromorphosis, but by the aid of Figs. 6, 10, and 13 one can readily show that there is neither the reversal of axial relations nor the development of one organ for another. Hence we do not have true heteromorphosis, but simply the swinging around of a portion

[1] "Experimental Studies of the Regeneration of Planaria maculata," Separat-Abdruck aus dem *Archiv für Entwickelungsmechanik der Organismen*. Bd. vii, p. 382.

of tissue as a whole, so as to give the anterior end a posterior direction, or pseudoheteromorphosis.

Perhaps the best example of pseudoheteromorphosis is found in Fig. 15, which was produced in the following manner. On Dec. 22, 1898, the worm was operated on by splitting its tail, as indicated by the line *a* in Fig. 13. Then a small anteriorly directed piece of tissue was partly isolated on the inner margin of the right tail *b*, which developed a head, as seen in Fig. 14, by Jan. 9, 1899.

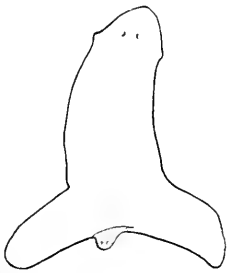

Fig. 15. — The worm of Fig. 14 in an expanded condition.

Fig. 15 represents the same worm in an expanded condition during locomotion.

Fig. 16 was produced in the same way as Fig. 15, except that the strip, which was isolated from the inner edge of the right tail, was cut longer, as indicated by the dotted line *c* in Fig. 13.

Neither Van Duyne nor Morgan gives evidence of having produced anything other than pseudoheteromorphosis.

4. *Critique of Evidence.* — In Van Duyne's first example of heteromorphosis (Fig. 3 of the plate) he figures a worm with two heads, one of which arose from the wound caused by taking a piece from its side by two cuts, a transverse one back of the right half of the head, and a longitudinal one from the inner end of the first cut to the tip of the tail.

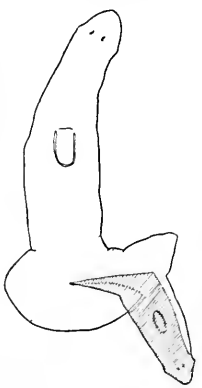

Fig. 16. — Pseudoheteromorphosis.

In order that this be an example of axial heteromorphosis it must have been regenerated from tissue which originally bore the same relation to the main axis of the worm as does the tail, *i.e.*, it must have been regenerated from tissue, the free end of which was originally posteriorly directed. The drawing does not clearly show this, but rather indicates that this head may have been regenerated on the anterior end of the newly formed tissue on the side of the worm and was forced to turn backward by the shoulder-like projection of old tissue.

Likewise in Fig. 4 of Van Duyne's plate there is no evidence that the heads may not have arisen from anteriorly directed tissue, as did the head in my Fig. 15. Fig. 5 of Van Duyne's plate gives no more evidence of being a tail than of being a partially developed head.

Morgan, in Fig. 36 of his paper, gives an example of what he considers to be axial heteromorphosis. He says: "The entire history of this piece is known, and there can be no doubt that two heads developed on opposite ends of the same cross-piece." Further he adds: "The bending of the heads to one side is due, in all probability, to the knife cutting somewhat obliquely to the long axis at the time that the piece was removed." May it not be more probable that we have here a case of the development of a head from each of the anterior corners of the piece? It is certainly reasonable to suppose this in the light of the evidence given. To determine whether this be an example of axial heteromorphosis or not, two things are necessary, *viz.*: (1) That we know the end of the piece which was originally directed anteriorly by some means other than the direction of its motion; and (2) that we know that the same end, which was the anterior end when the piece was first cut, continues to be the anterior end of the newly developed worm. Several cases were noticed where the piece, either from not having been cut squarely across or from some other cause, at first moved in a direction diagonal to its anterio-posterior axis, but afterwards, when the regenerated part developed normally, *i.e.*, in the line of the anterio-posterior axis, it again moved in a straight line. If the new tissue developed a little to one side of the anterio-posterior axis, as was sometimes the case, the piece continued to move in a diagonal direction, following the newly formed head. May not Morgan's Fig. 36 be an example involving conditions similar to these without involving axial heteromorphosis?

5. *Effect of Injury to One Part on a More or Less Different Part.* — In addition to the tendency to divide after the regeneration of new organs, referred to elsewhere, it sometimes happens that an operation on one part of the body produces an abnormality in some other part. Three interesting cases were

found where the eyes either divided, or became abnormally large and irregular in shape, and two where the pharynges developed abnormal proportions.

The first case was caused by an operation upon a planarian to produce a bud, as indicated in Fig. 6. Three times the bud divided off by fission, leaving the worm almost normal in appearance. After the third operation the eyes, which were crescentric in outline, began to deposit pigment in the concavity in irregular masses until the condition represented in Fig. 17 was produced, when the head separated from the body by fission.

The second case (Fig. 18) is that of a worm which had been operated on in a similar manner. The bud divided off and

FIG. 17.

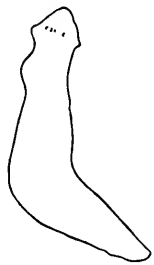

FIG. 18.

FIG. 19.

FIG. 17. — A worm in which the eyes have become abnormally large after being operated on.
FIG. 18. — A worm in which two new eyes developed after an operation upon its sides.
FIG. 19. — The dark part of the right eye divided after operation on the side of the worm.

almost immediately the eyes divided, giving four eyes. The one on the extreme left side of the head has the concavity on the right side, suggesting the possibility of its functioning as a right eye. Two others are in almost the normal position, while the fourth lies between them and a little to the left of the middle line of the head.

The third case (Fig. 19) is that of a worm which had been operated on in the posterior part of the body on the left side, producing a bud. When the bud had become half grown it divided near its anterior end. The right eye of the worm then divided in such a way as to produce two, one lying just anterior to the other. The head of this animal also separated from its body by fission soon after the division of the eye.

The two cases of abnormally developed pharynges were

found in two worms which had been split near the middle line of the body. One was split through the head back to the pharynx but not including it. After several operations two heads developed, and it was noticed that the pharynx was gradually increasing in width. This continued until the two heads were fully formed, when it had reached a size nearly twice that of the normal.

The other case was a worm whose tail had been split to the base of the pharynx. After the operation the pharynx increased continually in width until two tails were fully formed.

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ANN ARBOR, MICH., July 28, 1899.

THE STRUCTURE OF THE EYE OF SCUTIGERA (CERMATIA) FORCEPS.

JOSEPHINE HEMENWAY.

GRENACHER ('80), in his article entitled "Ueber die Augen einiger Myriapoden," described the structure of the eye of Scutigera (Cermatia araneoidea). Briefly reviewed, his account is as follows:

Externally the eye of Scutigera has the appearance of a true facet eye, consisting of one hundred of these "facets." To each facet there corresponds an ommatidium. Each ommatidium consists of a central crystalline body, surrounded by three tiers of cells; the distal tier of pigment cells, the middle and proximal tiers of retinular cells secreting on their inner edges a narrow band, the rhabdom. The crystalline body is composed of very irregular segments. These segments may be either cells or cuticular structures. In the adult eye they cannot be regarded as cells, as nuclei are not found in them, although Grenacher admits that at some time in their existence they may have been cells, later becoming modified and losing their nuclei. The possibility of their being secretion products he does not admit, as he finds no cells to which their origin could be traced. There are six to eight or nine of these segments.

The retinular cells with their rhabdoms embrace the proximal two-thirds or three-fourths of the crystalline body, the posterior portion of the retinular cells reaching to the basal membrane. Of the three tiers of cells surrounding the crystalline body, the middle tier, or outer retinula, is made up of from nine to twelve cells; the proximal tier, or inner retinula, of three to four cells. Sections through the proximal layer show that at this level the rhabdom is made up of four parts. Toward the extreme proximal end of these proximal retinular cells only three with their rhabdoms are visible in cross-

sections, the fourth having been pushed out. The nuclei of the retinular cells lie in the distal portion. The pigmentation of the eye consists partly of the pigment granules in the retinular cells and partly in the separate pigment cells. Of the latter there are three distinct groups: (1) a circle of from eight to ten large flattened cells, the outer tier of my description around the outer part of the crystalline body; (2) long, spindle-shaped pigment cells situated between the ommatidia, extending to the inner cuticula; (3) a third group, the supplementary cells of my account, is found on the posterior part of the retinula, between the retinular cells.

Grenacher also mentions the pigmentation of the optic nerve and the "inner cuticula."

Adensamer ('93), in his studies on this eye (Scutigera coleoptrata), confirms and completes Grenacher's statements. He differs in certain points.

The cornea of each ommatidium Grenacher regarded as externally convex, although there were individual differences. These differences Adensamer regards as stages in the development of the cornea.

In the adult eye frequently there were found in the crystalline body large yellowish enclosures, which had the appearance of fat drops. These are not to be confused with the nuclei for which Grenacher looked. Of the segments he found from seven to nine.

But in an individual 5 cm. long Adensamer states that he found nuclei in the crystalline body; thus he feels justified in calling the segments "cells."

As to the nerve fibers he was more successful than Grenacher, in that he saw the connection of the fiber with the outer and inner row of retinular cells. This he proved by sections. Just under the basal membrane there is a nerve connected with a muscle, which is entirely distinct from the optic nerve. Adensamer believes that this was probably mistaken by Grenacher for the real optic nerve. The latter consists of a bundle formed of the separate nerve fibers meeting proximal to the basal membrane.

Speaking of the superficial resemblance of the eye of Scutigera to that of insects and crustaceans, and the actual differ-

ences between them, Adensamer suggests calling the eye of Scutigera a "pseudo-facet" eye. Rosenstadt ('96) discusses the question as to whether the eye of Scutigera can be regarded as a true facet eye, reviewing the arguments of Grenacher and Adensamer. He also suggests a way by which an eye, as that of Scutigera, could be developed from a true facet eye.

The following work was done in the Biological Laboratory of Bryn Mawr College, under the direction of Prof. T. H. Morgan, to whom I am greatly indebted for valuable suggestions and criticism.

The species studied was Scutigera (Cermatia) forceps.

For sectioning, the best results were obtained by hardening the fresh material in corrosive acetic for fifteen minutes, then running it up through the successive grades of alcohol.

The dense pigment obscured all details, therefore a depigmenting agent, as KOH, was used (*cf.* Parker, "The Eyes in Scorpions," '87). The preparations were stained with iron-haematoxylin.

As a maceration fluid, a modification[1] of Béla Haller's fluid was used. Material left in it for a year gave excellent results. The separate ommatidia fell apart, and by gently tapping the preparation the individual cells of each ommatidium could be isolated.

By this means I have been able to make out more definitely the structure of the different component cells than have the authors mentioned above, and in some respects have been able to add some points to their results.

The eye of Scutigera forceps is nearly triangular in shape. The corneal hypodermis is faceted, one ommatidium corresponding to each facet. Each eye is composed of about two hundred individual units or ommatidia.

Fig. 1 *A* shows[2] a single ommatidium, its proximal end bordering on the inner cuticula or basal membrane.

[1] Béla Haller's mixture modified: two parts glacial acetic acid; two parts water; one part glycerine.

[2] The figures are all camera drawings: Fig. 1 *A* and *B* were drawn with a No. 7 objective; Fig. 1 *C* and *D* were drawn with an oil immersion $\frac{1}{12}$; Fig. 2 *A*, *B*, *C*, *D*, *E*, *F* were drawn with an oil immersion $\frac{1}{12}$.

Surrounding each ommatidium are elongated pigment cells, extending the entire length of the ommatidium (Fig. 1 *B*). At both distal and proximal ends these pigment cells become expanded, the pigment granules collecting in the expanded portions. At the proximal end this gives the pigmented appearance of the basal membrane, spoken of by Grenacher.

There are sixteen to eighteen of these pigment cells belonging to an individual ommatidium. The nuclei are visible without reagents, but are more clearly shown by methyl green.

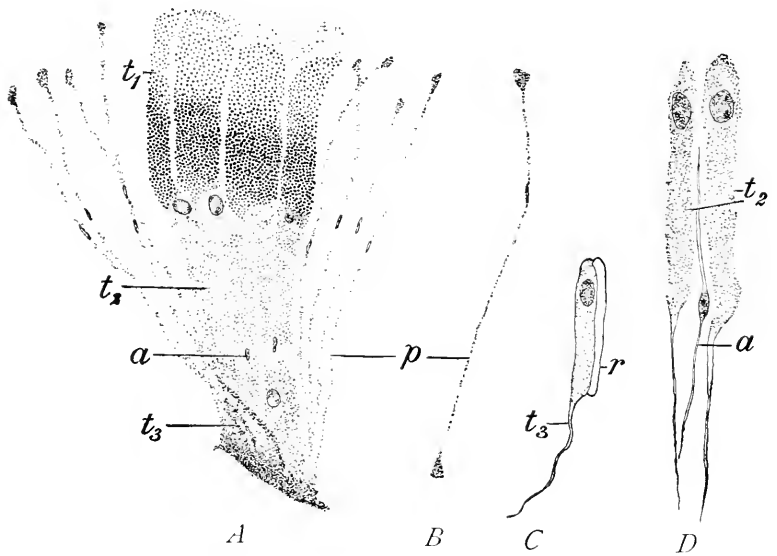

FIG. 1.

They are found at the same level as the nuclei of the middle tier of cells (Fig. 1 *A*). Each ommatidium consists of a clear, crystalline body, surrounded by three tiers of cells; the outer consisting of twelve (t_1), the middle of ten to twelve (t_2), and the inner tier of three to four cells, respectively (t_3).

The cells of the outer tier are large and flat and deeply pigmented at the proximal ends, the pigment granules being extremely large and round. The nuclei did not show in a macerated specimen, owing to the pigment.

The middle tier of cells are called by Grenacher the "outer retinular cells." They are longer and more narrow than the

cells of the outer tier, reddish in color, lacking the black pigment of the outer tier.

(Fig. 1) *D* t_2 shows two of these cells with the nuclei at the extreme distal portion. At the proximal end each cell is prolonged into an extremely fine "tail," which runs down between the cells of the inner tier and is continued through the basal membrane as a nerve fiber.

The cells of the inner tier have their proximal ends bordering upon the basal membrane. From the proximal ends fine processes continue through the basal membrane to form the nerve fibers. The cells are much broader than those of the middle tier.

Cross-sections through the different levels show the crystalline body occupying the central axis of the ommatidium, surrounded by a clear zone or rhabdom forming the inner parts of the cells of the ommatidium (Fig. 2 *B*, *r*). The clear zone is formed of the structures called by Grenacher the rhabdoms — a secretion product of the retinular cells. In macerated specimens these rhabdoms were visible upon the inner surface of each cell of the two proximal tiers (Fig. 1 *C*) and could be made to separate from the cell by tapping. The "tail," or nerve, is on the opposite side of the cell from the secreted portion. The secretions from the inner tier are thicker than from the middle tier, and in cross-sections appear roughly triangular in shape (Fig. 2 *F*). There were no nerve fibers observed for the outer tier, and it differs in this respect from the two inner tiers. In certain cases, after tapping, the outer cells unfolded, as it were, and spread out into a band. The distal ends are rounded, while the proximal ends are drawn down into a point which extends between the distal ends of the middle tier. Thus the nuclei of the middle tier are found between these points of the outer tier (Fig. 1 *A*).

The series of cross-sections (Fig. 2 *A*–*F*) are taken at the levels of the different nuclei.

I. The first section beneath the cornea is shown in Fig. 2 *A*. It represents the extreme distal portion of the ommatidia. A few large nuclei are found at this level, situated between the individual ommatidia.

II. The next figure (Fig. 2 *B*) is taken through the nuclei of the outer tier of cells, two sections intervening between *A* and *B*. These nuclei differ in shape from the round ones of the middle tier.

III. The next section (Fig. 2 *C*) shows two sets of nuclei, the larger ones (*n*) belonging to the middle tier of cells, the smaller (*p*) being the nuclei from the surrounding pigment cells (Fig. 1 *A*, *p*).

IV. Fig. 2 *D* shows a section through the nuclei of the middle tier of cells. This drawing is from the same section as *C*, but drawn at a lower level.

V. The following figure (*E*) is the fourth section after *D*. The round nuclei are from the clear cells or supplementary cells.

VI. Situated at about the same level as the nuclei shown in Fig. 2 *E*, but in the next section (Fig. 2 *F*), are the nuclei belonging to the inner tier of cells (Fig. 1 *A*, t_3).

The nuclei shown in Fig. 2 *E* belong to a group of cells lying between the two proximal tiers of cells. These cells are very different from any of the others found. They are colorless and contain no granules. Fig. 1 *D* shows two cells from the middle tier, between them one of these supplementary cells, in its natural position. The supplementary cells are extremely delicate, sending distally a fine process between the cells of the middle tier, and proximally between those of the inner tier. The nucleus is small and easily distinguished from that of a cell of the inner tier. The nuclei are found at the level of the distal ends of the inner cells. There are four supplementary cells.

The crystalline body is surrounded by the tiers of cells described above. It is composed of segments — "Grenacher's segments." These segments are cone-shaped. At the level of the nuclei of the inner tier (Fig. 2 *F*) these are not seen in cross-section, the rhabdoms, only, belonging to these cells being visible. In maceration preparations they often separate from each other at the proximal ends, while found joined at the larger distal ends.

According to Adensamer there are nuclei in these bodies

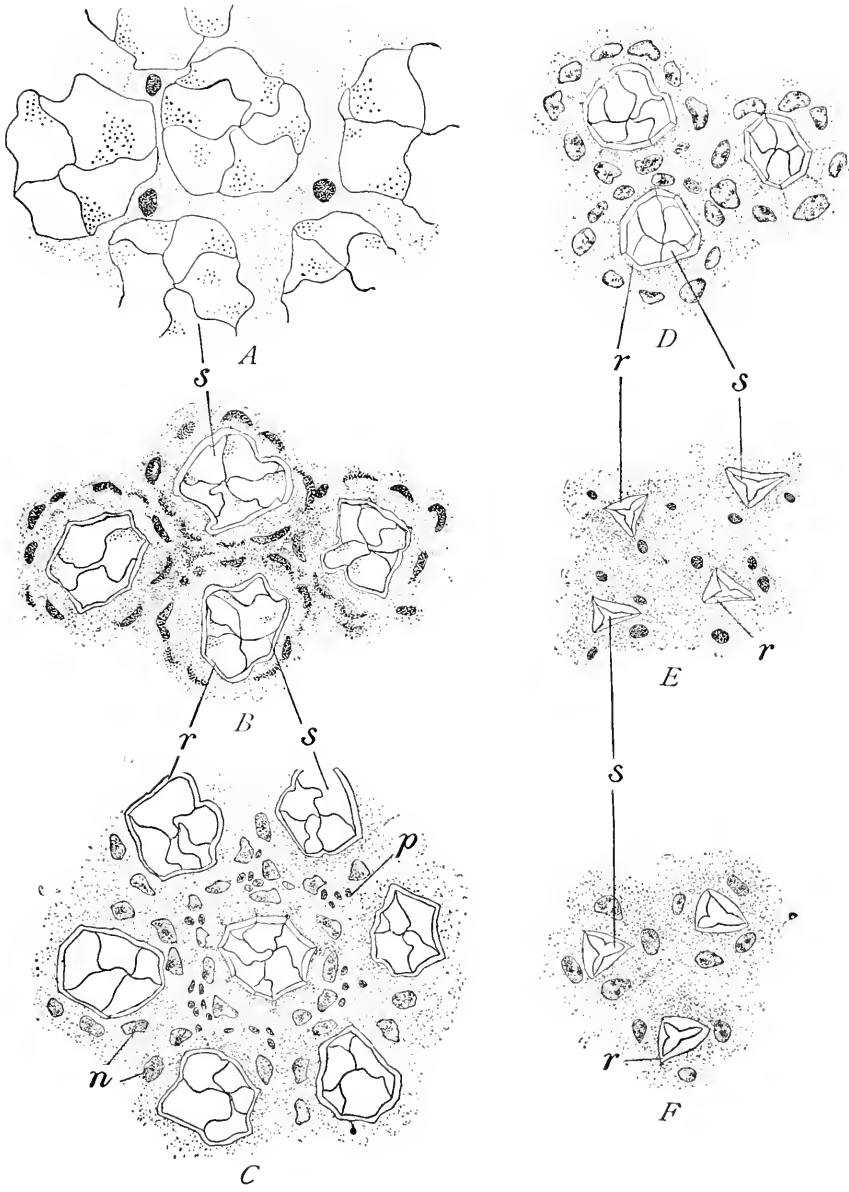

FIG. 2.

early in their existence, thus proving their cell nature. He also states that in an adult these can be vaguely seen. In no eye did I see an indication of nuclei in the segments of the crystalline body.

Cross-sections show the segments to be arranged in no regular manner. In a complete series of cross-sections one ommatidium was followed, and camera drawings at the high and low level were made of each section.

It was thus possible to trace each segment and find the number of segments and their relative position. In most ommatidia the number counted was ten to eleven, but in one ommatidium I was able to trace twelve. It must be understood that in a single section no more than six to eight appear. This can be seen by referring to Fig. 2.

SUMMARY.

The species described by Grenacher is Scutigera (Cermatia araneoidea); by Adensamer, Scutigera coleoptrata; by myself, Cermatia forceps.

The latter is the only American Scutigera.

The differences in the accounts are probably to be explained in part by the fact that the individuals studied were of different species.

(1) The number of ommatidia in each eye of Scutigera forceps is about two hundred. In Cermatia araneoidea (Grenacher) the number is given as one hundred.

(2) The crystalline body was found to be made up of ten to twelve segments, instead of six to nine. No nuclei were observed in these segments.

Each ommatidium is made up of the following cells:

(3) Elongated pigment cells surrounding each ommatidium, sixteen to eighteen in number (p, Fig. 1 *A*).

(4) An outer tier of pigment cells, embracing the distal portion of the crystalline cone, ten to twelve in number (t_1, Fig. 1 *A*).

(5) A middle tier of cells of ten to twelve (t_2, Fig. 1 *A*).

(6) An inner tier of cells situated at the proximal end of the

ommatidium, touching with their proximal ends the basal membrane. In the inner tier there are from three to four cells (t_3, Fig. 1 *A*).

The cells of (5) and (6) secrete, upon their inner surfaces, rhabdoms, and from the outer side send out a process constituting the nerve fibers.

These nerve fibers were mentioned by Adensamer, but his figures failed to show the direct connection between the fibers and the cells of the middle and inner tiers.

In macerated preparations I have been able to show this beyond doubt (Fig. 1 *C*, *D*), and in the ommatidium, before it has been separated into its component parts, have observed the passage of these fibers through the basal membrane.

The expanded proximal portions of the elongated pigment cells (Fig. 1 *B*, *p*) form the layer of pigment spoken of by Adensamer, as found on the basal membrane.

(7) Supplementary cells, four in number, are found at the same level as the cells of the inner tier. They are entirely different, and thus easily distinguished from the cells of the inner tier (*a*, Fig. 1 *D*).

(8) As shown in Fig. 2 *A* certain large nuclei were found in cross-sections at the distal part of the ommatidium. They are found only in the space between three ommatidia. They were not observed, nor the cells to which they belong, in maceration preparations.

Bryn Mawr College, April, 1900.

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BIOLOGICAL BULLETIN.

ABNORMALITIES IN THE CESTODE MONIEZIA EXPANSA. I.

IMPERFECT AND PARTIAL PROGLOTTIDS.

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In November, 1899, a large number of specimens of *Moniezia expansa*, a common parasite of the sheep, was obtained from the Union Stockyards in Chicago. Nearly every specimen exhibited one or more abnormalities in the form of the proglottids, but one specimen, some two feet in length, was found, which possessed over a hundred abnormal proglottids. This was incomplete, for in the oldest proglottids present the uterus had not yet appeared. The abnormalities in this individual are not different in kind from those found in others, but are much more abundant. Most of the cases described were selected from this specimen.

This paper, the first of a series, is devoted to a description of some of the simpler forms of abnormal proglottids. In the second paper a number of spiral anomalies will be described, and the third will include a general summary of the facts, together with some suggestions as to causes and significance.

The figures are all drawn with the aid of the camera from stained and mounted preparations. Figs. 2–6 are magnified about fifty diameters; all others about twenty. All except Figs. 7, 14, 15, 19, and 23 are taken from the single specimen mentioned above. These five figures are selected from different individuals.

Some of the figures show the dorsal side uppermost, others the ventral. The position is noted in most cases. In each figure the furrows of the lower side are drawn as broken lines. In cases where they gradually become shallower and disappear upon the surface of the proglottid, as they often do, the attempt is made to represent the general character of the line by a lighter or finer line in the figure on the upper side, and on the lower by longer spaces between the dashes composing the broken line. In the figures of abnormalities the testes are not represented. Nearly all figures show stages before the uterus appears.

The reproductive organs are represented schematically, for the exact details of structure are not essential to the object of this paper; but the position and relation of the organs is shown as exactly as possible.

Since it will be necessary to employ various terms with reference to the segments in the course of the description and discussion of the figures, it seems advisable, in order to avoid any possible confusion, to explain briefly the nomenclature employed. The terms "proglottid" and "segment" are used as synonyms; "anterior" and "posterior" possess of course the same significance as when applied to the whole animal; "transverse" is applied as referring to the direction perpendicular to the longitudinal axis of the animal, and parallel to the two flat surfaces, the ventral and dorsal; the "width" of a segment is equal to its transverse diameter; the term "longitudinal" refers to the direction parallel to the longitudinal axis of the animal and the "length" of a proglottid is equal to its longitudinal diameter. In the form under consideration the width of a proglottid is much greater than its length. The "thickness" of a segment is its dorso-ventral diameter. "Right" and "left" are used with reference to particular figures and do not always refer to right and left sides of the body. "Side" is used as referring to the region of the proglottid indicated by the preceding adjective, *e.g.*, "dorsal side," "right side," etc. The "inter-proglottidal furrow," "inter-segmental furrow" or "furrow" is the furrow or line which separates the proglottids. A "partial proglottid" is a portion of a proglottid incompletely or completely marked off by furrows. "Partial division" refers to the

incomplete separation of two proglottids or parts of proglottids, and the "partial furrow" is the furrow separating a partial proglottid from others; it may end free or may join another furrow. In many cases the furrows gradually become less and less distinctly marked and are said to become shallow as their depth is less than that of the normal furrow.

In anticipation of the summary it seems advisable to mention briefly some of the more important facts which may be gathered from the study of these abnormalities.

Taking as the basis for comparison the normal proglottid, numerous variations from this type are found. The segment may be longer or shorter than the normal, or may vary in length in different parts. The furrows bounding the segments may end at any point, leaving two or more segments partially united, or they may bend so as to run longitudinally. The furrows are evidently the expression of internal conditions, and where abnormalities in the furrows occur, the internal organs very often show abnormalities in arrangement and position which are very closely correlated with the position and development of the furrows. In brief, the position, development, and arrangement of the sexual organs are very closely correlated with the form and size of the proglottid. The organs which lie nearer the ventral side are affected chiefly by the form relations on that side, and those which lie nearer the dorsal side by the conditions there. This appears very clearly in many cases where the form relations on the two sides of the body do not correspond. Some cases appear to indicate that a certain degree of distinctness or separation, an "internal division," may exist without the appearance of distinct furrows. Between this condition and the normal, various degrees of division are indicated by shallower or deeper furrows. The various portions of the sexual organs, *e.g.*, the proximal and distal portions of the ducts, develop independently of each other *in situ*, and become connected secondarily, or in many cases remain separated. Abnormalities of the furrows are apparently due to the internal conditions in the growing regions. The abnormalities of the internal organs must be regarded as adaptations to the abnormal relations of form, size, etc., which already exist in the segment concerned.

Figure 1

Before proceeding to the description of the abnormalities a brief description of the normal anatomy of the proglottid is necessary. In this species the proglottids are always much wider than long, but the relation between width and length varies considerably both with age and with the degree of contraction. Fig. 1 is a figure, viewed from the ventral surface, of a normal proglottid at the stage when the testes are ripe, or a little later, *i.e.*, about the stage when fertilization occurs. The furrows between the proglottids are schematically represented by a single line here, as in most of the figures. As a matter of fact, the posterior edges of the surfaces of each segment lap over the

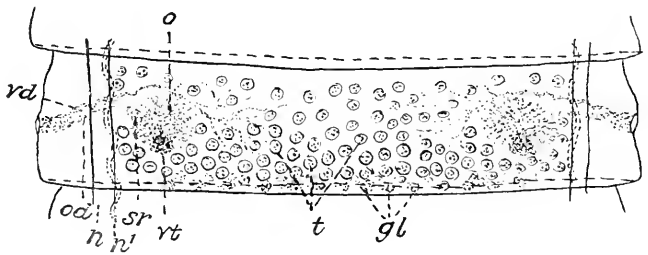

FIG. 1.

surfaces of the succeeding segment, *i.e.*, the furrow does not cut into the body perpendicularly to the surface but obliquely forward. Along the furrows on each surface, except near the edges of the segments, occur a varying number of small glands — the inter-proglottidal glands (Fig. 1, *gl.*), each of which opens by a distinct pore into the bottom of the furrow. At each side of the segment appear the two longitudinal nephridial tubes, the large ventral, *n*, and the smaller sinuous dorsal, *n'*. Transverse tubes, though visible in earlier stages, are very difficult to find later.

The terms "ventral" and "dorsal" are applied to the body of the cestode as follows: the ventral surface is the surface nearest which the ovaries and vitellaria lie, and the testes are situated near the dorsal surface.

Each proglottid possesses normally two pores lying near the middle of the two edges, but rather nearer the dorsal than the

ventral surface. The pore opens into the genital cloaca, or atrium, into which the male and female ducts also open. Following the female duct from this point, we find that it passes inward, somewhat anteriorly and dorsal to both of the nephridial tubes, then turns ventrally and posteriorly and opens into an enlarged portion, the seminal receptacle, *s.r.* Just beyond the seminal receptacle the ovary, *o.*, appears in the form of a rosette. The ovary consists of a mass of radiating branched tubules and is somewhat flattened in the same plane as the proglottid. The vitellarium, *vt.*, lies somewhat ventral and usually posterior to the ovary. At the stage shown in the figure the uterus does not appear, but in later stages it consists of an anastomosing set of tubes, which, after they receive the embryos, enlarge so as to fill nearly the whole proglottid. From this description it is seen that, although the ovary and vitellarium lie ventrally in the proglottid, the outer or distal portion of the oviduct lies dorsally. This point is important with regard to the relation of these organs in abnormal segments. Following the male duct from the atrium we find its terminal portion modified to form the cirrus. Beyond this the vas deferens, *v.d.*, follows the direction of the oviduct anterior to it, but is much coiled. It also runs dorsal to the nephridial tubes, but does not bend ventrally, as does the oviduct. Anterior to the middle region of the ovary it bends posteriorly and extends dorsal to the ovary toward the middle of the segment. Beyond the bend it begins to branch and soon breaks up into the fine tubules which connect with the testes. These latter, *t.*, lie scattered through the proglottid on the dorsal side, but are more numerous in the posterior half. They do not occur lateral to the nephridial tubes. Thus all of the male organs are nearer to the dorsal than to the ventral surface.

Description of the Abnormalities.

All the figures except 7, 14, 15, 19, and 23 are taken from a single chain. These five are taken from as many different chains, and on comparing them with the other figures it becomes evident that the abnormalities found so abundantly in the one specimen do occur, though less frequently, in very many individuals.

The figures all represent cases of partial division of segments, together with the accompanying abnormalities in the form and position of the genital organs. A classification is difficult, and, I think, unnecessary. In general the more simple and regular cases are discussed first, the complex ones later. Cases resembling each other are grouped together as far as possible.

Figs. 2–6 are taken from various points near the anterior end of the chain. They all show stages before the appearance of the genital organs. These cases, although differing somewhat in form, are grouped together here as furnishing some evidence for the conclusion that the abnormalities of this kind appear at the time the furrows are formed and are not due to a later division of proglottids. They are certainly as common in these earlier stages as in later ones. Following these are grouped the cases in which the furrows on the two surfaces correspond closely. These include Figs. 7–15, as well as Figs. 2, 3, 5, and 6 of the preceding group. In Figs. 7–15 the genital organs, though they may be abnormal in position, are nearly always fully developed. The remaining figures, 16–23, show cases which are more complex and in which the furrows on the two surfaces do not usually correspond. Moreover, in these cases some of the genital organs are commonly rudimentary or abnormally developed.

Figure 2.

This figure was taken from the extreme anterior end of the body. The furrows between the proglottids have become fairly distinct. As the dorsal and ventral furrows correspond exactly in position, only one surface is represented in the figure. Four abnormal segments, *a*, *b*, *c*, and *d*, are present. The segments *a* and *b* are both examples of partial division, one upon the right side, the other on the left. Here the partial furrows end free, not far from the middle of the segment in which they occur, so that the proglottid appears as if partially split from one edge. The two cases at the anterior

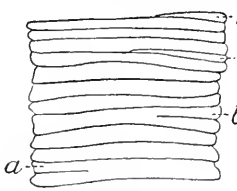

FIG. 2.

end, *c* and *d*, consist of partial segments on the right side. The separation of these is complete on both sides of the body.

Figure 3.

In this case two proglottids are incompletely separated on the upper side, because the furrow on the right side is slightly anterior to that on the left. The two parts of the furrow overlap slightly, *i.e.*, the left part extends past the inner end of the right part, and each ends free. On the lower side the furrow at the right bends anteriorly and meets the complete furrow anterior to it, thus marking off completely the small partial segment. The longer partial furrows correspond exactly on the two surfaces. Apparently the right and left portions of the furrows have been formed independently and have failed to meet.

FIG. 3.

Figure 4.

In the segment *a* this figure shows a case where the segment is of less than normal length at the left edge, and where, moreover, the bounding furrows on the lower surface do not extend to the edge but bend so as to meet on the surface of the segment a short distance from the edge.

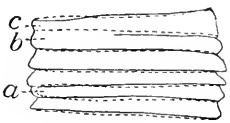

FIG. 4.

In *b* and *c* a rather simple case of partial division is represented. The partial furrow on the upper surface extends from the right edge to a point near the middle of the segment and there ends. At the left there is no furrow on the upper surface corresponding to this one, so the whole left half appears undivided. On the lower surface, however, the furrow between *b* and *c* is normal, extending across the whole body, meeting the upper furrow at the right edge and ending in a slight indentation on the left edge. At the right *c* is about twice as long as *b*, but at the left *b* is much the longer of the two. This difference is due to the fact that the furrows anterior to *c* are somewhat oblique.

Figure 5.

In this figure two variations from the normal form occur, both cases of incomplete separation or partial division. The partial segment *a* is completely separated on the upper surface from the segment in front, and its inner end is rounded, but on the lower surface the furrow between the two ends free, so that the separation is incomplete here. The segments *b* and *c* are incompletely separated by four distinct partial furrows, all of which, however, lie in the same transverse plane and must be regarded as portions of a single furrow. The largest portion is at the left side, extending to the middle of the body on each surface and of normal depth throughout. To the right of the middle a short partial furrow appears on each surface, the two being equal in length and in corresponding positions. At the right edge is a very short partial furrow marking off the two segments at the edge, but extending only a very short distance on either surface. The length on the two opposite surfaces of all the partial furrows, and especially of the two short entirely unconnected parts, is a point of interest. It is quite commonly, though by no means universally, the case that partial furrows, when they occur on the two surfaces, are of the same length on both.

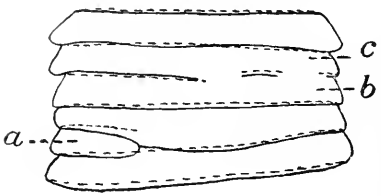

FIG. 5.

Figure 6.

At the stage shown here the inter-proglottidal glands have begun to appear in the furrows between the segments. This case shows a rather unusual form of partial proglottid. The part *a* is completely marked off on both dorsal and ventral sides from the rest of the proglottid by the transverse furrow between *a* and *c*, and by the nearly longitudinal furrow between *a* and *b*, thus forming a small, distinct, partial proglottid. The transverse furrow extends somewhat beyond the point where the longitudinal line joins it, thus partially separating a small portion, *b*, from

the remainder of the proglottid. At *d* a triangular depression appears in consequence of the fact that the contours of the portions *a*, *b*, and *c* are somewhat rounded at this point where all three meet. The same conditions are present in some degree on the lower surface also, so that the thickness of the body at *d* is very slight. Inter-proglottidal glands appear just anterior to the extra transverse furrow, thus showing the same relation to it as to the normal complete furrow. This is usually the case, provided the abnormal furrow attains a certain degree of depth.

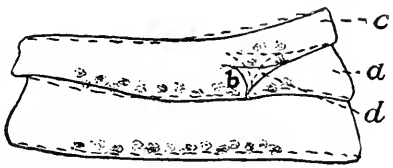

FIG. 6.

Figure 7.

This is a case of partial division seen from the ventral side. The segment is undivided at the left, and one genital mass appears. To the right of the middle, however, a short partial furrow appears on each surface, the two corresponding closely in position. The right edge shows clearly a division into two segments, and a very short furrow extends from it on to the ventral surface. In accordance with these indications of division in the right half two genital masses appear.

The fact that the two partial furrows correspond so closely on the two surfaces indicates that they are distinctly the result of internal conditions. Judging from the existence of the two genital masses and the short furrow at the right edge, it appears probable that division or separation exists in a certain degree between the two regions, even where the actual furrows do not appear. Many other cases support this view. It would appear that the individuality of the segment must attain a certain degree of development in order to cause the formation of furrows, and that, where only partial furrows exist, the division may be in many cases more complete than the furrows indicate.

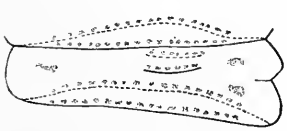
FIG. 7.

The short furrows on the two surfaces bear inter-proglottidal glands like the complete furrows.

Figure 8.

This case, though at a later stage of development than Fig. 7, resembles it. Two partial furrows appear, one on the dorsal, the other on the ventral surface, corresponding exactly in position and length, but entirely unconnected. The exact correspondence in position and length of these two entirely unconnected furrows indicates very clearly, as does the similar condition in Fig. 7, that the position of the furrows is determined by internal conditions, for it is difficult to understand how two perfectly similar partial furrows could arise on opposite surfaces of the body except as the expression of certain internal form-producing conditions.

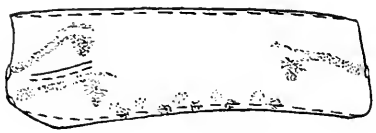

FIG. 8.

The genital organs are duplicated on the left side, but the two pores are approximated. The individuality of the two portions is apparently not sufficient to give rise to furrows at the edge, so that pores tend to appear near the middle of the edge. But the furrows extend almost to the edge, and the existence of two pores is undoubtedly the result of this position. The right side shows no trace of duplication.

Figure 9.

This figure shows three cases of partial division, and in all the partial furrows end free and correspond on the two surfaces. The partial furrows between *a* and *b* are most nearly complete, extending past the middle of the body. Between *c* and *d* they are shorter, and between *e* and *f* still shorter. In each case the two partial segments are longer than the corresponding single segment at the opposite edge, consequently oblique furrows appear between the three sets, but,

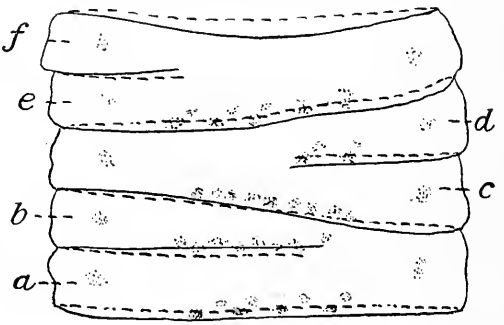

FIG. 9.

owing to the alternation in position of the partially divided regions, the length of the right and left edges of the whole group is the same, *i.e.*, the abnormality in form of each segment compensates for that of the others. Each partial proglottid possesses its own genital mass, so that there are five on the left side of the group and four on the right. All partial furrows that are long enough, *i.e.*, all except that between *c* and *f*, show interproglottidal glands, and all are of normal depth and distinctness. The decreasing length of the partial furrows from the posterior to the anterior set is noticeable, but whether it possesses any special significance or not is not clear.

Figure 10.

Four cases of partial division of proglottids occur here, three on the left and one on the right (*a*, *b*, *c*, *d*). In each case the partial furrows on the two surfaces correspond almost perfectly in position and length and end free, not far from the middle of the body. The relations at the edges do not differ from the normal except in the case of *b* at the right. This proglottid is partially divided at the left, but the undivided portion to the right is as long as the two partial proglottids at the left, though no furrows appear. The complete genital mass *g* appears at the normal distance from the furrows bounding the segment posteriorly, and a partial second set of organs, *e*, *f*, appears in the anterior region, consisting of the inner portion of the vas deferens, *e*, two small groups of cells just posterior to it, which probably represent the inner portion of the oviduct or the ovary, and entirely unconnected with these at the right edge a pore with

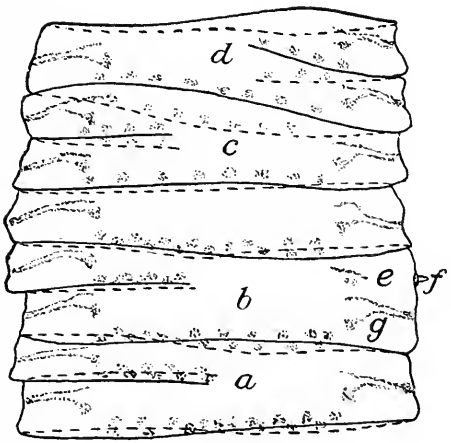

FIG. 10.

protruded cirrus, *f*, which has probably been forced out through the pore by the pressure during fixation. Here then is a complete set of genital organs and a second partial set occurring without any furrows between them. This condition is rare. I have found only one other similar case.

This appears to be a duplication of genital organs in a proglottid which is morphologically single, at least in its right half. I believe, however, that this case is simply another example of the fact that a certain degree of individuality may exist without the appearance of furrows, but may still be quite sufficient to lead to the partial formation of genital organs. The fact that the proglottid is divided on the left side into two parts by partial furrows of normal depth affords additional evidence for this view. It is evident that the causes leading to the formation of genital organs at *e* and *f* is much less efficient than normally, for the organs are extremely rudimentary and can never function in the normal manner.

The presence of furrows on the surface is, in general, simply the morphological expression of certain internal conditions. These relations differ in degree in different species, and, as is evident from the variations discussed in this paper, in this species also. This being the case, the logical conclusion seems to be that a certain degree of isolation or individuality may exist without the appearance of furrows on the surface.

In this rudimentary and incomplete set of organs, *e* and *f*, it is seen that the two parts, *e* and *f*, arise independently of each other. The pore and cirrus are absolutely unconnected with the inner portions of the ducts which are present. These facts show that the proximal and distal portions of the genital organs arise independently *in situ*, in, or as nearly as possible in, the position which is normal for each.

The cells of the incomplete set show the same degree of differentiation and the same reaction to the stain as the corresponding regions of the complete set, *g*. It seems probable, therefore, that both sets were formed at the same time. The differences between the two sets consist in the entire absence from the one of certain parts present in the other. As will appear below, a segment of less than normal length usually possesses only partial

genital organs. Here no actual furrows are present, but the relative positions of the two sets of organs, *g* and *e f*, indicate that the set *g* corresponds to a longer portion of *b* than does the set *e f*.

Inter-proglottidal glands appear in all of the partial furrows.

Figure 11.

This figure, representing a case of partial division, shows very distinctly an almost complete gradation in individuality from the right to the left, as indicated by the arrangement of the organs. At the right the partial furrows separate the segments in a normal manner, but the posterior segment is the shorter. Correspond-

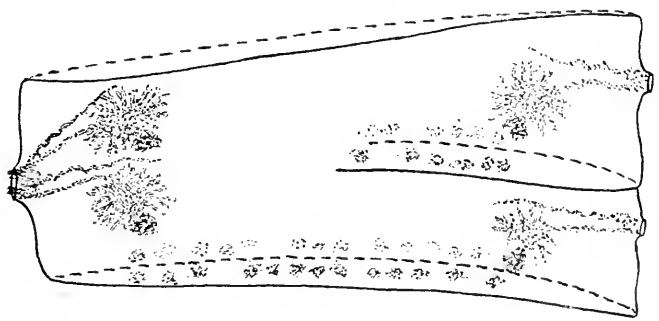

FIG. 11.

ing to the position of the furrows, two complete sets of organs appear on this side, but the posterior set, especially the ovary, is smaller and less fully developed than the anterior.

The partial furrows end, however, near the middle of the body, leaving the left half apparently undivided, and the left edge is considerably shorter than the right. That the two segments possess a certain degree of individuality beyond the region where the furrows end is indicated by the presence of two complete sets of organs and ducts, which are, however, closely approximated and open through a single pore situated at the middle of the undivided edge. Even the terminal portions of the two sets of ducts are distinct and two cirri are present. To judge from the arrangement of the organs it appears that from right to left the segments are less and less completely separated, until at the left edge the

conditions are nearly those of a single normal segment, so that only a single pore appears.

Inter-proglottidal glands lie in the partial furrows on each surface.

Figure 12.

The figure, a view from dorsal surface, shows three segments which are all incompletely separated at the right side. At the left the separation is complete, the furrows appear normal, and the genital organs in process of formation are normal in position and form. On the right the furrows separating the segments *a* and *b* end at *d* and *e*, before reaching the edge, the furrow on the ventral side becoming shallow and rather irregular in its course (*e*) but extending almost to the edge, while the dorsal furrow ends more abruptly at a greater distance from the edge (*d*). The furrows between the segments *b* and *c* do not reach the right edge, but end rather abruptly near it at *f*, the points of termination on the two surfaces of the body being about equidistant from the edge. Thus the whole right edge shows no traces of division into separate segments, but nevertheless possesses three genital pores, two of which are near together. The ovaries and vitellaria and the inner ends of the vasa deferentia at the right of *a* and *b* are normally situated with regard to the furrows, for at this distance from the edge the relations are practically those of two normally distinct proglottids. As we approach the right edge, however, the dorsal furrow, *d*, ends abruptly at some distance from the edge, while the ventral furrow, *e*, becomes more shallow and finally disappears near the edge. The terminal portions of the ducts lying nearer the dorsal surface are affected in greater degree by the relations on the dorsal surface, and we find here that as the ducts approach the edge they also approach each other, the approximation being almost wholly due to the abnormal direction of the ducts of the set *b'*. The organs at *a'* lie in the normal position, but those at *b'* lie

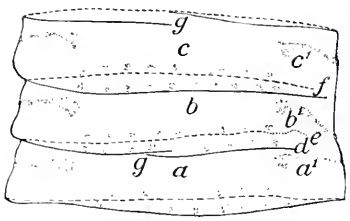

FIG. 12.

obliquely in their segment, the ducts extending outward and posteriorly toward the pore; but these positions are, I believe, due to the relations of the segments to each other. The fact must be recognized that in segments of normal length a complete set of organs capable of functioning tends to form, however abnormal its position; *i.e.*, the parts are formed independently and tend to unite in the normal manner. In this case the proximal portions of the organs *a'* and *b'* are formed in their normal position with respect to the furrows bounding the segment ventrally. The edge of *a b* shows no dividing furrow, so that it might be expected that a pore would appear at its middle. The furrows *d* and *e* approach near the edge, however, and the existence of a certain degree of "internal division" at the edge is probable. Thus two pores are formed instead of one, but are separated by less than the normal distance between pores of two successive segments. Apparently the degree of separation between the two segments at the edge is only slight, so that the edge is more or less like that of a single segment, and the middle region is the pore-forming region. But the two segments are sufficiently independent to give rise to two pores instead of one common to both; and these two pores, it will be noticed, are equidistant from the middle of the undivided edge of *a b*. But the pore in *b* is far posterior to the ovary, etc., and in order that the two may be connected the ducts must extend obliquely, as they do. In *a*, on the other hand, the pore is directly lateral to the proximal portions, and thus the ducts are horizontal.

The furrows between *b* and *c* extend almost to the edge, so that conditions here approach very closely to the normal. The organs *c'* in *c* are normally situated as if the furrow *f* were complete.

Two of the furrows on the dorsal surface are interrupted (*g g*) and the two parts overlap slightly in each case.

Figure 13.

The variation from the normal form shown here is almost identical with that shown in Fig. 12, *a* and *b*, except that here the two partial furrows bend anteriorly at the right. Both become

shallow and indistinct and terminate on the surface near the right edge. As in Fig. 12, *a* and *b*, two complete sets of genital organs appear on the right side, the posterior set being normal and the anterior set situated somewhat obliquely, with the pore near that of the posterior set. The positions of the two sets of organs are undoubtedly the result of conditions similar to those in Fig. 12, *a* and *b*, and are to be explained in the same way.

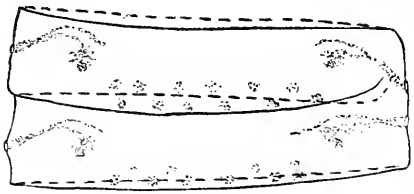

FIG. 13.

It is noticeable that the curve at the right ends of the furrows appears to have no significance as regards the position of the organs, which are situated as they would be if the furrows ended without bending forward. The furrows become very slight here, being little more than wrinkles on the surface.

Figure 14.

Two cases of partial division, *a b* and *c d*, are shown in this figure, viewed from the ventral surface. The partial furrows on the two surfaces correspond in both cases. Between *a* and *b* they extend from the left edge to a point just beyond the middle of the body, thus leaving almost the right half undivided, and, corresponding to the partial division, one set of organs is found at the right, while two appear at the left. The division between *c* and *d* is more complete, extending from the left edge over about three-quarters of the width of the body, and in this case, although the right edge itself shows no furrow, two sets of organs occur at the right as well as at the left, but their pores are much

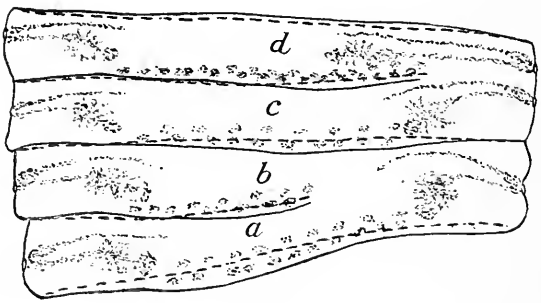

FIG. 14.

nearer together than at the left, where the separation of the segments is complete and normal. It appears from the arrangement of the organs at the right that the two segments *c* and *d* do preserve a certain degree of individuality in the region beyond the end of the partial furrows, for if this were not the case we should expect to find only one pore instead of two, a condition which does frequently occur. The position of the ovary and vitellarium at the right of *d* is peculiar. The ducts, instead of bending posteriorly, extend straight inward, and the ovary lies nearer the middle of the segment than the others. This position is apparently due to the form relations here. The distal portions of the two sets of organs at the right of *c* and *d* are approximated, but the partial furrows between *c* and *d* extend to the region of the ovaries, and *d* is slightly shorter in this region than *c*, so that the ovary and vitellarium in *d* take the position in which they can attain most nearly their normal development.

Inter-proglottidal glands occur in the partial furrows as well as in those which are complete.

Figure 15.

This figure shows a case of partial division in which the partial furrows are nearly complete. The segments are rather old, the ovaries and ducts being in process of degeneration and the uterus containing embryos (not drawn in figure).

At the left side the segments are normally bounded, and the genital organs are apparently normal. At the right the partial

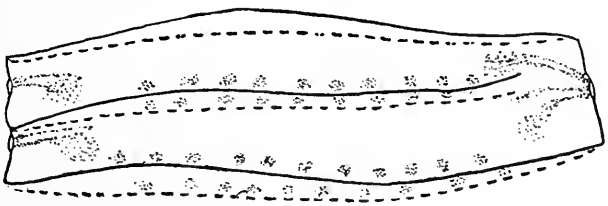

Fig. 15.

furrows end before reaching the edge, and two sets of organs occur, opening into a common pore. The partial furrows extend so nearly to the edge that in the ovarian region the two segments

appear almost normally separated, and accordingly two sets of organs appear. The edge, however, is undivided and shorter than the combined length of the two segments at the left, and only a single pore is formed, into which both sets open. This case shows much the same gradation from complete division to almost complete union, as is found in Fig. 11, but here the gradation occurs within a much shorter distance, for the furrows are nearly complete, while in Fig. 11 they extend only halfway across the body.

Figure 16.

The figure represents a peculiar case of partial division seen from the dorsal side. The two segments are completely separated at the left by partial furrows which extend to the middle on each surface. Corresponding to this separation we find two complete sets of genital organs. On the right the two portions are separated dorsally by a very shallow furrow which is interrupted at several points. This furrow passes the right edge and extends for a very short distance on the ventral surface, leaving all the rest of the right half of the ventral surface undivided. Corresponding to this incomplete separation we find abnormalities in the genital organs. There is one complete set of organs (a') in the posterior segment, and portions of a second set (b') in the anterior segment.

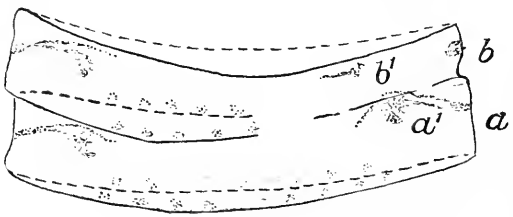

FIG. 16.

The ovary, vitellarium, and inner end of the vas deferens of a' lie nearly in the middle of the undivided ventral side, almost directly beneath the shallow interrupted furrow on the dorsal surface, thus indicating that their position is more directly affected by the conditions of the surface to which they are nearest, *viz.*, the ventral. The pore and atrium, on the other hand, appear on the edge of a, nearer the anterior than the posterior end. The partial furrow on the dorsal surface and the right edge is very slight, *i.e.*, the two partial segments, though

separated to a certain degree on this side, are still much less distinct than normal segments, and the pores and terminal portions of the ducts of *a'* are therefore found in a position only a little posterior to that which they would occupy if *a* and *b* were not separated at all.

The partial segment *b*, as marked off by the slight and interrupted dorsal furrow, is narrower than *a*. The complete set of organs, *a'*, lies nearly in the middle of *a b*, but since the two segments are sufficiently distinct dorsally for the formation of a slight furrow, there is a certain tendency for another set of those organs which lie near the dorsal surface to form in *b*, as is indicated by the presence of a pore with atrium and cirrus at the edge, and the inner portion of the vas deferens at *b'*. These parts are wholly unconnected, and there is no trace of female organs. The failure to develop a complete vas deferens is probably due to the fact that the segment *b*, as bounded dorsally, is of less than normal length and imperfectly separated from *a*. The parts of the male organs which do appear are identical with those which we find in Fig. 10, *b*, but in that case there is a trace of female organs also. These two cases are examples of a condition often found in short, imperfectly separated segments, *viz.*, the development of the innermost and outermost portions of the organs without connection. It appears as if the region of the pore and the inner portions of the ducts represent, as it were, the places of least resistance with respect to the formation of the genital organs, so that segments which are not sufficiently normal to give rise to a complete functional set of organs may form these two parts, but not the ducts connecting them.

The complete absence of female organs at the right of *b* shows very clearly that the formation of the ovary and vitellarium is connected with the conditions on the ventral side of the body, and the formation of the vas deferens with conditions on the dorsal side.

The shallow dorsal interrupted furrow at the right is without inter-proglottidal glands, probably because of its slight development.

Figure 17.

The figure represents two partially separated segments seen from the dorsal surface. At the right the division is complete and the genital organs are normal.

The ventral furrow extends without interruption about three-quarters across the ventral surface, but is somewhat irregular in its course. The dorsal furrow is interrupted at two points, once just to the right of the middle and again near the left side, leaving a short portion, *c*, entirely separated from the rest. This portion does not reach the left edge, but turns anteriorly near it and ends abruptly. The ventral furrow shows no portion corresponding to this portion, *c*, consequently the segments are visibly separated only on the dorsal surface in this region. The abnormal relations of the furrows are accompanied by abnormal conditions in the genital organs. The case is somewhat similar to the one appearing in Fig. 16, and confirms the conclusions reached in the discussion of that case. The posterior portion, *a*, is longer than *b* and possesses a normal set of organs normally situated, while in *b* there is a complete vas deferens and pore, but no trace of ovary, vitellarium, or oviduct. Analysis shows a very close relation between the organs and furrows. The case is very similar to Fig. 16, but presents some differences. The partial furrow *c* is dorsal, but is deeper than the furrow in Fig. 16; *i.e.*, the division between *a* and *b* is a little more complete here than there, and the ovary and vitellarium of *a* lie further posteriorly. A second set of female organs does not appear, probably because the region *b* is not separated from *a* on the ventral side and is considerably shorter than *a*, so that the single ovary and vitellarium serves for the whole length of *a b*. On the dorsal surface the partial furrow *c* shows that different relations exist, and here in the shorter portion, *b*, there is formed a complete vas deferens and pore. The pores in *a* and *b* are

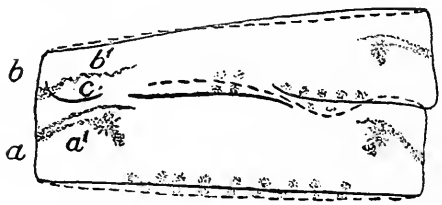

FIG. 17.

approximated, this being apparently due to the fact that the division is incomplete and the furrow *c* does not reach the extreme edge. Comparison of this figure with Fig. 16 is very instructive. The relations of the furrows at the left of Fig. 17 are almost the same as at the right of Fig. 16, the chief visible differences being that in Fig. 16 the furrow is shallower, but passes over the edge, while in Fig. 17 it is of normal depth but does not extend to the edge. In both cases the corresponding portions of the ventral surfaces are without furrows. As regards the genital organs in the shorter anterior portion *b* in the two cases, we find in Fig. 16, where the dorsal furrow is shallow, only the inner portion of the vas deferens and the pore appear, the two being entirely unconnected, while in Fig. 17, where the dorsal furrow is deeper and thus more nearly normal, a complete vas deferens is formed connected with its pore. Moreover, in Fig. 17 the furrow does not reach the edge, and the pore in it is situated somewhat posteriorly, while in Fig 16, where the furrow passes the edge, the pore is in the middle of the edge of *b*. In neither case does the region *b* show any trace of female organs. The conclusions regarding the causes of the conditions in Fig. 16 apply with equal force here. To my mind these two cases afford ample basis for the views expressed in this paper, but these are supported and confirmed by a mass of evidence from the other abnormalities discussed here, so that the conclusions reached become not only probable, but, I believe, incontestable.

Figure 18.

In this case a small partial segment is completely marked off by very slight furrows, and the anterior furrows show a very abrupt bend where the partial segment ends. In the complete segment lying just posterior the genital organs are normal, but in the small partial segment nothing but two small groups of cells appear, and it is impossible to determine just what portion of the organs they represent. The pore is entirely absent.

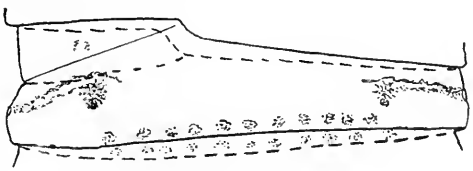

FIG. 18.

Figure 19.

In these segments the ovaries and ducts are degenerating, and the embryos are in the uterus (not shown in figure). The two segments seen from the ventral surface are incompletely separated ventrally by a partial furrow which does not reach the left edge. Dorsally the furrow between the two is complete. At the right the segments and genital organs are normal. At the left *a* is longer than *b* and is separated from it only dorsally. In *a* a complete set of organs appears, but situated somewhat farther anteriorly than the normal position, *i.e.*, approaching

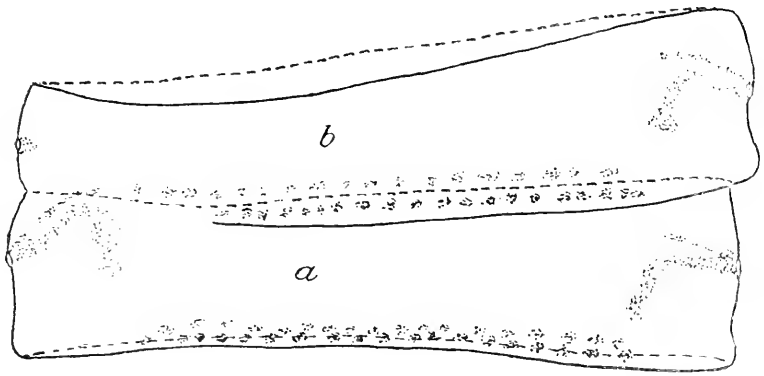

FIG. 19.

the middle of the undivided region of *a b*. The dorsal boundary between *a* and *b* is normal at the left, and the edge is divided, and in *a* we find a pore almost normally situated with respect to the form of the dorsal surface. In the shorter segment *b* the only indication of genital organs at the left is a pore, but this is placed nearly in the middle of the edge of *b*, *i.e.*, almost normally with respect to the dorsal boundaries. The fact that no other organs appear here is doubtless due to the shortness of this portion of the segment *b* and to its imperfect separation from *a*. As seen in Figs. 10, *b*, 16, 17, and 18, imperfectly separated segments of less than normal length usually possess more or less rudimentary organs. As noted, the two pores at the left of *a* and *b* are not quite in their normal positions, *i.e.*, they are separated by less than the normal distance, as is evident from a

comparison with the pores at the right. This approximation of the pores is evidently due to the incomplete separation of the two segments, which, though separated dorsally, are united ventrally. Thus, while the existence of the pores seems to be determined by the relations upon the dorsal surface, their position may be affected in some slight degree by the relations on the ventral surface.

Figure 20.

The series of abnormalities shown here is rather complex and may be considered most conveniently segment by segment. The ventral surface is uppermost.

The segment *a* is partially divided on the left side by a furrow which extends from a point on the ventral surface very near the edge around the edge to the dorsal surface, and for a short distance on the dorsal surface, where it ends free. The degree of separation is sufficient to cause the appearance of two distinct and complete sets of genital organs. At the edge the division is complete, and accordingly the pores lie in practically their normal positions on each side of it. The division, as indicated by the furrow, extends only a short distance on either surface, but farther on the dorsal than on the ventral surface, and the arrangement of the ducts, ovaries, etc., is in accord with these relations. The two ovaries, etc., are quite closely approximated, but the ducts diverge, thus indicating that the division becomes more complete with the approach of the edge. This case, like Fig. 10, *b* and *c*, illustrates, though in a less degree, the apparent existence of a certain degree of separation in regions where the furrows do not appear. Thus there is no furrow on either side immediately between the ovaries, yet two sets appear. That the division is more complete dorsally than ventrally is shown by the fact that the dorsal furrow is longer than the ventral, and the position of the genital organs accords with this fact as shown above. At the right *a* shows no trace of division, and a single normal set of organs is present.

The segments *b* and *c* are best considered together. At the right, before reaching the edge, both the dorsal and ventral furrows separating *b* and *c* bend anteriorly and become very slight,

being mere wrinkles on the surface. The ventral furrow can be traced to the anterior boundary of *c*, where it ends very near the edge, while the dorsal furrow ends free about midway of the segment. Thus the segment *c*, as bounded by the very shallow curved furrows, does not reach the right edge of the body at all on the ventral surface, and dorsally extends to the edge only anterior to the end of the curved furrow. The portion forming the edge is not separated from *b*. At the left the ventral furrow between *b* and *c* reaches the edge normally, but ends there, for the dorsal furrow, instead of extending to the edge and meeting the ventral, bends forward like the right ends of the furrows and becomes like them very shallow, a mere wrinkle, which is visible to the anterior end of the segment. Thus the portion forming the left edge in the region of *c* is connected on the ventral surface with *c*, but dorsally only with *b*, *i.e.*, there is a short spiral here. This case shows how a spiral may arise by the bending forward of one of the furrows to meet the next in front, instead of uniting with its fellow on the opposite surface. In nearly every case of spiral variation this bend occurs as it does here near the edge, though in many cases the furrow remains of normal depth. This case then is what may be called an incipient spiral modification.

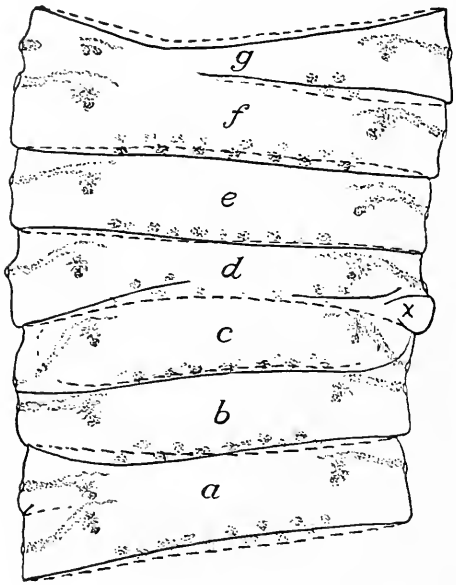

Fig. 20.

The spiral does not appear between *c* and *b* at the right, simply because both furrows bend forward, though the furrow does not completely separate the two segments, but ends free. The furrows anterior to *c* must be considered briefly before turning to the discussion of the genital organs of *b* and *c*. The dorsal

furrow is complete and takes a slightly curved course, but the ventral is divided into three parts. At the left one portion extends from the edge obliquely inward and anteriorly to a point near the middle, where it ends. The second portion lies on the right side, is almost transverse, and extends nearly to the right edge, overlapping with the third portion which reaches the edge at a point anterior to the corresponding dorsal furrow. Upon the edge it turns posteriorly and passes backward to the point where the dorsal furrow reaches the edge, and there it turns inward again, extends for a short distance, and terminates freely, thus almost surrounding a small region on the ventral surface at *x*. Notwithstanding these irregularities the furrows between *c* and *d* approximate to the normal conditions, but the ventral furrow is a little anterior to the dorsal, except in the short portion posterior to *x*. At the right relations are normal.

Returning now to the genital organs in the segments *b* and *c*, we find in each segment a complete set on each side. Considering first the organs in the left side of *b* and *c*, it is seen that in *b* the inner portions are normally placed, but the pore lies rather more anteriorly than its normal position. As noted above, there is a short spiral here owing to the course of the dorsal furrow in *c*, and the edge corresponding to *c* is not separated dorsally from *b*. This accounts for the position of the pore in *b*; *i.e.*, the organs in *c* are situated very much as they would be if there were no dorsal furrow at all between *b* and *c* in this region. The only indication of division on the dorsal surface in the region of the ducts is the very slight furrow curving forward. This seems not to affect the course of the ducts at all, for they cross it at right angles to reach the edge. The extreme posterior position of the pore in *c*, *i.e.*, its approximation to that of *b*, is evidently due to the same causes as the displacement of the pore in *b*, *viz.*, the absence of dorsal division in this region.

At the right in *b* and *c* somewhat similar conditions exist. The positions of the inner portions of the organs are about normal. As regards ducts and pores on the right, there is the same approximation as on the left. This end of the dorsal furrow in *c* is incomplete, ending, after bending forward, free on the surface just dorsal to the middle region of the ducts, and the ventral fur-

row also bends forward. The ducts in *c*, however, are situated as if the curved portions of the furrows were not present; that is, as if the furrows, especially the dorsal, ended about where they begin to bend.

The right edge corresponding to *b* and *c* is undivided, and the pores are accordingly approximated as on the left side. The separation of the two segments is normal up to within a short distance of the edge, and thus probably determines the existence of two separate pores, instead of the union of the two sets of organs in one.

The significance of the curved ends of the furrows in *c* requires a brief consideration. As mentioned above, they are very slight, being mere wrinkles, and though they are continuous with the normal inter-proglottidal furrows, they are not like these in appearance. The position of the genital organs does not appear to bear any direct relation to them, for the ducts cross them to reach the edge. Undoubtedly the slight development of these curved ends indicates a very incomplete separation of the parts which they bound, and, as will appear later, it is possible that such furrows do not always coincide with the real segmental boundaries.

The position of the organs in *c* and *d* appears to be nearly normal. At the right the pore lies very near the end of the abnormal ventral furrow, but about in the middle of the edge, as bounded dorsally, thus showing that its position is determined, at least largely, by the relations on the dorsal side. At the left the pore is approximate to the pore in *b*, evidently because of the absence of division on the dorsal surface at the edge.

The segment *e* is apparently perfectly normal, but *f* and *g* show abnormal relations, being separated on the right but united on the left. The partial furrows extend from the right edge a short distance past the middle of each surface and end free, the terminal portions being shallower than the rest. Thus the left side is without any true furrows, but the surface shows certain indications of a division between the two parts. From the end of the furrows to the edge there extends a depression in each surface too broad and indistinct to be called a furrow, but still apparently indicating a certain degree of separation (not shown in the figure). It reaches the edge in the slight depression between the two

pores at the left of the figure. The existence of this line of depression indicates, I believe, that *f* and *g* are really more or less distinct segments, even on the left, where no true furrow occurs. At the right *g* is as long as *f*, but is shorter at the left, and the furrows bounding it anteriorly are abnormal, for they are not transverse but extend from each edge somewhat posteriorly, thus making *g* very narrow just to the left of the middle. At the right the genital organs in *f* and *g* are normal and normally placed. At the left the organs in *f* are situated a little anterior to their normal position. We find, however, a second partial set of organs anterior to the first and showing relations almost identical with the rudimentary organs in *b* in Figs. 10, 16, and 17. The inner portion of the vas deferens appears, and just posterior to it lie small groups of cells which apparently represent a portion of the female organs. These parts are, however, entirely unconnected with the cirrus and pore, which are of normal size and appearance. Here again the inner and the outer portions have developed independently of each other, and the connecting ducts are absent. This case differs from those in Figs. 16 and 17, and resembles that in Fig. 10, *b*, in that a portion of the female organs appears here. In Figs. 16, *b*, and 17, *b*, a distinct furrow occurs on the dorsal side, but there are none ventrally; this condition indicating a more complete separation on the dorsal side than on the ventral, while in Fig. 10, *b*, as in this case, distinct furrows are absent on both sides in the immediate region concerned. Probably portions of both female and male organs occur in these cases, because the degree of separation, though slight, is the same on both sides. The incompleteness of the organs is doubtless due here, as in the other cases, to the small size of the segment.

The inter-proglottidal glands appear on all the furrows which lie within the zone of their formation. In the furrows between *f* and *g*, however, they are found only near the right side. The terminal portions of the furrows are shallow, and thus apparently insufficient to cause the glands to appear.

The region from which this figure was taken is not exceptionally abnormal, but was selected because it presents a number of different kinds of abnormalities near together.

Figure 21.

The figure represents four incompletely separated proglottids seen from the ventral surface. Between *a* and *b* the furrows at the left meet at the edge and extend over about one-third of each surface, ending free. At the right a peculiar curved furrow appears on each surface, and on the dorsal surface an oblique furrow extends posteriorly over *a* from the curved position almost to the posterior boundary of the segment. In accordance with the relation of the furrows, the genital organs at the left are normal, but on the right side of *a b* a peculiar set of abnormalities appears. Two distinct ovaries and vitellaria, *a'* and *b'*, appear, one in *a*, the other in *b*, but there is only one vas deferens, that in *b*. The oviduct from *a'* extends anteriorly and unites with the oviduct of *b'* near the seminal receptacle, and the common duct opens through the pore in *b*. In a number of cases I have found two sets of organs opening through a common pore, but the union of oviducts at a point so far from the pore is rare. The organs *a'* consist wholly of female organs, the vas deferens being entirely absent. It will be noted that the partial furrow on the dorsal surface in this region takes an oblique course. The right end of the curved partial furrow on the ventral surface takes a similar course. The ovary *a'* lies quite near these furrows and consequently there is no space for the development of the vas deferens in anything like its normal position. As the relative position of the various organs appears to be quite definitely determined in all cases, there is probably no tendency

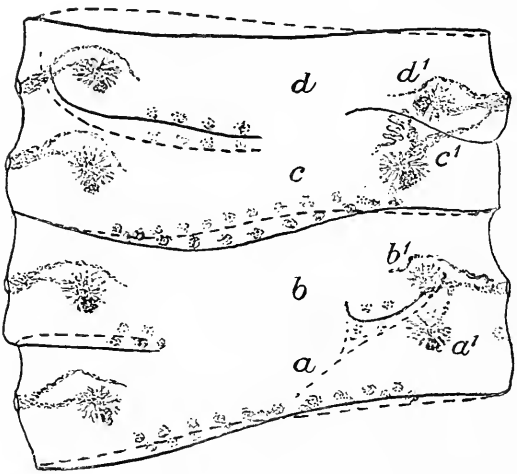

Fig. 21.

for the vas deferens to appear at all when it cannot be formed somewhere near its normal position. The partial furrows end just between the ovaries of *a'* and *b'*, and accordingly the two are quite closely approximated. This may be another reason why the vas deferens does not appear in *a'*, and it is, I believe, because of this approximation that the oviduct of *a'* unites with that of *b'* instead of running independently to the surface. There is a small rudimentary pore on the right edge of *a* which is wholly unconnected with the ovary *a'*, thus showing again the tendency for the terminal portions of the genital organs to develop separately in the segments of a low degree of individuality. The genital organs, *b'*, appear normal in form and constitution. The vas deferens is present here and in its normal relations. The pores in *a* and *b* are somewhat approximated, owing, apparently, to the fact that the edge is undivided, though division exists a short distance from it.

Between *c* and *d* at the right there is a distinct, though rather slight, furrow only on the ventral surface, and this furrow becomes somewhat oblique a short distance from the edge, *i.e.*, it extends somewhat anteriorly from the edge toward the middle. Its slight development is not clearly shown in the figure, but it is much less deep than the normal furrow. Dorsally there is no distinct furrow but only a shallow depression extending in the same direction as the furrow on the ventral surface and terminating in the corresponding region (not shown in the figure). As in the case of Fig. 20, *f* and *g*, I believe this depression represents what might be called a very rudimentary furrow, and its correspondence in this case with a distinct furrow on the ventral surface supports this view as regards both this case and Fig. 20. The genital organs, *c'* and *d'*, show peculiar relations. There are two complete sets opening by a common pore in *d'*. In *c'*, however, the vas deferens does not extend to the pore at all, but forms a complex coil just anterior to the ovary and *apparently opens directly into the seminal receptacle*. A small cirrus appears to be present in the enlarged terminal portion of the male duct which is seen in the figure. This is the only case where such a relation of the male and female organs has been found, unless it occurs on the left side of *e*, Fig. 22, where

it is impossible to determine the exact relations. In the organs at c' the portion of the seminal receptacle which lies between the ovary and the point of union of the male and female ducts is full of spermatozoa, while the outer portion is entirely empty, and this fact renders it certain that an actual union of the ducts with an opening does occur, and shows, too, that self-fertilization occurs as well.

It is important to note that here in c a vas deferens is formed, while in a, as mentioned above, the male duct is absent. The cause of this difference is indicated by the different direction of the partial furrows in the two cases. The partial furrows between a and b at the right extend obliquely backward posteriorly from without inward, and cut off from the segment a the region where the vas deferens would normally form, while the ventral furrow and the dorsal depression between c and d slant anteriorly, and thus a space is left in c anterior to the ovary where the vas deferens may form. The fact that the vas deferens opens into the seminal receptacle instead of extending to the pore, while the oviduct pursues a more nearly normal course, is perhaps not explicable on the basis of the form relations of the segments, but the suggestion offers itself that the close approximation of the two sets of organs, c and d, prevents its formation between them where it would naturally appear; so that it is confined wholly to the inner genital region. The oviduct of c' crosses the furrow to reach the pore instead of opening in its own segment. This is probably due to the fact that the degree of separation between the two segments is less than normal; for, as mentioned above, there is no distinct furrow on the dorsal surface, though ventrally the segments are sufficiently separated to give rise to separate ovaries. No pore at all is found at the right edge of c, and this is probably due to the same fact, *viz.*, that dorsally the degree of division is very slight, so that only one pore is formed for the two segments, though the position of this is apparently affected in some degree by the partial division which does exist, since it is placed somewhat anterior to the middle of the edge of c d.

In the genital organs d' of d relations are almost normal, but the oviduct is shorter than in c', and the ovary is thus nearer the edge of the proglottid. The oblique direction of the partial fur-

row may perhaps account for this difference in position in the two sets of organs, for the line connecting the centers of the two ovaries lies at right angles to the furrow separating them, and the ovary of *d'* thus lies in a region where the segment *d* is longer than it is in the region where the ovary would normally appear.

The relation of the furrows and genital organs at the left of *c* and *d* requires little comment. The organs are normal in all respects. The two partial furrows approach close to the edge, but turn forward, becoming very slight, and soon disappear. The pores are somewhat less than the normal distance apart, for the furrows do not quite reach the edge. The curve forward of the outer ends of the furrows apparently does not affect the position of the genital organs, this portion of the furrows being very shallow.

Inter-proglottidal glands appear in all the partial furrows except the one between *c* and *d* on the right, and their absence in this part is undoubtedly connected with the slight development of the furrow.

Figure 22.

In the series of segments shown here there are a number of more or less incomplete furrows, and each is accompanied by abnormalities in the genital organs. The figure is a view from the ventral side.

The two furrows between the segments *a* and *b* correspond closely in position, except at the right, where the ventral furrow turns forward just before reaching the edge and ends on the ventral surface, but the dorsal furrow continues to the edge, where it ends. At the left neither of these partial furrows reaches the edge, though both end near it, the dorsal furrow nearer than the ventral. The genital organs at the right of these two segments, *a* and *b*, appear normal in form and position. The ovaries are the normal distance apart, as might be expected from the character of the furrows in the ovarian region. The two pores are equidistant from the dorsal furrow between them. At first glance the right pore in *a* appears to be quite close to the anterior boundary of the segment, but it should be noted

that the notch in the right edge which appears to separate *a* from *b* is really in *a*, for the dorsal furrow reaches the edge anterior to it, and the two pores are equidistant from this furrow. At the left side of *a b* there are two complete sets of organs opening to the exterior through a common pore which lies in the middle of the undivided edge of *a b*. In the region of the ovaries the furrows are normal, and accordingly the ovaries are nearly the normal distance apart. The left end of *a* is short, so that the full normal distance between the ovaries is not attained. Since the

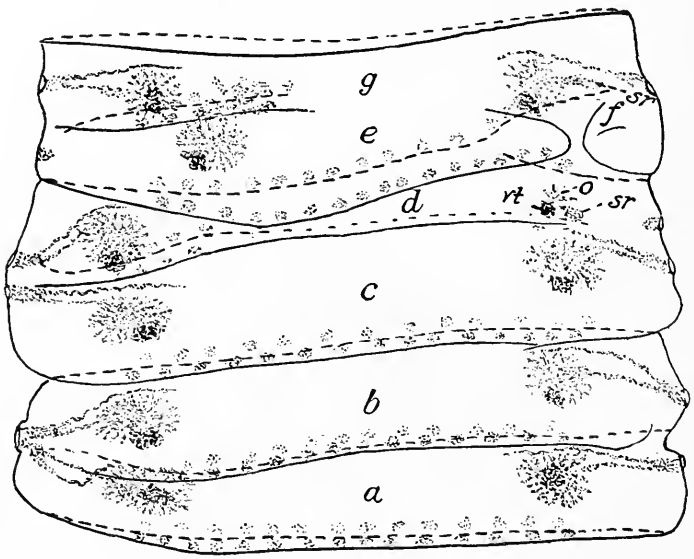

FIG. 22.

furrows do not quite reach the edge, it is undivided, and presents the relations of a single rather long proglottid. As might be expected, only one pore is present, though rather larger than normal, and into this the two oviducts and two vasa deferentia open, for the two sets of ducts approach each other as they reach the undivided region.

The segment *c*, of about normal length, and the segment *d*, which is of less than the normal length, except at the edge, are partially separated by two partial furrows which correspond very closely in position and extent on the two surfaces. The segment *c* is nearly the same length throughout, but *d* is longer at the

left edge than at the right and is very short in the middle region, and especially just to the left of it, in consequence of the bent course of the furrows bounding it anteriorly. At the right the two furrows between *c* and *d* end on the surface in the region of the ovaries, so that the right edge is undivided. At the left the furrows end very near to the edge, but do not reach it. The organs of the right side in *c* are normal; in *d*, however, they are rudimentary, consisting of a small imperfect ovary, *o.*, vitellarium, *vt.*, and a small closed and empty seminal receptacle, *s.r.*, and, entirely unconnected with these, a pore at the edge. No male organs except the cirrus appear. The absence of male ducts is perhaps due to the fact that this region of the segment *d* is shorter dorsally than ventrally, in consequence of the peculiar arrangement of furrows anterior to it. The pore of *d* is approximated to the pore in *c*, apparently because the furrows do not reach the edge. At the left edge *d* is of nearly normal width, though it narrows rapidly from the edge inward. Corresponding to its size the set of organs is of about normal size, like the left organs in *c*. These two sets open by distinct pores, which are, however, approximated.

The furrows anterior to *d* are very irregular. From the left edge they extend slightly posteriorly, thus almost separating *d* into two parts, then bend forward again and on the right end in a peculiar manner. The ventral furrow does not reach the right edge, but bends anteriorly and back upon itself, and ends on the surface. From the right edge the other portion of the furrow extends inward for a short distance, then curves back upon itself and ends. In the concavity of the curve near *f* a short isolated furrow appears. The furrow on the dorsal surface bends further anteriorly as it approaches the right edge and finally ends on the surface before reaching it. Posterior to this furrow lies another partial furrow corresponding to the right portion of the ventral furrow. It does not, however, bend back upon itself, but extends some distance to the left and then ends free on the surface. Thus a small region, *f*, is incompletely marked off as a partial segment on the dorsal surface, but ventrally the curved furrows divide into two parts. No genital organs appear in *f*.

The regions *e* and *g* are partially separated at the left by cor-

responding partial furrows, but at the right there is no separation, unless the region *f* be regarded as representing the right side of *e*. It is perhaps more correct to say that the right side of *e* is bounded ventrally by the left one of the two curved furrows, while dorsally *e* runs into *g*, and a small partial segment, *f*, mostly dorsal, laps over the edge to the ventral surface and fills the space left.

The furrows separating *e* and *g* on the left half of the body do not reach the left edge, though they end very near it. They are both rather shallow, thus indicating that the division between the two partial segments is less complete than normal.

The genital organs at the left of *e* present very peculiar and unusual relations. Ovary, vitellarium, and seminal receptacle of the normal size are present, and anterior to these and extending into *g* is a vas deferens which is closely coiled. This whole complex of organs does not lie in the normal position, but somewhat to the left of it, in the longest region of the partial segment *e*. I think it is possible that its position is due to the fact that the length is greater here than elsewhere. There is no trace of ducts leading to the edge; indeed, the oviduct beyond the seminal receptacle is absent, and the vas deferens does not extend even beyond the edge, but is coiled in a mass just anterior to the ovary. Doubtless this condition is due to the abnormally great distance between the organs and the edge. Careful examination of both surfaces of the region about the organs showed that there was no trace of a surface pore. I found, however, that the seminal receptacle was full of spermatozoa, a fact which indicates that the vas deferens opens directly into the seminal receptacle. The coils of the vas deferens were so dense and close, however, that it was impossible to find the connection. A pore corresponding to this set of organs exists at the left edge of *e*, but it is rather small and there is no trace of ducts leading from it. At the left of *g* there is a normal set of genital organs. On the right side of *e g* there is no division, unless, as suggested above, *f* be regarded as corresponding to *e*, and accordingly only one set of genital organs appears. In this the vas deferens is complete and normal, but the oviduct does not connect with the pore at all, ending instead with the seminal receptacle, *s.r.*, which is of

nearly normal size, but empty. It will be noted that furrows bounding *f* anteriorly end very near the region of the oviduct on both surfaces, and it seems probable that this abnormal condition is due to the position and direction of these furrows. The position of this set of organs as a whole is normal, and since the anterior of the two dorsal furrows does not reach the edge we find the pore in the middle of the edge *f g*.

The region *f*, although as large as some partial segments which possess at least rudimentary genital organs, shows no trace of any such. The ventral surface is cut by furrows in various directions, and this is probably the reason why no ovaries appear. The single pore at the edge of *g* is just between *f* and *g*, for the two are not separated at the edge, so that there was probably no tendency for another pore to arise in *f*.

Inter-proglottidal glands appear in all the transverse furrows which lie within the region of their occurrence, except the furrows between *c* and *d*. Here the glands appear only near the left ends of the furrows, but these portions are deeper and thus more nearly normal than the rest of these furrows.

Figure 23.

This figure, a dorsal view, shows two segments at a later stage of development, in which the uterus is formed, and the other

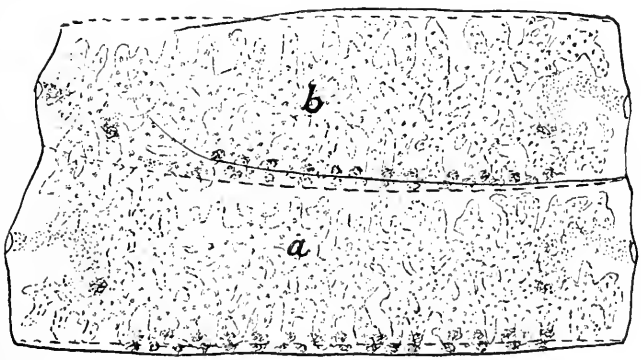

FIG. 23.

genital organs have undergone degeneration. The two segments are incompletely separated at the left, the ventral furrow being

shallow, but reaching the edge, and the dorsal furrow curving anteriorly and ending on the surface. The uterus is drawn in this case, and it is seen that the uteri of the two segments are continuous at the left, where the separation of the segments is incomplete. This is the only case of this kind figured, but continuity of the uterus is common in cases of partial division.

Regarding the other genital organs little can be said, as they are far advanced in degeneration. All appear to have been normal except at the left of *b*, where the pore and vitellarium are still visible, but no traces of ducts appear, and only a few cells in the ovarian region. A more or less rudimentary condition of these organs might be expected, for this portion of the segment is of less than normal length and dorsally is not marked off from either of the segments adjoining.

HULL ZOÖLOGICAL LABORATORY,
UNIVERSITY OF CHICAGO,
April, 1900.

A DESCRIPTION OF THE MALE OF PERIPATUS EISENII WHEELER.[1]

AUGUSTA RUCKER.

THIS new Peripatus from Tepic, Mexico, was named by Dr. W. M. Wheeler, of the University of Texas, and the female was described by him in the *Journal of Morphology* for October, 1898. It is from his material, which Dr. Wheeler has placed in my hands, and under his guidance, that I have obtained the following results. In this paper I have undertaken to give a description of the general external character of the male as differing from the female, and a description of its reproductive organs, with a brief account of the spermatophores. I hope in a short time to follow this up with the anatomical details, and later on to give the embryology of this most interesting animal.

The males proved to be so abundant in the material that an excellent opportunity presented itself for the study of this sex. Out of the original number, consisting of eighty-six specimens, thirty-two, on close examination, were found to be males. They are very much smaller than the mature females; in fact, several of the mature males in the material were smaller than embryo females (2 cm. in length) which I removed from the uterus. The largest of the males measured only 2.8 cm., while the largest female was 5.8 cm. in length. As to whether the sexes differ in color I cannot say, since a glycerine preparation used in softening the animals for sectioning has removed much of the color.

It has already been shown that this species varies in the number of its walking appendages, as do all the other well-known neotropical forms. The highest number of legs for *Peripatus Eisenii* is twenty-nine pairs, while the lowest is

[1] *Contributions from the Zoölogical Laboratory of the University of Texas*, No. 5. Director W. M. Wheeler.

twenty-four pairs.[1] Sedgwick's statement that the males have the lowest number of legs holds good here in every case except one. All those specimens having twenty-nine, twenty-eight, or twenty-seven pairs of legs were females, while all those with twenty-six, twenty-five (with one exception), or twenty-four pairs were males.

The number of these appendages is fixed at birth, as is also the case with *P. Edwardsii*, as Sedgwick has shown, and the

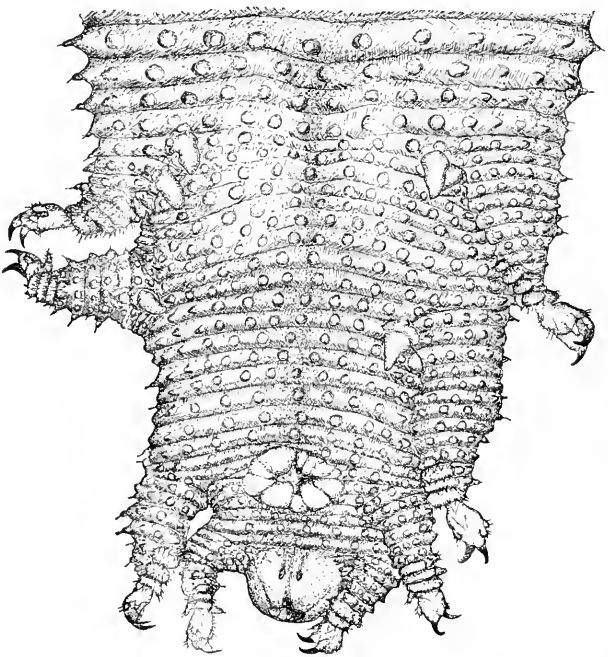

Fig. 1.

number of appendages of the mother is not necessarily transmitted to the embryo. From a mother with twenty-seven pairs of legs, three embryos were removed, each with twenty-eight pairs of appendages; and again from a mother with twenty-eight pairs of legs three embryos were removed, the two most mature of which had twenty-five pairs, while the less mature one had twenty-six pairs. These last three specimens had

[1] Dr. Wheeler mentioned in his paper one specimen with twenty-three pairs of appendages; this I was unable to find after carefully reëxamining all the males.

other external characters, apart from the number of appendages, in the appearance of the posterior portion of the body, which, embryos as they were, showed them to be males.

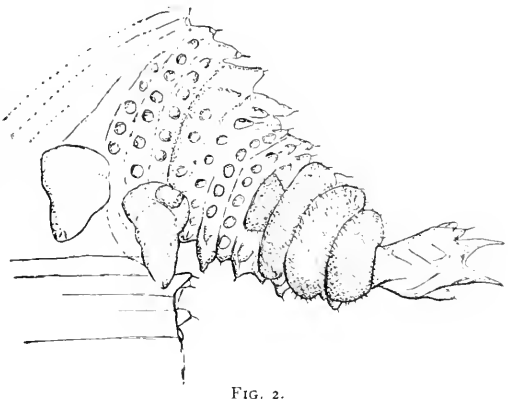

Fig. 2.

The anterior legs of the males are like those of the females, each possessing four pads and a pedal groove. The nephridial opening is on the second pad from the base, on the fourth and fifth leg, as in the female. On the third posterior leg the proximal pad becomes much reduced and entirely disappears on the penultimate leg, while on the last leg only the two distal pads remain, with a portion of the original second proximal pad.

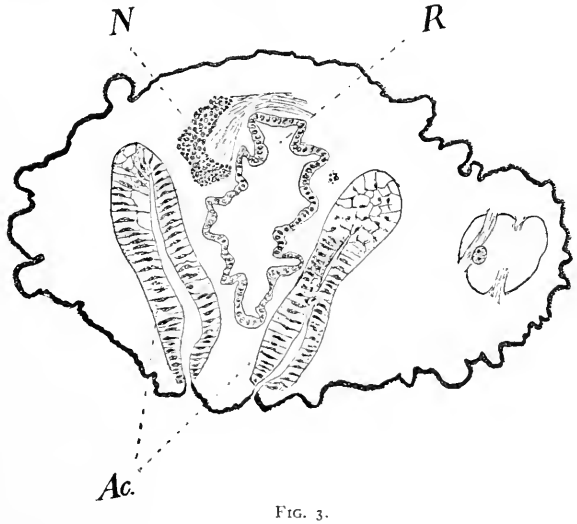

Fig. 3.

On the four posterior pairs of appendages there are no pedal grooves, and here begins the difference between the appendages of the two sexes. In the place of the pedal grooves, which are entirely wanting on the third and fourth posterior legs, there are two long, soft papillae for each appendage. This is invariably the sign of the male *Peripatus Eisenii*, and these papillae, with an opening at the tip for the outlet of the *crural*

glands, are always on the third or fourth posterior appendages. The only specimen with twenty-five pairs of legs, which did not have these tubercles, was opened and found to be a female. The position of these papillae can best be seen from Fig. 2, which is a camera lucida drawing of the left fourth leg. Fig. 1 is a drawing of the ventral surface of the posterior end of an animal 2.4 cm. in length. At first sight the fourth or third leg may appear to have only one papilla or none at all, but on closer examination the tip of the papilla will be seen to be surrounded by a circular ridge. Sections through these posterior legs of different individuals show that the tubercles are of uniform development in all males, and that they can be retracted or protruded in the living animal. The section also shows that the papillae are retracted only by involuntary muscle fibers inserted on these papillae. Fig. 4 represents a section through the fourth leg. The inner papilla is protruded, while the outer

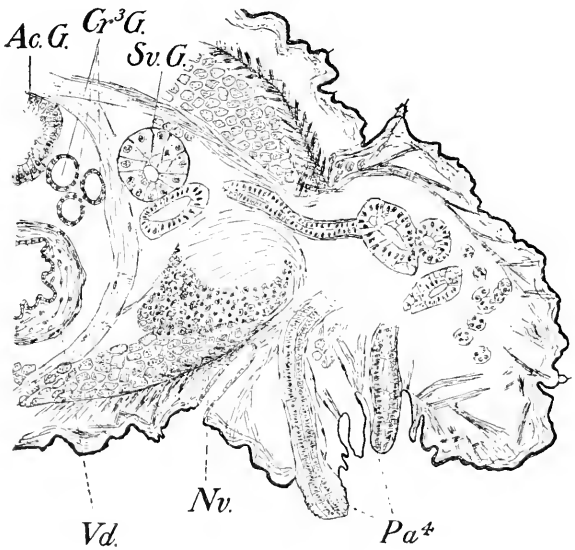

FIG. 4.

one is partially withdrawn. Fig. 5 is a section through the third leg, showing the inner tubercle more retracted than the outer one in Fig. 4. This tubercle has about reached its limit of retraction. The outer papilla was cut to one side, so as to

show the cup-shaped depression in which it rests and the distinct outline of the epidermis which makes it look like a diminutive pine cone.

The opening of the generative organs is, like that in the female, between the penultimate pair of legs; but this pair of

FIG. 5.

appendages, unlike that of the female, has no trace of a pedal groove, and the same may be said of the last pair. There is likewise no trace of the nephridium in the penultimate pair of legs, whereas the last pair possesses these organs, which appear in section with small external openings.

Just as there are crural glands in the male, which are wanting in the female, so also are there *accessory glands*. There is a pair of these glands which opens externally by two small slits situated between the generative and anal openings, about a fourth of the distance from the latter. Fig. 3 represents a camera drawing of a section through the orifices of these accessory cells.

Before leaving the consideration of the exterior of *P. Eisenii* it is well to speak of a thing of interest which relates to both the sexes, and which has not been mentioned before in connec-

tion with this species. It is a bean-shaped papilla that is always found in a depression on the dorsal surface of the leg where it joins the foot. Gaffron describes this papilla in *P. Edwardsii*. Sedgwick says it is also found in the Trinidad species and is probably characteristic of all the neotropical forms. The surface of the depression in which the papilla lies is smooth, while the papilla itself shows a distinct cell structure, the cells all converging toward the center. Fig. 6 represents a longitudinal section through the foot splitting the papilla.[1]

FIG. 6.

From the number of external outlets of glands connected with the generative tract, it is readily seen that the male repro-

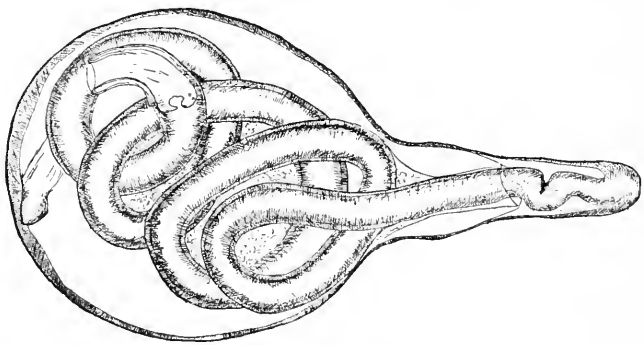

FIG. 7 *a*.

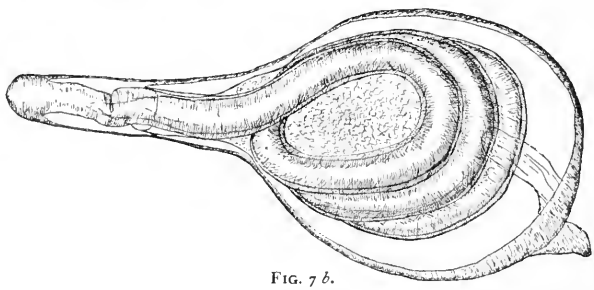

FIG. 7 *b*.

[1] It seems from the position of these papillae, especially when the foot is drawn in, that they are sensory. If this be true, the comparison of the foot of *Peripatus Eisenii* with the parapodium of the Chaetopoda is rather striking, the sensory papillae corresponding to the cirri.

ductive organs are much more complicated than those of the female. The latter has two fused ovaries, paired receptacula ovorum, paired receptacula semines, and paired uteri. The testes are large tubular organs beginning at about the posterior third of the body and running backward without much twisting to the seminal vesicles, which are somewhat larger in diameter. The seminal vesicles appear as dilatations of the testes, the right one of which is some distance in front of the left. The vesicles of all the specimens I have examined are full of the spermatogonia discharged from the testes, spermatocytes, and spermatozoa. The material was collected in October, when the testes were active. The seminal vesicles lead posteriorly into a pair of exceedingly convoluted vasa deferentia, the right one of which passes over and then under the nerve to join the left, which passes under the nerve. They then run forward side by side, as two small, very thin-walled, straight ducts, for some distance, till they unite to form a common duct. These paired portions of the vasa deferentia are quite full of spermatozoa. The unpaired portion of the testicular ducts is of great length, sometimes exceeding twice the length of the whole body. This tube is clearly divided into two portions, the first

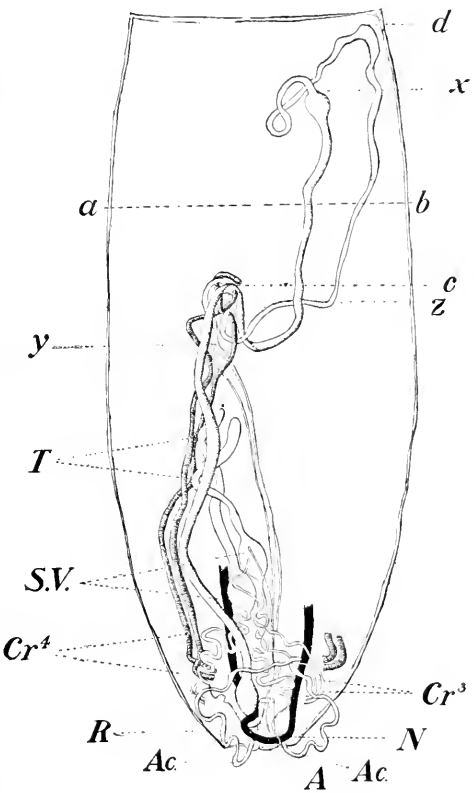

FIG. 8.

two-thirds of which are comparatively thin walled and lined with ciliated cells, while the last third has a non-ciliated epithelial lining and very thick muscular wall. This thick-walled portion terminates in an enlarged sack which might well be called the spermatophore sack, since it holds a spermatophore in nearly all the specimens examined. The sack opens on the exterior by means of the generative orifice between the penultimate pair of legs.

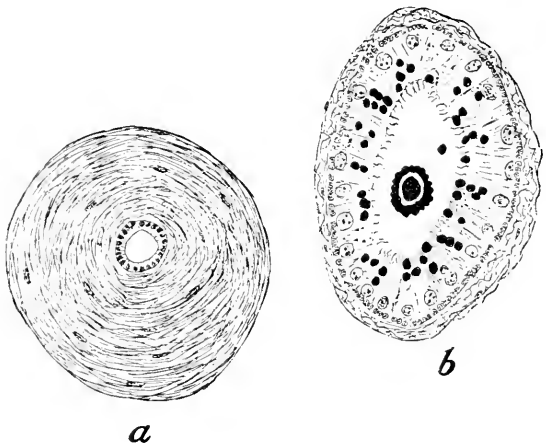

FIG. 9.

The portion of the vas deferens possessing the thick muscular wall does not constitute the spermatophore maker, as Moseley found in *P. N. Zealandiae*, but it is the thin-walled portion which has this function, though the epithelium is ciliated in that region.

Fig. 8 is a partially diagrammatic drawing of the male reproductive organs of *Peripatus Eiscnii*. The vas deferens from *c* to its termination has a thick muscular wall. From *y* to *d* and thence back to *c* the wall is comparatively thin, and the lining cells are at the same time ciliated and secretory. Especially active are the cells of that portion which begins at about *z* and ends at *d*. Here the most substantial portion of the spermatophore is made. In secretion great balls of a glutinous substance staining dark in haematoxylin are formed in the inner cells and given off. They become packed into the spermatophore rod in the most regular manner, making its surface appear to be marked off in regular hexagons, not indicated in my drawing. This rod receives lighter secretions as it passes along, carrying before it a packet of spermatozoa around which it becomes very much coiled in the dilated distal portion

of the vas deferens, or spermatophore sack. Here the coiled spermatophore seems to receive other layers of secretions which form a case of some thickness. Fig. 7 and 7 *a* are camera drawings of two views of a spermatophore, the pointed end of which projects forward in the vas deferens.

The crural glands which open out through the above-described papillae are found only in the male. These glands from the fourth pair of legs are large and extend almost half the length of the animal. They leave the lateral compartment of the body (unlike the same glands of *P. capensis*, which run their whole distance in this portion of the body) almost immediately to coil around the vas deferens. The crural glands of the third pair of legs are very thin tubes winding in and around the convoluted portions of the vasa deferentia, and around the seminal vesicles, where they end. The accessory glands are large tubes which are situated dorsally to the other organs; they run posteriorly (the right one going over and just under the nerve), to empty a very short distance in front of the anus.

In concluding this description, one point of great interest presents itself which cannot be overlooked. *This is the rapid sexual development of the males to maturity.* I observed that in sections of very small specimens which could not have been long from the uterus, the seminal vesicles were distended with ripe and rapidly developing spermatozoa. In a male embryo which was removed and sectioned, I found in the seminal vesicle not a few spermatozoa and spermatids in abundance. It would seem to follow from these conditions that the males of the neotropical species of Peripatus must be rather short-lived, and this fact will probably account for their scarcity.

UNIVERSITY OF TEXAS, AUSTIN, TEX.,
May 1, 1900.

BIOLOGICAL BULLETIN.

ABNORMALITIES IN THE CESTODE MONIEZIA EXPANSA. II.

C. M. CHILD.

1. *Spiral Abnormalities.*

In the cases described in this section spiral modifications of the segmentation are present in greater or less degree. Associated with these are often found examples of partial division resembling those described in Part I, *Biological Bulletin*, Vol. I, No. 5. Where these are closely connected with the spirals they are shown in the figures and briefly described.

Figs. 24, 26, 27, 30, 38, 39, are selected from a number of different individuals. The other figures are all taken from the single worm mentioned in Part I as possessing a very large number of abnormalities. Figs. 34 and 35, being taken from a point nearer the anterior end of the chain, where the size is much less than in older proglottids, are magnified about fifty diameters, the other figures about twenty.

For terms used in the description, the structure of the normal segment, etc., the reader is referred to the first paper (*Biol. Bull.*, Vol. I, No. 5).

Figure 24.

The principal feature of this figure is a case of partial division, which is in reality a short spiral. The proglottid *a* shows at the right a very short furrow extending from the edge a short distance over the upper surface and ending free.

The lower surface shows no corresponding furrow. The length of the proglottid at this side is somewhat greater than, but not double, the normal length, *i.e.*, it is not as long as two fused proglottids of the same age. Two groups of cells, the "Anlagen," of the reproductive organs or "genital masses," appear upon this side, however, as would be the case if the short partial furrow were complete. The furrow itself indicates the imperfectly double character of the segment, and the two genital masses show this still more clearly. At the left *a* is only half as long as at the right and possesses only a single genital mass. The partial segment *b* is completely separated from *a* both on the upper and lower surface, but is seen to be connected with *c* on the lower surface. The furrow separating *b* from *a* runs inward and somewhat anteriorly from the left edge for about one-third the width of the body, then turns and extends outward and anteriorly until it joins the complete furrow in front. Thus the small piece *b* is completely marked off on the upper surface, and though its edge at the left side is of normal length, it narrows to a rounded end. On the lower surface the relations are different, for the partial furrow between *b* and *c* on this surface ends free, while the complete furrow separating *a* and *c* at the right bends so as to pass posteriorly to *b* at the left and connects at the left edge with the furrow between *a* and *b*. The partial segment *b* is thus a short spiral, making less than half a turn. Notwithstanding its small size, it shows a genital mass as large and distinct as any at this stage.

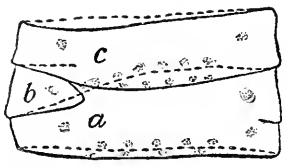

FIG. 24.

Figure 25.

Here two examples of partial division and a short spiral occur. Upon the upper surface the two partial proglottids *a* and *b* are incompletely separated, the partial furrow on the left side being longer than that on the right. The partial furrows at the right correspond exactly on the two surfaces, both ending free. The partial furrow on the upper surface at the left forms

the beginning of a spiral furrow which makes one and a half turns. It is oblique upon the lower side, running from between *a* and *b* at the left to the anterior edge of *b* at the right, then passing over the upper surface again as a complete transverse furrow anterior to *b*, and finally ending free on the lower surface. Thus the spiral segment *b* is open at both ends. If the furrow between *a* and *b* on the upper surface were complete, the spiral would begin between *a* and *b* at the right on the lower surface, and the furrow would thus make almost two turns. In the region where the genital masses appear the furrows show very nearly normal relations, and the position of the genital masses needs no comment.

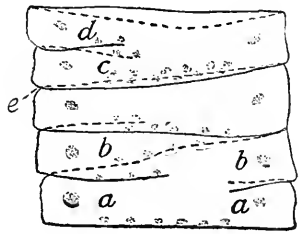

FIG. 25.

In *c d* another case of simple partial division occurs at the left, the partial furrow corresponding in position on the two surfaces. At the left two genital masses occur, while at the right, where *c d* is undivided and shorter than at the left, only one appears. All the partial furrows which extend far enough from the edges to lie within the region where the interproglottidal glands occur, possess them. The furrows between *a* and *b* on the right show none, as they are too short.

Figure 26.

This case consists of a short spiral in which the spiral furrow makes one and a half turns about the body. As the result of its course the partial proglottid *b* is formed, which unites on the upper surface with *a*, and on the lower with *c*.

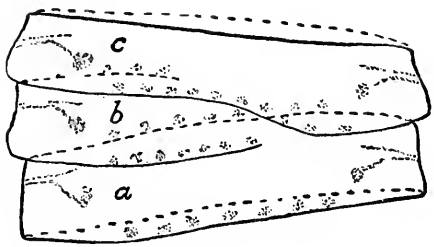

FIG. 26.

In the lateral regions the segmental boundaries are all normal, and, accordingly, the organs are situated nor-

mally, but at the left there are three segments and at the right only two, and a corresponding number of sets of genital organs is found.

Figure 27.

A spiral furrow making only a little more than half a turn appears in this case. At the left the upper surface of *a* is united at the edge with the lower surface of *b*, and at the right the lower surface of *a* unites at the edge with the upper surface of *b*.

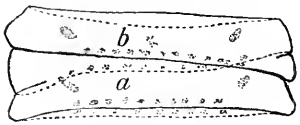

FIG. 27.

The only abnormality visible at this stage in the genital organs appears at the left in *a*. Here the genital "Anlage" is elongated and narrower than in the other cases. The proglottid is not sufficiently developed to show the ducts and pores, so that it is impossible to determine just what the situation of these organs will be.

Figure 28.

Here the natural relation of the dorsal and ventral surface is somewhat altered. The figure is drawn with the dorsal surface uppermost, and it is seen that the furrows on the dorsal surface lie further posteriorly than those corresponding to them on the ventral surface. The furrows bounding *a* posteriorly do not meet at the edge, as they would if normal and merely distorted by pressure or otherwise, but the end of the ventral furrow is anterior to the dorsal. The furrows *d* and *d'* would correspond to each other if normal, but as a matter of fact *d'* meets *e* at the left edge instead of meeting with its corresponding furrow *d*, thus producing a slight spiral. The furrows *e* and *e'* would meet at the two edges if normal, but here again the ventral furrow is considerably anterior to the dorsal except at the right edge, and its left end shows no indication of bending posteriorly to meet the latter. A somewhat similar condition is seen frequently in mounted specimens, but in most cases is simply a distortion due to the compression between glass plates during fixation. The real abnormalities such as occur

here can be distinguished by the fact that at one edge or the other or both the corresponding furrows on the two surfaces do not meet. That some distortion has also occurred in this case is probable from the fact that in the regions immediately outside and posterior to that of the figure otherwise normal segments are oblique dorso-ventrally, as if the dorsal surface had moved posteriorly over the ventral, or the ventral anteriorly over the dorsal. The segment *b* is bounded by a furrow beginning at *d''* and forming a spiral of nearly two turns, ending free on the ventral surface (*e'*). The genital organs *b'*, on the left side of *b*, lie almost between the dorsal furrow *e* and the ventral *d'*, and it is the only genital mass on the left for the whole spiral. The ovary and vitellarium, being nearer the ventral surface, appear between the furrows *d'* and *e*, while the ducts lying nearer the dorsal surface bend posteriorly, and their terminal portions appear posterior to the furrow *e* on the dorsal surface, and finally reach the surface almost midway between the dorsal furrows bounding *b*. At first glance it appears that if the position of the genital organs is correlated with the form of the proglottid, the duct should open somewhere in the region *c* instead of passing posteriorly under the dorsal furrow *e*, as it does. As a matter of fact, however, its position is the only one possible in the spiral proglottid *b*. Since the spiral segment *b* lies somewhat obliquely, *i.e.*, with its ventral surface somewhat anterior to the dorsal, the position of the organs at *b'* between the dorsal furrow *e* and the ventral *d'* is only apparent. In reality they are in about the normal position in their segment *b*. The outer end of the ducts is rudimentary, consisting of a scarcely visible strand of cells, and there is no enlargement in the region of the pore. Moreover, the inner end of the vas deferens instead of running anteriorly to the ovary and vitellarium, as is usual, is posterior to them, as seen in the figure (*b'*). This position of the inner end of the vas deferens posterior to the ovary is peculiar and is probably due to the oblique position of the segment *b*.

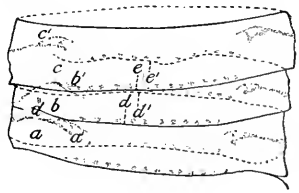

FIG. 28.

The rudimentary character of the terminal portion of the ducts is apparently due to the fact that the proglottid *b* is not wholly distinct from *a* in this region. The posterior dorsal furrow is interrupted at *d''*. The short portion extending to the left edge is not a furrow of normal depth but a scarcely visible fold upon the surface, and the left end of the main furrow at *d''* is also very shallow. On the ventral side there is no furrow corresponding exactly to the furrow *d'd''*, for *d'* is a spiral continuation of it. Therefore the only evidences of separation between *a* and *b* in this region are the slight furrows at *d''*. Since the degree of separation is so slight, the tendency to form a second genital pore and the terminal region of the ducts is probably very slight also, but is still present, as is evident from the figure. The testes are just beginning to appear (not represented in the figure), and their distribution corresponds exactly with the conditions on the dorsal surface.

Figure 29.

At the stage shown here the proliferating groups of cells forming the reproductive organs are visible, and the interproglottidal glands are more numerous. The variation is a spiral, the furrow making two complete turns. The posterior end of the spiral furrow appears between *a* and *b* at *e*. Upon the lower surface it is a complete furrow and is continuous with the furrow upon the upper surface between *b* and *d*. This bends anteriorly at the left instead of completing the furrow between *b* and *a*, and so separates *b* and *c* at the left edge, continuing over the lower surface as a complete furrow and passing once more to the upper surface between *d* and *c* at the right and finally ending free at *f*. The only portion of this continuous furrow which differs greatly in position from the normal is the part between *b* and *d* at the left on the upper surface, where it bends anteriorly and so fails to complete the separation between *a* and *b*. The spiral is the result of this bend

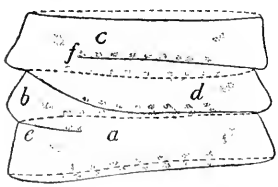

FIG. 29.

in the furrow, but since the furrow ends free at *c* and *f* both ends of the spiral proglottid bounded by it are open and connect respectively with *a* and *c*. The position of the genital masses is not affected by the presence of the spiral arrangement.

The general relation of the inter-proglottidal glands to the furrows is shown by the fact that the glands appear with the abnormal and partial furrows as well as with the normal.

Figure 30.

This figure shows two spirals situated in the regions designated by *a* and *b*. In each case the spiral is due to the curving of the furrow near the median line of the body. In the one case the curve is on the dorsal surface, in the other on the ventral. Since the curved furrows are on opposite surfaces and yet nearly parallel, the two spirals are opposite in direction. In both cases the ends of the spiral portions unite more or less completely with adjacent segments, owing to the fact that the furrows between them end free. In *b* this union is much more complete than in *a*. In *a* the spiral furrow makes two turns about the body, in *b* only one and a half as a continuous furrow. If, however, the partial furrows at the right in *b* be considered as a continuation of it, this furrow also makes two complete turns.

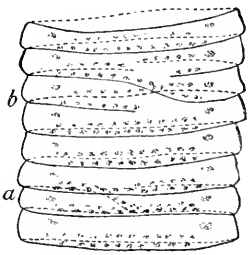

FIG. 30.

The lateral regions and edges of the segments are all normal in form, and we find all the genital masses normal in position.

Figure 31.

The figure is a view from the dorsal side of a series of segments, showing a number of abnormalities. The first of these is the small partial segment *b*, wedged in at the right between *a* and *c*. Its dorsal surface is greater than its ventral, and its edge is nearly as long as that of a normal segment. Dorsally the furrow between *a* and *b* ends free on the surface. The

corresponding ventral furrow turns anteriorly a short distance from the edge and meets the main furrow between *a* and *c*. Thus the ventral surface of *b* is completely marked off from other segments. Both the dorsal and ventral furrows between *b* and *a* are rather shallow. The organs in *b* are distinctly abnormal. A rather small ovary and vitellarium appear nearer the edge than in normal segments, probably because of the increasing length of the segment *b* nearer the edge. The oviduct is incomplete and ends bluntly, as the figure indicates.

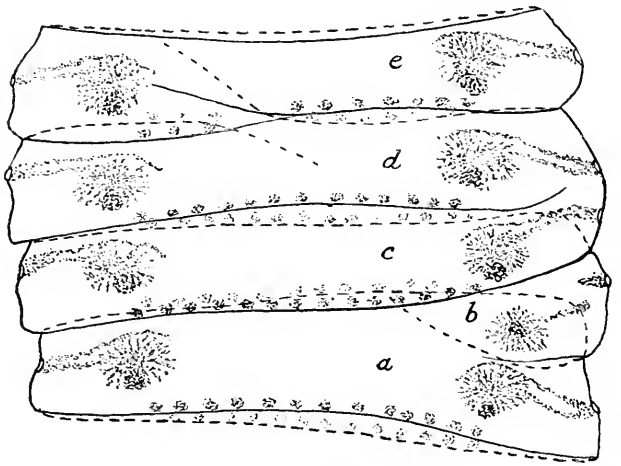

FIG. 31.

A distinct pore is present, and connected with it is a well-developed cirrus, but no trace of a vas deferens is found anywhere in the segment. The position of the various organs illustrates well the relation of each to the form of the segment in the region where it occurs. Thus the ovary and vitellarium, which appear from the dorsal surface to be near the posterior edge of the segment, lie midway between the bounding furrows on the ventral surface, and the oviduct, which extends somewhat dorsally from the ovary, runs obliquely forward towards the edge, so that it is normally placed with regard to the furrows on the dorsal surface. The pore lies near the anterior end of the segment. The ventral furrow bounding *b* anteriorly turns backward before reaching the edge and unites with the

posterior furrow, so that the region corresponding to the ventral side of *b* is cut into two parts, that nearest the edge being united with *c*, *i.e.*, taking *b* as it appears on the dorsal surface, we find that it is not separated from *c* at the edge. As *b* is bounded on the ventral surface it does not reach the edge of the body at all. The position of the pore is evidently connected with these peculiar relations. The dorsal side of *b*, together with *c*, forms a spiral. Beginning with the dorsal partial furrow between *b* and *a*, the spiral furrow makes two complete turns about the body.

The rudimentary condition of the organs in *b* is undoubtedly due to the small size of the segment. The ovary and the oviduct are more completely developed than the vas deferens. The segment *b* contains a number of testes and in some spermatozoa are visible.

The position of the organs in *a* needs no comment. The segment is of peculiar form, owing to the presence of *b*, but its genital organs are normally situated.

The furrows between *c* and *d* are abnormal. The dorsal furrow ends at the right without reaching the edge, and the ventral furrow turns posteriorly near the right edge and meets the posterior boundary of *c*. Thus the right edge of *c* and *d* is not divided by any furrow, but the dorsal furrow extends almost to the edge. The ovary and vitellarium at the right of *c* are normally placed with regard to the ventral boundaries, and the ducts and pore with regard to the dorsal boundaries. Both ducts cross the course of the ventral furrow at an angle to reach the edge, thus indicating that relations on the ventral side have little influence on their direction. At the right of *d* a normal set of organs occurs. The figure shows, however, that the two pores on the right edge of *c d* are near together. In the region of the inner ends of the ducts the segments are completely separated, and the distance between the two sets of ducts is normal here. As they approach the surface, however, the separation between the two segments on the dorsal surface becomes less and less complete, and the edge itself is undivided. Thus the pores tend to form near its middle, but the fact that the dorsal furrow extends so nearly to the edge

indicates that a certain degree of individuality exists up to and perhaps beyond the point where it terminates, and this, together with the length of the edge of *c d*, accounts for the presence of two pores instead of the union of both sets of ducts in a single pore.

Between the segments *d* and *e* the furrows are very abnormal. The ventral furrow is divided into two parts which overlap on the surface, the one turning anteriorly, the other posteriorly. The oblique portions are very shallow and do not bear interproglottidal glands.

The dorsal furrow is also in two parts. The one at the left does not turn posteriorly, but continues as a very shallow furrow over the region corresponding to that which the ventral furrows leave undivided, and finally unites with the right half. This latter, however, continues to the left, beyond this point, but turns anteriorly, running up into the segment and ending just dorsal to the ovary. The oblique portion is shallow, like the oblique portions of the ventral furrow, and bears no glands. The genital organs at the left of *d* and *e* are normal, however, doubtless because the growth has been normal in the regions where the organs occur. Only the oblique portion of the dorsal furrow approaches the ovary, but, as has been repeatedly shown, the position of the ovary is influenced only very slightly, if at all, by the form of the dorsal surface.

Figure 32.

At the stage of development shown in the figure the genital masses are becoming differentiated into the various organs. The female portion is mostly distinct from the male, and the strands of cells forming the ducts extend nearly or quite to the edge of the body, though the pores are not distinct as yet. The variation shown is a spiral in which the furrow makes two complete turns, the spiral segment bounded by it making one complete turn. The spiral begins on the right in the short furrow bounding *a* posteriorly and separating it completely from the proglottid behind; from this point it passes around the body, bending forward at the right side of the upper sur-

face to form the anterior boundary of *a*, then making one more complete turn and ending on the upper surface, thus leaving *b* and *c* incompletely separated at the right of the dorsal surface. The development of the genital organs is sufficiently advanced in this case to show the very intimate relation of these organs as regards position with the form and relations of the proglottids. The segment *a* possesses its own genital mass (a'), which is entirely separated from all the others. This is, however, of less than the normal size and does not reach the edge of the segment. It is divided into two parts in its inner portion, but the group of cells which would later form the ovary and vitellarium does not appear. In fact, the mass seems to consist largely, if not wholly, of portions of the two ducts. It will be remembered that the ducts lie farther dorsally than do the ovary and vitellarium. The figure is drawn with the dorsal surface uppermost, and it is only dorsally that the region *a* appears as a distinct partial proglottid. On the ventral surface the relations of the furrows are entirely different. It appears then that the dorsal region of *a* possesses a degree of individuality sufficient to cause the appearance of the organs proper to this region. The ventral region not being separated from *b*, the organs of the ventral side do not appear. Whether the organs would in later stages approach or reach the normal development it is impossible to state with certainty, but the evidence seems to be against such a view, for in all cases of similar abnormalities in much later stages the genital organs or parts, however rudimentary they may be, show the same degree of differentiation as those of normal segments.

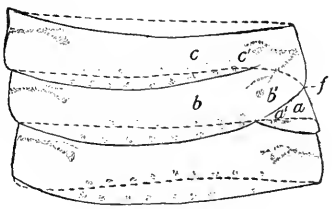

FIG. 32.

In the large, incompletely separated segments *b* and *c*, there appears another example of the close relation between the individuality of the segment and the presence and arrangement of the reproductive organs. At the left appear normal sets of organs in normal position. At the right, however, where the furrow on the dorsal surface is incomplete and that upon the

ventral surface bends posteriorly, two sets of organs (b' and c') appear whose ducts open into a common genital pore. Each of the sets is apparently complete, possessing the groups of cells which will form ovary and vitellarium, as well as the vas deferens. The inner portions of these two sets are situated much as they would be if b and c were normally separated from each other, *i.e.*, their position is nearly normal. The partial furrow on the dorsal surface, however, does not extend to the right edge of the body, but ends free before reaching it, so that b and c are united here, and correspondingly only one genital pore appears at d, and into this both sets of ducts open. But the question now arises as to the reason for the connection of the organs b' with this pore. Normally these organs would open on the edge at some point not far from f, but, owing to the arrangement of the proglottids in this case, f is the point of intersection of the furrows, *i.e.*, does not possess the features of the region where the genital pore normally appears, for this is upon the edge, about midway between two furrows. The only possible conclusion from the facts is that the direction of the ducts and their final connection with the pore are correlated with the form of the proglottids in this region and especially upon the dorsal side. This conclusion is confirmed by the fact that the ducts cross almost at right angles a furrow on the ventral side, thus rendering it evident that their arrangement is not affected by its presence. In short, ovaries and vitellaria arise separately in b' and c', because the relations of the ventral sides of the segments in that region are practically those which exist in two separate proglottids, and upon the dorsal surface the same is true in the immediate region of the inner portions of the organs. Nearer the edge, however, the relations on the dorsal side are those of a single segment, so that the two sets of organs approach each other and finally open in a common pore, which occupies a normal position with respect to the boundaries of the proglottid in its immediate vicinity.

Figure 33.

This figure shows a rather long spiral, together with a small completely separated partial proglottid. The furrows bounding the spiral begin between the partially separated segments *a* and *b* near the left side of the dorsal surface — the dorsal surface is uppermost in the figure — and make a little over three turns about the body. At the left side of the dorsal surface, between the segments *d* and *c*, the furrow becomes shallower, and on the left edge it terminates. The spiral segment enclosed by it makes a little more than two complete turns. In consequence of the course of the furrow, *a* and *b* are incompletely separated on the dorsal surface, but completely separated ventrally; the furrows bounding the regions *b*, *c*, and *d* do not correspond on the two surfaces, and finally *d* and *c*, which are distinct dorsally, are completely united on the ventral surface. These abnormal relations are accompanied by a number of corresponding abnormalities in the genital organs. At the left side *a* is distinct from *b*, and the genital organs *a'* on this side are normal and in normal position. At the left side of *b*, *c*, and *d*, where the spiral character of these segments becomes evident, the genital organs show marked abnormalities. At *b'* only two small groups of cells are found, representing apparently portions of the ducts; at *c'* and *d'* full sets of organs occur, but lie obliquely, and the ducts are elongated. It is evident that the pores and the greater portions of the ducts are normal in position with regard to the dorsal form relations of the segments. The oblique direction of the ducts is apparently due to the fact that the dorsal side of *c* and *d* bends forward near the left edge. Since the inner portions of the organs are formed at the normal distance from the edge, in order to reach the edge as they do, the ducts must be longer than the normal, for they must run obliquely.

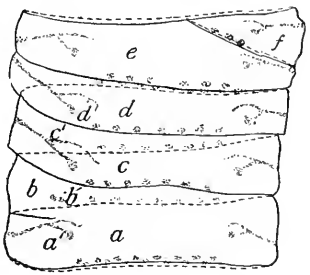

FIG. 33.

The dorsal sides of *b* and *c* both correspond in part, as

regards position, to the ventral side of *b*. The ovary of the set *c'* lies in *b* as bounded ventrally. Apparently the dorsal side of *c* and the ventral side of *b* are to be regarded as belonging together at the left, even though they do not occupy corresponding positions, as they do at the right. If this be the case, the organs *c'* show a close correspondence to the form relations. Upon the dorsal surface *b* is merely a small portion, intercalated, as it were, between *a* and *c* and incompletely separated from *a*. The genital organs are very rudimentary. The ventral organs found in *b* belong to the set *c'*, and there is no distinct ventral region corresponding to the dorsal side of *b*. Thus no ventral organs appear. Two small groups of cells (*b'*) are the only traces of genital organs in this region. These apparently represent portions of the ducts. This very slight development of genital organs is probably due to the small size and imperfect form of this portion.

The set of organs at *d'* shows much the same relations as that at *c'*. Its pore, however, is very close to the furrow between *d* and *e*, as is also the pore of the organs at the left of *e*, which are otherwise normal. The approximation of these pores is evidently correlated with the incomplete separation of *d* and *e* by a shallow furrow on the dorsal surface, and not at all ventrally.

On the right, at *f*, a small partial segment is separated from *e* by oblique furrows. It possesses a normal set of genital organs. The intercalation of *f* leaves the right edge of *e* very short, but the genital organs are, so far as appears, normal. Whether they will reach full development and normal size cannot of course be determined.

Figure 34.

The abnormalities figured here occur not far behind the scolex, where genital organs have not yet appeared. At *a* there is a small partial segment wedged in between two others at the left side. Just anterior to this is a spiral, beginning on the lower surface and making nearly two turns. The course of the spiral furrow is such that on the upper surface the segment *c* does not reach the left edge at

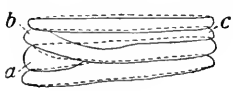

FIG. 34.

all, and on the lower surface the segment next to *a* narrows toward the left and ends at the edge.

Figure 35.

The figure shows a complex case of partial division (*a*) and a spiral of about four turns (*b c*). The region *a* is partially separated into two segments at the right, but at the left into three, the most anterior (*b*) forming the beginning of the spiral. On the lower side, just beneath *b*, there is a small region wholly marked off by furrows and not forming part of the spiral. The spiral *b c* is perfectly simple in form, though rather long. This case, like Fig. 34, was found near the anterior end of the chain, and neither genital organs nor inter-proglottidal glands are formed.

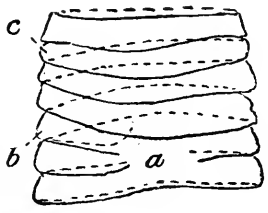

FIG. 35.

Figure 36.

The figure is a dorsal view of an extremely long spiral, which makes seven complete turns about the body. The spiral is due to the bending posteriorly of the ventral furrows near the right edge.

At the left the segments are all normal in form, and all of the genital organs are normally placed. At the right the curve in the ventral furrows produces complex relations in the various segments. All of the curved portions of the ventral furrows except the one anterior to *c* are much shallower than the transverse parts, as is indicated in the figure. In the one exception, the furrow anterior to *c*, the curved portion appears as distinct and deep as the rest of the furrow. In *a*, *b*, *d*, *e*, and *f* the inner portions of the organs of the right side are seen to lie in about their normal positions with respect to the boundaries of their segments. The ducts are parallel to the dorsal furrows and cross the course of the ventral furrows in each case, *i.e.*, they conform to the relations on the dorsal side. In the segment *c*, however, the ducts run nearly parallel to the

ventral furrows, crossing the dorsal furrow which forms the posterior boundary of *c*, and finally opening, together with the organs in *b*, into a single pore on the edge of *b*. This case appears to be an exception to the general rule of correlation between the arrangement of the genital organs and the form of the segment, for the ducts on the dorsal side cross the

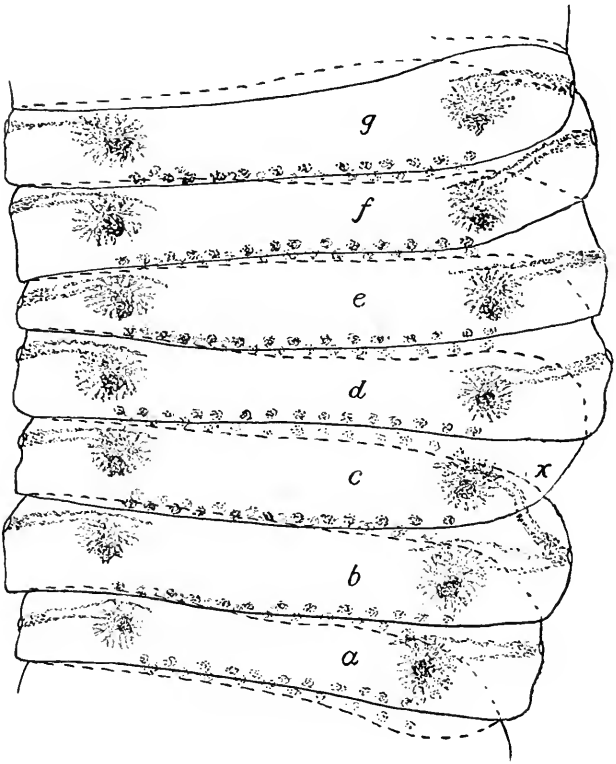

FIG. 36.

course of the dorsal furrow. As is evident from the figure, the ventral side of *c* and the dorsal side of *b* are very intimately connected at the right edge, more so than, for instance, the ventral side of *c* with the dorsal side of *d*. Moreover, the edge of *c* itself is oblique and very short, and the ventral furrow at *x* is deeper than the corresponding portions of the other ventral furrows. The course of the ducts from the organs at the right of *c*, differing as it does from the course of

the ducts in the other segments of the spiral, is undoubtedly determined by the relations existing here. Probably the small size of the dorsal side of *c* at the right is the real basis of the difference, for it is largely because of this that the ventral side of *c* is so intimately connected with *b* at the right.

The segment *g* is nearly normal in form in the region of the right ovary, and this lies in its normal position. Nearer the edge, however, the dorsal and ventral sides of the segment do not correspond, the ventral surface bending posteriorly, while the dorsal bends slightly in the opposite direction. The ducts and the pore evidently conform to the relations on the dorsal side, but they lie almost directly over one of the ventral furrows.

Figure 37.

This case comprises a number of segments which show an approach to the spiral form but do not quite attain it, since most of the furrows are not complete at the left. The figure is a dorsal view. It can easily be seen from the figure that if the furrows on the two surfaces were continued over the left edge, a spiral segment extending through the whole series would be formed. The manner in which a spiral arises is well illustrated by this case. The bending of the furrows near the edge on one surface is all that is necessary. Here the dorsal furrows bend anteriorly, while the ventral furrows remain straight, except between *a* and *b*, where there is a slight posterior curvature.

At the right the segments are all normally bounded, and the genital organs of the right side are normal in form and position. At the left, however, where the relations approach the spiral form, the organs show corresponding abnormal relations. At the left of *a* the anterior ventral furrow is normal in the ovarian region, but turns posteriorly near the edge, and the dorsal furrows bend anteriorly, so that the dorsal side of the segment appears curved forward at the left end. The ducts and pore show clearly the influence of this form. The course of the ducts toward the edge is oblique, *i.e.*, nearly parallel to the dorsal furrows in this region, and the pore lies nearly

in the middle of the edge as it is bounded dorsally. In *b* very similar conditions exist, but the bend in the dorsal surface of the segment is more pronounced than in *a*. The ducts are more oblique than in *a* and elongated, but preserve the same relations to the segment. The dorsal furrow forming the anterior boundary of *b* curves to such a degree that it does not reach the edge at all, thus leaving it apparently undivided, *i.e.*, not distinct from the edge of *c*. Near the middle of this common edge a single pore appears, and into this open the

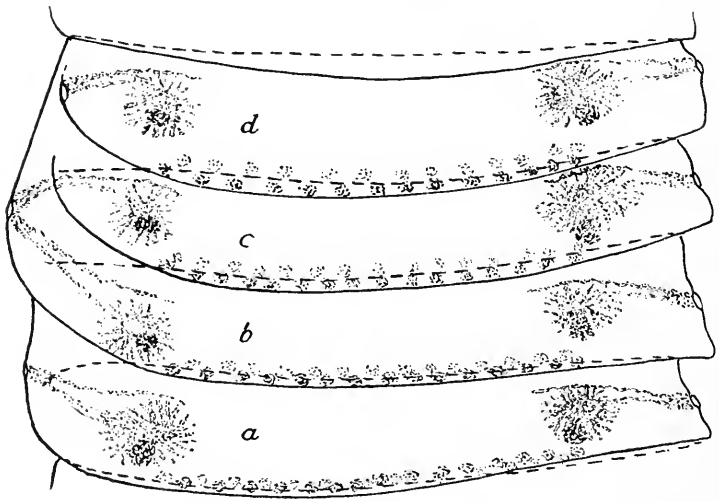

FIG. 37.

ducts from *c* as well as those from *b*. The ducts of the organs in *c* cross the course of the curved dorsal furrow to reach the edge, but this part of the furrow is very slight.

The organs at the left of *d* present an extremely interesting relation with respect to the furrow. The dorsal furrow between *c* and *d* turns anteriorly and runs parallel to the edge, but the furrow in front of *d* is straight. The ducts of the genital organs show no tendency to run parallel to the curved furrow, but meet it almost at right angles, and the pore appears in this furrow instead of upon the edge of the body. The furrow is deeper than the one posterior to it which crosses the ducts in *c*, apparently without affecting their position.

The difference in the relations in these two cases is undoubtedly due to the difference in depth of the two furrows. In the case of *d* the furrow is deep enough either to interrupt the course of the ducts or else to produce conditions approaching those at the edge of the body, and consequently the pore forms here instead of at the edge. The ducts are slightly shorter than the normal, but the inner portions of the organs show a perfectly normal arrangement.

2. *Other Abnormalities.*

Under this head are included a few cases of abnormalities of a different nature from those previously described. Two of these (Figs. 38 and 39) are cases of lateral duplication of the genital organs, and the other two (Figs. 40 and 41) are cases of alteration in position of the genital organs.

Figure 38.

The figure, a view from the ventral side, shows a number of abnormalities. Between the segments *a* and *b* the furrows are normal except near the right edge, where both curve posteriorly. On the ventral surface the furrow ends before reaching the edge, while dorsally it continues to the edge. The inner portions of the genital organs are normal, and the ducts extend in the normal direction toward the edge, but do not reach it. The pore lies on the curved dorsal furrow a short distance from the edge of the body, *i.e.*, on the dorsal surface. The terminal portions of the ducts are entirely normal in structure. Thus the abnormal edge formed by the curved furrow affords conditions which allow a normal pore and terminal organs to appear and so resembles closely the segment *d* in Fig. 37, except that there the furrow between *c* and *d* turns anteriorly instead of posteriorly. At the left of *a* the form of the segment and the organs are normal.

The segments *b* and *c* are incompletely separated on the ventral surface, and *c* is a spiral in consequence of the peculiar curve of the ventral furrow separating the parts *c* and *d*. On

the dorsal surface the furrows are normal, and the regions corresponding to *c* and *d* are parts of a single segment. Thus the spiral furrow bounding *c* and *d* begins ventrally between *b* and *c*, makes one turn, then bends anteriorly, separating *c* and *d*, next makes another almost complete turn and finally ends on the ventral surface anterior to *d*, so that *d* is not completely separated from the segment next anterior to it.

At the right of *b* the edge is very long in consequence of the curve in the posterior furrows, but there are indications that these curved portions of the furrows do not mark the

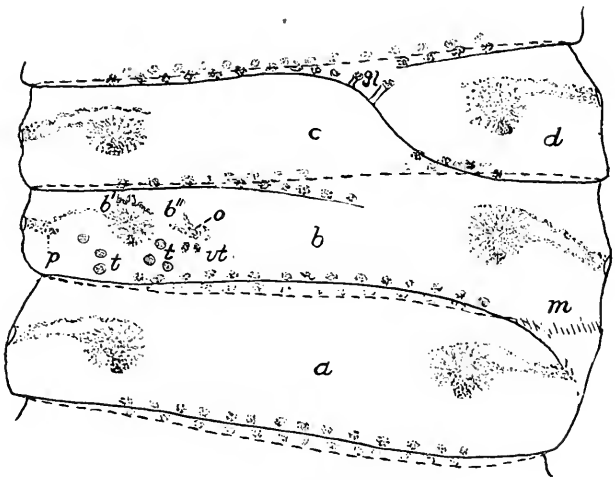

FIG. 38.

actual posterior boundary of *b*. Along the line *m* the cellular structure appears denser and stains more deeply, thus resembling in appearance the regions near the intersegmental furrows. There is no real furrow here, but the presence of this band of tissue similar to that which occurs along segmental boundaries indicates that the posterior boundary of *b* is here and not along the curved furrows; that is, these latter are mere wrinkles in the surface continuous with the intersegmental furrows. If this be the correct interpretation of the conditions here, it is evident that the ovary and pore at the right of *b* present the usual correlation in position with the form of the segment.

At the left of *b* peculiar conditions appear. Besides the organs (*b'*) in the normal position there is another partial set (*b''*) lying to the right of the first. The first set, although normally placed, is imperfect, for the ovary and vitellarium are rather smaller and less branched than usual; the oviduct, atrium, and pore are normal, but the vas deferens is not complete. Its inner end appears anterior to the ovary — near the letter *b'* — but it ends blindly posterior to the oviduct instead of in its normal position anterior to it. A peculiar condition appears in five or six of the testes (*t t*) near the edge. They are enlarged and packed full of spermatozoa, so that they stain like the vas deferens of this stage and are quite different in appearance from the other testes, though the testis cells can be distinguished in them with high powers. The inner portion of the vas deferens is also full of spermatozoa, but the seminal receptacle is empty, indicating that there is no outlet for the sperm into the female organs. In the normal organs of adjacent segments impregnation has already occurred. The accumulation of sperm in the testes (*t t*) is doubtless due to the imperfect development of the male ducts. The movement of the spermatozoa from the middle regions of the segment toward the edges having occurred as far as possible — the testes in the middle region are empty of sperm — they have accumulated in a number of testes near the edge and remain there, since there is no outlet to the exterior or to the female organs. This condition is found in one other case (Fig. 39).

The small size and imperfect development of the set of organs *b'* is probably due to the fact that the left half of the segment *b* is considerably shorter than the normal. The normal length at this age is about that of *a*, and this portion of *b* is only a little more than half as wide as *a*. At the right *b* is wider and normal organs occur.

The second set of organs (*b''*) is very small and rudimentary, consisting of a small simple ovary (*o*) and two small groups of cells representing the vitellarium (*vt*) without any traces of ducts. The orientation of these organs in the proglottid is apparently normal.

This transverse duplication of the female organs does not

appear to be connected with any visible abnormalities in the form of the segment or in the relations of its boundaries. The two sets of organs taken together probably do not represent more material than a single set of normal size. The left side of the segment *b* is somewhat shorter than normal, but in Fig. 39, *c*, where a similar duplication occurs, the segment is of very nearly normal length. The furrows bounding this region of the segment seem to be normal, except that the distribution of the inter-proglottidal glands in the dorsal furrow between *b* and *c* is rather irregular. None appear in this furrow in the middle region of the body, and only a few to the left of the middle. The furrow is normal in appearance, however, and the other furrows seem to be normal in every respect. The conditions found here may perhaps be due to the splitting of a single genital mass in earlier stages, but if this is the case no clue is afforded as to the cause of the splitting. If such a division should occur, later growth would undoubtedly increase the distance between the two portions. From a study of the early stages of the genital organs and their method of origin I am inclined, however, to believe that this extra set has arisen *in situ* and without connection with the set *b'*. If this is the case its appearance must be the result of certain internal conditions, which present no other visible manifestation.

This transverse duplication of organs constitutes a problem entirely different from that of their multiplication longitudinally. Whether or not it is to be regarded as the result of a kind of longitudinal division of the segment is doubtful. No organs except the ovary and vitellarium are duplicated in this case, *i.e.*, the organs on the ventral side only. This is likewise the case in Fig. 39. These two examples are the only ones of this nature which I have found so far, but it is hoped that additional material bearing upon this point may be discovered and may serve to throw some light on the factors concerned in the production of this peculiar abnormality.

The regions *c* and *d* of the ventral side are separated by a portion of the spiral furrow which runs almost longitudinally. At the right it forms the posterior boundary of *d*, but turns anteriorly and then continues as the anterior boundary of *c* at

the left. On the dorsal surface the furrows appear normal. Relations at the two edges are apparently normal, and the genital organs appear normal in all respects.

The relations of the inter-proglottidal glands to the abnormal furrows are interesting. Those portions of the furrow which run transversely show the glands in their usual position, but there are none in the region where the furrow departs from its transverse course. Two of the glands (*gl*) in the partial segment *d* present very peculiar relations to the furrow. Here the furrow bends posteriorly, but the last two glands appear at some little distance anterior to it and almost in line with the others and are connected with the furrow by distinct ducts of considerable length. In the posterior region of the curve two of the glands lie posterior to the furrow as it curves forward, but these open directly. The relation of the glands to this curved furrow affords further evidence in favor of the conclusion that the curved furrows do not always coincide with segmental boundaries. Here the glands do not follow the furrow in this curve, but lie at some distance from it and are entirely absent from that portion which departs farthest from the normal condition. It appears as if the glands follow the line of the real boundary, while the furrow does not. Nevertheless, as the presence of the ducts indicates, the glands tend to open in the furrow.

Figure 39.

The series of abnormalities occurring in the three segments represented here is in some respects the most peculiar that I have found in this species. The figure is a ventral view.

In the segment *a* the relations on the right are normal, but on the left there appears on the dorsal surface the anterior end of a spiral, the remainder of which is not drawn, as it makes only one turn and is similar to others already discussed. The ducts of the organs *a'* extend to the surface in accordance with the relations on the dorsal surface and thus open at a point on the edge which is dorsally a part of *a*, but ventrally in another proglottid.

The segment *b* is abnormally short, even more so dorsally than on the ventral surface. In accordance with this fact only partial organs are developed right and left (*lb'* and *rb'*). Ducts connecting with the surface do not appear at all, and on the left no pore is formed. On the right edge, however, a pore appears, of normal size and with atrium and a small portion of the oviduct extending inward from it. This portion was found upon examination to present the characteristic appearance of the oviduct and to possess a lumen, but was

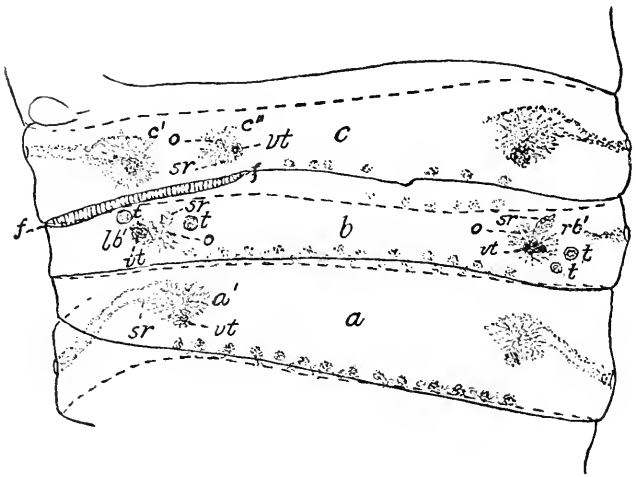

FIG. 39.

closed at the inner end. The reason for the appearance of a pore on the right edge and not on the left lies, I believe, in the fact that the right edge is longer than the left and thus presents more nearly the conditions of the normal edge. Each of the partial female organs *lb'* and *rb'* consists of a small ovary (*o*), a small vitellarium (*vt*), and the inner portion of the duct, terminating in a small, bladder-like, closed seminal receptacle (*sr*), which is empty. The organs of the dorsal surface are less nearly normal than those of the ventral. Testes appear, but their number is much less than the normal, even in proportion to the small size of the proglottid, for they are scattered very sparsely through the middle region, while other segments of this stage show large numbers of them. No traces of vasa

deferentia appear on either side. This rudimentary condition of the male organs is doubtless due to the extreme shortness of the proglottid. As on the left side of *b* in Fig. 38 the spermatozoa have accumulated in some of the testes in the lateral regions of the segment (*t t*). In this case there is no exit on either side of the spermatozoa, and the female ducts are incomplete and unconnected with the male ducts. Consequently the segment is not functional. The spermatozoa cannot fertilize the eggs of this or any other segment, and the eggs cannot be fertilized by spermatozoa from this segment or from any other.

The ventral furrow between *b* and *c* is distinctly abnormal, especially at the left. A normal furrow does not cut into the body vertically, but obliquely, and in such a manner that the posterior edge of each proglottid seems to overlap the anterior edge of the next succeeding. Over about two-thirds of its course the ventral furrow between *b* and *c* is normal in its relations, though slightly irregular in its course. Over the remaining third, however, — the shaded portion at the left marked *f*, — it is a vertical furrow widely open to the surface, and nearly twice as deep as the normal furrow by actual measurement. It cuts almost halfway through the body and thus separates *b* and *c* in this region much more completely than they are separated elsewhere. This portion of the furrow shows no inter-proglottidal glands, but they are present in the more nearly normal portion. The ventral furrow anterior to *c* is also abnormal at its left end. It is interrupted, one portion turning anteriorly, and the other curving near the edge so as nearly to enclose a small area. The dorsal furrow bounding *c* is normal.

In the segment *c* there are two normal sets of organs, the one situated normally, and the other nearly so ; but in addition to these organs a third set (*c''*) appears situated to the right of *c'* and consisting of a small ovary (*o*), a vitellarium (*vt*), and a small, empty seminal receptacle, which is closed. This case of transverse duplication of organs is very similar to the one figured in *b* in Fig. 38, and it is in the same region of the body, the two being separated by some thirty segments only. This second case does not afford any evidence as to the factors concerned

in the production of this form of variation. However, the position of the organs in *b* and *c* does bring to light some interesting facts regarding the orientation of the organs in the segment, indicating that this also is perhaps correlated with the "form" of the segment.

In the normal form of the female organs the vitellarium lies more or less completely posterior to the ovary, as is clear from many of the figures (see *a'* in segment *a* of this figure, for instance). The seminal receptacle appears at a point separated from the vitellarium by one-quarter of the circumference of the ovary, *i.e.*, about ninety degrees (note the position of *vt* and *sr* in *a'*, where they are normally situated). Now in the supplementary set of organs *c''*, in the segment *c* the vitellarium lies on the right side of the ovary, while the small rudimentary seminal receptacle (*sr*) is posterior. That is, the whole set of organs appears as if rotated through an angle of ninety degrees from its normal position. An oviduct, if present and normally oriented with respect to the ovary, etc., would lead to the shaded portion of the furrow *f*.

Turning now to the organs *lb'* at the left side of *b*, we find that the parts present in this set are the same as those found in *c''*, *viz.*, a small ovary (*o*), a vitellarium (*vt*), and a small closed seminal receptacle (*sr*). The orientation of this group, however, is different from that of *c''*. The vitellarium, instead of being in its normal position posterior to the ovary, lies at the left of it, while the small seminal receptacle (*sr*) is anterior to the ovary, instead of to the left. Here, then, the whole complex appears as if rotated through an angle of ninety degrees in the direction opposite to that in which the rotation of *c''* is conceived as having occurred. In consequence of this position, an oviduct, if present and oriented normally with respect to the other organs, would, as in the case of *c''*, open into the shaded portion of the furrow *f*.

Examination of the organs *rb'* at the right of the segment *b* shows that the relations there are more nearly normal. The vitellarium (*vt*) is somewhat posterior to the ovary, and the seminal receptacle, *sr*, though somewhat more than ninety degrees from the vitellarium, does extend in a nearly normal

direction, and if growth of the parts continued, the receptacle and the oviduct from the pore would meet. In brief, this set of organs shows what is practically the normal orientation, while *lb'* and *c''* do not.

The suggestion which offers itself in this connection is that the abnormal orientation of the organs *c''* and *lb'* is correlated with the presence of the furrow which lies between them. The furrow is on the ventral side, as are these organs. May it not be possible that the orientation of these two sets of organs with respect to this furrow is due to its extreme depth? They are oriented with regard to it as if it were the edge of the body, though no pores appear, opening into it. There is a considerable extent of free surface in the dorso-ventral plane on the sides of the furrow. The organs at *c''* are far from the real edge, but near this abnormal furrow, and their abnormal orientation appears to be a form of adaptation to the abnormal conditions. The complex of organs *lb'*, as described, is correspondingly oriented with regard to the furrow *f*. The question at once arises as to why this should be, since this set lies at the normal distance from the real edge. The answer to this question may lie in the fact that the left edge of the segment *b* and the region near it are very short — apparently too short to allow a pore and ducts to appear. The organs at *lb'* are much nearer to the furrow *f* than to the edge, and if the orientation of *c''* is determined by the furrow, that of *lb'* may be also. In the organs *c'* orientation and position are apparently normal. The pore lies rather far anteriorly, and this is probably due to the fact that *c* is incompletely separated dorsally from the segment next in front. The position and orientation of this set of organs may seem to be strong evidence against the conclusion that the orientation of *c''* and *lb'* is due to the presence of the furrow *f*, but here the edge is normal and the proglottid is of normal length, *i.e.*, normal relations are possible here, while they are not in the cases of *lb'* and *c''*. Furthermore, on the right of *b*, where the furrows are both normal, and the edge is wider than at the left, the organs are normally oriented and a pore is present, though the parts are not connected.

All who study the cases discussed in this and the preceding paper must, I believe, conclude that the position and arrangement of the genital organs in abnormal as well as in normal proglottids are very definitely determined by the form relations

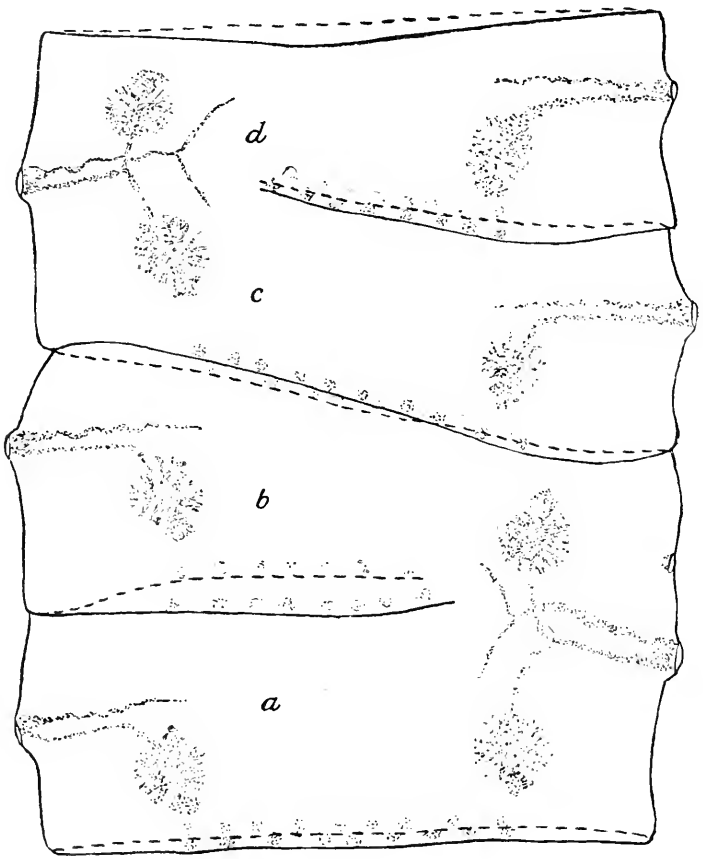

FIG. 40.

of their segment. The above suggestions have been made in the belief that the form relations may have some influence here, and in the hope of throwing some little light on the conditions in this particular case. Whether other similar cases, if found, will confirm them remains to be seen.

Figure 40.

Two cases of partial division are figured here as seen from the dorsal surface. The two are almost exactly similar, except that in one case the partial furrows extend from the left edge, in the other from the right. At the side of the body, which is completely divided in each case, two complete sets of genital organs normally situated are found. At the other side the inner portions are double, but the ducts unite to form a single

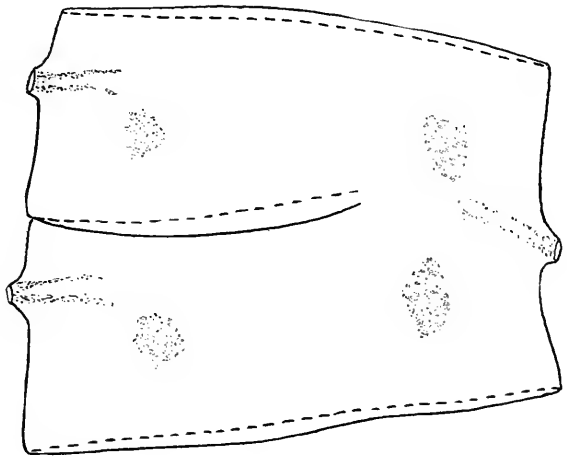

Fig. 41.

vas deferens and a single oviduct, and these open through a single pore, which is situated almost exactly in the middle of the undivided edge. The most remarkable fact is that the position of the anterior set is the reverse of that of the posterior set in each case, the oviduct running posteriorly from the ovary, and the vitellarium lying anterior instead of posterior to the ovary. The vas deferens also runs posteriorly instead of laterally. The arrangement of the organs is very evidently correlated with the incomplete separation of *a* and *b* and of *c* and *d*. The undivided edges of *a b* and *c d* are shorter than the divided edges, but the undivided edge of *a b* is longer than the undivided edge of *c d*, and it is interesting to note that in the region corresponding to *b* of the edge *a b* a second pore appears,

much smaller than the one posterior to it and without any ducts opening into it. Apparently the greater length of this edge has afforded space, as it were, for the formation of another pore, but the ducts connecting with it fail to appear. This case, like a number of others, shows that the pore may be wholly unconnected with the other organs, but that its formation is doubtless due to the general conditions that lead to the formation of the other portions of the set, even though the two parts do not unite.

Figure 41.

This case is very similar to the one shown in Fig. 40. The development is so far advanced that it is impossible to determine with certainty whether the division of the ducts is as complete as in that case. The cell-masses at the right representing the two ovaries and vitellaria appear about equal in size, and there are indications that they were connected with the single duct leading to the pore. It is impossible to determine whether the vas deferens divides or not.

Hull Zoölogical Laboratory,
University of Chicago,
May, 1900.

A CONTRIBUTION TO THE DEVELOPMENT OF PARYPHA CROCEA.[1]

CARRIE M. ALLEN.

My work has been carried on at the Zoölogical Laboratory of Syracuse University under the direction of Dr. C. W. Hargitt, to whom it is a pleasure to express my obligations for his kind suggestions and supervision throughout its progress, and for the pains which he has taken in furnishing me with the best of appliances and material. The material upon which the investigations have been made was collected by Dr. Hargitt at Woods Holl, Mass., during the summer of 1898. Through his kindness I had at my disposal an almost limitless supply killed and preserved by a number of methods. Picro-sulphuric acid and Perenyi's fluid both gave excellent results, but formalin proved unsatisfactory for histological work.

In most of my study I used preparations stained *in toto* in borax-carmine. The specimens were left in alcoholic borax-carmine for twelve hours, after which the stain was extracted by acid alcohol for from fifteen minutes to half an hour. In dehydrating they were left in each of the various grades of alcohol for thirty minutes, after which they were cleared either in cedar oil or chloroform. Both clearing agents gave good results, but the latter was preferable because of its rapid action.

In staining on the slide, iron-haematoxylin and double stain of eosin and haematoxylin both proved satisfactory.

In using the iron-haematoxylin the sections were fixed to the slide, carried down through the alcohols to 50 per cent, and placed in a 2 per cent solution of ammonio-ferric-alum for from thirty minutes to three hours. They were then washed in running water for twenty minutes, stained in 0.5 per cent aqueous solution of haematoxylin for from one-half hour to

[1] *Contributions from the Zoölogical Laboratory*, Syracuse University.

two hours, washed again in running water and cleared for a few seconds in iron-alum. After rinsing in distilled water they were plunged into 95 per cent alcohol, carried up and mounted in balsam. The best results were obtained by leaving the slides in each stain for an hour. This method was of greatest value in study of the segmentation of the egg. The cytoplasm appeared gray, chromatin fibers black.

In using the eosin-haematoxylin method the sections were stained for an hour in a 2 per cent solution of eosin in 90 per cent of alcohol, after which they were stained in a weak solution of Delafield's haematoxylin for twenty minutes. This stain gave very good general differentiation, and was of especial value in determining the origin of the sex cells.

A number of other stains and combinations of stains were used with fair success.

General Description of Parypha.

Parypha crocea is found all along the New England coast attached to floating timbers and the piles of wharves. It seems to prefer brackish water and partial sunlight, but often occurs in pure sea water.

This hydroid grows in colonies which arise from a single individual by a process of budding, and the sexes are always separate. The hydrorhiza is made up of a contorted mass of irregularly branched stems, from which the hydrocaulus of the individual hydroid arises. The stems bearing the adult polyps are usually two and a half to three inches in length, and short stems are sometimes found branching out from the main ones. Enclosing the stem is a horny, often annulated sheath, the perisarc. The polyp is borne at the top of a somewhat globular expansion of the hydrocaulus, and is almost conical in form, with a broad, saucer-shaped base. It contracts about three-quarters of the way up, forming a thick-walled, flexible proboscis, in the center of which lies the mouth, surrounded by a circle of short, thick tentacles with decurrent bases. Around the base of the polyp is a circle of long, slender tentacles, varying in number from sixteen to twenty-four. The medusoids

are borne upon long, slender, branched peduncles which arise a short distance above the tentacles of the lower row. All parts of the hydroid are made up of the two layers characteristic of all hydroids, but the mesogloea forms only a thin layer in the peduncles and tentacles and is not visible in the medusoids. The tentacles of both rows consist of a central axis of the endoderm, surrounded by a thin layer of ectoderm.

Origin and Morphology of Male Gonophores.

The medusoids in this species begin to appear early in the development of the hydroid, when the head upon which they are borne is less than a quarter of the size of the adult polyp. The first indication of their formation is a slight outpushing of the endoderm of the body wall a little above the axils of the lower row of tentacles. The ectoderm is pushed out and becomes thinner than in the adjacent parts of the wall. The papilla thus formed elongates into a peduncle communicating directly with the body-cavity of the polyp. From this peduncle arise short branches which may subdivide, and it is at the ends of these that the medusoids are borne. At first there is merely a thickened layer of endoderm surrounded by a thin layer of ectoderm, but when the length of the bud is about once and a half the width, the ectoderm cells at the tip begin to grow rapidly, forming a plug of cells with large nuclei and indistinct boundaries (Pl. I, Fig. 1). For a time the endoderm is forced back (Pl. I, Fig. 2), but it soon begins to grow down into the center of the plug, to form the manubrium, and around the outside to form the endodermal layer of the bell. All the cells between this layer and the manubrium are of ectodermal origin, and from them the reproductive elements arise. The sex cells increase in number, and to some extent in size, until they occupy the greater part of the bell. While this growth is taking place the cells at the distal end of the gonophore next the endodermal layer of the bell begin to differentiate, forming a thin, delicate layer which gradually extends around the gonophore and becomes the inner wall of the bell (Pl. I, Fig. 3). It is made up of cells much smaller than those from which they

are derived. Meanwhile the endodermal layer has thickened in four regions equidistant from each other at the distal end of the medusoid. At first the cells in the thickened region are irregularly arranged, but later they form themselves into two rows with a space between them. In a few cases no cavity was found, and in two of the gonophores examined it extended halfway around the bell. The remainder of the wall consisted of a single layer. Pl. I, Fig. 4, represents the condition found in most of the medusoids. Agassiz ('62), p. 259, states that there are neither radial nor circumoral canals in this species but the position and mode of development of these cavities leave little doubt that they are rudimentary radial canals. No circular canals were observed, and the radial canals were never found connected with the body cavity of the medusoid in any of the hundreds of sections studied.

Spermatogenesis.

The large nucleated cells lying between the manubrium and the inner wall of the bell become the sperm mother-cells, which finally break up to form the sperms. In the first division the karyokinetic figures are distinct and show spindles and prominent chromosomes. The later stages were difficult to study because of the minuteness of parts, and I was unable to demonstrate clearly the exact number of spermatozoa derived from a single germ cell, but I think four are usually formed. Their structure could only be made out in particularly favorable sections, but was easily demonstrated by crushing the gonophore and allowing the sperms to escape. They consist of a pear-shaped head with a very long, slender tailpiece. When fully developed the male gonophores are spherical, and the walls are so thin that their structure can only be determined by the use of very high powers. They bear no tentacles, although the ectoderm is sometimes thickened slightly in the regions where tentacles arise in the female. I examined carefully a large number of mature male gonophores to learn whether or not the ectodermal layer of the manubrium was formed and discovered a definite transparent layer next the

endoderm. No gonophores from which the sperms had been expelled were found, so I was unable to prove that this represented the ectoderm of the manubrium, but as that layer was not observed in the female until a very late stage, I think that there can be little doubt that it functions as such.

Origin and Morphology of the Female Gonophore.

The female gonophores arise in the same manner as the male and, in the early stages, are made up of the same parts, but later may always be distinguished by a circle of six or eight short, blunt tentacles at the distal end and by their more elongated shape. When filled with young they are nearly spherical and the tentacles mere papillae; but when the larvae have been set free the medusoids become elongate and the tentacles expand. Pl. I, Fig. 5, shows a section through two of these tentacles.

Oögenesis.

The primitive egg cells are developed in the same manner as the sperm mother-cells. I find no evidence whatever of ova either in the coenosarc of the stem, the body of the polyp, or the walls of the peduncle. There are in the endoderm of the polyp and peduncle numerous large, deeply stained cells with large nuclei which somewhat resemble eggs when cut in the right plane, but a careful study of a large number of sections reveals the fact that they are in reality highly differentiated endodermal cells. They are always in contact with the supporting layer and usually project beyond the other endoderm cells into the body cavity, neither of which conditions, according to Weismann (**83**), p. 70, occurs in egg cells. Moreover, these cells are much larger than the primitive ova and take a deeper stain than do the eggs in any stage of their development. They are very rich in protoplasm, and sometimes the outer surface is found sloughing off into the body cavity. This condition was even more marked in similar cells in Eudendrium ramosum, where they extend farther into the body cavity, and the discharge of portions of their protoplasm was

very evident. All this would indicate that they were glandular in function. They are largest and most numerous in the peduncle and occasionally one is found in the manubrium, but such cases are rare. It would be impossible to distinguish a section through the peduncle of a male head from that of a female, as these cells are equally conspicuous in both. Pl. I, Fig. 8, shows a number of these glands, one of which resembles an egg, but other sections through the same peduncle show that it is really in contact with the supporting lamella.

In the younger stages of development the manubrium of the female appears to consist entirely of endoderm, but when the gonophore is fully mature and the primitive ova have disappeared, a thin layer of ectoderm is found to be present. It consists of a single layer of much flattened cells with smaller nuclei than those of the germ-tissue cells from which they are derived.

Development of the Ovum.

The primitive egg cells make up the large mass of tissue lying between the manubrium and the inner wall of the bell. They are packed closely together, so that the outlines of the cells are more or less irregular. The nuclei are large and spherical and contain a prominent nucleolus which takes a very deep stain. The mass of protoplasm surrounding each nucleus is small, and the cell boundaries are very indistinct (Pl. I, Fig. 4).

As the gonophore grows older the nuclei of the germinal tissue become much larger and more prominent, the mass of protoplasm surrounding them increases in bulk, and the cell boundaries become more clearly defined. At this stage the nuclei appear as very large spheres, with the chromatin fibers arranged in a sort of network around the periphery. Within the layer of chromatin is a colorless mass, near the center of which lies the nucleus suspended by four or five slender threads, which run out to the layer of chromatin. These threads take a fainter stain than the chromatin fibers and are only visible in especially well prepared specimens.

The nucleolus is usually spherical or slightly elongated,

but in many cases it shows a varying number of short, blunt processes. This condition was most clearly seen in sections stained with ammonio-ferric-alum and haematoxylin.

Within the nucleolus are a number of small, transparent, highly refractile bodies, the nature of which will be discussed later. There is usually one of these in the nucleus of each primitive ovum, but some contain two. As the ova grow older the number increases and there are sometimes as many as four or five in a single nucleolus. The protoplasm of the cells is granular and often contains a few small vacuoles.

Up to this time the growth of the various cells of the germinal tissue has been about equal, but now several cells increase markedly in size, and often the greater number in one side of the gonophore are found to be thus growing. If, however, a large number take part in this early development, the cells in the opposite side of the gonophore decrease in size, both nucleus and cytoplasm becoming smaller. Soon a few cells attain greater size than the rest and develop very rapidly. Many of the cells in this and the preceding stages are found to possess pseudopodia-like processes quite similar to those figured by Doflein ('96) for Tubularia. Smallwood ('99) mentions the same condition in the eggs of Pennaria. The pseudopodia extend in between the other primitive egg cells, and the tips are more granular and take a deeper stain than the rest of the egg. Doflein ('96) has given much attention to the amoeboid forms assumed by eggs of Tubularia, and he inclines to the belief that these processes do not function as mouths by which the surrounding eggs are bodily engulfed. My results have coincided very closely, in most respects, with those of Doflein, but numerous cases were also observed where the outline of the absorbed egg could be definitely made out within the protoplasm of the absorbing egg. Even in these cases, however, the absorbed egg did not lie in a vacuole, as would the food taken in by the amoeba, and the outline could only be made out by the greater density of its protoplasm. It seems, therefore, that in this case also we have a blending of the protoplasm of the two cells rather than a digestion and absorption of the one by the other. There seems to be no great uniformity either

in the number or location of the primitive cells which finally become ova, although by far the greater number lie next the manubrium, and few, if any, develop on the outer surface of the germinal mass. I am inclined to agree with Doflein ('96), p. 65, that all of the cells of the germinal tissue have potentially the capacity of becoming eggs, but that those favored by better nourishment or advantage of position are the first to develop.

He says in this connection : "Das starke Wachsthum des Gonophors hat einzelne Lücken und Spalten im Gewebe entstehen lassen, und in diese wachsen nun die Keimgewebezellen mit ihren Fortsätzen hinein." But while in my investigations many such cracks were found, in most instances the pseudopodia extended between eggs where no crack occurred, and in the greater number of ova no pseudopodia were present at all. I am, therefore, led to the belief that proximity to cracks in the germinal tissue is not of controlling importance, although the eggs do undoubtedly take advantage of the room afforded by such cracks when present. Doflein ('96) also states that in Tubularia the growing eggs are always found next the manubrium or upon the outside of the germinal mass, unless cracks are present within the tissue. I have examined a large number of sections, and I find that in Parypha the eggs of the outer layer are the last to develop, but that those in the interior of the germinal tissue are often found considerably enlarged even in the younger gonophores.

When the growing cells have attained a diameter about three or four times that of the cells of the germinal tissue, the nucleus is found lying close to the periphery of the egg and is oval and transparent, the chromatin fibers being scarcely visible (Pl. II, Figs. 5, 6). The nucleolus takes a fainter stain, and in most cases contains a number of the refractile bodies already mentioned. Later these bodies apparently unite, as nearly the whole nucleus is often occupied by a single large one. Just what their character is I am unable to state, but they appear to contain oil, and certainly they are associated with the peculiar metabolism exhibited by the cell at this time (Pl. II, Figs. 5–7). In some of the eggs in which the nucleus had this peripheral position, its outline was irregular upon the

inner side so that it resembled the figure shown by Hickson ('90) to illustrate the stage in the fragmentation of the oösperm nucleus of Allopora. In the next stage the nuclear membrane is broken down and the nucleoplasm blends with the cytoplasm of the egg, from which it can only be distinguished by its homogeneousness and greater transparence (Pl. II, Figs. 7, 8). In other eggs having the same general appearance as the last no nucleus whatever is visible. I have several complete series through eggs in this stage, none of which show any signs of a nucleus, although they have been stained by a number of different processes, and I am perfectly confident that the nucleus would be visible if present. Hickson describes a similar condition in the eggs of Allopora, Milleopora, and Distichopora; and Dr. C. W. Hargitt tells me that in his opinion a like condition is to be found in Eudendrium, although he has not yet placed it beyond doubt.

Hickson ('93) has written an extended account of "nuclear fragmentation," in which he cites the opinion of a number of authors with regard to this much disputed question. After describing the stages observed in Distichopora he says: "I have described a process which can only be compared with the so-called free nuclear formation in the early insect embryos. Nuclei make their appearance in places which were previously devoid of any nucleus or nuclear structure. It is not reasonable, however, to assume on the insufficient evidence before us that "nuclear formation" does actually occur. It seems to me much more probable that minute fragments of nuclear substance scattered through the protoplasmic meshwork collect together in places, and form by their fusion true recognizable nuclei. In other words, the process we have under observation is rather one of "nuclear regeneration" than one of free "nuclear formation." He quotes Flemming and Ziegler as authorities most opposed to this view, both these investigators contending that any process of nuclear division other than that by mitosis is a sign of the degeneration of the nucleus and the approaching end of the life of the cell. Ziegler inclines to the opinion that nuclei which have arisen by amitotic division will never again divide mitotically. Opposed to these are the works

of Verson, Frenzel, Löwit, and others who, since the publication of Ziegler's paper, have called attention to cases of amitotic division of the nucleus which are certainly not followed either by nuclear degeneration or a cessation of cell multiplication. Altogether there seems to be constantly increasing evidence that such a fragmentation does occur in the ova of widely separate groups of animals.

Wilson ('96), p. 85, believes that the subject requires more study, but says: "There can be no doubt, however, that Flemming's hypothesis in a general way represents the truth, and that in the majority of cases amitosis is a secondary process which does not fall in the generative series of cell division."

Absorption.

At about the time when the transparent nucleus lies near the periphery of the egg the cytoplasm changes from a granular to a reticular structure. The boundaries between the large cells and those adjacent to them now begin to break down and the protoplasm to blend. This fusion may take place between two large cells or between a growing cell and a germ tissue cell. The former usually occurs first, the large cells near the manubrium fusing and then gradually taking in the germ cells which surround them. The nuclei of the latter are found lying in the protoplasm of the absorbing cell. Both conditions are shown in Pl. I, Figs. 6, 7.

The outline of the syncytium thus formed is very irregular, and parts of the walls of the constituent cells persist for a time, showing where the fusion has occurred (Fig. 7). Doflein ('96), p. 66, states that in Tubularia one large, well-nourished cell controls the absorption, and that as it grows its nucleus also increases in volume, and that the nucleus becomes the functional nucleus of the ovum, the other nuclei being gradually absorbed. In Parypha, as already stated, the nuclei of the growing cells disappear at an early stage so that only the nuclei of the smaller cells persist. It thus becomes impossible to tell which is the controlling cell.

Finally the mass of fused cells takes on the typical egg

form, the protoplasm near the periphery becomes more dense, and the absorbed nuclei are found in various stages of disintegration. The egg now lies on the outside of the mass of germinal tissue and next to the wall of the bell. No evidence of fusion with the primitive eggs was observed after this stage was reached, although the two were still in contact. It is quite evident, however, that the remaining germ cells grow and unite to form new eggs later in the history of the parent, since primitive eggs are often found in advanced stages of growth, while two or three nearly mature embryos still occupy the gonophore. In other cases the gonophores contained several embryos in various stages of development, but no primitive ova. Doflein ('96), p. 67, states that, although he was unable to obtain sections to illustrate adequately the point, he believes that the germ cells of Tubularia do unite to form new eggs after the larvae have left the gonophore. In Parypha there is no chance to doubt that new ova are formed even before the exit of the larvae.

Fertilization.

As is the case in many of the hydroids, the process of fertilization is shrouded in mystery. The fact that the eggs are developed in closed gonophores makes it difficult to decide just when fertilization takes place. In discussing the development of Allopora, Hickson states that he believes that fertilization occurs while the nucleus lies at the periphery of the egg, and previous to the time when it becomes irregular in outline. From the positions of the eggs in which these irregular nuclei were found, *i.e.*, next the manubrium, this might be the case here, but nothing was discovered which threw any light directly upon the matter.

History of the Pseudo-Cells.

The nuclei of the absorbed cells are found in various stages of disintegration within the ovum. Some of them resemble so closely the nuclei of the germ-tissue cells that, were it not for the position and the vacuoles within which they lie, it would be

impossible to distinguish them. Later the chromatin fibers lose their reticular arrangement and assemble into a varying number of small spheres just within the periphery of the nucleus, and at the same time the threads which support the nucleolus disappear. The ground material in which the chromatin is suspended, and which up to this time has been nearly transparent, now begins to react to the staining agents, and the structure of the nuclei becomes obscure. If, however, methyl-blue was used, this substance was only slightly affected, so that this stain proved most satisfactory for the study of the various phases exhibited by the retrograding nuclei, or pseudo-cells, as they are sometimes called. Many of the nuclei are often found in the process of division. The nucleolus lengthens slightly, and finally separates into two parts. Later the entire nucleus divides and part of the chromatin goes with each half. Cases in which the nucleolus had divided were very numerous, but very few were found in which the division was actually taking place. Pl. II, Fig. 11, shows such a one, and Fig. 10 represents a nucleus in which there were three processes on the nucleolus. No chromatin fibers were visible in either of these cases. The halves thus formed often divided again, sometimes before they were separated, and in some instances as many as six parts can be observed. The chromatin globules vary in number and size in the various parts (Fig. 12). In some of the nuclei the division is less regular, and portions are often found in the process of being absorbed into the protoplasm of the egg. Fig. 15 represents a nucleus in which the parts formed by the first division were of very unequal size. In the smaller the nucleolus has again divided, but the larger part has been partially absorbed. Often several of these nuclei are found in a single vacuole. Fig. 9 shows one in which there were seven in various stages of disintegration, but usually not so many are found. Doflein believes that they are carried into the vacuoles by currents in the protoplasm. All this goes to strengthen the opinion of Doflein that the absorbed nuclei take the place of the yolk-granules, which are wanting in this species, and that they are gradually broken down to serve as food for the developing egg. They persist through the entire

embryological development, being very numerous in the endoderm of the young hydroid when it escapes from the gonophore. Isolated ones are even found in the endoderm of the tentacles, as noted by Doflein, but I cannot agree with him that they are entirely confined to that layer.

Segmentation of the Ovum.

The egg, after assuming the typical form already described, goes into a resting stage, as a large number are found in that condition and without nuclei. Soon, however, an irregular mass of nuclear matter appears at one pole. Sometimes this forms a single mass, in other cases it is made up of two or three more or less isolated portions. Whether these are finally assembled to form a single nucleus, or whether two or three nuclei are thus produced, I am unable to say, as many of the sections in the later stages might be interpreted either way. In some of the eggs a single definite star-shaped nucleus was present, but in others there were two, and in one case four of these nuclei lying close together at one pole of the egg. There was nothing in these eggs to indicate that the nuclei had not been derived from a single nucleus, but, on the other hand, some of the disorganized masses of nucleoplasm could not but give the impression that more than one would be formed. However, the number is of minor importance, and the real interest attaches to the fact that such a reorganization occurs at all. That it does, I am fully convinced. I have examined a large number of sections with this question particularly in my mind, and am forced to the conclusion that the nucleus of the mature egg is formed by the reorganization of the fragments of the nuclear matter scattered through the cytoplasm.

The earliest stage in which definite mitosis was observed was in the egg shown in Pl. III, Fig. 1. In this three definite nuclei, one in a process of division, showed in a single section. Another section through the same egg revealed a fourth nucleus which, from its position, might have been derived from one of the others, but no spindles were observed. There were no signs whatever of segmentation planes in this egg. The development in the eggs of Parypha is very irregular indeed,

and seems to be governed by no single law. In some cases definite cell walls were found in the earlier stages, as in Fig. 2, where four cells had been formed, one of which contained two nuclei. In this we have only the stage next to the one last described, but in that there were no segmentation planes at all. In still later stages the development is quite as irregular. Fig. 5 shows a section in which six nuclei were visible, and other sections through the same egg contained several others, some of which were in the process of division, but no cell walls had been formed In Figs. 6 and 7 we have sections through much older eggs, but the same indefiniteness of structure prevails. From the foregoing illustrations it will be seen at once that there is little uniformity in the early development of the eggs of Parypha, either as to size of the cells formed or the number of nuclei that appear previous to the formation of the cell walls. Segmentation does, however, begin at one pole, and the greater part of the egg is for a time unsegmented. In no case did I find the egg divided into two equal parts, as Dr. Hargitt has sometimes observed in Pennaria eggs. Pl. III, Fig. 3, represents conditions similar to what is constantly met with in eggs of Pennaria. In total segmentation the ovum consists of a solid sphere of cells of more or less uniform size but with irregular outlines. They are very reticular in structure, and large vacuoles are numerous.

Formation of the Ectoderm.

Following the complete segmentation, the first indication of a differentiation into ectoderm was observed in an increased amount of cytoplasm in the outer layer of cells. These cells then divide radially, forming narrow cells, as shown in text Fig. 1. The two mitotic figures lay in adjacent cells, as shown in the drawing. In the next stage observed the ectoderm appeared to consist of two layers of cells much smaller than those of the endoderm, and distinguished from them by the greater density of protoplasm. The two layers appeared in this case to be dovetailed into each other, as shown in Fig. 2 of the text. In the fully formed ectoderm the cells are very elongate and somewhat

spindle-shaped, with one end broader than the other. Both the form of the cells and the position of the nuclei indicate that they have been formed from a condition like that in Fig. 2, and not by further delamination of the outside layer alone. At this stage the larva is made up of a solid mass of irregular cells with spherical nuclei surrounded by a single layer of much elongated cells. No segmentation cavity is formed. The origin of the germinal layers agrees, therefore, quite closely with that described by Hickson ('93) under *E. c.*, p. 52: "A sterrula is formed by precocious delamination. No segmentation cavity is formed, and segmentation is at first incomplete." Parypha is not mentioned by Hickson under this class, and Tubularia, the form most like Parypha in its general mode of development, he includes under another head. Dr. Hargitt informs me that nothing equivalent to true delamination or invagination occurs in Pennaria. It would, therefore, seem that no one, two, or even three laws of cleavage are sufficient to explain the varied conditions to be found in the segmentation of the hydroid egg.

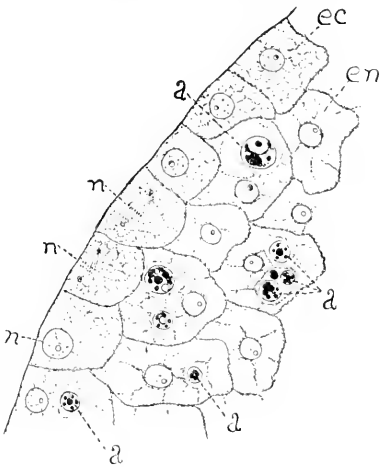

FIG. 1 × 560. — Early stage in the formation of the ectoderm of the embryo; *ec*, ectoderm; *en*, endoderm; *n*, nuclei; n^1, nuclei in the process of division.

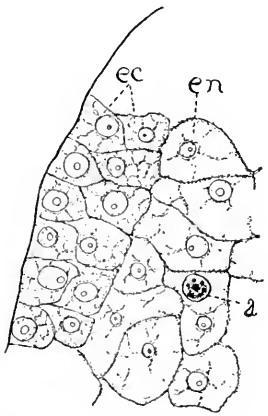

FIG. 2 × 560. — Later stage in the formation of the ectoderm; *ec*, ectoderm; *en*, endoderm; *a*, nuclei of absorbed cells.

The embryo now appears concave upon the side next the manubrium, but this is probably due to pressure and not to any intrinsic cause. After the formation of the ectoderm the two layers of the embryo evaginate at seven points so that a section through the region of the process appears star-shaped,

the rays at first being very short. These processes elongate to form the basal tentacles of the young hydroid. While this growth is taking place the convex side of the embryo becomes still more convex, and the concave portion between the tentacles evaginates and becomes convex also. In this way the endoderm cells in the center are split apart and the body cavity is formed. At first it is very irregular, but later the endoderm cells assume the typical endodermal form and arrange themselves in a single layer within the ectoderm, and the body cavity

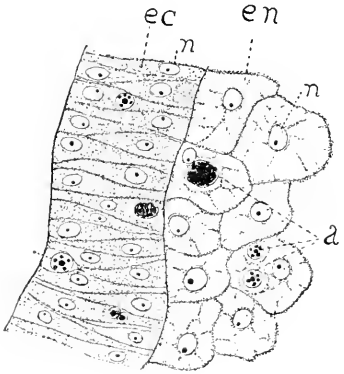

FIG. 3.

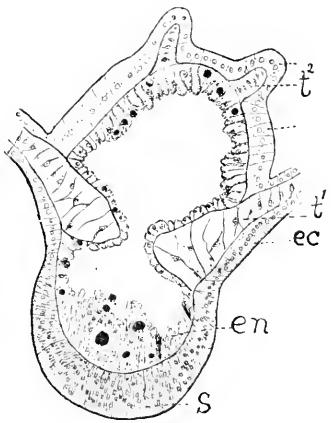

FIG. 4.

FIG. 3 × 560. — Fully formed ectoderm from convex side of embryo; *ec*, ectoderm; *en*, endoderm; *n*, nuclei; *a*, nuclei of absorbed eggs.

FIG. 4 × 190. — Young embryo ready to escape; t^1, basal tentacle; t^2, buccal tentacle; *s*, stalk; *ec*, ectoderm; *en*, endoderm.

takes on a form quite similar to that of a young polyp. From almost the earliest stage in the development of the ectoderm the cells on the convex side of the embryo appear much longer than upon the opposite side, and it is this portion which becomes the stem to which the young hydroid attaches itself. According to Agassiz the larva escapes in this condition, and the mouth and buccal tentacles are developed after it attaches itself. I have, however, obtained sections of a large number of mature larvae in which well-developed tentacles were present. Fig. 4 represents an embryo that was just leaving the gonophore. The body and the stem were both well developed, and the basal tentacles were nearly twice as long as the body.

At the buccal end there were five or six tentacles, a section of which is shown in the figure. Whether the mouth is developed at this time or later I did not decide.

Summary and Conclusion.

In a summary of the results obtained in this study, the following points should be noted:

1. The medusoid develops from a bud formed by an outgrowth of the body wall and shows itself first in a thickening of the endoderm.

2. The sex cells in both the male and the female are derived from the plug of ectodermal cells which is formed at the apex of the bud.

3. The medusoid is never set free and no circular canal is formed, although remnants of four radial canals are quite conspicuous.

4. The eggs grow by the absorption of the cells of the germinal tissue, a syncytium being thus formed.

5. The nuclei of the primitive eggs persist as pseudo-cells and are gradually broken down to serve as food for the growing embryos.

6. The pseudo-cells divide amitotically, but are finally absorbed by the growing egg.

7. The nucleus of the growing egg is absorbed at an early stage, but is re-formed, after the assumption of the typical egg form, from the fragments scattered through the protoplasm.

8. Segmentation is very irregular and nuclear division often outruns the segmentation of the egg.

9. The ectoderm is formed by radial delamination of the two outer layers of cells.

10. The embryo escapes as an actinula with both basal and buccal tentacles.

The results obtained in this investigation differ in several points from those of Agassiz, whose description of Parypha crocea is the only one that I have found. Clark ('93), to be sure, refers to the eggs and spermatozoa of this species, but gives no account of them. Agassiz states that he was unable to

find any trace of eggs, and that the embryos are developed from a large spherical portion which buds off from a granular mass of protoplasm formed by the separation of the endoderm and ectoderm in the medusoid bud. This granular mass he calls the "germ basis." A study of stained specimens in section shows clearly that this granular mass, or "germ basis," as he calls it, is really the mass of sex cells which have already been described. His opinion that the embryo was formed by the budding off of large portions of this mass probably arose from the fact that in the early stages of the development the eggs are packed closely together and the membranes are indistinct, so that the whole mass appears somewhat homogeneous. As the eggs grow, they become less granular and in time are entirely separated from the germ tissue. As to the radial canals, they would probably be overlooked, except in sections, as they are never functional. The tentacles of the embryo are, however, so well developed that it seems strange that he should not have observed them, since he has noted tentacles upon the female gonophore where they are less clearly defined.

SYRACUSE UNIVERSITY, May, 1900.

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EXPLANATION OF PLATE I.

FIGS. 1–7 × 190; FIG. 8 × 270.

FIG. 1. Young medusa bud showing the formation of the germinal cells from ectoderm of bud. *ec*, ectoderm; *en*, endoderm; *h*, germinal cells.

FIG. 2. Later stage, germinal cells separated from the ectoderm of the bud.

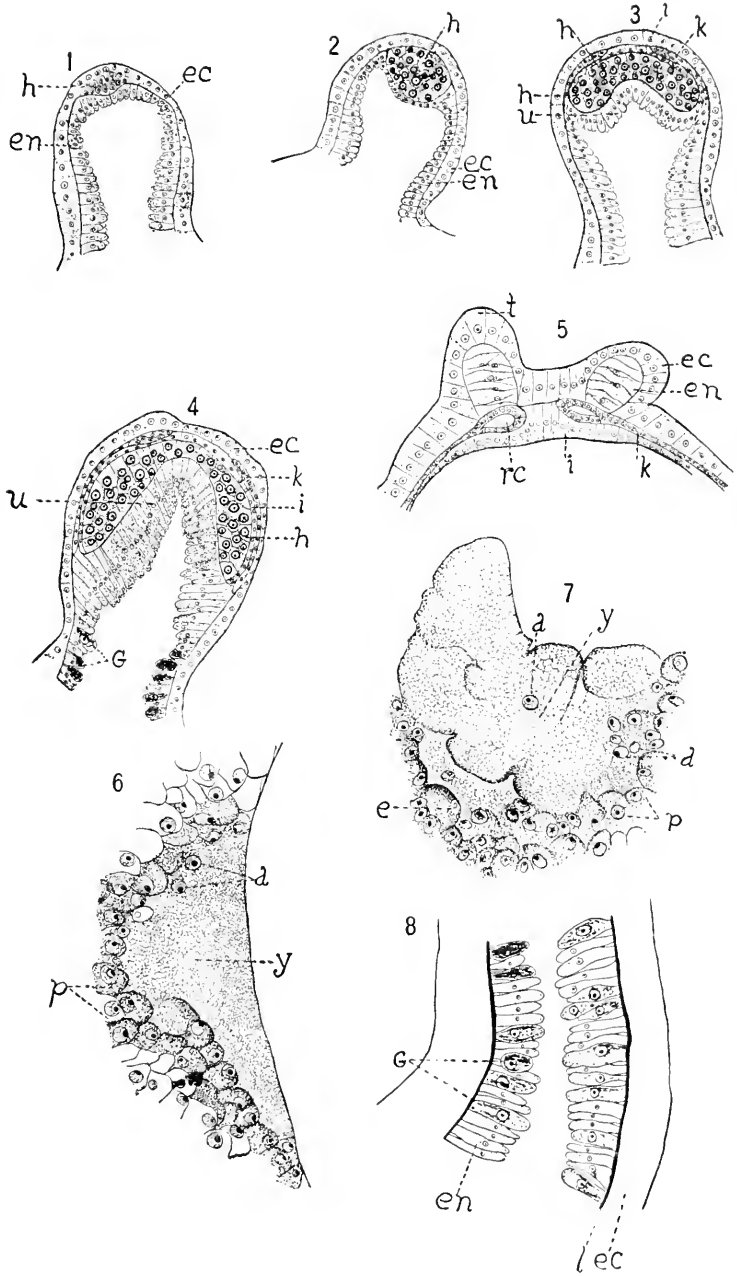
FIG. 3. Still later stage showing the mode of formation of the endodermal layer of the bell (*k*), the inner ectodermal layer (*i*), and the manubrium (*u*).

FIG. 4. Showing the layers of the bell completely formed.

FIG. 5. Distal end of mature female gonophore showing tentacles (*t*), rudimentary radial canals (*rc*), outer ectodermal layer of the bell (*ec*), and endodermal layer (*k*), inner ectodermal layer (*i*).

FIGS. 6, 7. Showing growth of the egg by the absorption of the primitive egg cells (*p*). Syncytium thus formed (*y*); nuclei of absorbed cells (*a*); young growing cell (*e*).

FIG. 8. Longitudinal section through peduncle from female head showing gland cells (*G*).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3
h
k
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4
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t
ec
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rc
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k
6
d
y
p
7
a
y
d
e
p
8
G
en
ec

EXPLANATION OF PLATE II.

FIG. 1 × 127; FIG. 2 × 118; FIGS. 3–8, 10–15 × 765; FIG. 9 × 495.

FIG. 1. Growth of ovum (*e*) by absorption of primitive cells (*f*).

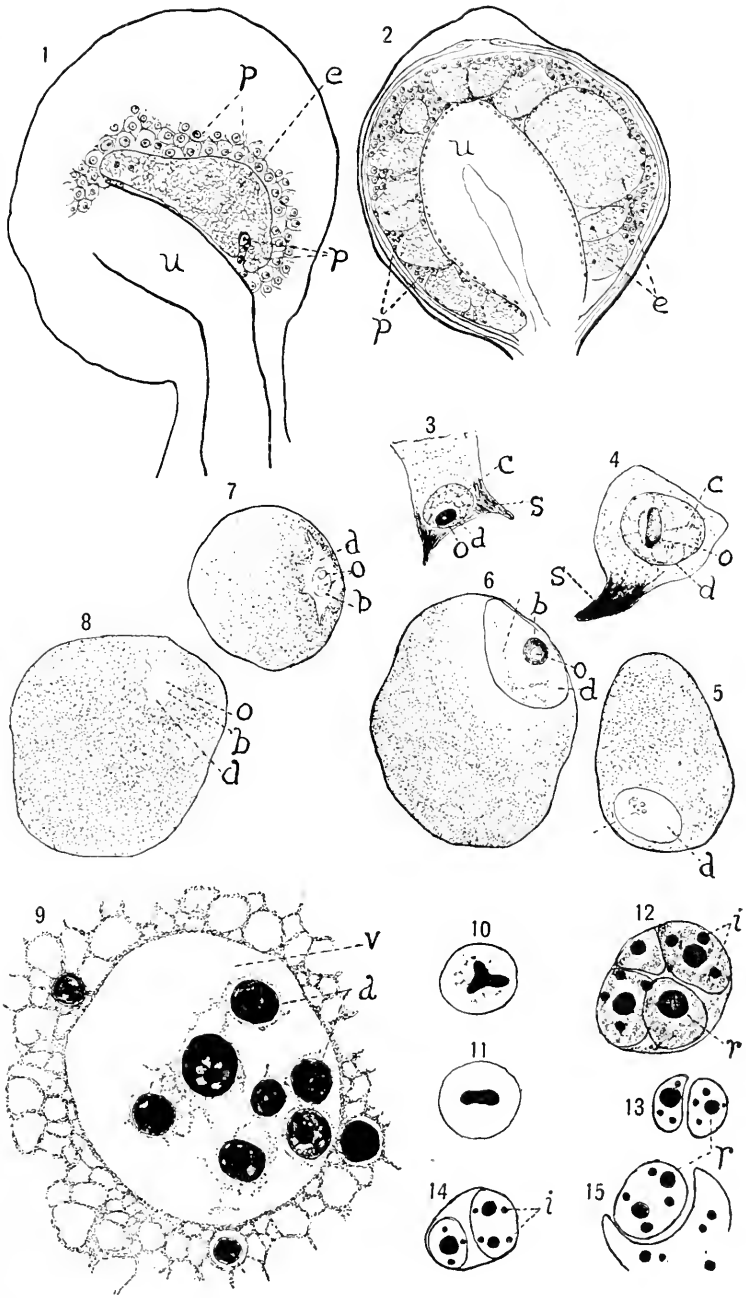
FIG. 2. Showing the number of growing primitive egg cells to be found in a single gonophore.

FIGS. 3, 4. Primitive egg cells in early stage of development showing pseudopodia (*s*); nucleus (*d*); oil drops (*o*); chromatin fibers (*c*).

FIGS. 5–8. Later stages showing the disappearance of the nucleus of the growing egg. *d*, nucleus; *b*, nucleolus; *o*, oil drops.

FIG. 9. Vacuole (*v*) in segmenting egg showing nuclei of absorbed cells (*a*) in various stages of disintegration.

FIGS. 10–15. Retrograding nuclei of absorbed cells. Nucleolus (*r*); assembled chromatin fibers (*i*). In Fig. 15 a portion of the nucleus has been absorbed; the smaller part is in the process of division, the nucleolus having already divided.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b
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7
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8
o
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9
v
d
10
11
12
i
r
13
r
14
i
15

EXPLANATION OF PLATE III.

FIGS. 2, 6 × 115; FIGS. 1, 3–5, 7 × 152.

FIG. 1. Young ovum showing three nuclei (n). n^1 in the process of division. No segmentation planes visible; a, nuclei of absorbed cells.

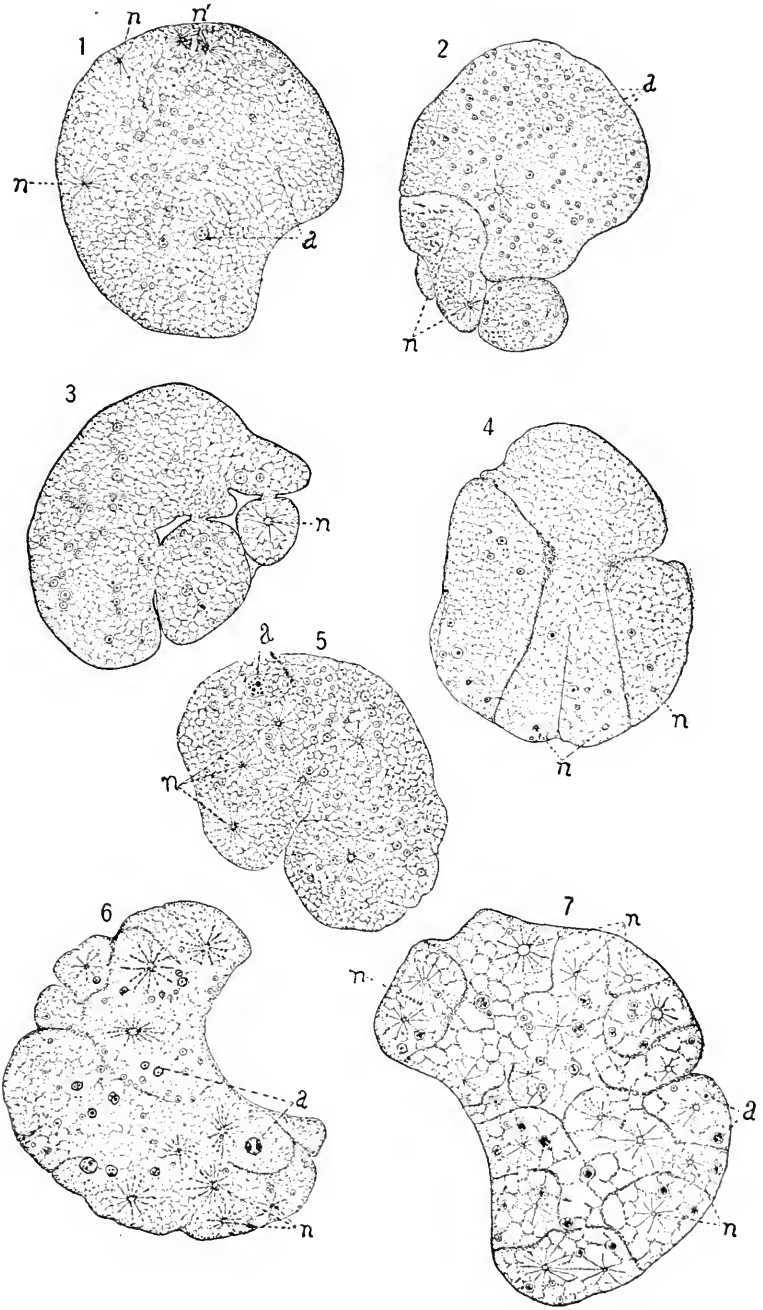
FIGS. 2, 3. Slightly later stages; segmentation planes well marked. n, nuclei; a, nuclei of absorbed cells.

FIG. 4. Still later stage of segmentation.

FIG. 5. Section through an egg containing fifteen or sixteen nuclei, but no well-defined cell walls. n, nuclei; a, nuclei of absorbed cells.

FIG. 6. Later stage; cell boundaries indefinite.

FIG. 7. Advanced stage of segmentation; cells irregular in outline, cytoplasm very reticular; n, nucleus; n^1, nuclei in process of division; a, nuclei of absorbed cells.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d
n