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EMBRYOLOGY AND METAMORPHOSIS

OF THE

MACROURA.

BY

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WITH FIFTY-SEVEN PLATES.

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[With fifty-seven plates.]

CHAPTER I.

INTRODUCTION.

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By W. K. Brooks.

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No great group of animals is more favorable than the Crustacea for the study of the history and significance and origin of larval forms, for these animals possess a number of peculiarities which serve to render the problem of their life history both unusually interesting and significant, and at the same time unusually intelligible; nor are these peculiar features exhibited, to the same degree, by any other great group of animals.

The body of an arthropod is completely covered, down to the tip of each microscopic hair, by a continuous shell of excreted matter, and as this chitinous shell is not cellular it can not grow by the interpolation of new cells, nor can it, like the excreted shell of a mollusk grow by the deposition of new matter around its edges, for there are no such growing edges, except in a few exceptional cases, such as the barnacles. Once formed and hardened the cuticle of an arthropod admits no increase in size, and as soon as it is outgrown it must be discarded and replaced by a new and larger one. The new shell is gradually excreted, in a soft condition, under the old one, and as soon as this is thrown off the new one quickly becomes fully distended and solid. As a result, from the very nature of the chitinous shell and the method of renewal which its structure entails, the growth of an arthropod, from infancy to the adult condition, takes place by a series of well-marked steps or stages, each one characterized by the formation of a new cuticle and by a sudden increase in size.

In most arthropods the newly-born young are very different in structure from the adults, and growth is accompanied by metamorphosis. As the changes of structure are necessarily confined to the moulting periods, the stages of growth coincide with the stages of change in organization, and there is none of the indefiniteness which often characterizes the different larval stages of animals with a more continuous metamorphosis. On the contrary the nature of each change is as sharply defined and as characteristic as the structure of the adult itself. As the moulting period is frequently a time of inactivity the animal may then undergo profound changes without inconvenience, and the successive steps in the metamorphosis of an arthropod are not only well marked, but often very profound as well.

In these features all the other arthropods are like the Crustacea, but another consideration, the fact that, with few exceptions, the higher Crustacea are marine, renders the problem of their life history much more intelligible than that of any other class of animals.

So far as the ontogenetic history of the metamorphosis of a larva is a recapitulation of ancestral stages in the evolution of the species its retention at the present day must depend to a great degree upon the persistency of those external conditions to which the larval stages were originally adapted.

This is true at least of all free larvæ, which have their own battle to fight and their own living to get, and while a larva inside an egg or within a brood pouch may possibly recapitulate obsolete ancestral stages, the survival of a free larva depends upon its adaptation to its present environment.

As compared with the ocean the inorganic environment of terrestrial or fresh-water animals is extremely variable, and changes in climate, elevation, and continental configuration are accompanied by corresponding changes in enemies, competitors, and food, so that the conditions which

surround a modern terrestrial larva must, in nearly every case, be very different from those under which the remote ancestors of the species passed their life, but while this is also true, to some degree, of marine animals their inorganic environment is comparatively stable, and the persistence of so many ancient marine types shows that the changes in the organic surroundings of marine animals take place much more slowly than corresponding changes on land.

This fact, joined to the definite character of the changes which make up the life history of a marine crustacean, renders these animals of exceptional value for the study of the laws of larval development, and for the analysis of the effect of secondary adaptations, as distinguished from the influence of ancestry; for while Claus has clearly proved that adaptive larval forms are much more common among the Decapods than had been supposed, his writings and those of Fritz Müller show that no other group of the animal kingdom presents an equal diversity of orders, families, genera, and species in which the relation between ontogeny and phylogeny is so well displayed, but, while proving this so clearly, Claus' well known monograph also shows with equal clearness that this ancestral history is by no means unmodified, and that the true significance of the larval history of the higher Crustacea can be understood only after careful and minute and exhaustive comparison and analysis.

Greatly impressed by this fact, I began nearly ten years ago to improve the opportunities that were offered by the marine laboratory of the Johns Hopkins University, for obtaining more complete and detailed knowledge of the larval stages of a number of Macroura, and this work has been prosecuted at every opportunity up to the present time. Some of my results have been published in my monograph on Lucifer, in the Phil. Trans. Royal Soc. for 1882, and others are incorporated in my report on the Stomatopoda collected by H. M. S. *Challenger.*

This memoir contains the life histories of a number of additional species based in part upon my own studies at Beaufort, North Carolina, and at Green Turtle Key and New Providence in the Bahama Islands, but chiefly upon the researches which one of my students, Mr. F. H. Herrick, has carried on under my general supervision. In 1886 he undertook, at my suggestion, the study of the embryology and metamorphosis of the Macroura, and devoted three years to this subject under my direction, and the results which follow are almost entirely due to his zeal and energy. He has completed the study of several subjects upon which I had previously made a beginning, so that my own unfinished notes have been incorporated with his researches, and our respective shares in the work are as follows: The chapter on Gonodactylus is entirely based upon my own researches; the chapter entitled "*Alpheus*, a study in the development of the Crustacea," is entirely the work of Mr. Herrick; the one on the metamorphosis of Alpheus is based upon our combined studies, and that upon Stenopus is almost entirely the work of Mr. Herrick, as my own contributions to this life history are of minor value except so far as they supplement his work.

I shall now give a brief outline or summary of the chief results which are described in detail in each chapter.

THE LIFE HISTORY OF STENOPUS HISPIDUS.

During the six seasons which I spent at Beaufort, North Carolina, I captured in the tow-net, at different times, some six or seven specimens of a remarkable pelagic crustacean larva, all of them well-advanced and in nearly the same stage of development.

Nothing was learned of the earlier larval life nor of the adult form of the animal, although enough was made out to show that it is one of the few Macroura which, like Peneus and the Sergestidæ, have retained the primitive or ancestral metamorphosis, and that its secondary modifications are very slight as compared with those of ordinary macrouran larvæ, and also that the Beaufort larvæ are new to science. (See Pls. IX and X.)

These larvæ have the full number of adult somites and appendages, and in side view they are very suggestive of the Sergestidæ. They are very much larger than ordinary pelagic larvæ and are quite different from any known forms of Macroura.

The chief locomotor organs are the last pair of thoracic legs, which are extremely slender, as long as the entire body of the larva, ending in flattened elliptical paddles, which are used as sweeps for rowing through the water. They are stretched out in front of the body near the

middle line and are then swept backwards and outwards, describing at each stroke a circle equal in diameter to about twice the length of the body. By the vigorous use of these oars the larva skims rapidly through the water, and its movements are not unlike those of a Gerris upon the surface of a fresh-water pond.

Notwithstanding the importance of a complete knowledge of the life history of the animal to which this sergestid-like larva belongs, I was unable to complete the study at Beaufort, although I made careful drawings of two stages and filed them away for future use.

Immediately upon our arrival at Green Turtle Key, in the Bahama Islands, early in June, 1886, our attention was at once attracted to a small, graceful, brilliantly colored prawn which was found in abundance among the coral. (See Pl. v.) It proved to be *Stenopus hispidus*, a species which is chiefly known to naturalists through specimens from the Indian and South Pacific oceans. It has been recorded as occurring in the tropical Atlantic, but our knowledge of the adult has been very scanty and imperfect, and nothing whatever has been known regarding its life history until Mr. Herrick devoted himself to its thorough investigation.

It is an active, timid animal, and is one of the most brilliantly colored of the crustacea. As it is also one of the most widely distributed, it is noteworthy that while its color markings are so prominent and conspicuous they are extremely well fixed and constant; so much so that the specimens from the Indian Ocean and the South Pacific agree with those from the West Indies down to the most minute markings.

The adults are found in pairs, a male and a female swimming together side by side and exhibiting evidence of strong conjugal attachment to each other.

The most noteworthy fact in its history is its world-wide distribution, and the question whether this can be a result of any peculiarity in its structure or habits at once suggests itself.

We should expect, on general principles, to find the least specialized species the most widely diffused; and one which holds its ground in so many parts of the world, and without any change of structure finds a safe and congenial home in seas so widely separated, might be expected to be of indefinite or slightly specialized habits, but this is not the case. In structure, in habits, in color, and in external appearance, and also in its metamorphosis, Stenopus is one of the most highly specialized of the crustacea; and it owes its ability to survive in many seas to the accuracy and delicacy of its adjustment to a narrow range of conditions, rather than to indefinite and vague adaptation to many conditions.

Its antennæ are unusually long and slender, and the acuteness of its senses, together with its very remarkable alertness; the quickness with which it perceives danger, and the rapidity with which it escapes; have undoubtedly aided it in holding its own wherever it has gained a foothold in a suitable locality, and no crustacean, with the exception, possibly, of Gonodactylus chiagra, is better adapted for life in a coral reef.

It is well protected from enemies by a thorny armor of hooked spines, which cover all the upper surface of its body and limbs, and as all the hooks point forward the attempt of an enemy to swallow a Stenopus must be difficult and painful.

These facts no doubt account for its survival, and the length of its pelagic larval life is beyond question an aid to its wide dispersal and to the discovery of new homes.

While we cannot state that the adult will not at some time be found upon the Atlantic coast of our Southern States, there is no evidence that this is the case, and the larvæ which were obtained at Beaufort, North Carolina, were undoubtedly hatched from eggs which were carried upon the abdominal appendages of parents in the West Indies or on the Florida Keys; and these larvæ had therefore wandered more than six hundred miles from their birthplace. The species might therefore be diffused through a chain of coral islands six hundred miles apart, from a single starting point, in a very small number of generations.

The eggs, which are very small, are laid at night, and the segmentation, which Professor Herrick has thoroughly studied by sections, is entirely confined to the nuclei, the yolk remaining undivided; Stenopus therefore presents a most pronounced type of centrolycethic segmentation.

The great mass of the egg consists of a homogeneous mass of yolk granules, which takes no part in the process of segmentation and probably contains no protoplasm. This yolk is aggregated around a central nucleus, which divides, probably indirectly, into two, four, eight, sixteen

nuclei, and so on until the number is very great. As this process of division goes on the nuclei, each with an investing layer of protoplasm, gradually migrate to the surface of the yolk, and at last form a superficial investing layer around a central yolk, out of which all the protoplasm has been withdrawn.

The yolk does not divide up into typical yolk pyramids, although the outlines of the blastomeres are sharply indicated by transitory superficial furrows.

The embryonic area is soon marked out as a region where the nuclei are densely crowded, and the point of invagination is indicated by a solid ingrowth which penetrates the yolk to form the inner layers of the embryo. The subsequent stages of embryonic development were not followed in detail.

The larva hatches in the afternoon, and during the following night the parent moults and lays another brood of eggs.

At the time of its escape the larva is a Protozoea, and its later history is of great interest, since it unites features of resemblance to Lucifer, Sergestes, Peneus, and to the prawns in general, with individual peculiarities in which it differs from all of them.

At the time of hatching (Pl. VII and Pl. XI, Fig. 25) it has sessile eyes, locomotor antennæ, an enormous mandible, a deeply forked telson, a long rostrum, and a complete series of appendages as far as the first pereiopods, which are essentially like the third maxillipeds. The long hind body has no appendages and is only vaguely divided into somites.

Five or six hours after hatching it changes into a true zoea, much like that of an ordinary macrouran (Pl. VIII). The carapace becomes much enlarged; the rostrum is shortened to less than half its former length, the mandible becomes small, the forks disappear from the telson, the eyes become stalked, the antennæ are shortened like those of a zoea, and the maxillipeds become the chief locomotor organs.

As these larvæ could not be reared in captivity the later stages were studied from captive specimens, but Professor Herrick has proved that the Beaufort larvæ are either young Stenopi or else the larvæ of some closely allied species which is at present unknown.

A specimen a little older than the oldest Beaufort specimen was captured at Nassau (Pl. XII). It is in the Mastigopus stage, with greatly elongated eyes, and with antennæ which are gradually approximating to those of the adult. The third maxillipeds are now extremely long and are the largest of all the limbs, while the huge, oar-like fifth pereiopod of the preceding stage is now reduced to a rudimentary bud, and the fourth is also reduced to a two-jointed rudiment.

It thus appears that, as in the Sergestidæ, the last two pairs of "walking legs" are shed after the Mysis stage, to be again reconstructed in the Mastigopus stage. After several moults the Mastigopus larva gradually assumes the adult form, the principal changes being the shortening of the eyes and the reacquisition of the fourth and fifth pereiopods.

ALPHEUS.

The genus Alpheus includes a large number of small, brilliantly colored crayfish-like Crustacea, which are widely distributed, although all are essentially tropical. Two species range as far northward as the coast of Virginia, but the true home of the genus is the warm water between tide-marks or near the shore in coral seas, and they occur in the greatest abundance and variety in all the sounds and inlets among coral islands. They are well adapted, in structure as well as in habits, for a life among the coral, and of all the Crustacea which abound upon the coral reefs the genus Alpheus is one of the most common and most thoroughly characteristic (Pl. I, II, and IV).

Nearly every mass of sponge or algæ or of coral rock or living coral which is fished up from the bottom and broken to pieces contains specimens of one or more species of Alpheus, and pieces are often found which fairly swarm with these little animals.

A few of the species wander over the bottom, and wandering individuals of other species are found occasionally, but their true home is in the tubes of sponges and the holes and crannies in the porous coral limestone, or under the broken shells and fragments of limestone which lie upon

the bottom in shallow water. Occasionally they inhabit short, vertical burrows, which they construct for themselves in the sandy mud, but most of the species pass their life hidden in the shelter which they find upon the reef.

The most conspicuous characteristic of the genus is the great enlargement of the claws of the first pair of walking legs. Both claws are large, but one of them is enormous, and it serves as a most formidable weapon of offense and defense. In some species this large claw nearly equals the body in size, and it is usually carried stretched out in front of the body, but one species carries it folded down under the body and hidden, ready to be instantly pushed out to make a rapid thrust at any enemy.

In nearly all the species the large claw terminates in hard, powerful forceps. The claw or dactyle is provided with a plug, which fits into a well or socket in the other joint and probably serves to prevent dislocation. When the forceps are opened the dactyle is raised so that the plug just rests in the mouth of the socket. As soon as the claw is released it is suddenly and violently closed, as if by a spring, and the solid stony points striking together produce a sharp metallic report, something like the click of a water hammer, and so much like the noise of breaking glass that I have often, when awakened at night by the click of a little Alpheus less than an inch long, hastened down to the laboratory in fear that a large aquarium had been broken. In the open water the report is not so loud as it is when the animals are confined in small aquaria, but Alpheus is so abundant in all the Bahama Sounds that a constant fusilade is kept up at low water all along the shore. The animals are remarkably pugnacious and they will even attack bathers. They are known to the inhabitants of the out islands as "scorpions," and are much dreaded, although their attacks are harmless to man. The snapping propensity is exhibited both in the water and out by both sexes, and if two males or two females, either of the same or different species, are placed together in an aquarium, a most violent combat at once takes place, and quickly ends by the destruction of one or both. Some species appear to pinch with the large claw, but it is more frequently used like a saber for cutting a slashing blow. The edge of the movable joint is sharp and rounded, and the animal advances warily to the attack with the claw widely opened and stretched out to its full length. Watching its opportunity it springs suddenly upon its enemy, instantly closing its claw with a violent snap and a loud report, and cutting a vertical sweep with its sharp edge. I have often seen *Alpheus heterochelis* cut another completely in two by a single blow, and the victim is then quickly dismembered and literally torn to fragments.

The abundance of these animals in coral seas is well shown by the fact that of the twenty species which are known to inhabit the shores of the North American continent we found twelve, or more than half, upon a little reef at Dix Point, a few rods to the eastward of our laboratory at New Providence, in the Bahama Islands.

Of the thirteen species which we found in the islands several are new, and as none of them have ever been adequately described, an illustrated, systematic description of all the species is now in preparation by Mr. Herrick. The present memoir deals only with the embryology and metamorphosis of the genus. This is a new field, for nothing whatever has as yet been published upon the embryology of any species of the genus, and all our knowledge of the metamorphosis is contained in two short abstracts without illustrations on the metamorphosis of a single species, *Alpheus heterochelis*. Eggs have now been obtained from all thirteen of the Bahama species, and the first larval stages of most of them have been reared from the eggs in aquaria in the laboratory, and the metamorphosis has been traced from actual moults.

THE METAMORPHOSIS OF ALPHEUS.

One of the most remarkable results of our study of the various species of the genus Alpheus is the discovery that, while there is such a general similarity as we might expect between the larval stages of the different species, the individuals of a single species sometimes differ more from each other, as regards their metamorphosis, than the individuals of two very distinct species. This phenomenon has been observed by us and carefully studied in two species—*Alpheus heterochelis* and *Alpheus saulcyi*—and it is described in detail, with ample illustrations, in the chapter on the metamorphosis of Alpheus. In the case of the first species the difference seems to be geographical, for while all the individuals which live in the same locality pass through the same series

of larval stages, the life history of those which are found at Key West is very different from that of those which live on the coast of North Carolina, while those which we studied in the Bahama Islands present still another life history. In the case of the second species—*Alpheus saulcyi*—the difference stands in direct relation to the conditions of life. The individuals of this species inhabit the tubes and chambers of two species of sponges which are often found growing on the same reef, and the metamorphosis of those which live in one of these sponges is sometimes different from that of those which inhabit the other. In this species the adults also are different from each other, but as we found a perfect series of transitional forms there is no good reason for regarding them as specifically distinct, and in the case of the other species—*Alpheus heterochelis*—we were unable, after the most thorough and minute comparison, to find any difference whatever between adults from North Carolina and those from the Bahama Islands, although their life histories exhibit a most surprising lack of agreement. In fact, the early stages in the life of *Alpheus hete-rochelis* in the Bahama Islands differ much less from those of *Alpheus minor* or *Alpheus normani* than they do from those of the North Carolina *Alpheus heterochelis*, and, according to Packard, the Key West *heterochelis* presents still another life history.

In the summer of 1881 I received the American Naturalist with Packard's very brief abstract of his observations at Key West upon the development of *Alpheus heterochelis*, and read with great surprise his statement that this species has no metamorphosis, since, while still inside the egg, it has all the essential characteristics of the adult. As I had under my microscope at Beaufort on the very day when I read his account a newly hatched larva of the same species and was engaged in making drawings to illustrate the metamorphosis of which he denies the existence, and as my experience in the study of other Crustacea had taught me that all the larvæ of a species at the same age are apparently facsimiles of each other down to the smallest hair, Packard's account seemed absolutely incredible, and I hastily decided that, inasmuch as it was without illustrations and was written from notes made many years before, it involved some serious error and was unworthy of acceptance. This hasty verdict I now believe to have been unjust, since my wider acquaintance with the genus has brought to my notice other instances of equally great diversity between the larvæ of different specimens of a single species.

The phenomenon is, however, a highly remarkable one and worthy the most thorough examination, for it is a most surprising departure from one of the established laws of embryology—the law that the embryonic and larval stages of animals best exhibit their fundamental affinities and general resemblances, while their specific characteristics and individual peculiarities make their appearance later.

As in most animals the adult life is most important, the adults have a more diversified environment than the young, and the divergent modification which is continually taking place to perfect the adjustment between such organism and its conditions of life chiefly affects the adults, so that specific characters and the slight differences between varieties or races are usually confined to the adults, while the embryos and larvæ are, as a rule, more generalized.

This is true to a marked degree of those animals whose young are nursed or protected or cared for in any way by their parents, and while it is less true of those animals whose independent life begins very early, yet the same law holds with them also; and the chief scientific value of embryology lies in the fact that a knowledge of the early stages in the life of animals enables us to trace their broad affinities and to distinguish them from more recently acquired differences; for the early stages of two related forms of life share in common their more fundamental characteristics and are essentially alike, while the adults differ from each other and exhibit the divergent specializations which are of more recent acquisition.

It sometimes happens, however, that the early stages of two closely related species differ greatly. This may occur when the larvæ of the one species lead a free, independent life, while the young of the other species are protected in some way by the parent. For example, the complicated metamorphosis which is so characteristic of starfishes is almost totally absent in those starfishes which are provided with brood-pouches. The same relation may also be exhibited when the larvæ of one species of a genus have become adapted to a mode of life very different from that of the larvæ of the other species of the genus. Thus those species of Æginidæ whose larvæ are para-

sitic multiply asexually during the larval life and build up complex communities, while nothing of the sort occurs in those species with free larvæ.

Many similar cases might be given, but we must bear in mind that they are all very different from the one now under examination. In all such cases the difference is between the larvæ of two distinct species, while in Alpheus we have a similar difference between the larvæ of individuals of a single species.

Among other animals it is not very unusual for certain individuals which are placed under conditions exceptionally favorable for embryonic development to be born in a more advanced stage than the normal for the species, and in such cases the larval metamorphosis is abbreviated by the omission of the earlier stages.

This abridgment of the larval life is not common, but many cases are known, and if the history of Alpheus were simply another illustration of this process of abbreviation it would not be at all anomalous, although the existence of three well marked and fixed grades of abridgment in *Alpheus heterochelis*, in three widely-separated localities, would still be remarkable and interesting.

The life history of the North Carolina form of this species is more abbreviated than that of the Bahama form, and the metamorphosis of the Key West form is still more shortened, but, in addition to the abridgment, the different forms also present most important differences in structure and in the order in which the appendages are developed; differences which are much more fundamental and profound than the mere length of the larval life.

The various larval forms are described with so much detail in the chapter on the metamorphosis of Alpheus that it is not necessary to repeat them here, but the following very brief outline will serve to call attention to a few of the most conspicuous features:

As several distinct species of the genus Alpheus pass through a long metamorphosis, each stage of which is almost exactly the same in all the species, we may safely assume that this is the primitive or ancestral metamorphosis which was originally common to all the species. It has been traced in *Alpheus minor* by me at Beaufort, North Carolina, and by Mr. Herrick in a similar species at New Providence. Mr. Herrick has also traced it at New Providence for *Alpheus normani* and *Alpheus heterochelis*. In all these forms the larva hatches from the egg in a form which is very similar to Fig. 2 of Pl. XVI, and very shortly after hatching it moults and passes into the second larval stage, which is the one from which Fig. 2 was drawn. This larva has all its appendages fully developed and functional as far backwards as the third pair of maxillipeds. Following these are three bud-like rudiments, to represent the first, second, and fifth thoracic limbs, and posterior to these a long, tapering, imperfectly-segmented abdomen, ending in a flat triangular telson.

The locomotor organs are the plumose antennæ and the exopodites of the three pairs of maxillipeds.

After the second moult the larva passes into the third stage, which is shown in Pl. XVI, Fig. 1, and Pl. XVII, Fig. 1. The first and fifth thoracic limbs are now functional; all the abdominal somites are distinct and movable, and the uropod, or sixth abdominal appendage, has appeared, and its exopodite is functional and fringed with plumose hairs, while its endopodite is rudimentary. The five abdominal appendages have not yet appeared.

The first thoracic leg, which was represented by a bud in the preceding stages, has now acquired a flat, basal joint and a swimming exopodite like those of the maxillipeds, but its endopodite is rudimentary.

The fifth thoracic limb is fully developed and is the most conspicuous peculiarity of the larva at this stage of development. It has no exopodite; its basal joint is not enlarged nor flattened, and its long, cylindrical, slender shaft is prolonged at its tip into a long lance-like hair, which projects beyond the tips of the antennæ.

After its third moult the larva passes into the fourth stage, which is shown in Pl. XVIII, Fig. 3.

The carapace now begins to extend over the eyes, and the ears make their appearance in the basal joints of the antennules. There are now five pairs of plumose locomotor exopodites, belonging to the first, second, and third maxillipeds, and the first and second thoracic limbs. Between the latter and the elongated fifth thoracic limb are buds to represent the third and fourth. The telson has become narrow and elongated, and the uropods are fully developed, although there is as yet no trace of the other abdominal appendages.

After the fourth moult the larva passes into the fifth larval stage, when it resembles Fig. 1 of Pl. XXI, so far as concerns the anterior end of the body, from which it differs greatly as regards the telson and uropods. The eyes are now well covered by the carapace, and the swimming organs are the seven pairs of exopodites belonging to the three maxillipeds, and the first four thoracic limbs. The first five pairs of abdominal appendages are now represented by buds, like those shown in Pl. XXI, Fig. 1, but the telson and uropods are nearly like those of Fig. 3, in Pl. XX. The telson is narrow and much elongated, and its marginal spines are very small.

During the moults which follow, the abdominal appendages become fully developed, the eyes become completely covered by the carapace, the antennule develops a scale, the antennæ elongate, the swimming appendages of the midbody disappear, these appendages assume their adult form, and the animal gradually becomes like the young Alpheus shown in Pl. XX, Fig. 2.

This life-history is common to *Alpheus minor* at Beaufort and New Providence and *Alpheus normani* and *Alpheus heterochelis* at New Providence, although the latter species presents a totally different life-history at Beaufort. Before it hatches, this form, as shown in Pl. XX, Fig. 1, reaches a degree of development which bears a general resemblance to stages two and three of the Bahama form, with certain differences which are pointed out in the sequel.

Immediately after hatching it assumes the form which is shown in Pl. XIX, Fig. 2, and Fig. 1. The animal has now all the somites and appendages of the adult, but all behind the maxillipeds are rudimentary, and there is little power of locomotion. The first moult occurs in a few hours, and the larva assumes the form shown in Pl. XX, Fig. 3, when it is no longer a larva but a young Alpheus. The eyes are almost completely covered by the carapace, the ear is well developed, the flagellum of the antenna has elongated, and the other appendages have assumed the adult form. An older specimen is shown in Pl. XX, Fig. 2, and a still older one in Pl. XVII, Fig. 3. Careful comparison will show that no exact parallel can be drawn between any larval stage of this form and a stage of the first form, and that we have to do with something more profound than simple acceleration of development. The Bahama *heterochelis* has, at first, three, then four, then five, and then seven fully developed and functional exopodites, while the North Carolina form never has more than three. As regards the thoracic region and the first five abdominal appendages the Beaufort larva, at the time of hatching, is more advanced than the fourth larval stage of the Bahama form, while the uropods are like those of the Bahama form at the time of hatching.

In the latter the first and fifth thoracic limbs are the oldest, and the others appear in succession, while all five pairs appear together in the Beaufort form. In the Bahama form the uropods appear before and in the Beaufort form after the others, and many minor differences show that we have to do with profound modification of the life history rather than with simple acceleration.

Packard's short account of the development of those specimens of this species which occur at Key West shows that these differ from the Beaufort specimens about as these latter differ from the Bahama specimens.

The second species is probably *A. saulcyi*, although Guérin's figure and description of this form are not in accord with it in some important points. It is found in the Bahama Islands, living in the tubes and chambers of two species of sponge, a green one and a brown one. Those found in the green sponges have many small eggs, while those found in the brown sponges have only a few large eggs. The eggs from the green sponge hatch in the stage shown in Pl. XXI, Fig. 1. It has rudimentary gills, the eyes are imperfectly covered, the antennules and antennæ are beginning to assume their adult form, and the exopodites of the three pairs of maxillipeds are the chief organs of locomotion, although all the appendages are represented. The abdominal feet are rudimentary, however, and the uropods are covered by the cuticle of the telson.

Very soon after hatching the larva moults and assumes the form shown in Pl. XXI, Fig. 2. The eyes are more completely covered, the antennules and antennæ are elongated, the thoracic limbs have the adult form and the pleopods are all functional.

In twenty-five or thirty hours after hatching it moults for the second time and passes into the third stage, which is shown in Fig. 8. It is no longer a larva, but a young Alpheus, with all the structural characteristics and pugnacious instincts of the adult.

In a few cases the development of this species is still more accelerated, and a few eggs from animals taken from the brown sponge hatched in the stage shown in Fig. 8, instead of the stage

shown in Fig. 1. The following notes on the variations in the coloration and habits in Alpheus, particularly in *A. saulcyi*, are taken from a paper by Mr. Herrick published in the Johns Hopkins University circulars.

VARIATIONS IN THE HABITS AND COLORATION OF ALPHEUS.

Some of the species of Alpheus are usually or even universally found living as parasites within the water tubes of sponges, and it is extremely interesting to find that individuals of the same species, living in different species of sponges, may themselves differ greatly in color and in habits.

A large brown sponge, *Hircinia arcuta*, which is not to be mistaken, grows on the shallow reefs and off the shores of many if not all the Bahama Islands. This is called the "loggerhead sponge" by the fishermen, and is found from just below low tide mark out to one-half a fathom or more of water, where its great size and sooty brown color distinguish it at once on the white bottom. If a sponge colony of this kind be pulled and torn apart, one is certain to find it swarming with a small species of Alpheus, which quarter themselves in the intricately winding pores of the sponge. Hundreds, or even thousands of individuals might be collected from a single large specimen. These animals vary from one-eighth to three-fourths of an inch in length. They are nearly colorless, excepting the large chelæ, which are tipped with brown, reddish orange, or bright blue. The females are so swollen with their eggs or burdened with the weight of those attached to the abdomen that they can crawl only with great difficulty if taken from the water. The eggs are few in number and of unusually large size, their diameter varying from one twenty-second to one twenty-fifth of an inch, and their number from six to twenty. These are most commonly yellow, but may be either bright green, olive, flesh color, brown, or dull white.

Another quite different sponge grows on all the reefs in from one to two fathoms or more of water. There are several varieties of this, which may be told by their olive-green color, yellow flesh, and clumpy, irregular shape, as well as by the putrescent mucus which some of them pour out when broken open. In nearly nine out of ten of these sponges one will find a single pair of Alphei which resemble those living in the brown sponge in most particulars, although they differ from them in several important points. They are distinguished by their large size, and by their peculiar and very uniform color. They vary in length from two-thirds to one and two-thirds inches. The females exceed the males greatly in bulk owing to the great size and number of their eggs.

Both sexes are nearly transparent and colorless excepting the large claws, which are bright vermilion-orange (Pl. IV). The female is practically inert during the breeding season (which lasted during our stay, March to July), and at such times is well protected in her sponge, or against any green surface, by the bright green ovaries which fill the whole upper part of the body, and by the mass of similar colored eggs attached to the abdomen below. Only two pairs, or four individuals, out of a hundred or more which were examined showed any variation from these colors. In these the eggs were yellow, and the pigment on the claws more orange than red. The table which follows shows the variations between two large females taken respectively from the brown and green sponges, and between the size, number, and color of the eggs.

Habitat of Alpheus.	Length of ♀	Number of eggs.	Diameter.	Color.	Color of adult.
Brown sponge....	*Inches.* ½	19	*Inches.* $\frac{1}{22}$	Yellow (variable).	Large chelæ, red, blue, or brown.
Green sponge	$1\frac{5}{16}$	347	$\frac{1}{25}$	Usually green; in this case yellow.	Large chelæ, always orange-red.

These two forms, apparently distinct, are seen however, by closer examination, to belong to the same species, although they show very interesting variations. The Alpheus living in the brown sponges tends to vary in several ways, chiefly in size and in the color of the body and eggs. The rostrum usually has three spines, but occasionally only two are present, the median one being lost. It is evident that these animals are perfectly protected from outside enemies while within the tortuous mazes of the sponge, as their numbers would show. Parasites such as Isopods, how-

ever, are not uncommon.	There has thus been no chance or need for natural selection to act along the line of color.	On the other hand, possibly, the Alpheus of the green sponge does require color protection, since the females are very sluggish during the breeding season, which extends over a good part of the year.	This animal is certainly well protected against any green surface, as already stated.	But as will be shown, natural selection has probably nothing to do with it.	The bright coloring of the tips of the claws, which only are protruded from the place of concealment, recall the similarly colored heads of boring annelids which abound on the reef, and may have a protective significance.	This evidence, however, is not very reliable.

The colors of certain crustacea, and also the color of their eggs, are known to vary greatly with the surroundings.	In the Alpheus parasites in the brown sponges these colors vary considerably where the surrounding conditions are the same.	However, the color of the ovarian eggs is always the same as that of those already laid, and although these animals were kept for several days at a time in differently colored dishes, we never observed any very marked change in the color of the eggs, but these experiments were not continued long enough or carefully enough to be conclusive.	The eggs of *Alpheus hecterochelis* are almost invariably of a dull olive color, while as in the case of the parasite of the green sponge, about one in a hundred has bright yellow eggs.	In the first case at least this is possibly an instance of reversion to one of the original colors from which the green was derived by natural selection.	In most species of Alpheus the color of the eggs is fixed and uniform, and as already suggested may have a protective significance, but in a few other cases where this is not true, the color is not only variable in different individuals, but probably also in the same individual.

In order to explain the variations which we find in these two forms, we must assume either (1) that the parasites of the green sponge are a fixed variety with distinct habits, or (2) that they represent individuals which have migrated from the brown sponges and adapted themselves to their new surroundings, or further (3) that only those chance individuals with orange-red claws and bright-green eggs, which occasionally occur in the brown sponge, find their way to the smaller green species, where they acquire great vigor and size.	This last supposition is evidently untenable.	If moreover the two forms, which were at first supposed to be specifically distinct, represent fixed varieties, we ought to find the young or at least adults of all sizes in both sponges, whereas it is only in the large brown variety that any small or undersized individuals occur, while a single pair, of large and tolerably uniform size, is invariably found in the exhalent chambers of the green sponges.

These and other considerations render it probable that the second (2) proposition above stated is the correct one, viz, that the parasites of the green sponges were born in the brown variety, and after attaining considerable size migrated thither, where they adapted themselves at once to their slightly different surroundings, growing to three or four times their former size, and the females acquiring bright green eggs, which become a source of protection in their new habitat.	This view implies the greatest variability in color and in size of the individual, and in the color of the egg, which is more remarkable from the fact that it is quite unusual in this genus.

THE EMBRYOLOGY OF ALPHEUS.

At my suggestion Mr. Herrick undertook, in 1886, the study of the embryology of Alpheus, and devoted a considerable part of his time for three years to this subject, and while he carried on the work under my general supervision the results which he has reached are entirely his own, and my share in the chapter which is devoted to this division of the subject is only that of an instructor.	I must call attention, however, to the fact that Mr. Herrick's studies were begun at a time when our knowledge of the embryology of the higher Crustacea was far less complete than it is at the present time.	From time to time brief abstracts of the progress of the research have been written by Mr. Herrick and published in the Johns Hopkins University circulars, and the following corrected summary of his results contains the substance of these preliminary reports.

The work was begun at Beaufort, North Carolina, and the eggs of the two species of Alpheus which occur there were carefully examined and preserved for laboratory research, but much better and simpler material was afterwards obtained at the Bahama Islands, the early stages were much more thoroughly studied, and the development of the animals was traced in detail, step by step,

from the first nucleus of the fertilized egg, through all the embryonic and larval stages, up to the adult condition. The eggs of each of the thirteen species which occur in the Bahamas were obtained and studied sufficiently to ascertain what are the specific differences in development, and four species were studied exhaustively, in detail. These four are *Alpheus heterochelis*, Say; *A. minus*, Say; *A. saulcyi*, and the Bahama *heterochelis*. Unless otherwise stated the following notes on the early stages refer to the last species. The development in the egg is the same for all, excepting *A. minor*, which will be referred to separately.

This prawn has proved to be a good subject in which to study the origin and rôle of certain much disputed bodies, which are met with in several Crustacea, the "secondary mesoderm cells."

SEGMENTATION OF THE NUCLEUS AND OF THE YOLK.

The egg when laid, is enveloped by a single membrane, the chorion or shell, to which is added the secondary membrane of attachment. If the nucleus is unfertilized, it is not able to initiate the process of segmentation. The fertile nucleus divides, and its products pass towards the surface, until a syncytium of eight nuclei is formed. Either just before or after the division of these, the yolk undergoes segmentation simultaneously over the whole surface into a similar number of partial pyramids. Each yolk pyramid has a large nucleus at its base, while its apex fuses with the common yolk mass in the interior of the egg. The process is now a regular one until 128 to 256 small segments are formed. The rate of cell multiplication is then retarded over one-half of the egg, while it still continues and perhaps is accelerated over the remaining portion of it. The egg thus loses its radial symmetry and becomes two-sided. It is important to notice that no products of the segmentation nucleus are left in the interior of the yolk. The superficial pyramidal structure is lost; the primitive blastoderm is established, and there now takes place a general migration of nuclei from the surface to the yolk within, but principally, as would be expected, from that part of the egg where the blastoderm cells are most numerous, corresponding to the future embryo. This is followed by a partial secondary segmentation of the food-yolk into balls. The yolk-ball is apparently formed about the migrating nucleus, but as the latter is moving, this segmentation is irregular.

Mr. Herrick has been able to follow very closely the entire process of segmentation in Stenopus, where it is substantially the same as that just described, except that there is no general migration of cells from the surface, prior to invagination. This is also true of Pontonia domestica, and it is quite probable that the majority of macroura pass through the same phases in their early development.

Alpheus minor is anomalous from the fact that the products of the first nucleus instead of multiplying by regular binary division, multiply indirectly, and give rise to numerous nuclei, many of which degenerate, before the blastoderm is formed.

THE INVAGINATION STAGE. —

A slight invagination occurs where the superficial cells are thickest, and the egg becomes what has been generally regarded as a modified gastrula. The depression is shallow, and does not form an inclosed chamber within the yolk. The included cells multiply rapidly, and form a mass of nearly similar elements, some of which pass into the yolk. The protoplasm surrounding the nuclei of these cells is prolonged into a reticulum, which encloses myriads of small yolk fragments, and probably digests them by an intracellular process, after the manner of feeding amœbæ. The thickening in front of and surrounding the pit, which is now obscured, is the rudiment of the abdomen. Anteriorly the "procephalic lobes" or more properly the optic disks make their appearance on either side of the long axis of the embryo, as circular patches of ectoderm. Meantime nuclei wander from the cell mass below the abdominal plate to all parts of the egg. Some pass to the opposite side, and take up a position beside the flattened epithelial cells, of what was the primitive blastoderm. The majority, however, pass forward and upward in divergent lines from the sides of the abdominal plate, and eventually large numbers of these wandering cells settle down over the dorsal surface of the embryo.

PRODUCTS OF CELL DEGENERATION.

At the beginning of the egg-nauplius period, when numerous wandering cells have passed forward and joined the inner surface of the embryonic ectoderm, certain new bodies begin to appear in great numbers. They vary in size from small refringent particles to bodies nearly as large as ordinary nuclei. The latter stain deeply and nearly uniformly, but with high powers it is often possible to demonstrate a clearer zone about them, which might be mistaken for a layer of cell protoplasm. How do these bodies, the so-called "secondary mesoderm cells," originate and what is their function? As to their origin there can be no doubt whatever. They arise by a process of degeneration from the embryonic cells or nuclei, chiefly from those wandering cells just described. Many of the latter may be seen to be swollen out and their chromatin divided into coarse grains and balls of various sizes. The wall of the cell breaks down and thus sets the chromatin granules free, or, more correctly, the products of the degenerating chromatin.

These degenerating bodies are most marked in the fully developed egg-nauplius, where there is a large accumulation of them around the œsophagus and at the bases of the rudimentary appendages. After this stage they generally disappear from these regions. Somewhat later, however, when there is a well developed nervous system and six pairs of post-naupliar appendages, a patch of ectoderm cells on the surface of the egg opposite the embryo proper becomes noticeable. It reminds one of a median unpaired "dorsal organ." A slight invagination apparently takes place at this point, but at any rate a number of cells pass into the surrounding yolk, and these give rise in the way described, to a swarm of minute particles of chromatin products.

Before any pigment is deposited in the eyes, it is easy to demonstrate the presence of blood corpuscles in the stream of plasma which bathes the nervous system. They have the adult characteristics, that is, they possess a deeply staining nucleus and a clear irregular body. In the nauplius stage, moreover, some of the larger "secondary mesoderm cells" have a similar appearance, but there is no evidence that they ever become blood cells. Mr. Herrick's study of these bodies has shown that Reichenbach's views on the function of secondary mesoderm cells of Astacus are probably erroneous. According to this naturalist they arise from the nuclei of the endoderm cells, forming the ventral wall of the primitive stomach, and are converted into mesoderm.

THE GERMINAL LAYERS.

The apparent plasticity of the embryonic cells and layers and the comparative tardiness with which they are clearly differentiated can not fail to impress anyone who follows closely the early stages of development. The cell mass developed around the invaginate area, forming the thoracic-abdominal process, can not be artificially divided into layers. It certainly represents very largely the primitive mesoderm, but some of its elements pass to the opposite pole of the egg and become almost indistinguishable from the superficial ectoderm, although it will be shown that they do not pertain to this layer. A part of this mass remains as the mesoderm of the rudimentary abdomen, while many of the cells which migrate from it degenerate and perform a nutritive function.

The endoderm does not appear as a definite layer until the egg-nauplius stage. It arises from wandering cells which assume a peripheral position, and, joining the cells of the hindgut, form the walls of the mesenteron.

THE EYE.

The optic discs appear as patches of ectoderm, one cell thick on either side of the long axis of the embryo in front of the rudimentary abdomen. Before the appendages are definitely formed, these have become thickened ectodermic discs. This thickening is due (1) to delamination, or to a division of cells in a plane parallel with the surface; (2) to emigration of cells from the surface, due to crowding or to a division of superficial cells in a plane at right angles to the surface. A disc of cells is thus formed which gives rise chiefly to the eye and its ganglia. The cord of cells uniting the two optic discs represents mainly the future brain. The eye proper is due to the differentiation of the outer layer of the cells of this disc, while the ganglion is developed from the inner layer. For fuller results of later studies not represented by these partial and preliminary notes, reference must be made to Mr. Herrick's completed paper and to the summary of the whole history of the development in the egg given at the end.

GONODACTYLUS CHIRAGRA.

There are few orders of animals of which we are more ignorant than we are of the Stomato-pods. They are well known as museum specimens, and every natural-history cabinet contains one or two, which have been brought home as rare curiosities from distant seas; but we know hardly anything of the habits of the living animals. They are abundant and widely distributed, but like most rapacious animals they are very alert, taking alarm at the slightest disturbance and retreat-ing to the depths of their burrows at the bottom of the ocean, where they are so completely hidden from observation that their capture is difficult, and any attempt to study them in their homes is almost out of the question.

The habits of Squillæ are tolerably well known, and in my report on the Stomatopoda, collected by H. M. S. *Challenger*, I have given an account of the habits of Lysiosquilla based upon observa-tions made at Beaufort, North Carolina; but, except for a few scattered and fragmentary notes in the various descriptive papers, this is the whole of our knowledge of the order. During the sea-sons of 1886 and 1887 I was so fortunate as to find in the Bahama Islands *Gonodactylus chiragra* living in localities which were peculiarly favorable for observing its habits, and I am now able to supplement my report upon the *Challenger* collections by an account of this interesting species, of which little had hitherto been known, except the fact that it is the most cosmopolitan of the Macroma abounding on the shores and islands of all tropical and subtropical seas.

I also obtained its eggs in abundance and succeeded in rearing the young from them in aquaria, and am now able to make a contribution to a subject upon which there were hitherto no direct observations, for it is a noteworthy fact that while the older larvæ of Stomatopoda have long been known, and while many genera and species of them were carefully figured and described and named by the older naturalists before their relationship to the adult Stomatopoda was sus-pected, not a single species in the whole order has, so far as I am aware, been reared from the egg and in this way identified with its specific adult.

While the adults usually inhabit burrows in the bottom the larvæ swim at the surface of the ocean, and as none of the animals which are captured in the surface net exceed them in beauty and grace, their glass-like pelagic larvæ are familiar to all naturalists who have had an oppor-tunity to study the surface fauna of the ocean. Their perfect transparency, which permits the whole of their complicated structure to be studied in the living animal, their great size and rapacity, the graceful beauty of their constant and rapid movements, can not fail to fascinate the naturalist. Unfortunately they are as difficult to study as they are beautiful and interesting, and notwithstanding their great abundance and variety, only two or three of them have been traced to their adult form.

Unlike most Malacostraca the Stomatopoda, instead of carrying their developing eggs about with them, deposit them in their deep and inaccessible burrows under the water, where they are aërated by the currents produced by the abdominal feet of their parents. The eggs quickly perish when deprived of this constant current, and as it is very difficult to obtain them at all, I know of no Stomatopod which has ever been reared from an egg under observation. The older larvæ are hardy and are easily reared, but they are seldom found near shore, and microscopic research is so difficult at sea that I know of only two cases in which they have been kept until they assumed the adult form. As I have stated in my report on the *Challenger* Stomatopoda, I have reared a young Lysiosquilla excavatrix from an old larva which was captured at the surface, and Faxon has in the same way obtained the young Squilla empusa. The young larvæ are common near shore, but as they seldom survive a moult in captivity they can not be identified in this way.

The growth of the larvæ is slow and the larval life long, and as they are as independent and as much exposed to changes in their environment and to the struggle for existence as the adults they have undergone secondary modifications which have no reference to the life of the adult, and are therefore unrepresented in the adult organism. The larvæ have been arranged in genera and species, but their generic characteristics are quite different from those upon which the adult genera are based, and this is true in a still greater degree of their specific characteristics. As they undergo great changes during their growth different stages have been described as distinct species or even genera, and it is not easy to select from the rich gatherings which are brought home by

collectors the successive stages in the history of a single species.   Like the adults, they are widely distributed, and a gap in a series from the North Atlantic may be filled by a specimen from the coast of Australia or the Sandwich Islands, and the collection from a single locality may contain the larvæ of several widely-separated species of adults in all stages of growth as well as the larvæ of deep-water species which are as yet entirely unknown.

The attempt to unravel the tangled thread of the larval history of the Stomatopods is therefore attended with very exceptional difficulties, and the earlier writers were content to rest after the bestowal of generic and specific names upon the larvæ.   As I found after the *Challenger* collection was placed in my hands that it was very rich in larvæ, I attempted to determine, by comparison, the larval series for each genus, and the methods which I employed for making the comparison are fully stated in my report.   As one of the results of this comparison I ventured to describe the general characteristics of the larva of the genus Gonodactylus (p. 113), and in Pl. XII, Fig. 5, of that report I figured a larva which I ventured to call the larva of Gonodactylus.   A comparison of that figure with Pl. XV, Fig. 11 of this memoir will show that this determination was correct, for the larva of *Gonodactylus chiragra* which is here described is so much like the one figured in the *Challenger* report that they belong, in all probability, to the same species.

CHAPTER II.

THE LIFE HISTORY OF STENOPUS.

By Francis H. Herrick.

This paper is the result of observations made at Beaufort, North Carolina, in 1881 and 1883, and at Nassau, New Providence, in 1887. The marine laboratory of the Johns Hopkins University was stationed at the latter point in the Bahama Islands from March until July of that year, and with the means thus generously afforded, I was able to considerably extend my studies upon the Crustacea of these coral islands.

Professor Brooks found a number of peculiar pelagic larvæ at Beaufort, and it is very probable that they represent a part of the life history of *Stenopus hispidus*. Plates IX and X, illustrating two important stages of these very interesting larvæ, are contributed by Professor Brooks, and the descriptions of these stages are based entirely upon his observations.

While the material gathered in a sojourn of a few months at the seashore is in many instances incomplete, it seems worth while to bring out this sketch of the Stenopus, inasmuch as nothing was previously known of its development, and indeed but very little concerning the adult form. *Stenopus hispidus* is, in fact, generally known to naturalists as occurring only in the Indian and South Pacific oceans. It was at first quoted from the Atlantic (Cuba) by Von Martens (7) in 1872, and it has not since been reported from the Western Continent, so far as we are aware, until we rediscovered it at Abaco, Bahama, in 1886, but any assiduous collector on West Indian coral reefs must somewhere have hit upon it (v. Appendix I).

As the eggs are quite small, as is the case in all Crustacea with a protozoa stage, they are not particularly well suited for study by means of sections, and no special attempt has been made to trace out the history of the germinal layers, a subject which can be dealt with to better advantage in other species. The Stenopi breed readily in aquaria, and several series of eggs, illustrating fully the segmentation, and some early phases of development were prepared, and the sections were afterwards made in Baltimore. These are given on Pl. VI. They are especially interesting, since the segmentation is like that of Penæus studied by Haeckel, who relied wholly upon surface observations.

The ova were immersed in Kleinenberg's picrosulphuric acid and afterwards hardened in alcohol. This answered sufficiently well for the purpose in hand, although it rendered the eggs more resistant than is desirable.

I.—THE NATURAL HISTORY OF STENOPUS.

The Bahaman Stenopus (Pl. V) measures from 1½ to 1¾ inches in length. All the appendages are long and generally quite slender and delicate, especially the antennæ, which give to this form a very characteristic appearance in the sea. These are snow-white. They are carried widespread and arch outwards in graceful curves. The flagella of the second or outer antennæ are two and a half times the length of the body. In the act of swimming these are bent backward and outward, while the outer division of the first or inner antennæ is carried upward, and their inner branch is directed forward.

The body is pure white or nearly so, excepting three broad transverse bands of reddish scarlet. The first or most anterior of these color bands covers the front of the animal, involving the eyes and bases of the antennæ, and in some cases it extends behind the rostrum as far as the mandib-

ular or "cervical" groove. The second is nearly confined to the broad tergal surface of the third abdominal segment, while the third zone crosses the last abdominal somite and impinges on the tail fin. The appendages are all colorless excepting the third pair of legs which carry the large pincers. These are similarly marked with four bands of the same bright color. As shown by the colored plate two of them encircle the great claws, a third belongs to the carpus, and the fourth to the meros or fourth segment of the limb. The bases of the third and sometimes of the fourth and fifth thoracic legs are tinged with bright blue. The ovaries often give to the dorsal surface of the females a light-greenish cast.

There is but little variation in the size and character of these markings in the same sex or in different sexes, but it is most remarkable to observe how constant these colors are in individuals of the species from different parts of the world. We possess two colored drawings of this species* (which will be referred to again), one by Adams (5), from a living-specimen taken in the China Sea, and the drawing of Dana (6), who found the species on the coral reef of Raraka, one of the Paumotu Islands, and at Balabac Passage, north of Borneo. Both of these, and especially the Samerang plate, essentially agree with our Bahaman specimens, which in color seems to be the more faithful copy of nature. Here the basal joints of the thoracic legs are colored blue as in the Nassau form. Why should Stenopus, coming from different seas, retain the same colors and markings, to a nicety of shade and pattern, while a cosmopolite like *Gonodactylus chiragra* (a Stomatopod) presents such wide color variations as to be as unlike as possible, so that scarcely any two taken from the same place have a similar color pattern? To this question we can not at present give a satisfactory answer.

Alcohol soon removes all trace of color from the body, but the spots on the legs remain for a longer time as light orange red. Both sexes are of nearly the same size, and, as already stated, alike in color.

Being thus brilliantly decorated with the American colors, our crustacean soon acquired with us the name of the "Bandanna Prawn." As we see this animal swimming deliberately in the water we are reminded of some strange and fantastically colored insect. It is by far the most showy, and for its size the most attractive, member of that giant family, the Crustacea, which have their dwelling on the reef. One day, when out upon a wading and diving expedition, a pair of these prawns was discovered by turning over a plate of loose coral, and was easily captured by slowly raising the slab from the water into the boat; for this species, unlike some shrimps, is quite helpless when once out of its element. More frequently, however, they led us to a long chase.

There seems to be considerable attachment between the sexes, since they are invariably found in pairs, the male and female swimming side by side. On a still day they may be found clinging to the mosaic of sponges and living coral, which form the reef bottom, but if disturbed they suddenly become very active, and, darting backward by sudden jerks, dive into some chink, out of reach of the hand net.

Several females both hatched and laid eggs in aquaria in the month of June, but the breeding season, as inferred from the capture of locomotor larvæ, probably extends throughout the spring and summer months, if not throughout the entire year.

The eggs are very numerous. They are nearly spherical and measure one-fiftieth of an inch in diameter. They were always of the same light opalescent-green color. The ova are laid at night, but the process was not observed.

Three different females hatched their broods on the afternoons of June 4, 14, and 24, respectively, and moulted and laid eggs during the following nights. As these animals invariably moult just before laying their eggs, the latter are probably fertilized at the time they are laid. The hatching of one brood lasted about 9 hours, from 2 o'clock in the afternoon until well into the following night. By 10 o'clock the same evening some of the larvæ had moulted for the first time. The eggs are closely felted to the abdomen, and, as in all Decapods, they are cemented together by a secretion which possibly comes from the oviducts during ovulation. They are fastened by the same substance to the hairs which fringe the bases of the pleopods, chiefly to those of the first and second pairs.

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* Besides Milne-Edwards figure (4), evidently made from a specimen in which the natural colors had been removed by alcohol. (See remarks, etc., under Section IV.)

After a moult the colors are, as is usual, very bright, and the moulted skin, as it stands intact supported by the antennæ, may easily be mistaken for the living animal. These prawns make no sounds and appear to be very timid. The surface of the whole anterior body and of the large claws is thickly beset with tooth-like spines, the points of which are bent forward, and these may be regarded as an admirable protection against being swallowed head first by an enemy. It is also interesting to notice that the spines of the hinder part of the body project backward, and may thus be of service to Stenopus when attacked from the rear. Their long sensitive antennæ or "feelers" and well-developed eyes doubtless warn them of approaching enemies, which, by their rapid angular movements, they may easily escape. The extraordinary development of the eyes in the older larvæ (Pl. II) is remarkable.

The geographical distribution of *Stenopus hispidus* is very interesting.* H. Milne-Edwards, in his "Histoire naturelle des Crustacés" (3), gives the habitat of *Stenopus hispidus* (Latreille) as the "Indian Ocean," following Olivier (1) and the older writers. In the "Règne Animal" of Cuvier, third edition, "Les Crustacés," p. 137, he says: "We know of only one species, reported from the Australian seas by Peron and Lesueur." The Samarang naturalists (5) met with it on the coasts of Borneo and at the Philippines in 1843–'46. Dana, in 1838–'42, on the Wilkes Expedition (6), found it in the South Pacific at the points already noticed. In 1872 E. von Martens (7) describes the species for the first time from the Atlantic, in a collection of Cuban crustacea made by Dr. J. Gundlach, and de Man in 1888 (9) quotes it from Amboina in his monograph on the Decapoda and Stomatopoda collected in the Indian Archipelago by Dr. J. Brock.

We can now add to this list the Bahama Islands (Abaco and New Providence). We have also the interesting fact that the larva was taken on our coast at Beaufort, N. C., whither it had probably been carried by the warm waters of the Gulf Stream. We may therefore expect to find the adult Stenopus on the Florida Keys, but not much farther north, since this is essentially a tropical form.

We thus have in *Stenopus hispidus* another instance of not only the same genus, but also the identical species, occurring on the eastern shores of two continents. It seems not impossible that the prolonged larval period which this animal possesses may have played an important part in its geographical distribution. This may be also true of *Gonodactylus chiragra*, but on the other hand it can not be asserted of Limulus. In the last case the Asiatic and American forms are specifically distinct.

II. SEGMENTATION AND EARLY PHASES OF THE EGG.

The prawn, which hatched her zoëa brood on the 4th of June, laid eggs the next morning probably at about 6 o'clock, and as soon as discovered some of these ova were hardened at intervals of a few hours during the next two days. In this way a complete history of the segmentation was obtained.

First stage.—The first eggs preserved (probably 5 to 6 hours after ovulation) are perfectly opaque, nothing but the light-green yolk corpuscles showing through the shell or egg-envelopes. Thin sections prove that the segmentation nucleus has divided, and that its two products lie remote from each other. Physiologically speaking, we now have two cells, each consisting of a deeply staining nucleus and perinuclear protoplasm. The first segmentation is evidently central. What takes place is briefly as follows: Primitively we have a central nucleus, about which protoplasm is gathered. Around this again is the great mass of yolk, and the whole is encapsuled by the protective chorion and the secondary membrane of attachment. The first division involves only the nucleus and surrounding protoplasm. The products as independent bodies now leave their central position and seek the surface of the egg. In one instance one of these has reached the surface (shown in Pl. VI, Fig. 1), while the other is only halfway there on the opposite side. The superficial cell, as seen by the figure, has the same characters as when buried in the yolk. In

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* The reason for considering the Bahaman form identical with the Hispidus of Olivier, Latreille, Milne-Edwards, Adams, Dana, and others are given on page 351.

another egg of the same phase neither cell is quite at the surface, so that the example given in Fig. 1 may be taken to illustrate a tendency, not a rule.* The yolk (Fig. 1, Y. C.) consists here, as in subsequent stages, of homogeneous and tolerably uniform green corpuscles. No vacuolar cavities are to be seen.

Second stage.—Four and one-half hours later the second segmentation is going on or is already completed. The egg from which Fig. 2 was taken contains four nuclei with perinuclear protoplasm. It was cut into a series of 50 sections, of which the second represented is the twenty-first. Nuclei occur in sections 21, 25, 29, and 35, none being as yet superficial. A portion of section 21 (Fig. 2) is shown under a higher power in Fig. 3.

Third stage.—After three hours and twenty-five minutes have passed the third phase is reached and we have eight cells, around which the yolk is superficially constricted into eight corresponding lobes or segments. A surface view of this entire egg and also a section through it are shown in Pl. VI. Figs. 5 and 6, and a tangential section of one of the nuclei and lobes is given with more detail in Fig. 4. The constriction furrows appear to be considerably deeper than they actually are, and we might predicate a total segmentation of this egg without the knowledge which the section affords. We have here a merely superficial indentation of the yolk, the great central mass of which is undivided. It is a close approach to the yolk pyramid stage seen in Astacus, Alpheus, Hippa, Palæmonetes, and many other Decapods. The dividing planes, Figs. 7 and 8 (unless artificially produced), do not penetrate into the egg. The furrows extend inward to a plane just below or on a level with the nucleus.

Each nucleus with its outer protoplasm may be spoken of as the *cell*, and it is hardly probable that there is any protoplasm like that surrounding the nucleus in the other parts of the egg. The nuclei increase gradually in size, as seen by comparing the figures of successive stages, and the surrounding plasm, which they manufacture out of the yolk, is also of greater bulk. Each is a flattened, oval disc, shown well in transverse section in Fig. 5 at *a*, and tangentially in Fig. 4. It contains coarse grains and granules of chromatin, and the enveloping protoplasm radiates visibly but a short distance between the yolk spherules. The long axis of each nucleus lies in a plane parallel with the surface. Cell multiplication is in all cases indirect, as my observations show to be the case with several other related forms, and this is undoubtedly the rule not only with the segmenting eggs of the Decapod Crustacea, but with those of all the Metazoa. There seems to be an exception in the case of *Alpheus minor*.

Fourth stage.—After another interval of an hour and five minutes there are sixteen cells resulting from the fourth segmentation. The blastomeres are less sharply marked at the surface and more distinctly polygonal. Six nuclei are cut by the section given in Fig. 7. They are nearer to the surface than in the former stage.

Fifth stage.—The egg represented by Fig. 8 is three hours older than the last and has thirty-two cells and the same number of superficial segments. Up to this time the egg has exhibited radial symmetry. The nuclei are quite near the surface of the egg. They are more spherical and the investing protoplasm is less conspicuous than formerly. The fissures between contiguous blastomeres are becoming less and less prominent.

Sixth stage.—After a longer period, nine hours and forty-five minutes, the process of regular division into smaller and smaller superficial segments has proceeded until 128–256 of these bodies are formed. The cells lie at the surface, just under the chorion, and form a continuous envelope, the primitive blastoderm about the central yolk. This yolk mass is not segmented, nor does it include any nuclei which have not participated in forming the blastoderm. In one or two instances a cell was observed just below the service. This may be interpreted as either having never reached the surface or as having been there and moved below it towards the interior. But the general statement is doubtless true that all cells reach the surface, and that there is no extensive migration to the interior, as there is in Alpheus, before invagination.

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* It now seems probable to me that this superficial cell represents the male and the central cell the female pronucleus. A small, deeply staining body, which I interpret as an undoubted polar cell (not shown in Fig. 1), lies underneath the chorion, not far from the superficial cell.

Seventh stage.—In three hours and three-quarters from the last phase the blastodermic cells have spread more rapidly at a given point on the egg, which loses its radial symmetry in consequence. There is thus formed the embryonic area or first trace of the embryo proper.

Eighth or invagination stage.—Three and a half hours later a portion of the blastoderm in the embryonic area is invaginated, that is to say, some of its cells pass below the surface in a body, and the invagination stage is reached. The invagination is solid, or nearly so, as is the case with nearly all Decapods. Fig. 9 represents an oblique section of one end of an egg, through the area of invagination, *Ig*. The epiblastic cells contain small oval nuclei. There are no yolk cells in the interior of the egg. The vitellus is here segmented into large, irregular fragments, each of which is composed of yolk corpuscles similar to those seen in Fig. 4. It is just possible that this fracture of the yolk, which is commonly seen in the eggs of other Crustacea, is artificially produced at least to some extent, at this stage.

Ninth stage.—After another period of three and a half hours, while the external change is not marked, the invaginated cells have rapidly multiplied and given rise to a considerable cell-mass below the surface at that point.

Tenth stage.—In thirteen and a half hours from the last stage, or when the embryo is fifty-two hours old, important changes have been effected. In surface view the embryo presents a heart-shaped or somewhat three-sided area. The optic discs appear as widely separated patches of ectoderm, united to the thoracic-abdominal plate, a mass of cells which forms around, but chiefly in front of, the point of ingrowth. Sections through this egg show a considerable thickening in the optic discs, and an accumulation of large granular cells in the abdominal area. These latter undoubtedly represent some of the primitive mesoderm and endoderm.

The phenomena just recorded are given in a more condensed form in the following table, which shows the age and corresponding growth of the embryos at the successive stages. The age of the first stage is assumed to be 6 hours, which is probably not far from the truth.

In the above account we are constantly dealing with different eggs, and assume of course that they are all at any given time in the same phase of development. While this is not strictly true, it is very nearly so. The eggs are at first about on a par, and it is only later that some become handicapped, producing those slight differences which may be seen in embryos from the same female.[*]

Time of hatching June 4, a. m., early.   Temperature 80° F.   Diameter of egg $\frac{1}{20}$ inch.

Stage.	Age of egg.	State of development.
1	6 hrs	2 cells.
2	11½ hrs	4 cells.
3	14 hrs. 55 min.....	8 blastomeres.
4	16 hrs	16 blastomeres.
5	19 hrs	32 blastomeres.
6	28 hrs. 45 min.....	128–256 blastomeres.
7	32½ hrs	First trace of embryo.
8	35½ hrs	Invagination stage.
9	38½ hrs	Pit obscured.
10	52 hrs	Optic discs and abdominal plate formed.

We thus have in Stenopus a type of the so-called "centro-lecythal" segmentation, exactly comparable to that of Penæus, and essentially like that which is probably characteristic of a large number of the Decapod Crustacea. The fact that all the protoplasm of the egg enters into the blastoderm and that no yolk cells are now formed, is of some interest, and this subject, will be considered more fully in a paper on the development of Alpheus.

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[*] This is not true of the American lobster, *Homarus americanus*, in which I have made a very complete study of the segmentation process. In a batch of segmenting lobster's eggs, there is a decided lack of uniformity. Some ova which afterwards continue to develop, remain with yolk unsegmented until the third or fourth day after fertilization.

III. METAMORPHOSIS, OR PERIOD FROM THE TIME OF HATCHING TO THE ADULT STATE.

A. Protozoëa or first larva (length=4^{mm}).—Stenopus leaves the egg as a protozoëa, which may be compared to one of the early larvæ of Penæus or Sergestes, but it is unlike either of them. This first larva, which is very long and slender, is so coiled upon itself in the egg that the tail fin overlaps the posterior end of the carapace. It requires considerable time after casting off the shell to uncoil and straighten its appendages, especially the antennæ and the long rostrum which was bent under its body.

The figure on Pl. XI exhibits some of the grotesqueness of this larva. This drawing was made from an animal which had just wiggled out of its egg shell and was uncoiling its appendages. The huge antennæ are partially unfolded, while the rostrum R., is scarcely visible. Drawings of parts of this immature protozoëa are seen in Pl. VII, Figs. 11–16, and the larva itself as it finally appears, about two hours after hatching, in Fig. 11. If we compare with this the younger form in Fig. 25, we notice some details, chiefly of a quantitative kind, in which they differ. Immediately after leaving the egg the epidermic structures grow rapidly; hairs or setæ are developed on all the appendages, and the tail-fin acquires some new characters. The first larva does not swim well until several hours after hatching.

The Stenopus protozoëa (Pl. VII, Fig. 11) is 4^{mm} long, the rostrum alone being 1½^{mm}. It is colorless, excepting the dark eyes and a few scattered blotches of brownish pigment upon the sides of the body or on the tail-fin. It swims chiefly by aid of its largely developed antennæ, which are directed forward as shown in the plate. These, with the rostrum, add considerably to the apparent length of the body and serve to distinguish it, without the aid of a lens, from the second larva (Pl. VIII, Fig. 17), which soon follows and swims about in the aquarium with the others. It is further characterized by the very large size of its mandibles (Pl. XI, Fig. 25, Md.) and by its forked telson-plate, adapted for swimming. The forked locomotor tail-fin and large hairy antennæ mark the protozoëa stage in Crustacea generally. The carapace is only feebly developed, not nearly reaching to the bases of the appendages. It is prolonged in front into a huge tapering cone, the rostrum, which is nearly half the length of the body. This is beset with short spines and reaches considerably beyond the antennæ. About four segments of the abdomen are distinguishable from before backwards (Fig. 25). The first and second, which latter is the largest, carry lateral spines, and the upper surface of the second segment is also prolonged posteriorly into a median spine. The tail-fin at the time of hatching is sharply forked (Fig. 13) and is furnished with 6 pairs of rudimentary setæ, of which the median pair is the shortest, besides a pair of outer non-plumose bristles (Figs. 11, d, and 13, a.). In the course of a few hours this organ has become functional and appears as shown in Fig. 11. The hairs grow out and acquire thick lateral fringes; the outer pair (next to *a*) become rudimentary, and three additional pairs of toothlike bristles make their appearance on the sides of the telson-plate.

The eyes are sessile. The inner or first antennæ (Fig. 25, AI) are jointed, unbranched appendages. Each is tipped with a bunch of about four long sensory filaments and with a single seta. A single plumose hair also springs from the distal end of the penultimate joint on its inner side. The outer antennæ are biramous. The inner branch consists of a simple stem, tipped with at least two long hairs. The outer division is segmented at its extremity, and is garnished with plumose setæ, chiefly on the inner margin, there being one or two to each segment. The gland at the base of the antennal peduncle is conspicuous.

The mandibles are of enormous size in comparison with the other appendages. A view of the labrum and right mandible is given in Pl. VII, Fig. 15. They are simple blades with rounded edges, covered with minute horny teeth. There is no palpus. The first maxilla (Fig. 12) consists of two stout branches tipped with bristles, and in the case figured they are spotted with pigment. The second maxilla is a broad lobulated plate (Fig. 10). Each lobe is provided with hairs, excepting the outermost which corresponds, in part certainly, to the scaphognathite. Only a single bristle was detected on this lobe in the specimen from which the drawing was made.

The three maxillipeds have each an exopodite, which is considerably larger than the other branch, and which is furnished near the tip with not less than three pairs of locomotor hairs. The undeveloped condition of these latter in an embryo just hatched but unable to swim, is well shown by

Figs. 14 and 16, which represent the first and third maxillipeds of the right side, as seen from below. The endopodites of the second and third pairs possess four joints, of which the terminal one carries setæ. There is one pair of thoracic limbs consisting of a stout locomotive exopodite, similar to that of the second and third maxillipeds just described, and of a very short, indistinctly segmented endopodite. The latter is armed with two terminal and three lateral plumose hairs on the inner side.

B. *First zoëa or second larva* (length, $\alpha = 5^{mm}$).—Five or six hours after hatching the protozoëa moults into a form which superficially resembles the macrouran larval type. (Pl. VIII, Fig. 17.) The carapace of this larva has grown down so as to cover the basal joints of all the appendages, and it also extends behind them. The rostrum is reduced to from one-half to two-thirds its former size, and does not surpass the antennal hairs.

There is still put one thoracic segment with its appendages. All the abdominal segments are formed, but none show any traces of limbs. The lateral spines of the first and second somites are missing, but the median unpaired spine of the latter is greatly developed, and extends to nearly the end of the third somite. The sixth somite, which carries the zoëal telson, is equal in length to the third, fourth, and fifth combined. The fan-shaped telson, viewed from below, is represented in Fig. 20. Comparing this with Fig. 11, we observe that it is no longer conspicuously forked. The median notch has a short unpaired spine. There are six pairs of feathered hairs, the outer ones still being rudiments exactly as in the first larva, and a non-plumose spine which ends the series; the three rudimentary spurs seen in Fig. 11 being wanting. The eyes, which have acquired short stalks, protrude slightly.

The antennæ are shorter and are now no longer so important as organs of locomotion. The terminal joint of the inner antenna is reduced, but otherwise this appendage is but little changed. The outer antenna ends in a stout hook, which is succeeded, on the indented margin of the inner side, by a series of eight feathered hairs. The second joint of this appendage also bears a serrated hooked spine at its outer extremity. The mandible is without a palp. It has a serrated edge, and a prominent, inferior, compound tooth (Fig. 18).

The inner branch (coxopodite) of the first maxillæ (Fig. 19) carries three simple and three compound spines, while the outer division consists of three segments with stout, plumose hairs, as shown in the figure. The second maxillæ (Fig. 21) are considerably altered from the form shown in Fig. 10. There is an outer lobe (scaphognathite), bearing one large hair directed backwards and at least four others which point in the opposite direction. The inner portion is lobulated into six or more parts, all of which are well provided with stiff hairs.*

The first maxilliped is shown greatly enlarged in Fig. 22. Examining this in connection with Fig. 14, we find that the exopodite consists of one segment and bears a limited number of hairs (here two) at its apex. The endopodite is segmented and carries numerous hairs, which are continued in small tufts along the inner margin to the base of the limb. The chief swimming organs are the first and second maxillipeds and the first pair of thoracic legs. The inner branch of the latter is considerably developed, and nearly equals the expodite in length.

There is a large irregular spot of red pigment on each side of the anterior half of the body just above the base of the third maxilliped. The lobes of the liver (L) begin now to show distinctly through the carapace. The food yolk, which is present in small quantities in the stomach of the protozoëa (Fig. 25), is finally absorbed. It was probably owing to this and to the fact that I gave the larvæ no food that suited their taste that they never reached the second moult, although they passed a number of days in this condition. In course of several trials the animals at this stage always became greatly crippled by particles of organic matter adhering to their body and invariably starved. For later stages, therefore, connecting this zoëa with the adult, we have to rely upon larvæ collected at the surface of the ocean.

C. *Mysis or Schizopod stage.*—It is evident that the zoëa of the stage B passes into a mysis-like form through the intervention of one or more moults, and we have two larvæ already noticed belonging to the close of this period. They were collected by at Beaufort, N. C., July 14 and 15,

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* The distal or terminal lobe represents the endopodite; the lobes next this stand for the basipodite, while the second (?) proximal division at the base of the appendage correspond to the coxopodite.

1883.   In the Beaufort specimen (Pl. IX) all the segments and appendages of the body are present, and all of the latter are functional, excepting the first five pairs of abdominal feet, which are rudimentary buds.   The carapace is well developed, and terminates in front in a slender serrated rostrum, which is much shorter than in previous stages.   The eyes are now large and prominent, being mounted on long stalks.   These organs, which are sessile in the protozoëa, undergo marked changes in both size and form in the course of development.   They reach a maximum in a later stage, and are correspondingly reduced during the passage from the latter to the adult.

The inner antennæ are biramous; the outer are reduced to a long narrow scale, armed with bristles.   The third pair of maxillipeds and first, second, third, and fourth pairs of thoracic legs bear prominent swimming exopodites.   The fifth pair of pereiopods characterize this larva by their great length, and by the huge, paddle-shaped segment, which bears the small, terminal claw. There is no exopodite to this appendage.   The endopodites of the first, second, and fourth pereiopods are nearly equal; the third-longer.   The first five abdominal segments are of equal size and, as stated, carry rudimentary feet.   The sixth segment, however, is long and narrow, and has the uropods well developed.

D.   *Mysis stage.*—The larva of stage C moulted into a form (Pl. X) resembling the last, with the addition of several important features.   The inner antennæ consist, as before, of a segmented stem with two terminal appendages.   The first and third segments of the antennular stalk are short, while the second is very long; spine nearly equal to length of basal segment; inner flagellum very slender, shorter than the outer branch; the proximal, thickened portion of which carries several (three) bunches of sensory filaments.

The antennal scale is as long as the antennular peduncle.   The flagellum of the antennæ now appears as a slender filament, nearly twice the length of the scale.   Possibly it is formed, as in Penæus, from a bud-like remnant of the inner ramus of this appendage in the protozoëa.   The third pair of maxillipeds and first to fourth pairs of thoracic legs are as in the previous stage, with conspicuous exopodites fringed with setæ.   The endopodite of the fourth pair is longer than that of the third; the fifth pair are twice as long as the fourth; and the breadth of the penultimate segment is much reduced.

The first, second, and third abdominal segments are equal; the sixth is narrow, equal to length of fourth and fifth.   The telson is narrow, tapering, three times as broad at base as at apex; the uropods are one-fourth larger than telson.   Pigment is found as before, in the extremities of the segments of the appendages.   Large spots also appear on the abdomen and eyes.

E.   *Mastigopus stage.*—On June 15 an older larva than the one just described was obtained in the ocean outside the harbor at Nassau.   It agrees in the main with the mastigopus of Sergestes. The carapace ends anteriorly in a short spine or rostrum, which is bent up at an angle of about 40 degrees with the body.   The eyes are mounted on very long naked peduncles.   Both pairs of antennæ are biramous.   The outer flagellum of the first or inner pair of antennæ is the longest (Pl. XI, Fig. 26), and it bears four or five bunches, containing in all about a dozen sensory filaments. The inner branch is a bud.   The second antennæ extend as far forward as the joint of the first pair, where the inner flagellum is given off.   The flagellum of the second pair is wound into a short spiral coil.

The exopodites of the second pair of maxillipeds are rudimentary (Pl. XI, Fig. 31).   The third maxillipeds are now the stoutest appendages, and equal in length the third pair of thoracic limbs. The first and second thoracic legs are slender; the third pair is the longest and the terminal segment is bifid; the fourth is a short two-jointed rudiment; the fifth, corresponding to the huge oar-like appendage of stage C, is reduced to a bud.   *It thus appears that, as in the Sergestids, the last two pairs of walking legs are shed after the mysis period, to be reconstructed again in the mastigopus stage.*

All the abdominal appendages are functional.   (Pl. XI, Fig. 27.)   The last segment of the abdomen is nearly equal in length to the three preceding.   It is laterally compressed, and more nearly resembles the adult form.   In the act of swimming this larva carries the abdomen bent at nearly a right angle to the rest of the body.   It is colorless, excepting areas of red pigment at the bases of the abdominal feet, and spots on the lower portions of the antennæ and eye-stalks.   There is also a transverse band of the same color on the anterior part of the carapace.

F. *Mastigopus stage.*—After it had been kept three days this larva passed through a moult, by which only slight changes were introduced. The fourth pair of walking legs is now distinctly jointed, the fifth remaining as a bud. The flagellum (endopodite) of the second pair of antennæ uncoils and speedily lengthens. The terga of the first and second abdominal somites bear on the lower lateral margins of each side a short tooth. The larva lived four days without further ecdysis. Figs. 26, 27, 30, and 31 are from this stage.

G. *Mastigopus stage* [Pl. XI, Figs. 28, 29, 32–34, Pl. XII], (Length = 9ᵐᵐ).—An older larva, caught in the net on May 7, is shown on Pl. XII. The most striking features of this form are the long trailing antennæ (flagella of the outer pair), the actual length of which is about 1 inch, which is more than twice the length of the larva. The remarkable eyes which this animal possesses give it a very odd appearance. They are placed at the extremity of club-shaped stalks, each of which is nearly 2ᵐᵐ long. The distance between the eyes is 4.7ᵐᵐ. In passing to the adult stage the eye-stalks are much reduced. The outer antennæ have a short peduncle; a long scale, armed with stiff hairs on the inner margin, and a long flagellum, all very much as in the adult prawn. (Pl. XII, and Pl. XIII, Figs. 40, 41.) The first pair of antennæ are much less like the adult form. (Pl. XII and Fig. 40). The stalk is longer and more slender than in the full-grown condition. The flagella are short, the inner one still rudimentary, and the sensory hairs are retained.

The carapace has developed on it a lateral furrow, which is surmounted by a conspicuous spine placed on either side at a point one-third the distance from the rostrum to the posterior end of the carapace. · The rostrum is short and stout, bent upward, and does not reach beyond a line passing through the vesicula anditoria. The front of the carapace bears also a short dentiform process on each side below the rostrum. These are the only indications of the future spinous armature of this region of the body. The abdomen and abdominal appendages are about as represented in Fig. 27. The telson is a short triangular plate, garnished with short bristles, and is terminated by a pair of very small spines. The uropods are provided with a close fringe of interlocking, plumose hairs, which are longest on the inner margin. The outer lamella is one-third longer than the inner and three times as long as the telson.

The first and second maxillæ of this larva are represented in Figs. 28 and 29. In Figs. 12, 19, 29, and 38 we have four stages in the evolution of the first maxilla, and we see that it undergoes comparatively little change. No trace of a palpus (endopodite) was seen in the specimen examined (Fig. 29), the appendage consisting of a small inner (coxopodite) and a larger outer knob-shaped branch (basipodite), each armed with short tooth-like spines. The second maxilla has also the adult character. (Figs. 28, 42.) It consists of an elongated outer plate (scaphognathite), fringed with a single row of plumose hairs; a palp-like endopodite, and an innermost lobulated division (basipodite and coxopodite), each part carrying a few bristles.

The first maxilliped of stage F is given in Fig. 30. It consists of a basal portion (coxopodite), which bears an inner and larger lobe (basipodite), having bristles on its proximal border; an exopodite tipped with a pair of bristles, and of an intermediate bud (endopodite) bearing a single bristle. Part of the second maxillipeds is shown in Pl. XI and also in Fig. 31 (St. F.). The exopodite is rudimentary. The outer segments are covered with spinous bristles. We see already a resemblance between these appendages and their adult forms. (Figs. 43, 45.) The third pair of maxillipeds are still the largest limbs. (Pl. XI, Mxp. III.) The terminal joint bears several long spines. Compare with the adult limb seen in Fig. 46.

The pereiopods are slender appendages, of which the third pair are longest, as in the adult; the second are longer than the first; the fourth and fifth are rudimentary. One of the first pair of pereiopods is represented in Fig. 33. This appendage is nonchelate, unlike the adult stage; all its segments are armed with long spines, and there is a cluster of serrate bristles on the inner side of the proximal end of the terminal segment, and near it a similar cluster on the next. Similar tufts of hair are found on the adult appendage. (Pl. XIII, Fig. 47.) The terminal joint of the second thoracic limb is shown in Fig. 32; the basal extremity of the third, the fourth, and fifth are given in Fig. 34. The second and third pair are chelate; the fourth is rudimentary; the fifth is still a bud. The abdominal appendages, excepting the sixth pair described above, are all uniramous. (Fig. 27.)

This larva is colorless, excepting large spots of reddish pigment, distributed much as in the previous stage. There is a spot near the extremity of the eye-stalk and similar ones on the abdomen. Some of the appendages are also tipped with brownish red. The attainment of the adult characters is now mainly a question of the further growth of parts already present.

The above outline gives us a pretty complete history of the metamorphosis of Stenopus. Between stages B and C a lacuna occurs, but it is not difficult to bridge over this gap. The development of Stenopus is especially interesting, inasmuch as it combines certain features of the metamorphosis of Penæus, Sergestes, Lucifer, and the Prawns in general, but it differs essentially from any of them. Detailed comparisons are purposely omitted in this paper, but we will call attention to the apparent similarity of the second larva of Stenopus (Pl. VIII, Fig. 17) to the zoëa of *Callianassa subterranea*, figured by Claus.* The length in each case is 5ᵐᵐ. He says, p. 54:

> Die jungen Callianassa larven besitzen beim Verlassen der Eihüllen eine ansehnliche Grösse, sind sehr langgestreckt und tragen drei spaltästige Füsspaare, von denen sich das Vordere schon wesentlich der Formgestaltung des späteren Maxillarfusses nähert. Der lange Stirnschnabel, sowie die Bestachelung des Abdomens, dessen zweites Segment mit einem besonders langen Rückendorn bewaffnet ist erinnern an die oben beschriebene larve.

which applies perfectly to the Stenopus zoëa, except that the latter has the first thoracic segment with its appendages, while, according to Claus, the first zoëa of Callianassa has not, although his figure is not clear on this point. The rostrum, eyes, antennæ, second maxillæ, and maxillipeds are nearly identical in the two forms. The differences are in the shape of the telson and in the condition of the thoracic appendages. The tail fin has a convex posterior edge, a median and two lateral, short spines, and eleven intermediate pairs. The rudiments of the sixth pair of abdominal appendages show through the integument. Behind the maxillipeds, already "die kurzen, schlauchförmigen Anlagen sämmtlicher Thoracalfüsse unter dem Integument bemärkbar sind."

Among the Prawns, Penæus has apparently preserved most completely the ancestral history of the Decapod Crustacea, and for this reason a thorough knowledge of the development of related species is very desirable.

IV. THE ADULT.

STENOPUS (Latreille).
　　　　Cancer (Herbst).
　　　　Palæmon (Olivier).
　　　　Stenopus (Latreille) Léach, Desmarest, Roux, Milne, Edwards, Adams, Dana, etc.

Diagnosis of Stenopus hispidus (Latreille).—Body nearly cylindrical. Carapace with prominent rostrum and distinct transverse groove. Outer antennæ with long, bristle-bordered scale bent under the inner antennæ toward the middle line. Second maxillipeds with epipodite and long exopodite. Third maxillipeds very long and appendicular, with a rudimentary exopodite at base. First, second, and third pairs of pereiopods chelate. The first and second pairs quite slender, ending in small shears. Third pair longest, bearing the large claws. Fourth and fifth pairs of pereiopods slender and nonchelate. Carpus and propodus of the same articulated into numerous rings. First pair of pleopods uniramous in both sexes, all the others biramous.

Special description.—Length, 37–44ᵐᵐ (1½–1¾ inches). There is little difference in size between the sexes, but the females are usually a trifle the larger.

Color: Body invariably white, crossed by three bands of reddish crimson. Appendages colorless, excepting the third pair of pereiopods, which are encircled by four wide zones of the same color. These markings are not of uniform tint, but vary from bright scarlet to mottled orange red. The basal joints of at least the third and fourth pairs of thoracic legs sky blue. Antennæ snow white. For further particulars under this heading, see Pl. V, and Sec. I.

The carapace (Fig. 37) presents a marked transverse fossa. It is covered with short dentiform spines, largest on the front. The rostrum is elevated, extending hardly beyond the basil joint of the inner antennæ. It ends in a sharp terminal spine and carries six to seven stout, curved teeth on the dorsal median line, besides a single spinule projecting downwards near the tip. From the single dorsal row of teeth two similar rows diverge, extending back to the transverse furrow. The

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*C. Claus : " Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceen-Systems." Wien, 1876. Taf. VIII, Fig. 1; also Figs. 2–7.

rostrum also bears on each side a single row of about four teeth projecting forward. The under side is unarmed. Several large spines occur in the angle behind the eye and on the basal joints of the antennæ.

The epidermic spines, which are characteristic of the Hispidus, though not confined to this species, are found upon the dorsal surface of the entire body, on the third pair of pereiopods and on the bases of the appendages generally. The first, second, fourth, and fifth pairs of thoracic legs are destitute of conspicuous spines. The spines of the carapace and anterior abdominal terga are bent forward; those of the fourth, fifth, and sixth abdominal somites and of the tail fin are appressed, stouter, nondentilate, and point backwards.

The telson is arrowhead-shaped; its free edges are garnished with short, closely set hairs; it has a median groove, bordered on either side by a longitudinal elevated ridge, bearing spines; it hardly surpasses the uropodal lamellæ. The eyes project at right angles to the long axis of the body. They have dark brownish black pigment and are mounted upon short, stout stalks, covered with small prickles. The labrum consists of a semicircular bar, the convex surface of which points forward and bears two nearly median spines projecting downward. From its concave border is suspended a lingulate appendage, which is supported by a thin, median, and vertical plate. The inner antennæ (Fig. 40) bear very long flagella, the disposition of which has already been noticed (Sec. 1). The segments of the stalk are armed with stout denticles, and each division of the proximal portion of the outer flagellum or exopodite bears externally a sharp spine.

The outer antennæ (Fig. 41) possess at their base a long, narrow scale (exopodite), which is traversed by longitudinal grooves. Their inner borders, which meet in the middle line, are fringed with closely set hairs. The stalk or protopodite is spiny, and the flagellum or endopodite is two and a half times the length of the body of the animal. The mandibles (Fig. 39) bear very large palpi, and have blunt interlocking teeth; a transverse furrow divides the cutting surfaces of each. The first pair of maxillæ (Fig. 38) consist of an inner (coxopodite) and outer branch (basipodite), with a slender endopodite. The outer division or coxopodite is thickly beset with strong spines. The second pair of maxillæ (Fig. 42) are furnished with an elongated plate, the "bailer" or scaphognathite, which is fringed with hairs, an inner lobulated portion (basipodite and coxopodite), and an intermediate endopodite, which bears several plumose hairs at its distal end.

The first pair of maxillipeds (Fig. 43) consist of an inner lobulated portion (coxopodite and basipodite), thickly studded with short bristles, an outer triangular plate (epipodite), and two intermediate appendages. The innermost of the latter (endopodite) terminates in a stout spine. It consists of two segments armed without by a row of long plumose hairs. The whip-like, appendage exopodite next this is twice as long and is bordered with short hairs. In the second pair of maxillipeds the basil portion consists of several lobules, tufted with hairs, and a small, external epipodite. There is a stout incurved endopodite, with hirsute terminal joints, and a long, slender exopodite. A transparent lamella springs from the outer side of the proximal half of the the endopodite, and bears plumose hairs on its free margin.

The third pair of maxillipeds (Fig. 46) are long and conspicuous, somewhat less slender than the first or second pairs of thoracic legs. The inner and outer borders are fringed with long hairs. The outer border is denticulated; the distal extremities of the segments, as of the ischiopodite, produced into a sharp spine. The basipodite is small, bearing the persistent and rudimentary exopodite, which is a slender palp equal in length to the ischiopodite. The first pair of dereiopods (Fig. 47) are small, slender, and chelate. The second pair of pereiopods are similar to the first pair, but longer.

The third pair of pereiopods, the "great chelæ," differ somewhat in size, the right being sometimes larger and sometimes smaller than the left. The chela is compressed and slightly twisted. There is a single row of stout regular denticles, forming a saw-tooth edge on either margin of the "palm," and several rows of lesser spines on the broad sides. There is also a longitudinal groove extending to the base of the dactyle. The carpus is prismatic and bears about five rows of large teeth. The ischium is more cylindrical, but similar. The dactyle and propodus possess each a prominent tooth, which fits into a corresponding depression.

The fourth pair of pereiopods (Fig. 48) end in short bifid dactyles, the terminal claw bearing a shorter proximal one below. The propodus is superficially segmented into from five to seven rings, which vary in size. The right propodus may have five rings, the left seven. The carpus is articulated into ten to twelve segments, commonly twelve, of variable or equal size. The fifth pair of pereiopods is similar to the fourth, but shorter. The propodus bears from six to seven segments, the carpus from eight to twelve. In the fourth and fifth thoracic legs the number of rings into which the propodus and carpus are divided differ within the above limits in different individuals of either sex and on the right and left sides of the same individual. The pleopods are all biramous, excepting the first pair, in which the endopodite is suppressed as shown in Fig. 44. This pair of appendages is much smaller in the male. In the female the first swimmerets are nearly as long as the following pairs and are fringed with long setæ.

Measurements (in millimeters).

[Locality: Nassau, New Providence, Bahama Islands.]

Sex	♂	♀	♂	♀	♂
Length from tip of rostrum to end of telson	37	43	44	44	40
Length of carapax, including rostrum	14.5	16	......	......	......
Greatest breadth, including spines	8	10	......	......	......
Greatest depth, including spines	7.5	10	......	......	......
Length of rostrum	4.5	......	......	......	......
Distance between transverse furrow and tip of rostrum	9	10	......	......	......
Length of first abdominal tergum	1	1.5	......	......	......
Length of second abdominal tergum	2.5	3	......	......	......
Length of third abdominal tergum	5	5.5	......	......	......
Length of fourth abdominal tergum	3	3	......	......	......
Length of fifth abdominal tergum	2.8	3	......	......	......
Length of sixth abdominal tergum	4.5	5.5	......	......	......
Length of telson	8	9	......	......	......
Greatest breadth of telson	3	4	......	......	......
Length of eye-stalk	3	......	......	......	......
Greatest diameter of eye	2	2	......	......	......
Breadth between eyes	6.5	7	......	......	......
Stalk of inner antennæ	45	......	......	......	......
Length of terminal segment of the same	1	......	......	......	......
Length of inner flagellum of the same	73	......	86	......	......
Length of outer flagellum of the same	75	......	98	......	......
Length of scale of outer antennæ	9	......	......	......	......
Greatest breadth of the same	1.8	......	......	......	......
Length of stalk of outer antennæ	1.5	......	......	......	......
Breadth of stalk of outer antennæ	1.5	......	......	......	......
Length of flagellum of outer antennæ	92	......	119	......	......
Breadth of flagellum of same at inner end	0.4	......	......	......	......
Length of third maxilliped	18.5	......	......	......	......
Length of terminal joint of the same	2.5	......	......	......	......
Length of basal joint of the same	5	......	......	......	......
Breadth of basal joint of the same	1	......	......	......	......
Length of exopodite of the same	5	......	......	......	......
Length of first pereiopod	20	......	......	......	......
Length of propodus of same	5	5	......	......	......
Breadth of propodus of same	1	1	......	......	......
Length of dactyle of same	2	2	......	......	......
Length of carpus of same	6	8	......	......	......
Length of second pereiopod	27	......	......	......	......
Length of propodus of same	6.5	7	......	......	......
Length of dactyle of same	3	3	......	......	......
Breadth of propodus of same	1.5	2	......	......	......
Length of carpus of same	9	11	......	......	......
Length of meros of same	7	8	......	......	......
Length of left third pereiopod	48	53	......	......	......
Length of chela	19	22	......	......	......
Greatest breadth of same with spines	5	6	......	......	......
Greatest depth of same with spines	3	4	......	......	......
Length of dactyle	7	9	......	......	......
Width over tooth of dactyle	2.1	2.5	......	......	......
Length of carpus of same	9.5	12	......	......	......
Greatest breadth of carpus without spines	3	3	......	......	......
Greatest breadth of carpus with spines	4	4	......	......	......
Length of meros of same	11	12	......	......	......
Length of right third pereiopod	46	51	......	......	......

Measurements (in millimeters)—Continued.

Sex	♂	♀	♂	♀	♂
Length of chela of the same	18	19			
Greatest breadth of same with spines	5	5			
Greatest depth of same without spines	4	3			
Length of dactyle of same	7				
Width over tooth of dactyle	2				
Length of carpus of right third pereiopod	9	11			
Greatest breadth of same with spines	4	4			
Greatest breadth of same without spines	3	3			
Length of meros of same	12	12.5			
Length of fourth pereiopod	36				
Length of dactyle of same	1.5	1.5			
Length of propodus of same	5	5			
Number of rings in propodus	5	5			
Length of carpus of same	14	18			
Number of rings in carpus	12	12			
Length of meros of same	10	11			
Greatest breadth of meros	1.4				
Length of fifth pereiopod	30				
Length of propodus of same	5	6			
Number of rings in propodus	6	6		✓	
Length of carpus of same	15	16			
Number of rings in carpus	13	12			
Length of meros of same	9.5	11			
Length of first pleopod	3	7			
Length of third pleopod		9			
Length of inner lamella of same	4	6			
Breadth of inner lamella of same	1.5	2			
Length of outer lamella of same	4	6			
Length of inner lamella of uropod	6.5	8			
Length of outer lamella of uropod	7	9			
Greatest breadth of outer lamella of uropod	3	3.5			

REMARKS.—The earliest figure of Stenopus hispidus with which I am acquainted is that of Olivier, published in 1811 under the name of *Palæmon hispidus* (1, Pl. 19, Fig. 2). In this drawing the third thoracic leg of the right side is represented as rudimentary. In explanation of this he says: "La pince gauche manquoit et paroissoit repousser. Dans un autre, c'étoit la droite qui manquoit et paroissoit repousser de même." The next drawing appears in Milne Edwards's Atlas (3, Pl. 25, Fig. 13) of 1837. Like Olivier's plate this is crude and faulty.

A second and very much better likeness of the Hispidus by Milne Edwards came out in Cuvier's Le Règne Animal (4, Pl. 50, Fig. 20). This is represented as pale straw color and was evidently made from an old alcoholic specimen. Some of the parts are also figured. Adams's figure (5, Tab. XII, Fig. 6), already noticed, and his brief description agree essentially with the Nassau form. The antennæ are not in their natural position, and should probably be more than twice as long as represented. Of the habits of the species he says: "The Stenopus, Sicyonia, and Penæus, usually swim in a slow, deliberate manner forwards, and occasionally with a sudden jerk propel themselves backward. They keep at a considerable distance from the shore and seem to love deep still water, never appearing when the surface of the sea is ruffled." The drawing by Dana (6, Pl. 40, Fig. 8) represents the antennæ of this animal for the first time in a natural position. The antennal and antennular stalks are, however, much too slender, compared either with Adams's figure or with the Nassau form. The length is given as 3 inches, while the Stenopus on the plate measures about 2¼ inches. So far as it goes his description agrees in the main with my own. He says: "The legs of the first and second pairs and of the fourth and fifth are colorless, and they are extremely slender, much more so than in the drawings hitherto giving of the Hispidus; third pair is about one-fourth longer than body, fourth joint of second pair nearly twice as long as hand; fourth joint of fourth pair 12-jointed, and fifth joint 7-jointed; tarsus minute (p. 606)."

This *extreme* slenderness does not appear in the specimens examined by me, nor is it apparent in Adams's figure, which is one of the previous drawings referred to by Dana. In making the drawing of the Nassau Stenopus (Pl. V) great pains were taken to represent all the appendages

in their natural positions, and in their true relative proportions. In Adams's plate the fourth joint of the fourth thoracic leg has 16–17 rings, the fifth joint 8 rings. In the Nassau form the carpus has 10–12, the propodus 5–7 rings. In details like this, where the right and left sides of the same individual are often unlike, it would be surprising to find agreement. Von Martens's short notice of the Cuban occurrence does not give us much additional knowledge, but there is no doubt that the alcoholic specimens examined by him belong to the same species as that described in this paper. He says: " Ich weiss keinen erheblichen Unterschied zwischen diesen cubanischen Exemplaren und den indischen anzugeben, welch letztere ich bei Amboina gesammelt habe. * * * Nur erscheinen die indischen im Leben bunt roth gezeichnet, in Spiritus blass orange und mehr hartschälig, endlich scheint Carpus und Hand des dritten Fusspaars bei ihnen minder vier-seitig, doch ist dieser letztere Unterschied gering und fliessend." He then adds that he would not be surprised if it should turn out that the West Indian form was specifically different from the East Indian.

So far then as we can judge from the figures and meager descriptions in our possession, the Asiatic Stenopus hispidus can not be regarded as specifically distinct from the American form. Perhaps a point of difference worthy of remark is the length of the body from rostrum to end of telson, which is given as $2\frac{1}{2}$ and 3 inches by Adams and Dana respectively. None of the Nassau specimens which I have measured were more than $1\frac{3}{4}$ inches long. The data upon this point are not conclusive, and, in view of our knowledge of local variations in this respect, can not be regarded as of much importance. It is hoped that the descriptions and measurements which are here given will afford a basis for future comparisons with the Pacific Stenopus hispidus.

List of species.

So far as I can learn, only five species of the genus Stenopus (Latreille) have been described, viz:

(1) *Stenopus hispidus* (*Latr.*):
> Distribution : (*a*) Indian Ocean, Borneo, and Philippines (Adams).
>> (*b*) Paumotu Islands and Balabac Passage, north of Borneo (Dana).
>> (*c*) Amboyna, Cuba (Von Martens).
>> (*d*) Abaco and New Providence, Bahama Islands.
>> (*e*) " Red Sea, Indian Ocean, Indian Archipelago, New Guinea " (de Man).

(2) *Stenopus spinosus* (*Risso*):
> Mediterranean (Heller), teste Von Martens and de Man.

(3) *Stenopus ensiferus* (*Dana*):
> Fiji Islands.

(4) *Stenopus semilævis* (*Von Martens*):
> (One specimen in the Berlin Zoölogical Museum, purporting to have come from the West Indies. Length 12^{mm}. Von Martens.)

(5) *Stenopus tenuirostris* (*de Man*):
> Amboyna: Length 24^{mm}. (More closely allied to Stenopus spinosus of the Mediteranean than to Stenopus hispidus, and is the representative of the former in the Indian Ocean ; de Man.)

STENOPUS LITERATURE.

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(5) *Adams and White :* The Zoölogy of the Voyage of H. M. S. Samarang, 1843–6, p. 61, London, 1850.
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(7) *Martens, E. v.:* Ueber Cubanische Crustaceen ; nach den Sammlungen Dr. J. Gundlach. Archiv. f. Naturgesch., 38. Jahrg., Bd. 2, 1872, p. 143.
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(9) *De Man, J. G.:* Bericht über die im indischen Archipel von Dr. J. Brock gesammelten Decapoden und Stomato-poden. Separat-Ausgabe aus dem Archiv. f. Naturgesch., 53. Jahrg., pp. 215–600, 17. Taf., Berlin, 1888.

CHAPTER III.

THE HABITS AND METAMORPHOSIS OF GONODACTYLUS CHIRAGRA.

By W. K. BROOKS.

(With Pl. I, III, XIV, and XV.)

THE STRUCTURE AND HABITS OF THE ADULT.

This well-known species is found along the shores and islands of all tropical and subtropical seas, and our collections contain specimens from the Atlantic, the Pacific, and the Indian Oceans. Among the many localities where its presence has been recorded the following may be named: Bermuda, Florida Keys, Bahama Islands, Cuba, St. Thomas, Brazil, Mediterranean, Cape St. Roque, Samboanga, Samboanga Banks, Nicobars, Red Sea, Amboina, Indian Ocean, New Guinea. It is subject to but little variation, notwithstanding its very wide distribution, and also notwithstanding the fact that there are several other distinct species of Gonodactylus extremely similar to chiragra, and distinguishable from it by only very minute differences. There is a well-marked chiragra-like group of species all so close to each other that their divergence from each other must have been comparatively recent, and in view of this fact it seems remarkable that one of these species should so persistently retain its identity when exposed to such a wide diversity of conditions.

The species may be thus characterized: Stomatopoda with the sixth abdominal somite separated from the telson by a movable joint; the hind body convex; and the dactyle of the raptorial claw without spines and enlarged at the base; rostrum consisting of a transverse proximal portion more than twice as wide as long, with subacute antero-lateral angles and a slender, acute median spine which does not quite reach to the bases of the eyes; carapace nearly rectangular, three-fifths as long as wide, leaving the dorsal surface of the second thoracic somite completely exposed; antero-lateral angles semicircular and projecting beyond the median gastric area, which is nearly flat, and bounded by two nearly parallel gastric sutures, which are continued to the posterior edge of the carapace, which is nearly transverse with rounded postero-lateral angles; the transverse cervical suture is faintly marked, distant from the anterior margin about two-thirds of the length of the carapace; second thoracic somite, somewhat narrower than the carapace, with acute lateral angles; the eight following somites equal in width and wider than the carapace; the third, fourth, and fifth thoracic somites about equal in length; the lateral margins of the third are straight, with rounded angles, and as wide as the dorsal portion; the fourth is narrowed a little towards the lateral edge, and the fifth still more so; dorsal surfaces of the free thoracic somites and of the first five abdominal somites smooth; hind body convex; all the abdominal somites have marginal lateral carinæ, which are nearly linear, with the anterior end only a little wider than the posterior end; postero-lateral angles rounded in the first four abdominal somites, rectangular in the fifth, and acutely pointed in the sixth; there are no dorsal carinæ on the first five abdominal somites, and no median dorsal carina on the sixth, which carries three pairs of swollen convex lateral carinæ, which are equal in length and end posteriorly in acute spines, which are occasionally wanting on the submedian pair; the external carina is much less swollen than the others, and it unites at its posterior end with the laterial marginal carina; the spines of all the carinæ project beyond the posterior edge of the somite and lie in the same transverse plane.

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S. Mis. 94——23

The fifth abdominal somite is somewhat longer than those in front of it, and about twice as long as the sixth. The telson sometimes presents slight variations, but most of its characteristics are well marked, so that there is usually no difficulty in distinguishing the species by examining it. It is considerably wider than long, and its median portion is occupied by a rounded prominence, which consists of three broad, convex rounded carinæ, none of them ending in spines; the median one is longer than the others and spatulate at its posterior end, while the others have both ends obtusely rounded and alike; external to the proximal end of each lateral carina, and almost directly under the tip of the second, or intermediate dorsal carina of the sixth abdominal somite there is a small polished hemispherical tubercle. The edge of the telson is folded into six teeth, of which the submedians are largest and project farthest backwards; the tips of the intermediates are distinct and reach about half way to the tips of the submedians; the laterals are obsolete on the dorsal surface, although thin, small tips are distinctly visible on the flat ventral surface of the telson; each of these six teeth carries a dorsal carina; that of the lateral is marginal and nearly linear, while the others lie in the dorsal axes of the teeth and are thick and convex; that which lies above the submedian tooth is short, and lies in the same longitudinal plane as the external carina of the median prominence of the telson, while that which lies above the intermediate tooth runs nearly to the anterior edge of the telson; the median edges of the submedian teeth are minutely serrated, slightly concave, and meeting at an acute angle. There is a minute, nearly obsolete, tooth in the angle between the submedian and the intermediate, and the tips of the submedians are occasionally, but exceptionally, tipped by movable acute spines. The dorsal surface of the basal joint of the uropod ends posteriorly in an acute spine with a small lobe on the outer side of the base; its ventral surface ends posteriorly in a curved process divided into two acute curved spines, of which the outer is much the stouter and usually considerably longer than the inner, although they are occasionally nearly equal; the outer one has no marginal tooth. The paddle of the exopodite is about half as long as the second joint, which carries a central terminal immovable spine, and usually eleven—rarely twelve, and still more rarely ten—movable spines, of which nine are marginal and the tenth and eleventh terminal, largest, and central to the paddle. The eyes are cylindrical, with rounded corneæ, and the first and second antennæ are about equal in length, and more than half of the second joint of the shaft of the first antenna is exposed in front of the eye.

In the Bahama Islands this species presents two well-marked color variations, which occur side by side, specimens of both sorts being often found in burrows less than an inch apart. In the one form the color is a uniform dull-olive without spots or markings of any sort, as shown in Pl. III; while the other form, which is copied in Pl. I, Fig. 2, is more transparent and is delicately mottled over the entire dorsal surface in an intricate but constant pattern of greyish-green pigment so distributed as to form three transverse bands across the carapace and the large joints of the raptorial claws and fine transverse bands across the telson, while over the rest of the dorsal surface it forms a complicated reticulum. This difference is not sexual, for I found both males and females of each color; nor is it distinctive of age, for, while all the largest specimens were of the uniform green color, I found specimens of each color of all sizes except the largest. It is not probable that there are two constant color varieties living side by side in the Bahama Islands, and I am disposed to think that the mottled transparent specimens are those which have recently moulted, and that the color becomes more uniform as the cuticle hardens.

In the Bahama Islands this species inhabits burrows which it constructs in the coral rock or in masses of coral in shallow water, and, as nearly all the localities where its presence has been recorded are in the coral area, it is probable that this habit is pretty generally retained by the species all over its habitat. I have found it most abundant in lagoons and sounds on shelving beaches which are bare or nearly bare at low tide; and when a beach of this description is overhung by a limestone cliff, from which fragments fall into the water, each fragment is honeycombed by their burrows. A crack or natural depression in the rock seems to be selected by the animal when about to construct a new burrow, for most of the burrows opened into such cracks. The mouth of the burrow is nearly circular and only a little larger than the body of its inhabitant, but just within it widens out into a flask-shaped cave (Pl. III), with smooth, even walls and regular curvature, and large enough for the animal to coil up or turn around inside it. Most of the burrows are horizontal, but many are vertical with the opening below, and a few are vertical with the opening above.

The animals usually rest coiled up, with the eyes and antennæ directed outwards, just within the mouth of the burrow. They are always on the alert and reach out and snap at every small animal which approaches, even when it is two or three times larger than the Gonodactylus. They rarely pursue their prey, at least in the day time, and while a bait held near the mouth of the burrow will usually tempt them as far out as the body can be stretched without leaving the burrow they seldom go any further. In aquaria they are much more active at night than in the daytime, and they may possibly wander more in search of prey at night than I have ever seen them do in the daytime. They are solitary in their habits, and I have never found two in the same burrow. They are pugnacious to an astonishing degree, and their fighting habits, as I have observed them in aquaria, are so fixed and constant that they must be constantly exercised by the animals when at home. When two specimens are placed together in an aquarium they at first appear to be unconscious of each other, but more careful examination will show that their eye stalks are in constant motion following each movement of the enemy. They soon assume a position in which they are face to face, although they may be on opposite sides of the aquarium, and the constant motion of their eye stalks shows how intently each movement is watched. Soon one attempts to get behind the other, but each such attempt is frustrated, until finally they are brought close together, face to face, and soon one springs suddenly upon the other and attempts to pinch some unprotected part. They then spring apart and eye each other again to repeat the attack at short intervals until one is disabled; the other then springs upon him and soon tears him limb from limb, disjointing all the free somites of the body and tearing out and devouring the flesh.

I was not able to learn how the burrows are made, for none which I kept in captivity made burrows. The regularity and smoothness of the burrows and their adaptation to the shape and size of the body indicate that they are constructed by the animals themselves. The habit of burrowing in hard rock instead of soft mud is a fortunate one for the naturalist; for, while it is almost impossible to obtain the eggs of an ordinary Stomatopod without using a steam dredging machine; it is easy to get those of Gonodactylus by breaking up the rock in which it lives.

While adult Stomatopods are abundant and widely distributed, their eggs are almost unknown, for most of them inhabit deep burrows under the water, where it is no easy matter to capture the adults, and even when these are caught they do not carry eggs even in the breeding season, for the eggs are not fastened to the appendages as they are in most Crustacea, but are deposited at the bottoms of the inaccessible burrows. As they are dependent upon the aëration which is produced by the current of water which the parent pumps through the burrow by means of the valve-like paddles of the abdominal feet, they die when deprived of this current. The eggs are sometimes obtained, but unless they are found in an advanced stage of development it is difficult to rear them, and I know of no Stomatopod which has been reared from the egg under observation except the Bahama *Gonodactylus chiragra*. As the pelagic larvæ are large and conspicuous they are often captured at the surface of the ocean in the tow net, and the number of genera and species of Stomatopod larvæ which have been described is nearly equal to the number of adult species which are known, and the opportunity to identify even one of these larvæ by actually rearing it from the egg is a most noteworthy and important occasion.

The habits of the Bahama Gonodactylus afford this opportunity; for the nature of the rock which it inhabits prevents the construction of a deep burrow, and as the fragments of rock may easily be carried ashore and broken up the eggs can be obtained without difficulty. At the time of my first visit to the Bahamas I was engaged in correcting the proofs of my report on the *Challenger* Stomatopods, and one of the motives of the expedition was the hope that I might possibly obtain Stomatopod eggs. A day or two after our arrival Dr. E. A. Andrews brought me a Gonodactylus and a bunch of yellow eggs, which he had picked out of a rock which he had broken to pieces while searching for Annelids. The eggs were newly laid, and, while they were obviously those of some crustacean, there was no evidence that they belonged to Gonodactylus except the fact that they were found among the fragments of a rock which also contained this animal. As soon as I saw the eggs and heard how they had been obtained I started for a point where the beach was covered with fragments of coral rock. It was then late in the afternoon and growing dark, but I waded into the water and carried ashore as large a rock as I could lift. After I had thrown this on to a larger rock and broken it to pieces there was just daylight enough to show me

the Gonodactyli scattering in all directions, and the masses of yellow eggs which were spattered over the large rock which I had used as an anvil; but the problem was solved, and I went home and to bed, confident that I should next day get all the embryological material I needed.

As shown in Pl. III, the animal molds or shapes the mass of eggs into a hemispherical cap, which fits over the convexity of the hind body and lies between it and the stone wall of the burrow. The parent reaches out to snatch at passing prey, but so long as she is undisturbed she remains in the burrow. When the burrow is broken open she quickly rolls the eggs into a ball, folds them under her body in a big armful, between the large joints of her raptorial claws, and endeavors to escape with them to a place of safety. The promptness with which this action is performed would seem to indicate that it is an instinct which has been acquired to meet some danger which frequently presents itself. It would seem as if a cave in a solid rock were a pretty safe refuge from all enemies except a naturalist with a geological hammer, and it is difficult to say what the accident is which has thus been provided against. The larger heads of growing coral are often broken off by the waves, and loose fragments of rock are overturned by severe storms, and it is possible that, when alarmed by a violent shock, it flees from its cave to escape the danger of being crushed when the rock is torn from its place and turned over. At any rate its habit is the reverse of that of most burrowing animals, for they usually retreat to the depths of the burrow when alarmed. This is true of all the Stomatopods which I have had an opportunity to observe except this species, and the chief use of the burrow of *Squilla empusa* is for refuge in danger, while *Lysiosquilla excavatrix* darts down its burrow at the least alarm and can not be driven out even when the sand has been dug up on all sides of it.

THE METAMORPHOSIS OF GONODACTYLUS CHIRAGRA.

That feature of the life of Stomatopods upon which new data are most to be desired is the history of the early larval stages, and an abundant supply of the eggs of *Gonodactylus chiragra* rendered it an easy matter to obtain this history for that species. I also obtained a complete series of eggs for studying the embryology, but, as a few preliminary sections showed that this was of slight interest and that there is no essential difference from other Macroura as regards the egg embryology, this subject was not studied.

Most of our knowledge of the metamorphosis of Stomatopods is based upon the comparative study of collections of alcoholic specimens, and the direct observations on living larvæ are very scanty. In 1882 Faxen published an account (Selections from Embryological Monographs compiled by Alexander Agassiz, Walter Faxon, and E. L. Mark, I Crustacea, Cambridge, 1882, Bull. Mus. Comp. Zoöl., Vol. IX, No. 1, Pl. VIII, Figs. 2 and 3) of observations made three years before upon a young *Squilla empusa* which he had reared from an Alima larva; and in a paper which was published in 1879 I described (On the larval stages of *Squilla empusa*) a series of similar larvæ which I had studied while they were alive, and which was sufficiently complete to warrant the statement that they were the young of *Squilla empusa*, and that this species probably hatches from the egg in the *Alima* stage. In my report on the *Challenger* Stomatopods (Report of the Scientific Results of the Voyage of H. M. S. *Challenger* during the years 1873-'76, XVI, part XLV, 1886) I have given an account of the metamorphosis of *Lysiosquilla excavatrix* which I had reared at Beaufort, N. C.; but except for these observations our knowledge of Stomatopod metamorphosis rests upon the comparative study of preserved specimens, and, while the series which are picked out from miscellaneous collections sometimes present pretty satisfactory evidence as to the adults which they represent, this sort of indirect evidence can not be conclusive.

Large and varied collections of larvæ have been compared for the purpose of selecting those which form stages in the same series, and of ascertaining as accurately as possible the adult affinities of the oldest larvæ, by Claus (Die Metamorphosen der Squilliden, *Abhandl. d. k. Gesellsch. d. Wiss., Göttingen*, Bd. XVI, pp. 1-55, Pls. I-VIII, 1871) and myself (*Challenger* Rep., pp. 81-114). My own report was, so far as this subject goes, a supplement to Claus's work, for in its preparation I availed myself of his methods and results, amplifying and completing many of his observations, and confirming some of his results and correcting others. Combining his work with my own, I devoted a chapter of my report to the discussion of the larvæ, and gave a scheme or outline of the probable metamorphosis of each genus of adult Stomatopods.

Stomatopod larvæ or Erichthidæ, as they were named before their larval nature was suspected, have been divided into four genera, *Erichthoidina*, *Erichthus*, *Squillerichthus*, and *Alima*. Of these four the first, *Erichthoidina*, is simply a younger stage in the life of the *Erichthus*, and the third, *Squillerichthus*, a fully-grown larva of the *Erichthus* type, so that the genera become reduced to two, *Erichthus* and *Alima*. Of these two genera, one, *Alima*, is much more sharply defined than the other, *Erichthus*, which contains a number of divergent types, of which I have shown that five may be clearly distinguished, and I have proposed, for these five, names which indicate the adult genus to which each corresponds. I have shown that there are many reasons for believing that all *Alimi* are *Squilla* larvæ; *Alimerichthus*, the larvæ of *Chloridella*; *Erichthalima*, the larvæ of *Coronida*; *Lysierichthus*, the larvæ of *Lysiosquilla*, and *Pseuderichthus*, the larvæ of *Pseudosquilla*. The remaining larval type may be distinguished from the *Lysierichthus* by the shallowness of its carapace, which is not at all infolded, and by the position of its postero lateral spines, which arise very close to the dorsal middle line; while it may be distinguished from the *Pseuderichthus* larvæ by the length of the posterolateral spines, which are at least half as long as the carapace, and also by the fact that the telson is wider than long and longer than the long outer spine of the uropod. For this larval type, which was represented in the *Challenger* collection by many specimens, I proposed the name *Gonerichthus*, giving, at the same time, many reasons for regarding it as the larva of the genus Gonodactylus. Several of these larvæ were selected and shown in Pl. XII, Fig. 5, Pl. XIII, Fig. 9, and Pl. XV, Figs. 1 and 5, of my report; and I pointed out that in all of these larvæ, as in the young Gonodactylus, the sixth abdominal somite has a pair of submedian spines near its posterior edge, and its posterolateral angles are produced into acute spines. The telson is slightly wider than long, and its submedian spines are long and slender, but shorter than they are in *Pseuderichthus*. The telson is notched on the middle line, and there are from fourteen to twenty small secondary spinules on its posterior edge, between the submedians. There is one small secondary spinule internal to the base of the lateral marginal spine, another internal to the base of the intermediate, and a third midway between this and the submedian.

In Pl. XV, Figs. 5 and 6, of my report, as in the young Gonodactylus, the outer edge of the proximal joint of the exopodite of the uropod is fringed by nine marginal spines, the terminal one longest, and the outer spine of the basal prolongation is much longer than the inner, but not so long as it is in *Pseuderichthus*. A comparison of the telson of the young Gonodactylus with that of the other larval types will show that the one now under discussion is the only one which exhibits this resemblance, and as this larva never exhibits any traces of marginal spines on the dactyle of the raptorial claw it must pertain to some known adult with an unarmed dactyle or else to a new genus. It is not probable that a larval type which is so common pertains to an unknown adult genus. The larvæ are not *Protosquilla*, as this genus has the telson fused with the sixth abdominal somite, while it is free in the older larvæ; nor are they *Pseudosquillæ*, for they have no movable spinules on the tips of the submedian spines of the telson; and as all the other genera of Stomatopods except Gonodactylus have the dactyle armed, the only remaining genus is Gonodactylus, and the structural characteristics of the oldest larvæ indicate that they are the young of species in this genus.

Led by these considerations I did not hesitate to speak of these larvæ, in the *Challenger* report, as Gonerichthi, or young Gonodactyli, and to give this larval form as one of the diagnostic characteristics of the genus. This determination rests, however, upon circumstantial or indirect evidence; and, while the evidence is quite conclusive, I was nevertheless pleased to obtain more positive proof from the larvæ which I reared from the eggs of *Gonodactylus chiragra*.

Like many other Crustacea which inhabit the coral reefs, this species has its metamorphosis abbreviated and it hatches from the egg in an advanced condition. It is shown just before hatching, seen from behind in Pl. XIV, Fig. 1, and from in front in Fig. 2. The large yolk covers the dorsal surface, and the larva is doubled on itself, so that the telson and the tip of the abdomen are visible in a front view. The first five abdominal somites are indicated before it leaves the egg, and the first five pairs of abdominal appendages are fully developed, although the other appendages, with the exception of the mandibles and the large raptorial second maxillipeds, are either absent or rudimentary. The eyes are large, and even before hatching they are movable, although they are nearly sessile.

The larva, immediately after hatching, is shown in side view in Pl. XIV, Fig. 3; in ventral view in Pl. XV, Fig. 8, and in dorsal view in Fig. 7 of the same plate. The carapace is nearly half as long as the entire animal, and its posterior border, which is deeply emarginated, crosses the midde line over the posterior edge of the tenth somite; the somite which carries the appendages which are usually called, in the decapod Crustacean, the second pair of legs. There is a short, rather stout rostrum, and the anterior end of the carapace, which covers about half the eyes, is nearly semicircular. The posterolateral spines are short and curved outwards; there are no secondary spines external to their bases, but there is a small median dorsal spine on the posterior edge of the carapace, while the anterolaterals are absent. The antennule consists of a two-jointed shaft with two flagella, one terminal and the other arising from the dorsal surface of the distal joint of the shaft. The antenna consists of a rudimentary exopodite, which is cylindrical and ends in five swimming hairs, although it is of little use in locomotion. The large eyes are subspherical, nearly sessile, and they touch each other on the middle line dorsal to the antennules. The mandibles are enormous and the two pairs of maxillae rudimentary, as are also the first pair of maxillipeds, while the second pair, the large raptorial limbs of the adult, are well developed, although the dactyle is not folded backwards upon the penultimate joint or propodite. The third, fourth, and fifth maxillipeds, corresponding to the third maxillipeds and first and second ambulatory limbs of decapods, are rudimentary, and the three following appendages are absent, although all the corresponding somites are indicated as well as their ganglia. The abdomen is about twice as wide as the thoracic region and somewhat more than half as wide as the carapace. The first five somites are distinct and all end in acute posterolateral angles. The suture which separates the fifth from the unsegmented region, which represents the sixth and the telson, is obscure, and this region is longer than wide.

The abdominal appendages gradually decrease in size from the first and largest to the fifth pair, but all have their adult structure, except that they carry no gills and all are functional. The telson has four marginal spines on each side. Its posterior edge is slightly notched and carries seven or eight pairs of minute movable spines. The newly hatched larvae swim actively about by means of their abdominal feet, not by flexing and extending the abdomen, and notwithstanding the presence of a great mass of food yolk in the walls of the stomach they eat voraciously. By a lucky chance I found their proper food at once. Several bunches of the eggs of some unknown Nudibranch were in the aquarium in which the first brood hatched, and the larvae, nearly a thousand in all, soon settled down upon them, covering them completely, and at once began tearing them off and eating them. When washed away from them by means of a jet of water they swam about the aquarium for a short time, but soon settled down upon the eggs again. As these eggs are not very abundant they can hardly be the only food of the young larvae, although I could find nothing else that they would touch, and they refused the eggs of all other Nudibranchs. At this stage the heart consists of a large anterior chamber in the region of the second maxillipeds and a large dorsal vessel running as far as the fifth abdominal somite, with a pair of ostia in each somite.

After about sixty hours they moulted and assumed the form which is shown in side view in Pl. XIV, Fig. 4. The rostrum and the spines on the posterior border of the carapace have lengthened, but its shape and relative size are about as before. The second antennae are more clearly divided than before into a shaft and a scale, which has lost its hairs and is more flattened. The first pair of maxillipeds have made their appearance in the adult form, and the second pair are much larger than before, and the dactyle is now folded back onto the edge of the flattened penultimate joint. In all other respects the larva is like the younger one, but a little longer and with less food yolk. In about a week after hatching they moulted again and passed into the third (Erichthus) stage, which is shown from above in Pl. XV, Fig. 9, and in side view in Pl. XIV, Fig. 5. The rostrum is now greatly elongated and reaches to the tips of the antennules. Small anterolateral spines have made their appearance, as well as a small spine external to the base of each posterolateral. These latter are greatly elongated and very slightly divergent. A great change in the shape of the carapace has taken place, as will be seen by comparing Fig. 7 of Pl. XV with Fig. 9. Its lateral margins are nearly parallel, and its greatest width only a little exceeds that of the abdomen. Its posterior border is now nearly transverse and crosses the middle line above the last thoracic somite. The

sixth abdominal somite has separated from the telson, but its appendages are not yet developed. The scale of the antenna is now fringed with hairs, and the eyes are divergent, with well developed stalks. The raptorial claws have greatly increased in size and are beginning to approximate to the adult form, while at the earlier stage they closely resembled the chelæ of the third, fourth, and fifth pairs of maxillipeds of an adult Stomatopod. From this time on to the end of its larval life the young Erichthus of *Gonodactylus chiragra* presents the characteristics of that larval type for which I have proposed the provisional name Gonerichthus; and, while the resemblance grows stronger as the larva grows older, it is unmistakable even now, and still clearer after the next molt, when it assumes the form shown in Pl. XIV, Fig. 6, from above, and obliquely from below in Pl. XV, Fig. 10.

The antennulary flagella are now beginning to elongate, and that of the antenna is now represented by a bud, but there are no new appendages, although the sixth abdominal somite is now indicated. Although it is very much younger than the Gonerichthi shown in my *Challenger* report in Pl. XV, Figs. 1, 5, 6, and 11, it resembles these larvæ in the following features as well as in many minor points: The rostrum is long and reaches beyond the tips of the antennules, and it has four or five median teeth on its ventral surface. The anterolateral angles of the carapace end in acute spines pointing forwards, and the anterior edges are inclined towards each other, so as to make at the base of the rostrum an angle a little greater than a right angle. The lateral borders of the carapace are nearly parallel, and the posterolateral spines long, slightly divergent, and with a small acute spine external to the base of each. The carapace covers all the five thoracic somites and all or nearly all of the first abdominal, and its posterior border is transverse. The median dorsal spine, which was carried on the posterior edge of the carapace of the younger larvæ (Figs. 3, 4, and 5 of Pl. XIV), has disappeared, although it persists until a much later stage in the larvæ shown in Figs. 1, 6, and 11 of the *Challenger* report. The hind body is now nearly three-fourths as wide as the carapace.

The lateral margins of the telson still carry, as they did during the earlier stages, four nearly equal marginal spines on each side; of these the most anterior is the *external*, the next the *intermediate*, the third a secondary spinule, and the fourth, which, at the stage shown in Fig. 6, Pl. XIV, forms the posterolateral angle of the telson, is the *submedian*. The posterior border between the submedians is very slightly notched and nearly transverse. All the *Challenger* Gonerichthi are very much older than this larva, and their telsons are more developed. The spines especially are much more elongated; but in Figs. 5 and 6 of Pl. XV of the report the secondary spine can be clearly recognized about halfway between the submedian and the intermediate.

With the assumption of the form shown in Pl. XV, Fig. 10, the habits of the larva undergo a sudden change. Up to this time, while able to swim briskly about by the use of their abdominal appendages, they spent most of their time near the bottom of the aquarium, seldom going up more than an inch or two, although they are quite able to reach the top of the water, which was about 10 inches deep, and when masses of Nudibranch eggs were suspended near the surface of the water they quickly discovered and fastened upon them.

Up to this time, also, they were peaceful and did not attack each other. Several hundred survived the molt which precedes the beginning of their pelagic life, but all of them soon died and none passed this stage, which is the one shown in Fig. 10. They now left the bottom, and became restless, swimming continually at all levels in the water. They refused to touch the eggs of which up to this time they had been so fond, and I could find nothing else which suited their appetites, but their proper food is, beyond question, small swimming animals of some sort, for they now began fighting among themselves, and when two met they would seize each other with their raptorial claws, and then tumble over and over together, until they struck the bottom, when both died. The survivors would not touch the dead bodies, although most of them soon shared the same fate, and the rest became weak and soon died.

At the same time that I was studying the growth of the captive larvæ I captured several older ones in the surface net, and one of them somewhat older than Fig. 10 is shown in Figs. 11 and 12. The third, fourth, and fifth maxillipeds are now developed and are like those of the adult; and

the three pairs of free thoracic legs, and the uropods are represented by buds. An umber of moults and probably an interval of many weeks intervenes between this stage and the one shown in Pl. xv, Fig. 11 of the *Challenger* report.

The life history of this species of Gonodactylus, in the Bahama Islands at least, is thus seen to be extremely simple. It hatches as an Erichthus and remains an Erichthus until it assumes its adult form; and as the successive appendages make their appearance they have from the first the structure which they are to retain through life. The statement which I made in my *Challenger* report (p. 55), that Gonodactylus hatches from the egg in the Erichthoidina stage and subsequently changes into an Erichthus, is an error, at least so far as Gonodactylus chiragra is concerned, although it is possible, in view of the great variation which we have observed in a single species of Alpheus, that in other regions, where the adults have different habits, the larva may hatch in a younger stage. Coral-dwelling crustacea seem to exhibit a tendency towards the abridgment of their metamorphosis, and it is not at all improbable that other species of Gonodactylus may have an Erichthoidina stage.

The *Challenger* collection contains a bottle of very minute and young larvæ in the Erichthoidina stage, and one of these is shown in Fig. 3 of Pl. xii of my report. Comparison between this and the newly hatched Erichthus of our species, Pl. xiv, Fig. 3, will show many points of resemblance, and future research may possibly prove that it is the larva of Gonodactylus, although the statement that all Gonodactyli hatch as Erichthoidinæ is an error.

CHAPTER IV.

THE METAMORPHOSIS OF ALPHEUS.

By W. K. Brook and F. H. Herrick.

(With Pls. I, II, IV, XVI to XXIV.)

Section I.—The Metamorphosis of Alpheus minor from Beaufort, North Carolina.

This small species is found in abundance at Beaufort, North Carolina, and in the Bahama Islands, and it is no doubt widely distributed along our southern coast. At Beaufort it is found in shallow vertical burrows in the sandy mud which forms the bottom of most of the land-locked sounds between tide marks. It is also met occasionally in shells, and under loose stones and oyster shells.

During its development, between the time when it hatches from the egg and the time when it acquires the adult form, it passes through a long metamorphosis, divided into many stages. Its life history has been traced by one of the authors at Beaufort, and by the other at Nassau, and the individuals from both these localities pass through exactly the same series of changes. As we also find that other species, such as *Alpheus normani*, pass through the same metamorphosis, the life history of *Alpheus minor* may be regarded at the primitive or ancestral life history of the genus, which originally characterized all the species; although it is now retained in its perfect form by only a few, and has undergone secondary or recent modifications in the others.

THE FIRST AND SECOND LARVAL STAGES.

The stage in which the larva hatches from the egg is of very short duration, as it molts and passes into the second stage within a few hours after hatching. No drawings of it were made before the change, but this is very slight, and the description of the second stage holds true in all essentials of the first stage, except that the tips of the exopodites of the three pairs of maxillipeds, and the plumose hairs on the antennules and antennæ are not fully extended until after the change.

The second larval stage is shown in Pl. xvi, Fig. 2, and in Pl. xvii, Fig. 2, and various organs of the larva during the first stage are shown in Pl. xvi, Figs. 4, 6, 7, and 8, and Pl. xviii, Fig. 4. In Pl. xvi, Fig. 4, is the antenna of the first larval stage, Fig. 6, the first maxilla, Fig. 7, the second maxilla, Fig. 8, the mandible, and Fig. 4 of Pl. xviii, the first maxilliped. As shown in Pl. xvii, Fig. 2, and in Pl. xvi, Fig. 2, the locomotor organs of the larva during the first and second stage are the plumose exopodites of the antennæ and of the three pairs of maxillipeds. There are no functional appendages posterior to the maxillipeds, and the large eyes are freely movable and entirely uncovered.

The larva has all its appendages fully developed and functional as far back as the third pair of maxillipeds. Following these are three bud-like rudiments of the first, second, and fifth pairs of thoracic limbs, and posterior to these a long tapering abdomen, divided into six segments, there being at this time no joint between the telson and the sixth abdominal segment. During the first

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stage there are no traces of any abdominal appendages, but in the second stage, the outlines of the sixth pair are faintly visible under the cuticle of the telson, as shown in Pl. XVI, Fig. 2. The stomach is almost completely free from yolk, and the surface of the body is marked by red and yellow pigment spots, which are very constant in position and number, and are well shown in the figures.

As shown in Pl. XVI, Fig. 2, the antennule consists of a stout shaft composed of a long basal portion with no trace of an ear and a much shorter distal joint, which carries externally a much shorter and smaller joint with four sensory hairs, and internally a long slender plumose hair, which is not fully extended until after the first moult. At this stage this hair is almost sessile upon the shaft, although its base is destined to give rise to the long flabellum of the antennule of the adult.

The antenna has a large exopodite, which is fringed with plumose hairs, and is an efficient organ of locomotion. During the first larval stage this exopodite, which is destined to become the flat scale of the adult antenna, is cylindrical and distinctly annulated, as shown in Pl. XVI, Fig. 4. At this stage it is divided into a basal portion and five movable joints, about equal in total length to the basal portion. After the first molt the annulations become less distinct, although the "scale" is still cylindrical, as shown in Pl. XVI, Fig. 2. The basal joint of the antenna is about equal in length to the "scale," undivided, and it carries upon the inner edge of its distal extremity a small, short, movable joint, with a single, long, plumose hair, which is "telescoped" before the first moult, but fully extended afterwards. This short joint is the rudimentary antennal flagellum, which in the adult is equal in length to the entire body of the animal.

The mandible is shown in Fig. 8. It is deeply cleft into two branches, the outer one with two rows of large, strongly marked dentations, and the inner one with a rudimentary palpus, two rows of hairs, and a finely serrated cutting edge. The first maxilla is very small, but it does not appear to be rudimentary. It is shown in Pl. XVI, Fig. 6. No exopodite could be made out. There is a small endopodite, with one long, plumose hair, and two basal joints, one with two sharp cutting hairs and the other with one. The second maxilla is shown in Pl. XVI, Fig. 7. The two basal joints are feebly indicated, and each carries three slender, simple hairs. The endopodite carries two terminal hairs, and the flat exopodite is fringed by seven. I could not determine whether these hairs are plumose or not. The three pairs of maxillipeds are functional and they present features which are characteristic of the genus Alpheus (see Pl. XVI, Fig. 2). Each has a large, flattened, polygonal, basal joint, which carries upon its inner edge a few short, sharp teeth, and upon its outer edge a long, flat exopodite, with plumose swimming hairs, and an endopodite which presents several peculiar features.

The endopodite of the first maxilliped is very short and two-jointed, that of the second is somewhat longer and five-jointed, while that of the third is very greatly elongated, without traces of joints, and ending in a long, simple hair which, as shown in Pl. XVIII, Fig. 4, is telescoped before the first moult, but immediately afterwards becomes lengthened, as shown in Pl. XVI, Fig. 2, until it reaches forward beyond the tips of the antennules and antennæ. Following the maxillipeds are three pairs of buds to represent the first, second, and fifth pairs of thoracic limbs. The first bud consists of a single branch, which is shown by its subsequent history to be the exopodite. The second has two branches, a short exopodite, and an extremely short endopodite, while the third consists of a somewhat longer, but still rudimentary, shaft, which represents the endopodite of the fifth thoracic limb, and has no trace of an exopodite.

The hind body is divided by joints into five abdominal somites, behind which is a long undivided region to represent the sixth abdominal somite and the telson. Before the first moult none of the abdominal appendages are present, but after this molt the sixth pair are faintly indicated under the integument of the telson, as shown in Pl. XVI, Fig. 2. The telson itself is broad, subtriangular, with its posterior border nearly straight and transverse. It carries eight pairs of stout plumose hairs, of which three pairs are much longer than any of the others and nearly equal. This set of three spines is placed at the angle of the posterior edge on a lobe or elongation, which, while it is so slightly marked as to scarcely interrupt the triangular outline, is still very distinct and easily recognizable. Of the remaining five spines on each side of the middle line, one is on the external border, and the other four on the posterior edge between the group of three and the middle line. The internal one is very small and might easily be overlooked.

THE THIRD LARVAL STAGE.

(Pl. XVI, Fig. 1.)

After molting the second time the larva assumes the form shown in Pl. XVI, Fig. 1. It is also shown, much less enlarged, in side view in Pl. XVII, Fig. 1. The first and fifth thoracic limbs are now functional, the second is represented by a bud, all the abdominal somites are distinct, and the sixth abdominal appendage has made its appearance. The first five abdominal appendages are still unrepresented, and the endopodite of the sixth is rudimentary, although its exopodite is fully developed and functional.

Those appendages which were present in stage two have undergone little change. The external branch of the antennule has, in place of the four sense-hairs of the earlier stage, only two, which are much longer than before. The long terminal hair of the inner branch has lost the marginal hairs of the earlier stage and is now simple, while two plumose hairs have made their appearance on the lower surface of the distal joint of the shaft. The scale of the antenna is still cylindrical, but the annulations which marked it during the earlier stage have disappeared. The flagellum still consists of only one short joint, and the long terminal hair which it carried at the earlier stage has disappeared. The mandibles, maxillæ, and maxillipeds are about as they were before, but the endopodite of the third maxilliped has almost completely lost the long terminal hair of stage two, and has also become relatively shorter, and is now divided into four joints.

The first thoracic leg, which was rudimentary in stage two, has now acquired a flat basal joint and a plumose exopodite, like those of the preceding appendages, but the endopodite is represented only by a rudimentary knob or bud upon the anterior edge of the basal joint. The second thoracic limb is, as it was at the earlier stage, a two-lobed bud. No buds have as yet appeared between it and the base of the fifth thoracic appendage, which is now fully developed and forms the most conspicuous peculiarity of this stage in the development of Alpheus. It has no exopodite, its basal joint is not enlarged nor flattened, and its long, slender, cylindrical shaft, made up at this stage of four joints, is prolonged at its tip into a long, slender, tapering, simple hair, the end of which reaches beyond the tips of the antennæ when the appendage is in the position shown in the figure Pl. XVI, Fig. 1. The appendage seems to have little power of motion and it seldom deviates much from the position shown in the drawing, being usually carried closely pressed against the ventral surface of the body between the bases of the other appendages, with its tip directed forward. All six abdominal somites are distinct and movable, but the first five have as yet no traces of appendages. The first four somites are short and equal, the fifth is nearly as long as the first four together, and the sixth is very narrow and almost twice as long as the fifth. The endopodite of the sixth abdominal appendage is present and of considerable size, but it is not as yet functional, although the exopodite, which is not very much larger, is fringed by six long, plumose, swimming hairs and is used in locomotion. The two spines which are carried upon the lateral margins of the telson at an earlier stage have disappeared, and there is less difference than before in the relative sizes of the others, but the general form is the same.

FOURTH LARVAL STAGE.

The subsequent history of *Alpheus minor* was traced by one of the authors at Beaufort and by the other at Nassau, but as the stages which follow were found to be almost exactly like the corresponding stage of other species which had already been drawn, it did not seem to be advisable to make new figures, and in the remainder of the description the illustrations which are referred to actually represent the larvæ of other species. After its third molt the larva of *Alpheus minor* passes into its fourth stage, when it becomes almost exactly like the fourth larval stage of *Alpheus heterochelis*, shown in Pl. XVIII, Fig. 3. There is little change at the anterior end of the body, except that the carapace now begins to extend over the eyes, and the ears have made their appearance in the basal joints of the antennules. The mandible has lost its outer branch, and the basal joint of the second maxilla, Pl. XVI, Fig. 5, carries on its inner edge three hairy lobes. There are now five pairs of swimming appendages in place of the three of stages one and two, and the four of stage three. These five are the exopodites of the first, second, and third maxillipeds

and those of the first and second thoracic legs. The endopodites of the maxillipeds are as before. The endopodite of the first thoracic leg, which was represented in stage three by a rudimentary bud, now appears to be entirely wanting. The second thoracic limb, which in stage three was represented by a bilobed bud, now consists of a basal joint, with a large, functional, plumose exopodite and a rudimentary, bud-like endopodite. Between this appendage and the base of the fully developed fifth thoracic limb there is a row of buds to represent the third and fourth thoracic limbs, which became developed after the next molt. The fifth is about as it was in the preceding stage, and it carries no trace of an exopodite. The abdomen is about as before, except that the endopodite of the sixth abdominal appendage, the only one yet represented, is now fully developed and fringed like the exopodite by long, plumose, swimming hairs. The telson has become elongated and narrow, and the spines upon its posterior end are much smaller than before.

THE FIFTH LARVAL STAGE.

None of the figures of the larvæ of other species exactly represent the larva of *Alpheus minor* after the next molt. The eyes are now partially covered by the carapace, and the swimming organs are the seven pairs of fully developed exopodites belonging to the three pairs of maxillipeds and the first four pairs of thoracic legs. At this stage these four pairs of appendages reacquire their endopodites, and the anterior end of the body is similar to that of the larva shown in Pl. XXI, Fig. 1, from which, however, it differs greatly as regards the telson and the sixth abdominal appendage. The first five abdominal appendages are now represented by buds like those shown in Pl. XXI, Fig. 1, and in Pl. XIX, Figs. 1 and 2, but the terminal portion of the abdomen is nearly like that of Fig. 3 in Pl. XX. The telson is greatly elongated, narrow, and its terminal spines are very small.

THE OLDER LARVAL STAGES OF ALPHEUS MINOR.

During the successive molts the abdominal appendages become fully developed, the eyes become completely covered by the anterior edge of the carapace, the antennæ become elongated, the antennule develops a scale, the swimming exopodites of the maxillipeds and thoracic legs disappear, these appendages assume their adult form, and acquire gills, and the animal gradually becomes like the one shown in Pl. XX, Fig. 2, which is a young Alpheus of another species.

THE METAMORPHOSIS OF ALPHEUS HETEROCHELIS FROM THE BAHAMA ISLANDS.

In the Bahama Islands this species passes through a series of stages which, except for a few minor differences of detail, are exactly like those in the life history which has just been described.

This fact is remarkable when it is known that the life history of the same species is very different at Beaufort, North Carolina, and that Packard has described still another life history for specimens of the same species which he studied at Key West.

FIRST LARVAL STAGE.

The Bahama specimens hatch from the egg in the stage shown in side view in Fig. 1 of Pl. XVIII. As this larva agrees in all details of its structure with the first stage of *Alpheus minor* shown in Pl. XVII, Fig. 2, already described, no further description is necessary.

THE SECOND LARVAL STAGE.

Like *Alpheus minus* the Bahama specimens of *Alpheus heterochelis* molt within a few hours after hatching, but they undergo no essential change, and Pl. XVI, Fig. 2, exhibits all the essential characteristics, although this figure was drawn from a specimen of *Alpheus minor*.

The most noteworthy specific difference is in the relative length of the marginal spines of the telson. In the first and second larval stages of both species there are eight pairs of spines, one pair on the outer edge and seven on the posterior edge, as shown for *Alpheus minor* in Pl. XVI, Fig. 2, and for *Alpheus heterochelis* in Pl. XVI, Fig. 3. In both species the pair next the median line are rudimentary and the next pair very small, but the three which arise from the rounded angle of the

telson are much more nearly equal to the others in *Alpheus heterochelis* than in *Alpheus minor*. If, as seems probable, the triangular telson of the *macrouran zoëa* is a secondary modification of the deeply furcated telson of a more ancient protozoea, then the first larval stages of *Alpheus minor* are in this respect more primitive or protozoean than those of *Alpheus heterochelis*.

THE THIRD LARVAL STAGE.

This is shown from below in Pl. XVIII, Fig. 2, and a comparison with Fig. 1 of Pl. XVI will show its very close resemblance to *Alpheus minus* at the same stage. The only essential difference between them relates to the rudimentary thoracic limbs. In both species the first thoracic limb has a functional swimming exopodite and a rudimentary endopodite, and in both the fifth thoracic limb has a greatly elongated jointed cylindrical endopodite and no exopodite, but between these limbs *Alpheus heterochelis* has buds to represent the other three pairs of thoracic limbs, while *Alpheus minor* has buds for only one pair, and the other buds do not appear until after the next molt.

THE FOURTH LARVAL STAGE OF ALPHEUS HETEROCHELIS.

This is shown from below in Pl. XVIII, Fig. 3, and there are no noteworthy differences between it and *Alpheus minor*.

THE LATER STAGES OF THE BAHAMA ALPHEUS HETEROCHELIS.

The transformation of the larva into the adult Alpheus occupies a number of molts, and the general character of the changes will be understood by the study of Pl. XIX and XX, although these plates were drawn from Beaufort specimens of the species.

THE METAMORPHOSIS OF ALPHEUS HETEROCHELIS FROM BEAUFORT, NORTH CAROLINA.

As shown in Pl. XX, Fig. 1, this, before it hatches from the egg, reaches a stage of development which somewhat resembles stages two and three of the Bahama specimens. There are many important differences however, and the stage in which it hatches is not directly comparable with any stage in the life of the Bahama form, nor in that of *Alpheus minor*. Just before hatching it has, like the Bahama form immediately after hatching, three pairs of fully developed swimming maxillipeds, but it also has buds to represent all five pairs of thoracic legs. The antennary scale and flagellum are much more advanced than they are at a much later stage in the Bahama form, and the abdomen is much more distinctly segmented. The larva, immediately after hatching, is shown in side view in Pl. XIX, Fig. 2, and in ventral view in Fig. 1. The antennule and antenna are shown on a larger scale in Figs. 3 and 4, and the mandible and first and second maxillæ in Figs. 5, 6, and 7 of the same plate. The animal now has all the appendages which are present in the adult, but all behind the maxillipeds are rudimentary, although they all become functional after the first molt, as shown in Pl. XX, Fig. 3.

The antennule, Pl. XIX, Fig. 3, has a long cylindrical shaft made up of three joints fringed with plumose hairs and terminating in an exopodite with sensory hairs and an endopodite or flagellum, which is short and rudimentary but much longer than it is in the younger stages of the Bahama specimens. The antenna, Fig. 4, presents even greater differences. The flagellum is about as long as the scale, and two jointed, while the scale itself is flat, although its tip still presents traces of a primitive segmented condition. It is, however, of little use in swimming, and in fact the larva has at this stage only very feeble locomotive power. The eyes are stalked and movable and almost completely uncovered. The mandible is simple and without a palpus, as shown in Fig. 5. The first maxilla, Fig. 6, is very small, but apparently it is not rudimentary as its two lobes carry cutting hairs. The second maxilla, Fig. 7, is a broad flat plate, very much more developed than that of the newly hatched Bahama specimen shown in Pl. XVI, Fig. 5.

The three pairs of maxillipeds (Pl. XIX, Fig. 1) are almost exactly like those of the newly hatched Bahama larva (Pl. XVIII, Fig. 1) or those of the *Alpheus minor* at the same stage (Pl. XVI, Fig. 2), but the thoracic appendages (Pl. XIX, Fig. 1) are entirely different, and the ventral surface of the body is covered by a mass of limbs closely crowded, all pretty well developed, but all as yet

functionless.   Careful examination shows that there are five pairs (the five pairs of thoracic limbs), and that all but the last pair are biramous.   In all, the exopodites are longer than the endopodites, which decrease in length from in front backwards, while the endopodites increase in length.   The later history of these limbs shows that the exopodites never become functional, as they do in the Bahama form.

All six abdominal somites are distinct, although the line separating the sixth from the telson is faintly marked.   The first five pairs of abdominal feet are represented by five biramous buds projecting beyond the outline of the body, while the sixth pair are only faintly outlined under the cuticle of the telson, which itself presents a most important difference from that of the young Bahama larva, as it is not triangular, but spatulate; and of the eight pairs of setæ the three pairs which in *Alpheus minor* lie on the lobe at the angle of the telson are not on a distinct lobe, nor do they differ in size from the adjacent setæ.

This larva molts a few hours after hatching, and at once undergoes the most profound changes, and assumes the form shown in Pl. XX, Fig. 3.   It is no longer a larva, but a young Alpheus. The eyes are almost covered by the carapace, the ear is well developed, and all the appendages are present and functional and essentially like those of the adult.   The antennule has two flagella, each with several joints.   The flagellum of the antenna is more than twice as long as the scale and is composed of twenty-two joints, while the scale has its final form.

The first maxilla (Fig. 5) has a large club-shaped lobe, fringed with short hairs, and a rudimentary endopodite, while the second maxilla (Fig. 6) is a broad flat plate with cutting lobes and a short, rod-like endopodite.   The three pairs of maxillipeds (Figs. 7, 8, and 9) have assumed the characteristic Macrouran form and are no longer concerned in locomotion, while the thoracic limbs have elongated into the five pairs of ambulatory appendages of the adult, although they still retain their rudimentary exopodites.   The abdomen is now like that of the adult, and the telson (Fig. 4) is long and narrow.   An older specimen is shown in Fig. 2 and a still older one in Pl. XVII, Fig. 3.

Comparing the history of the Bahama form with that of the North Carolina form, the most conspicuous peculiarity, and that which first attracts attention, is the great abbreviation of the latter.   The Beaufort specimens hatch in a much more advanced condition than the Bahama specimens, and, while the latter pass through many larval stages, the former quickly assume the adult form.   This is not all, nor is it even the most fundamental difference between them.   The development of the Beaufort specimens is not simply accelerated; it is profoundly modified, so that no exact parallel can be drawn between any larval stage of the one and a stage of the other.   The statement that the Beaufort specimens pass, before leaving the egg, through stages which are exhibited during the free life of the Bahama specimens would do violence to the facts; for the difference between them is very much more fundamental than this statement would imply.   For example, the Bahama form has at first three, then four, then five, and then seven schizopod feet with functional swimming exopodites, while the Beaufort form never has more than three.   As regards the thoracic region and the first five abdominal appendages the Beaufort larva, at the time of hatching (Pl. XIX, Fig. 1), is more advanced than the fourth larval stage of the Bahama form (Pl. XVIII, Fig. 3), while the sixth pair of abdominal appendages are like those of the Bahama form at the time of hatching (Pl. XVI, Fig. 3).   In the Bahama form the first and fifth thoracic limbs are the oldest, and the others appear in succession from in front backwards; all five pairs make their appearance together in the Beaufort form.   In the Bahama form the sixth pair of abdominal feet appear before and in the Beaufort form after the others.   Many minor differences of the same general character show that we have to do with profound modification of the life history rather than with simple acceleration.

THE DEVELOPMENT OF ALPHEUS HETEROCHELIS FROM KEY WEST.

According to Packard's account the specimens of *Alpheus heterochelis* which occur at Key West differ from those which occur at Beaufort in about the same way that the latter differ from those from the Bahamas, as the metamorphosis appears to be entirely absent in the Key West specimens.   Packard states that, while still inside the egg, they had all the appendages of the adult in essentially the adult form.   There were five pairs of thoracic legs and the first pair had large

chelæ, and the eyes were nearly sessile. In this case also there seems to be modification as well as acceleration, as Packard says that there were only five pairs of abdominal feet and that these were well developed. It may seem to some that the fact that these three forms present such great and constant differences in development is a reason for regarding them as three distinct species, but, whether we hold that they belong to one, two, or three species, they will still furnish proof of the existence of profound modifications in the life histories of adults which have remained almost exactly alike.

Careful and minute comparison between adult specimens from Beaufort and Nassau showed the closest agreement in nearly all particulars (v. Chap. v, Pt. First, Section II), and it has therefore seemed best for us to regard them as belonging to a single species; the more so since our discovery that different individuals of another species found at Nassau (*Alpheus saulcyi*) differ from one another during their larval stages in somewhat the same way that the Beaufort specimens of heterochelis differ from the Bahama specimens.

Alpheus minor and *Alpheus heterochelis* are very distinct species. The adults have diverged from one another so far that one could not possibly be mistaken for the other; yet the life history of the Bahama heterochelis is so exactly like that of *Alpheus minor*, both at Beaufort and in the Bahamas, that the same figures of the early stages will serve for both; for the larval stages of heterochelis have undergone local modifications, while the adults have remained almost absolutely unchanged, except as regards the reproductive elements and their product.

Section V.—Larval development of Alpheus saulcyi.

An egg of *Alpheus saulcyi* just ready to hatch is shown in Pl. XXI, Fig. 5. The large claws are plainly visible through the transparent shell. The antennæ are folded back alongside the body, while the abdominal and closely packed thoracic appendages are directed forward. The telson overlaps the head.

First larva (length, $= \frac{15}{100}$ inch).—Fig. 1 shows the larva as it is just hatched. It belongs to the variety found in the brown sponges. The various parts may be seen more highly magnified in Pl. XXI, Figs. 4, 6, 7, 9, and Pl. XXII, Figs. 1–8, 12. In both varieties the animal hatched as a schizopod, loosely infolded in a larval skin, but not invariably, as I have noticed that in one or two cases, where females of the longicarpus with very few, perhaps half a dozen eggs, produced young, the metamorphosis was completely lost, the larvæ being in a stage corresponding to that usually attained after the second molt and represented in Pl. XXI, Fig. 8 This is referred to again at the end of the section.

To return to the first larva (Pl. XXI, Fig. 1); this is fifteen one-hundredths of an inch long. It is semi-transparent and colorless, except for spots of characteristic red and yellow pigment sprinkled freely on the abdomen, the telson, and appendages. Rudimentary gills are present and a remnant of unabsorbed green yolk is conspicuous in the stomach. The carapace covers the bases of all the thoracic appendages but the last pair. It is produced forward into a short simple spine, the rostrum, which extends between the eyes. There is a rudiment, on either side, of the ocular spines (Pl. XXII, Fig. 6), which soon grow forward and give to the front the characteristic trident shape. The eyes project forward, only the extreme base of the stalk being covered by the carapace. A median eye or ocellus is present just below and between the bases of the lateral eye stalks.

Both pairs of antennæ are biramous and jointed. The antennules (Fig. 8) consist of a stout peduncle, a short endopodite, and a shorter bud or outer branch, which bears several bunches of sensory filaments. The peduncle is composed of three segments, as in the adult; the basal joint being four times the length of either of the other two, and bearing on its outer side a rudimentary aural scale. The upper margin of each joint carries one or more plumose hairs. The antennæ (Pl. XXII, Fig. 7) are formed on the adult plan. There is an inner antennal stalk consisting of two joints, bearing a rudimentary flagellum, and an outer scale or exopodite. The distal margin of the exopodite is garnished with plumose hairs and carries a short outer spur.

The mandibles (Fig. 12, drawn from a larva after the first moult) are deeply cleft, as in the adult. The outer branch is dentated at its distal end and carries a palpus. The first maxillæ (Fig. 6,

shown with more detail in Fig. 3, Pl. XXII) have adult characters. They are biramous. The endopodite is stout and toothed at its apex. The more slender outer division bears a short spine near the distal end. In the second maxillæ (Fig. 6, Pl. XXI) the scaphognathite or respiratory plate is most prominent. This is now composed of an anterior portion, bordered with from six to twelve long plumose hairs and a posterior, rudimentary, and hairless lobe. The inner division (endopodite) has the adult form, while the innermost lobes of the adult appendage (Pl. XXIV. Fig. 9) are unrepresented.

The maxillipeds are all biramous appendages, and their exopodites are the principal swimming organs. The endopodite of the first pair is short and stout and divided at its tip. That of the third pair is three-jointed and equal in length to the exopodite. In the first pair of thoracic legs (Pl. XXI, Figs. 4 and 7) the inequality of the chelæ is very marked, and, as we have already seen, it is so for some time before hatching. Individuals differ somewhat in this respect. The articulations of the carpus and meros are distinct. The exopodites of this and of the three succeeding pairs of thoracic limbs are tipped with rudimentary invaginated hairs. The second pair of pereiopods (Pl. XXII, Fig. 1) are chelate, but the articulations of the carpus are not distinct. The third pair of pereiopods (Fig. 2) end in bidentated dactyles and have short exopodites. The fifth pair are without swimming organs.

All the abdominal appendages are present and functional, excepting the sixth pair. They have only very short hairs until after the first moult. The first pair (Pl. XXII, Fig. 5) consist of a larger outer and smaller inner blade. This endopodite remains rudimentary in the adult male, but nearly equals the exopodite in length in the female, as will be seen by reference to Pl. XXIV, Figs. 4 and 5. This convenient sexual mark probably appears early, but can not be relied upon at this stage. The second (Pl. XXII, Fig. 4) and three succeeding pairs of pleopods have a stout base, an outer blade like that of the first pair, and a shorter endopodite which bears on its inner margin a lobule or palp. The sixth pair, or uropods (Pl. XXI, Fig. 9), are not yet free. The inner and smaller divisions point forward, meeting on the middle line. The telson, which terminates the body, covering the outer uropodal limbs, is a rounded, spatulate plate, with a median notch. Its free posterior edge is fringed with seven pairs of plumose spines, the first or median pair being rudimentary, and the next four succeeding pairs long and nearly equal.

Second larva (length, $\frac{16}{100}$ inch).—The first moult takes place either immediately or very soon after hatching. The animal as it now appears is shown in Pl. XXI, Fig. 2. The principal external changes thus produced are the following: (1) The rostrum and ocular arches extend farther over the eyes. (2) Both divisions of the antennules are considerably extended. The flagella of the antennæ are from three to four times their former size and are articulated into twenty to thirty rings, the scale still not passing the peduncle. (3) The thoracic appendages have more of the adult characteristics. The articulations of the carpus of the second pair are distinct. The exopodites of the first four pairs are functional, and the last pair has grown forward. (4) The pleopods presently acquire swimming hairs; the telson plate is free and the uropods are functional for the first time. (5) The last thoracic segment is still uncovered and the eyes are incompletely hooded.

Third larva (length, about $\frac{1}{6}$ inch).—The third larva as it appears after the second moult, which takes place in twenty-five to thirty hours after hatching, is represented in Pl. XXI, Fig. 8. It has now the general adult character, and can not be called a larva in the strict sense. At even this early age the pugnacious instinct is strong, and although only about one-sixth of an inch long, it snaps audibly the fingers of its large "hand," which is carried extended forward. It also swims on the bottom of the jar in all respects like the adult. Only a few globules of yolk remain in the stomach. The gills are now quite prominent. They are evidently functional to some degree, and were so, possibly, at an earlier date. The yellow and red pigment cells have nearly all disappeared or are temporarily withdrawn from view.

A most prominent change at the second moult is the extension forward of the rostrum and the ocular spines, which form a hood over each eye. The antennal peduncle surpasses the scale, and its flagellum nearly equals the carapace in length. As in the adult, the large chelæ are very prominent. The exopodites of the thoracic appendages have dwindled to rudiments. The view of the head of a four-days old Alpheus is shown in Fig. 3, Pl. XXI.

The fourth form (after third moult).—When six or seven days old the third moult is passed, but only slight changes are introduced. The small chela and the inner and outer antennæ of this phase are given in Figs. 9, 10, 16, Pl. XXII. The inner branch of the antennules is still relatively short; the basal or aural spine extends to nearly the end of the first joint. The bristle-bordered plate of the antennæ has now developed a considerable spine near its outer extremity, a rudiment of which appears in the first larva (Fig. 7). This represents the squamal spine, to which the plate is ordinarily attached, in the adult. The spine is here developed from the plate. The latter may disappear, as we shall see further on, to be finally regenerated from the base of the spine. The small chela has the adult form.

The fifth form (after fourth moult).—These animals moulted the fourth time ten days after hatching. Very little change was apparent, except in size, and beyond this point we did not follow them.

METAMORPHOSIS OF ALPHEUS SAULCYI FURTHER ABBREVIATED.

As was stated above, the metamorphosis of *Alpheus saulcyi* may be still further accelerated so as to practically disappear altogether. This fact is illustrated by a young Alpheus hatched in a glass dish April 25 (Fig. 17, Pl. XXII). The prawn (var. *longicarpus*) was taken from a brown sponge. The eggs, half a dozen in number, were slow in developing. The small chela is shown in Fig. 15.

This phase corresponds with that usually attained after the second moult (shown in Fig. 8, Pl. XXI), with which it corresponds in size and color. All the thoracic and abdominal appendages have nearly the adult form, the exopodites of the former being rudimentary, as in Fig. 8. The large chela is most prominent, being nearly as large again as the smaller one. The eyes are partly hooded, but not so much as the four-day old prawn represented by Fig. 3. The Alpheus had to be held in a compressorium in order to be drawn, so that the parts are slightly distorted by pressure. At the time of hatching most of the hairs on the appendages generally are in a rudimentary condition.

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V.

ALPHEUS: A STUDY IN THE DEVELOPMENT OF CRUSTACEA.

By Francis H. Herrick.

CONTENTS.

INTRODUCTION.

The observations offered in this memoir were undertaken at Beaufort, North Carolina, in June, 1885, at the Marine Zoological Station of the Johns Hopkins University. But little was accomplished, however, until the next and following seasons, 1886–'87, when I enjoyed the advantages of this laboratory in the Bahama Islands.

A part of this memoir was accepted as a thesis for the degree of Ph. D. by the Board of University Studies of the Johns Hopkins University in May, 1888.

I take this opportunity of thanking Professor Brooks for his invaluable counsel, aid, and encouragement from the beginning to the end of the work.

At Nassau, New Providence, during a sojourn of four months (March to July, 1887), I had the rare opportunity of a making a comparative study of a large number of Crustacea. At least thirteen species of Alpheus were discovered on the coral reefs and shores of New Providence, and in all these the eggs have been obtained, and in nearly all the larvæ or first zoëas have been hatched in aquaria. Many of these forms are new or but little known, and when the means of publication is found it is hoped that their comparative and systematic zoölogy can be fully illustrated.

The majority of the decapod Crustacea have a long and complicated metamorphosis. That in a few forms the early stages are jumped, so that the young hatch in practically the adult condition, is a remarkable fact, and the discovery of a probable cause for this phenomenon in Alpheus is one of the most interesting results of that part of our work which deals with the metamorphosis of the genus.

The development of Alpheus has never, I believe, been previously studied, excepting the metamorphosis of the two Beaufort species, so that there is no work of others to refer to, which bears directly upon our subject. But the literature of the Arthropods is very great, commensurate indeed with the size of the group. During the progess of this work a number of important papers have appeared which are referred to either in the text or in notes. While much is known of the Arthropods as a whole and of that large division of them included under the Crustacea, it is probably true that a great deal of this knowledge is of a very fragmentary and unsatisfactory nature. There is great need for detailed and full accounts of the development and organogeny of many forms in order that the relations of the various members of the Arthropod type may be clearly established.

The present work may be regarded as a contribution toward supplying the need just mentioned, but how imperfectly it is unnecessary to say.

The plan of making observations upon other Crustacea for comparison with the more detailed studies of Alpheus has been as yet only partially carried out. The early stages of *Stenopus hispidus*, *Homarus Americanus*, and *Pontonia domestica* have, however, been followed, and less completely those of *Hippa talpoides* and *Palæmonetes vulgaris*.

Spence Bate (3) states that the shortened development of Alpheus was first described in his memoir, with drawings, communicated to the Royal Society in 1876, from a specimen procured in the Mauritius. He named his specimen *Homaralpheus*, "from the impression that species producing a Megalopa could not be placed in same genus as those producing a Zoëa." He says: "The original of my drawing is 2^{mm} in length and was procured from a specimen 14^{mm} long, resembling the figure that I have given of *Alpheus minus*, Say. An inspection of this drawing (3, Pl. CXXII, Fig. 1) leaves some doubt as to whether there was not an error in referring this form to the genus. The general shape is unlike that of Alpheus, the abdomen being three times as long as the carapace, and there appear to be only three pairs of thoracic appendages behind the chelipeds.

Packard (46) in 1881 was the first to describe a shortened metamorphosis for *Alpheus heterochelis*. In some brief notes published in the American Naturalist of that year, he states that both this and the small green Alpheus (*A. minus*) occur in abundance at Key West, Florida, in the excurrent openings of large sponges. This fact is interesting, and probably significant also, as will be later shown. Packard describes the first larva of this Florida form as much further advanced toward the adult state than is the first zoëa of the Beaufort species, according to the observations of Brooks. In fact it more nearly agrees with the first larva of a Bahaman Alpheus soon to be described, in which the metamorphosis is nearly lost. The Nassau form of *Alpheus heterochelis* has, as I have recently ascertained, a *complete metamorphosis*. The bearings of these facts will be discussed further on.

The larval development of the Beaufort Alphei was studied by Brooks (7) and a short abstract of his results was published in 1882. This is all, I believe, that has been previously done on the embryology of these Crustacea. Several abstracts of the present work appeared in 1887–'88 (20–22).

METHODS OF WORK.

Several species of prawns, such as Stenopus and Pontonia, repeatedly laid eggs while kept in aquaria, and doubtless I should have succeeded equally well with Alpheus, if sufficient pains had been taken. As it was, only two or three individuals gratified me in this respect, but in each case the ova failed to develop. The animals were therefore taken from the sea with eggs in the earliest phases of development, and were kept under observation in an aquarium for the length of time required. The ova were then carefully removed from the pleopods, and were hardened at intervals of thirty minutes or one hour or a longer time, according to the phase or age of the embryo. By obtaining a number of series in this way the whole life history within the egg could be followed, and by

this means I was able to observe the peculiar movements of the wandering cells and the formation of germ-layers, which are often very difficult to interpret, when we rely upon material taken by chance.

Experience with the use of Perenyi's fluid in preparing the eggs led me to discard this reagent altogether, and to substitute for it Kleinenberg's picro-sulphuric acid, made up either with water or 30 per cent alcohol. The alcoholic solution works equally well and economizes time. The Perenyi is too violent and uneven in its action. While it serves fairly well in some cases, it generally swells out the membranes or shell by the rapid endosmosis, and distorts some part of the egg or embryo in consequence. The egg is frequently deformed and the shell ruptured. The ova should be transferred directly from the killing fluid to 70 per cent alcohol, and they will then generally retain their normal shape, and can thence be removed to alcohol of a higher grade for permanent keeping. If, however, they are carried from the Kleinenberg fluid to a weaker alcohol (30 per cent), distortion is sure to follow, the capsule bursting and the egg sometimes exploding.

Preparations of the entire embryo as well as sections were made, but very little was attempted with the living egg. For surface preparations the hardened ova were first punctured to allow the fluid to penetrate the shell more easily and they were then stained entire, in Kleinenberg's hæmotoxylon. They were afterwards shelled, when this was possible; saturated with paraffin by the *turpentine-paraffin* method, and were then mounted. While the paraffin was congealing they were carefully placed in position with a hand lens. This last important and often troublesome process was rendered easy by the differential property of the stain, which affects only the embryonic cells, leaving the ylok, which in preserved eggs is of a light straw color, unaltered. The embryonic tissues are thus made to appear nearly black on a light background. The embryo was then cut away from the rest of the egg by the microtome razor; attached to the slide by collodion and mounted in balsam; or the egg was cut in two and both halves were similarly treated. All drawings which represent surface views excepting Fig. 10 were made from objects thus prepared.

In general, Kleinenberg's hæmotoxylon proved to be the best staining fluid, and it is especially useful in this case, where the massive yolk contains numerous elements, the relations of which it is important to determine. The carmines are less serviceable, since the food yolk is also affected by them. Soda carmines (Beccari's formula) proves to be incapable of removing pigment from the eyes, although it is specially recommended for this purpose. This may be easily effected by soaking the entire tissues in very weak solutions of nitric acid for a considerable length of time. Gaule's quadruple stain of hæmotoxylon, eosin, saffranin, and nigrosin was also tried with excellent results, but this method is very laborious, and since our inquiries do not extend in most cases, to cell structure it is unneccessary.*

Perenyi's fluid is sometimes available for swelling the chorion and thus aiding in its removal, although the embryo is liable to injury. It is also helpful in studying the egg with low powers. The food yolk, which is often dark green, is affected less actively by this reagent than the embryonic tissue. The latter is turned to a waxy whiteness and is thus clearly defined for a short time, but the yolk is soon decolorized unless the eggs are transferred to water, becoming pink, and finally light yellow after preservation in alcohol.

PART FIRST.

I.—THE HABITS AND COLOR VARIATION OF ALPHEUS.

Some facts of general interest have been gathered from a study of the Alpheus in its natural environment on the coral shores and reefs of the Bahamas, and in giving these we will limit ourselves mainly to the three species which have contributed the material for the history of the embryo, viz: *Alpheus minus* Say, from Beaufort, N. C., *A. heterochelis* Say, from Beanfort, N. C., and Nassau, New Providence, and *A. saulcyi*, from Nassau, New Providence. The genus Alpheus comprises numerous species spread over a large part of the globe, many of which are closely connected by intermediate forms. From North America upwards of twenty species of Alpheus have been described; five are known to inhabit the eastern coast of the United States, three from Florida, and two others (*A. minus* and *A. heterochelis*), which range from Panama to as

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* In studying the development of the lobster, which has also a large egg, I have found it necessary to adopt new methods, especially in the treatment of the eggs for surface preparations. In most cases the egg-membranes are best removed by the aid of hot water.

far north as Virginia. From Florida and Cuba nine species are recorded. I have found twelve species of this prolific genus, or about one-half the number described for the whole American continent, inhabiting the beautiful little reef of growing coral called Dix Point to the eastward of Nassau Harbor and along the margins of the little bay which was just in front of our laboratory. Another species (*A. websteri* Kingsley), first reported from Florida, was also discovered on Green Key reef, a few miles from Nassau.

From collections which I made at Abaco and Andros Islands, I am led to believe that the different species are quite generally distributed in the Bahamas, and as these islands have probably been largely populated from the South, we may expect the same forms to occur at Cuba and at other West Indian Islands. This genus, however widely distributed, is essentially tropical and abounds in all coral seas. Of the great family of the Crustacea which make their home on the submerged reefs of growing coral, Alpheus is perhaps the most prominent and thoroughly characteristic. They pop out of almost every rock which is brought up from the bottom, and every loose head or block of growing coral, with its clusters of algæ, sponge, and sea fans, which you pull from the reef, resounds with the click of their little hammers.

Some of these animals lead a semi-parasitic life in sponges, or seclude themselves in the porous limestone which forms the solid floor of the beach, and others, again, live under loose shells and stones in the white coral sand. Some are highly and beautifully colored, and with few exceptions the pigment is characteristic of the species for any locality. In all cases the claws of the first pair of walking legs are enormously enlarged and serve as formidable weapons of defense so remarkable in this genus, and in most there is the greatest disparity in the size of these claws, one, either the right or left, being the larger. One species, the habits of which are peculiar, carries the larger of these claws so folded under the body as to be completely concealed. It can, however, quickly withdraw this weapon and make a rapid thrust when an enemy comes near.* By the scissor-like blades of the large claws a sharp metallic report is produced. This is true of nearly all the species, and so abundant are many in these islands that a constant fusilade is kept up along some of the shores at low tide. This snapping propensity is shared by both sexes whether in or out of the water, and it is undoubtedly correlated with their pugnacious habits. If two males or females of the same or different species are placed in the same aquarium, they will dismember each other in a very short time, and one is usually literally torn to pieces.

The sounds emitted by *Alpheus heterochelis* are the loudest I have heard from any member of this genus. We frequently kept this species in glass dishes in our room for several days at a time, and sharp reports like the explosion of a small torpedo or pop gun were heard at intervals through the day and night. It sometimes swims with its large claw so widely opened as to suggest dislocation. This weapon then reminds one of a cocked pistol, and the report apparently follows in the same way that the click follows the impact of the hammer on the lock. I have given this mattter no closer attention, but find that Mr. Wood-Mason, who is quoted in a notice on "Stridulating Crustacea"† in "Nature," (65) has offered another explanation. According to this observer the sound always accompanies a sudden opening of the claws to their fullest extent, and may be caused either by impact of the dactyle upon the joint to which it is articulated or "by forcible withdrawal of the huge stopper-like tooth of the dactylopodite from its pit in the immovable arm in the claw." It seems most probable to me that the sound is caused by impact, and most likely by the rapid closure of the finger into its socket.‡

* This species is entirely new. The large concealed claw suggests a poison apparatus. The "fingers" are exceedingly slender and sharp at the points. Although kept for over a week in an aquarium it emitted no sounds.

† According to Wood-Mason sound-producing organs in Crustacea were first brought to notice by Hilgendorf, in V. der Decker's "Reisen in Ost-Africa (Crustaceen)," and were afterwards observed by himself in his dredging expedition to the Andaman Islands. The stridulating organs—scrapers and rasps—may be either on the carapace and appendages or on the appendages alone.

‡ Both Kent and Wood-Mason speak of the sounds emitted by the Alphei as if produced by the extension or opening of the claw. As pointed out above, it is just the other way, the sound following upon the impact of dactyle and propodus, when the tooth of the dactyle is not pulled out of its socket but driven into it. None of the conditions of piston movement are present. The walls and floor of the pit are relatively soft, while the tips of the claw are dense and stony. The "click" can be artificially produced when the claws are clamped with rubber, whether the "stopper" is present or not.

In *Alpheus heterochelis* the dactyle of the large pincers is a curved blade which shuts down into a groove on the occludent margin of the "thumb," and closes over the latter like a pair of shears. The huge stopper-like tooth is borne on the inner and proximal edge of the dactylopodite and fits neatly into a corresponding pit in the "thumb," in line with the groove just mentioned. The object of this plug is evidently to steady the movable dactyle and to prevent lateral strain and the dislocation which might result, and thus to give it a strong grip on any object which it has seized. In alcoholic specimens in which the relations of the parts are well preserved the stopper works freely in and out the well, and not like a "tightly packed piston from a cylinder closed at one end."

(The claw is widely opened, before the sound is produced, but the sound is not produced while the claw is open, but at the instant when it is violently and suddenly closed. It is due to the impact of the "thumb" and "finger," and I have frequently seen specimens of *A. heterochelis,* when prepared for combat, facing each other for several seconds with claws distended to the utmost. In these cases the "snap" does not come until the claw is closed. In fighting the claw is not used as a clasper, but as a saber. The sharp external edge is a weapon of such efficiency that I have seen individuals killed and almost cut in two by a single blow.—W. K. B.)

A large brown sponge, *Hircinia arcuta,* which is not to be mistaken, grows on the shallow reefs and off the shores of all the Bahama Islands which I visited. It is found from just below low tide mark out to one-half a fathom or more of water, where its great size and sooty brown color distinguish it at once on the white bottom. These "loggerheads" are round and much flattened (the smaller ones more vase-shaped), and of a coriaceous texture; they sometimes measure $1\frac{1}{2}$ feet in diameter. There is commonly one, sometimes two, large exhalent chimneys into which small fish, young spring lobsters, and other Crustacea, often beat a hasty retreat. It is easily broken open since it has no consistent skeleton. If a sponge colony of this kind is pulled and torn apart, one is certain to find it swarming and crackling with a small species of Alpheus, which quarter themselves in the intricately winding pores of the sponge. The sounds emitted from every fragment of these mutilated sponges remind one forcibly of "those made when sparks are taken by the nuckles from the prime conductor of a small electrical machine," as Wood-Mason remarks. Hundreds of individuals may be collected from a single large specimen.

These animals have an average length of about 12^{mm}. They are nearly colorless, excepting the large chelæ, which are tipped with brown, reddish orange, or bright blue. The females are so swollen with their eggs or burdened with the weight of those attached to the abdomen that they can crawl only with great difficulty, if taken from the water. The eggs are few in number and of unusually large size, their diameter varying from one-twenty-second inch to one-twenty-fifth inch, and their number from six to twenty. These are most commonly yellow, but may be either bright green, olive, greenish white, brown, brownish yellow, or dull white. The ova and ovarian eggs have always the same tint in the same individual. Although translucent and apparently colorless, upon close inspection the body is seen to be sprinkled with cells of reddish and yellow pigment.

Another quite different sponge grows on all the reefs in from one to two fathoms or more of water. There are several varieties of this, which may be told by their olive green color, yellow flesh, and clumpy, irregular shape, as well as by the putrescent mucous which some of them pour out when broken open. In about nine out of ten of these sponges one will find a single pair of Alpheus (rarely more than this), which resemble those living in the brown sponge, but differ from them in several important points. We are concerned at the present with the color variations only. They are distinguished by their large size (averaging about 23^{mm} in length) and uniform color. The females exceed the males greatly in bulk, owing to the large size and number of their eggs. In both sexes the large claws are bright red (v. Pl. IV, and for details section IV).

The female is practically inert during the breeding season, and at such times is well protected in her sponge or against any green surface by the bright green ovaries which fill the whole upper part of the body and by the mass of similarly colored eggs attached to the abdomen below. Only two pairs, or four individuals, out of a hundred or more which were examined showed any variation from these colors. In these the eggs were yellow, and the pigment on the claws was more orange than red. The table which follows shows the variations between two large females taken, respectively, from the brown and green sponges, and between the size, number, and color of the eggs.

Habitat of Alpheus.	Length of ♀.	Number of eggs.	Diameter.	Color.	Color of adult.
	Inches.		Inches.		
Brown sponge...	½	19	²⅕	Yellow (variable)....	Large chelæ, red (blue or brown in others.)
Green sponge....	1⁵⁄₁₆	347	¹⁄₆	Usually green; in this case yellow.	Large chelæ, orange-red.

These two forms, although apparently distinct. are seen, however, by closer study to belong to the same species; but besides the more superficial variations just mentioned, there are others of a more remarkable character, the morphological significance of which is considered in sections IV and V.

Of this species, *Alpheus saulcyi*, Guérin, it is necessary, for descriptive purposes, to distinguish two varieties, viz:

Alpheus saulcyi, variety *longicarpus* (from brown sponges),
Alpheus saulcyi, variety *brevicarpus* (from green sponges).

These two varieties shade completely into each other by numerous intermediate forms. The *longicarpus* varies greatly in size and in the color of the body and eggs (besides the other more profound variations mentioned in section V), while the *brevicarpus* type from the green sponges is more uniform in size and stable in color and other characters. The former variety is well protected from outside enemies while in the tortuous mazes of its sponge, as its great numbers would show, if any evidence under this head were needed. The enemies which invade them successfully seem to be parasites.*

Possibly the variety inhabiting the green sponge does require color-protection, especially since the females are very inert during the breeding season. They are, indeed, admirably protected when exposed on the green surface of sponges, algæ, etc. The bright color on the tips of the large claws, which only are protruded from the places of concealment, recall the similarly colored heads of boring annelids, which abound on the reef, but this fact may have no significance.

It seems quite probable that if we have in this Alpheus a case of protective coloring, it is due very largely to individual adaptibility. This view implies great individual plasticity, which does not appear in any of the species of Alpheus known to me *within a restricted area*.

The colors of certain Crustacea, and also the colors of their eggs, are known to vary greatly with the surroundings. In the Alpheus, parasitic in the brown sponges, these colors vary considerably where the surrounding conditions are the same. However, the color of the ovarian eggs is always the same as that of those already laid, and, although these animals were kept for several days at a time in differently colored dishes, I never observed any very marked change in the color of the ovary, but these experiments were not continued long enough or carefully enough to be conclusive. The eggs of *Alpheus heterochelis* are almost invariably of a dull olive color, while, as in the case of the parasite of the green sponge, about one in a hundred has bright yellow eggs. In the first case at least this may possibly be an instance of reversion to one of the original colors from which the green was selected. In most species of Alpheus the color of the eggs is fixed and uniform for any locality, and, as already suggested, may have a protective significance; but in a few other cases, where this is not true, the color is not only variable in different individuals, but probably also in the same individual.

Alpheus heterochelis from Beaufort, N. C., is uniformly of a dark olive-green color, with some red and blue on the appendages. It lives in the beds of oyster shells, which are more or less

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* A parasitic Isopod, probably a *Bopyrus*, is found on both the varieties, but is most common with the dweller in the brown sponge. It appears as a tumid bunch, firmly rooted in the branchial cavity or to the under side of the abdomen. In this connection I will mention another curious parasite which was found infesting the eggs of a single female taken from a brown sponge at Abaco. This is a large, spherical, unicellular organism in the encysted state. The egg, with the embryo, is packed full of them. (v. Fig. 199 and section IV, Part Second.)

In looking over a collection of unpublished drawings of Crustacea, made by the associates of Louis Agassiz and deposited in the library of the Museum of Comparative Zoölogy of Harvard College, I find a sketch (by H. J. Clark, December 23, 1857) of a *Bopyrus* taken from the branchial cavity of *Alpheus heterochelis*.
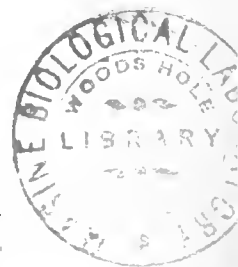
exposed at low tide. *Alpheus minus* has a similar environment and is similarly colored. *Alpheus heterochelis* from Nassau, New Providence, on the other hand, lives under loose stones, amid the white coral sands of the beach, and is noticeably transparent, looking as if the color had been bleached out of it. The body is sprinkled with dots of brown pigment. The claws and legs are pale greenish. Young and old are invariably colored alike.

In a collection of adult Alpheus of either sex of the same or of several species, where there is a difference in size of the large claws, it is noticed that either the right or the left, indifferently, may be the greater. As we will see, this differentiation of the chelæ begins in one instance before the animal is hatched. Is this right and left handed condition to be explained by inheritance from the parents? In about forty larvæ of a small brood of *Alpheus sauleyi*, all invariably had the *left* claw enlarged, and in a smaller number (all that were preserved), from another female of the same species, the left chela was also in each case the larger. This would indicate that the young of the same mother have always the same claw, either right or left, the greater, and that this phenomenon is one of direct heredity from the parents. But to prove this it is only necessary to trace right and left handed broods to parents which are themselves right and left handed, respectively. This, unfortunately, I have not done, as my attention was not called to the subject while at the seashore.*

The breeding season of Alpheus begins at Beaufort, N. C., about April 1. It covered the period of our stay at Nassau (March to July), and probably began earlier and lasted considerably later.† There the temperature is high and remarkably constant, the annual range being about 15° (temperature of air 70° F. in March, 80° in June), and in consequence the early phases of development are rapidly passed. Not one prawn in a hundred was found with eggs in an earlier stage than that of yolk segmentation.

II.—VARIATIONS IN ALPHEUS HETEROCHELIS.

A renewed comparison of *Alpheus heterochelis* with the Nassau form lends support to the conclusion already reached that we here have to do with two varieties of the same species. There are certain differences, which systematic zoölogists might regard as of specific value, but they are no greater than we have proved to exist among individuals of the same species living in the same sponge. (v. Section V.)

The Nassau specimens average smaller, but the chief difference lies in the shape of the small chela. The propodus of this appendage in the Nassau form is relatively shorter and thicker in both sexes. Both fingers are nearly cylindrical, and covered with hairs, which are distributed either singly or in tufts. In the Beaufort *heterochelis* there is a striking variation in the small chela which appears to have escaped detection. Judging from the small collection at my command it is a sexual variation. In the females the small chela is like that of the Nassau form, but is usually longer and slenderer. The dactyle is about one-half the length of the propodus. In the males the dactyle is relatively much shorter, and has a median longitudinal carina which is continued into the apex of the claw. In transverse section the dactyle is trihedral, with two concave sides, corresponding to the deep groove on either side of the keel. These grooves are fringed with a row of stout plumose setæ. Similar rows of setæ occur on the sides of the opposing "thumb."

Perhaps the most interesting variation which I have observed in the Beaufort *heterochelis* has reference to the size of the egg. The eggs in this locality have an average diameter of about one

* Mr. J. J. Northrop, of Columbia College, while at Nassau in the winter and spring of 1890, kindly offered to collect for me some specimens of *Alpheus sauleyi* with young. On February 10 he collected six females, five from green sponges, one of which had a brood of sixteen young, and one small female with three larvæ from the "loggerhead" sponge. In the first instance the left chela was the largest in the *mother* and in *each of the sixteen young*. In the latter, two had the right claw enlarged and one the left. The inference is suggested that when the claw of the same side is invariably the greater in all the young, this character is doubly inherited from both father and mother, but the data are insufficient to settle this point.

† Professor H. V. Wilson found this species breeding around Green Turtle Key from July until December. Mr. Northrop found newly hatched young early in February. It therefore breeds the year through, which is probably true of many of the Crustacea.

twenty-fourth inch, but two females were found which carried a few bunches of very small eggs, normally glued to the anterior swimmerets. These eggs measured only one fifty-third to one sixty-fifth inch in diameter, that is, the contents of the smaller was about one-twelfth that of the larger egg.

This occasional production of very small eggs exhibits a tendency, which is still present in the species of this locality to-day, to revert to its old metamorphosis long since laid aside.

III.—THE ABBREVIATED DEVELOPMENT OF ALPHEUS AND ITS RELATION TO THE ENVIRONMENT.

Related species, as a rule, resemble each other more in their early stages of development than in their adult state. This is not, however, invariably true, since all animals, whether young or adult, must adapt themselves to their environment or be destroyed. It is probable that animals in all stages of growth are equally plastic and tend to vary with the varying conditions of life.

The early life in large classes of the animal kingdom, as fishes, birds, and mammals, is spent either in the protecting membranes of the egg or within the body of the parent, and is thus but slightly affected by *external conditions*, and suffers little change in consequence. In other groups, on the contrary, and in the Crustacea in particular, the case is very different. Here the young are usually hatched in a very immature condition, and lead a life of their own at the surface of the ocean, wholly independent of their parents. They have accordingly adapted themselves to this mode of life, and the variations thus entailed have led to the production of the zoëa, a locomotor larva, fundamentally different from the adult. We may regard the zoëa as a secondary, adaptive form, directly descended from an ancestral protozoëan type. After passing a longer or shorter period (usually of several weeks) at the surface of the sea, the adult state is gradually reached through a complicated series of changes, and the animal adapts itself to new conditions on the sea bottom or on the shore.

Now, if the habits of the adult and larva should tend to converge, if the adults should adapt themselves to an entirely new environment, which it is necessary for the young to become fitted for at once as soon as hatched, we would expect that the zoëal stages, formally assumed to bridge over a gap which no longer exists, would be dropped or shifted to the egg. This seems to have actually taken place, and is illustrated in a remarkable manner in the genus Alpheus.

Most of the species, which are very numerous, inhabit the shores, in common with many related forms, and, as already stated, they abound on coral reefs. They all, as a rule, hatch as zoëa-like and have a complicated metamorphosis. Two species have been discovered, however, which have adopted a parasitic life, and in each the larval period is accelerated. In one, which is semiparasitic, the metamorphosis is partially abbreviated; in the other, which is completely parasitic, the metamorphosis is completely lost. Still more interesting and significant is the fact that *one of the species in one locality is nonparasitic and has a complicated metamorphosis, while the same species from another locality is parasitic and has the metamorphosis abridged.*

We will now consider more particularly the history of these two forms, in order to make a clearer comparison. The species are—

(1) { *Alpheus heterochelis*, from Nassau, New Providence.
{ *Alpheus heterochelis*, from Beaufort, North Carolina.
{ *Alpheus heterochelis*, from Key West, Florida.
(2) *Alpheus sauleyi*, from Nassau, New Providence.

ALPHEUS HETEROCHELIS FROM THE BAHAMAS.

This species, found at Nassau, exemplifies the development common to the genus, as seen, for instance, in *A. normani* (Kingsley), which is closely associated with it, *A. minus* Say, and in many other Bahaman forms. It is one of the common species at Dix Point, and may be found in abundance on the shore of the little bay, in pools left by the ebb tide, under shells or loose fragments of coral.

First larva (length = $\frac{1}{9}$ inch).—The three pairs of maxillipeds, each with long exopodites ending in feathered hairs, are the principal locomotor organs. Two pairs of rudimentary thoracic legs are present. All the abdominal segments, but none of their appendages, are formed.

The antennules consist of a stout jointed stalk, the terminal segment of which bears four sensory filaments. A long plumose spine springs from the extremity of the second joint on the inner side.

The antennæ are biramous, the two branches arising apparently out of a common basal segment. The outer division is a scale-like plate. It bears on its extreme inner border a row of plumose hairs, eight to ten in number. The endopodite is slender and shorter than the scale. It terminates in a short spine or denticle, from near the base of which springs a long plumose hair. The eyes are large and uncovered. The mandible is simple.

The telson is a broad triangular plate, the terminal side of which is garnished with the characteristic zoëal spines, the number, relative size, and position of which vary slightly in the different species. There are in this case eight pairs of these spines. The first or median pair is rudimentary; the second is not half the length of the third. The lateral angles of the plate are each prolonged into a short lobe, bearing three spines. There is no marked median notch, but there is a slight median depression. The rudiments of the sixth pair of abdominal appendages are plainly seen.

Second larva.—With the first molt the endopodites of the maxillipeds lengthen. Three pairs of rudimentary pereiopods are now present, the last of which are the longest. Of the pleopods only the sixth pair are represented, whether free or not was not observed.

ALPHEUS HETEROCHELIS FROM BEAUFORT.

The peculiar metamorphosis of the Beaufort *Heterochelis* was described in 1884 by Brooks, who also showed that in this respect it departs widely from the associated *Alpheus minus.*

The form in question is hatched as a larva with preparations for the schizopod stage. It has the usual swimming organs, but all the thoracic legs are present in the condition of rudimentary buds. The abdominal segments are formed, and the buds of the first five pairs of feet belonging to them. The eyes are not completely covered by the carapace. At the first molt the rudiments of the sixth pair of abdominal feet are added, and the larva undergoes profound changes. All the appendages are now functional and the eyes are nearly hooded. With later molts the adult characters become more pronounced, but the marked difference of the great claws appears only after several months.

ALPHEUS HETEROCHELIS FROM FLORIDA.

The short description, given by Packard in 1881, of the first larval stage of this species from Key West, where it inhabits sponges, has already been alluded to. From this we infer that the development is considerably more abridged than in the Beaufort case. This is also indicated by his figure of one of the abdominal appendages. He says: The eyes are nearly sessile, the yolk nearly absorbed, although the embryo (in the egg) was near the time of hatching. The antennæ are "well developed." All the thoracic legs are present, their joints distinct, "the first pair about twice as thick as the others, the claws rather large, but not so disproportionately so as in the adult form, but as much so as in the larva in the second stage of the lobster. Abdomen broad and flat, spatulate at the end, much as in the adult. There were five pairs of abdominal feet or swimmerets, each with endopodite and exopodite, like those of the second larval stage of the lobster."

ALPHEUS SAULCYI FROM THE BAHAMAS.

In this form, the metamorphosis of which is fully described in another paper, we have either an abridged development in which the general adult characters, very marked in the first larva, are all acquired in twenty-four hours after hatching, or a case where the short metamorphosis is done away with entirely, so that the animal leaves the egg in the full adult form.

Comparing the histories just given with the one before us, we find that the first larva of *Alpheus saulcyi* is about equivalent to the third larva of the *Heterochelis* from Beaufort, and rather more advanced than the first larva of this species from Florida.

The eggs of the Alphei, with the development unabridged, are invariably small and quite numerous. In the two species, however, with shortened metamorphosis, the ova are fewer and many times larger. Moreover, as would be expected, the degree of abbreviation is correlated with the

size and number of the eggs. These and the other facts which we have been considering are given in tabular view below:

Species.	Habits.	Metamorphosis.	Number of eggs.	Diameter of egg.	Length of female.
				Inch.	Inches.
Alpheus minus (from Beaufort).	Non-parasitic	Complete	*500	$\frac{1}{24}$	$\frac{1}{2}$ – 1
A. heterochelis (from Nassau)	....do	....do	300–500	$\frac{1}{4}$ – $\frac{1}{50}$	$\frac{3}{4}$ – $1\frac{1}{4}$
A. heterochelis (from Beaufort)	....do	Abridged	150–300	$\frac{2}{4}$ – $\frac{2}{7}$	1 – $1\frac{3}{4}$
A. heterochelis (from Florida)	Semi-parasitic	....do	....	....	....
A. sauleyi (var. brevicarpus)	Completely parasitic	Nearly lost	100–350	$\frac{3}{4}$	$\frac{1}{4}$ – $1\frac{3}{4}$
A. sauleyi (var. longicarpus)	....do	Completely absent (in some cases).	5–20	$\frac{2}{4}$ – $\frac{1}{25}$	$\frac{1}{4}$ – $\frac{2}{3}$

* Number not accurately determined.

The eggs of Alpheus are usually spherical when freshly laid, but they change their shape, becoming more elongate in course of development and increase somewhat in size.* The eggs of *A. sauleyi* are usually oblong. They vary from one twenty-eighth to one twenty-third of an inch, taking the mean of the long and short diameters. The extreme limits of the number of eggs vary somewhat from the numbers given above, which are the average limits.

In the genus Alpheus we thus have several stages in the abbreviation of the metamorphosis between the macrouran zoëa stage and the adult form. What is the cause of this gradual suppression of the zoëa like form? The conclusion seems to be unavoidable that in the Bahaman species this shortened life of the larva is directly related to the conditions of life. As the adults of the species in question became more and more dependent upon a semiparasitic† mode of life, it would be clearly beneficial to reduce the larval period, in order that the young might be hatched fitted to live in an environment similar to that of the adults. If the zoëa brood were swept out to sea by the tides, and were to spend several weeks in the larval condition at the surface of the ocean, the chances for large numbers to find particular sponges along the shores, when the adult state was reached, would be greatly lessened. It is likely that the larvæ of this Alpheus are never carried far from the shores, but while they undoubtedly leave the sponge in which they are born, they probably establish themselves very soon in a new one. (The young remain a short time after hatching, attached to the swimmerets of the mother.)

This supposition is strengthened by what we know of the peculiar history of *Alpheus heterochelis*. The Nassau heterochelis probably never changed its adult habits or adopted a parasitic mode of life; consequently it has retained undisturbed its complex larval development. The Floridian form has become a parasite, and its metamorphosis is accelerated as the result. From this the Beaufort Alpheus with its less abridged development has doubtless been derived (the species extending northward from the Gulf of Mexico), and it is within the possible, at least, to suppose that in this form the metamorphosis, once lost by parasitism, is now being reëstablished.

No fewer than three species of macroura, together with the Alpheus above described, occur in the large brown sponges (*Hircinia arcuta*) of the Bahama islands. These (one of which is also an Alpheus) live in the larger oscula, are less regular in their occurrence, and evidently have not adopted a stationary parasitic life. In none of them is the metamorphosis of the larva abbreviated. *Alpheus minus* is also reported as occurring in the large exhalent openings of sponges at Key West, but in this case we do not know, first, whether this is a fixed or only a transient habit, and secondly, we know nothing of its metamorphosis under these conditions.

Thus while in Alpheus the abbreviated metamorphosis may be explained as an adaptation to a parasitic mode of life, the question is probably often complicated by conditions which are not easy to determine. There is a general tendency among the higher forms of certain groups, as in the Cephalopods among the Mollusca, to reach the adult conditions rapidly by omitting some of the early embryonic stages.

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* An egg of *A. sauleyi* var. *longicarpus*, just ready to hatch (Pl. XXI, Fig. 5), measures $\frac{1}{100}$ by $\frac{1}{100}$ inch.

† The Alphei which inhabit sponges are commensals rather than parasites in the strict sense. They derive protection from the sponge colony, and receive the benefit of the circulating currents of water which are set up within it.

An abridged larval development has been attributed to the following macroura: The lobster *Homarus americanus;* the crayfishes; *Hippolyte polaris; Palæmonetes varians; Palæmon potinna; Palæmon adspersus* and *Eriphia spinifrons* (as first observed by Rathke, according to Packard); *Bythocaris leucopsis* (observed by G. O. Sars, according to S. I. Smith); *Alpheus heterochelis,* and *A. sauleyi.* To this list we must probably add the names of many deep-sea decapoda, *Munidopsis, Glyphocrangon, Elasmonotus inermis, Sabinea princeps, Acanthephyra gracilis,* and *Pasiphaë princeps,* as inferred by S. I. Smith, on account of the extraordinarily large size of their eggs. An egg of remarkable dimensions is that of " the little shrimp (*Parapasiphaë sulcatifrons,*) which carries only fifteen to twenty eggs, each of which is more than 4 millimeters in diameter, and approximately equal to a hundredth of the bulk of the animal producing it—a case in which the egg is relatively nearly as large as in many birds!" "Although the great size of the eggs," says Prof. Smith, " is highly characteristic of many deep-water species, it is by no means characteristic of all, and the size of the eggs has no definite relation to the bathymetrical habitat, and is often very different in closely allied species, even where both are inhabitants of deep water (59)."

The larval life of both terrestrial and fresh-water Crustacea is generally short as compared with that of marine forms, and the case of the crayfish may find an explanation in the well-known law that fresh-water life tends to shorten the development, as is shown in a remarkable manner in the fresh-water variety of *Palæmonetes varians,* described by Boas (4). Why, on the other hand, it is beneficial for the lobster to abbreviate its larval development is not plain, since its young at the present time hatch apparently under the same conditions as other pelagic larvæ, and, like them, swim at the surface of the ocean. S. I. Smith (58) and Ryder (55) have given accounts of the larval history of the lobster. (Since this paper was written I have undertaken a revision of this subject, and the results will be given in a fully illustrated report to the United States Commissioner of Fish and Fisheries.) While this animal hatches in a precocious state its life at the surface is by no means short, since, according to Ryder, it ordinarily requires seven weeks to pass through six molts. The first larva hatches in a schizopod stage, but there are no abdominal legs and the antennæ are somewhat rudimentary. The first ecdysis, according to Ryder, does not occur until from three to six days after hatching.* It is in the second stage that the second to fifth pairs of abdominal appendages make their appearance.

The third stage is preceded by a molt ten to fifteen days after hatching, and now the appendages of the last abdominal segment are formed. After the fourth molt (fifth stage) the young lobster, now 14ᵐᵐ long, quite closely resembles the adult. It swims more on the bottom. The flagella of the antennæ are equal to the cephalo-thorax in length. The exopodites of the thoracic legs are reduced to bare rudiments. The chelipeds show adult characters. The first pair of swimmerets are developed in the seventh stage, at the end of which there is a decided difference between the great claws.

It will be seen that the fifth stage in Ryder's account, attained at the end of the third week, nearly corresponds with the third larva of *Alpheus sauleyi* (Fig. 8, Pl. XXI) as it appears twenty-four hours after hatching, but the latter has the more decided adult characters. The young Alpheus is further advanced than the lobster at the time of hatching and reaches maturity in a remarkably shorter period.

Boas calls attention to the fact that while the young of the salt and fresh water forms of *Palæmonetes varians* are very different, the adults of these two varieties resemble each other very closely. Much more remarkable is the case of *Alpheus heterochelis,* even if we regard the Nassau form as a distinct species, and that of *Alpheus sauleyi,* where we have the same species living in the same sponge, hatching now as a larva and now as a form possessed of all the external adult characters.

Both the long and short metamorphosis has been attributed to the West Indian shore crab *Gegarcinus.* This highly colored crab (*Gegarcinus ruricola*) is very abundant at Nassau, and from its exceptionally large egg we may safely infer that the development has here been shortened. Fritz Müller (42) has found abbreviated development in the South American crabs, *Trichodactylus* and *Æglea* ("mountain crab").

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* A delicate moulted skin, which is easily overlooked, either comes off with the egg membranes at the time of hatching or is shed shortly after, as my own observations have clearly shown.

The habits of the hermit crabs, though secondarily acquired in comparatively recent times, have had no tendency to shorten the larval period. This is also true of the *Pinnotheres*. Similarly the commensalism of such forms as *Pontonia domestica*, which lives in the mantle cavity of several species of Pinna, has in no way affected its development.

IV.—THE ADULT.

The Alpheus whose development has just been traced was provisionally named *Alpheus præcox* (22), in allusion to its greatly accelerated metamorphosis. It has since been found to agree in most particulars with the description and figure of *Alpheus saulcyi* given by Guérin in Ramon de la Sagra's History of Cuba (18). In Guérin's drawings the long spine (squamal spine) of the antennæ is represented as continuous throughout its length with the scale, and the carpus of the second pair of thoracic legs as divided into three segments. The segmentation of the carpus of this appendage is one of the most constant of specific characters. If these figures are accurately drawn, the two forms in question are certainly not specifically identical; but though not at first able to satisfy myself on this point, or to decide from the short and imperfect description, it seemed best after further study to adopt Guérin's name.

The systematic zoölogy of the genus Alpheus is in a very unsatisfactory state, and in the absence of adequate and well executed drawings, and too often with only vague or general descriptions, the attempt to identify the less known species is apt to be attended with most doubtful success.

It is now necessary to complete the account of the metamorphosis of this Alpheus by giving a description of the adult form. The *Alpheus saulcyi* resident in certain green sponges found on the Bahama reefs is regarded as the typical form of this species.

DIAGNOSIS.

Carapace ends anteriorly in three spines. The median spine or rostrum inclined, especially in the female; arises from the edges of the carapace, like the lateral or orbital spines; barely surpasses the latter in length; without keel. Body and appendages generally smooth; large chela slightly twisted, smooth, no transverse constrictions; small chela subcylindrical, short; dactyle nearly straight, slender, one-half as long as propodus; carpus of this appendage short. Aural spine of inner antenna variable in length; rarely surpasses the middle of the second segment. Basal segment of outer antenna is produced into an outer, inferior spine, and an upper rudimentary spur; articulated with it is a squamal spine, on which is developed a conspicuous scale. Carpus of second pair of thoracic legs superficially segmented into five parts.

SPECIAL DESCRIPTION.

Length: Smallest found in green sponges, 9.5^{mm}, ♂; largest, 42^{mm}, ♀; average length, 25 to 30^{mm}. Females exceed the males a little in length, and greatly surpass the latter in size when swollen with their eggs.

Color: The color of this form is shown in Pl. IV. Large claw vermillion above, fading out towards proximal half, and nearly colorless below. On upper face of claw a transverse colorless band is often seen. Small chela often tinged with red, also the terminal segment of the third pair of maxillipeds. Body, pale, translucent, with scattered cells of reddish or yellow pigment, subject to quantitative variation, and visible to the naked eye on close inspection or by aid of a lens.

A young male which was kept for several days in an aquarium molted and lost completely the bright color of its claws. Sexes are colored alike, excepting the eggs and ovaries of the female, which are bright green.

In one or two instances a pair of these Crustacea were found which exhibited a variation from these tints. In these cases the male and female were of light-reddish orange and the claws deep orange red, darkest on the "fingers"; eggs and ovaries of female golden yellow. Length of ♀, 33^{mm}. Number of eggs attached to abdomen, 347. The male in this case also, after a moult, was apparently colorless, contrary to the rule that upon molting the colors are enhanced.

The carapace is smooth, translucent, and, like the abdomen, takes on more or less the hue of the yellow or green ovaries. It ends anteriorly in a trident, formed by the median rostrum and

ocular spines. The rostrum is short, subacute, broader at base than long, feebly convex above, without crest. The orbital spines are separated from the rostrum by a shallow superficial groove, and the marginal notch on each side has a regular V-shaped outline. Length of spines and width of notch are slightly variable.

The lateral compression of carapax is not marked. Frontal angle (angle made by middle line above and below rostrum, greater in ♀ than in ♂. In some females with the carapace bulged out by the ovaries the angle is as great as 45°. In males without conspicuous "forehead" frontal angle, 10°.

The telson ends bluntly. It is two-thirds as broad as long, and twice as broad at base as at apex. There is a single pair of short spines at the posterior extremity on either side the middle line, and two (or more) separate spines upon either side further forward. There is a wide and shallow median depression.

The compound eyes are conspicuous, owing to their dark pigment and the transparency of the carapace, and in the largest adults they show no traces of degeneracy. There is a permanent *ocellus* (Pl. XXII, Fig. 18), which occupies the same position and has the same characters as at birth. It consists of a pigmented body embedded in a short median papilla, situated below the compound eyes and between the bases of the antennules.

The antennules (Fig. 4, Pl. XXIII) consist of a three-jointed stem or protopodite, an exopodite, and endopodite. The first segment of the stem is largest and bears an external spine (aural spine), which protects the auditory sac. The latter is large and conspicuous in this genus. It usually contains some pigment cells and grains of sand. Second segment about half as long as first; third, four-fifths as long as second. Endopodite one and one-half times the length of stalk, slender. Exopodite compound, a slender flagellum branching from near the end of the stouter proximal portion. On the under side of the latter the sensory filaments (olfactory setæ) are borne, distributed in seven to ten bunches of two to three in a bunch.

The antennæ (Fig. 8, Pl. XXIII) are composed of three parts—a basal portion (protopodite), which carries a squamous spine (exopodite), and on its inner and lower side a long three-jointed stem, which bears a flagellum (endopodite).

The protopodite consists of a proximal segment (coxopodite) and a larger distal one (basipodite). A prominent papilliform process is seen on the inner side of the coxopodite at its point of junction with the basipodite. Upon it the duct of the green gland probably opens to the exterior. The basipodite is continued into a prominent spine below and into one or more rudimentary spurs above. To it is articulated a long, stout, scale-bearing spine. The scale plate, usually shorter than the spine and attached to it for less than half its length, is fringed on its inner free edge with plumose setæ. The antennal stem or peduncle consists of two short proximal segments and a long distal one, which carries the multarticulate flagellum. The latter is often hairy, and is two to three times the length of the peduncle. The relative lengths of the different parts for an average specimen is shown in Fig. 8, Pl. XXIII, and in Pl. IV.

The mandibles (Fig. 3, Pl. XXIII) are strongly bifurcate, as is characteristic of the genus. The larger division is finely tuberculated, while the masticatory surface of the slenderer branch is raised into sharp teeth. This bears a jointed palp (endopodite) on the inner side. The mandibular palpus is short; its terminal segment large and hairy.

The first maxilla (Pl. XXIV, Fig. 7) consists of three divisions—a smaller branch (endopodite), a larger branch (basipodite), divided at the apex and terminated by several long spines, and a larger spatula-shaped fork, the maxillary surface of which is beset with spines (coxopodite). (v. Description of figure.)

The second maxilla (Pl. XXIV, Fig. 9) is composed of three portions. (1) The long respiratory plate; the "bailer" or scaphognathite, fringed with a row of setæ. (2) An outer and lobulated division (coxopodite and basipodite), the inner edge of which are closely set with bristles, and (3) a median rudimentary endopodite.

The first pair of maxillipeds (Fig. 7, Pl. XXIII) are made up of a long, strap-shaped exopodite, with jointed setæ at the extremity and a small setigerous plate at its base; a small, two-jointed endopodite, protopodite, and epipodite. The protopodite is divided by a fissure into two lobes, a larger (basipodite), with dense rows of bristles on its maxillary surface, and a smaller division (coxopodite). The epipodite is an oblong plate, united by a short stalk to the protopodite.

The second pair of maxillipeds (Fig. 6) has a long, strap-shaped exopodite, like that of the first pair. The endopodite is incurved, and segmented into at least four parts. The dactylopodite or terminal segment is the longest, and is thickly studded with serrate bristles and setæ. There is a small oval epipodite.

The third pair of maxillipeds (Fig. 5) consist of a basal piece (coxopodite) and a long two-branched appendage. The large branch consists of three distinct segments—a long proximal one (basipodite (?) and ischiopodite), a shorter one (meropodite), and a long terminal segment (carpopodite, propodite, and dactylopodite). The exopodite springs from the base of the first segment, and is about equal to it in length. The lower surface of the two terminal joints is covered by numerous transverse rows of serrated bristles, and the end of this appendage is armed with several spines.

The first pair of pereiopods or walking legs bear the great chelæ ("hands" or "shears"). The chelæ are very unequal. Large claw (relatively larger in ♂) smooth, slightly twisted; outer and upper border sometimes marked by a linear crest; several spurs or tuberosities near the articular surface of the dactyle; dactyle shaped like end of pruning knife, its concave inner margin and tooth-like point shutting into a groove of the opposing "thumb." This groove of the propodus is continuous with the well, in which the stopper-like tooth of the dactyle fits. It is bounded by a rectangular process above and a less prominent one below. Tips of fingers barely overlapping. Dactyle sometimes overreaches propodus. Thumb (or extremity of propodus from joint of dactyle) one-third to one-half length "palmer portion" of propodus. Dactyle works somewhat obliquely. Tips of fingers simple. Propodus sometimes hooked.

Small claw (Fig. 3, Pl. XXIV) usually carried bent downward. Fingers nearly equal; three-fourths as long as palmer portion of hand; bent slightly downward and outward; propodus subcylindrical; half as broad as long; tip simple or slightly bifid. Small bunches of setæ on fingers.

Second pair of pereiopods (Fig. 1, Pl. XXIII): The characters of this appendage appear to be remarkably constant and of considerable specific value. They end in a small claw, the fingers of which are provided with bunches of long hairs. Carpus superficially constricted into five rings or segments. First or proximal segment nearly equal to 2+3+4+5. Second, third, and fourth of nearly equal length; fifth equals 2+3.

The third, fourth (Fig. 2, Pl. XXIII), and fifth pairs (Fig. 1, Pl. XXIV) of walking legs are similar to each other, the fifth pair being shortest. Each ends in a short, horny dactyle which is bifid at apex, the primary claw bearing a smaller secondary tooth at base. Propodus little shorter than meros in the fifth pair, and carries numerous bunches of short setæ on its under side. There are also found in this region of the propodus four to six stout appressed spurs.

The first pair of pleopods is specially differentiated in the sexes, and forms one of the most convenient marks of distinction. The first abdominal limb of the male is shown in Fig. 4, Pl. XXIV, and the corresponding appendage of the female in Fig. 5, and the typical appendage in Fig. 6. In the unmodified limb the protopodite carries as usual the two branches—endopodite and exopodite—each fringed with long setæ. The endopodite is a little longer than its fellow and bears a rudimentary secondary branch, which springs from near the middle of its inner edge. In the male (Fig. 4) the appendage is considerably reduced. The exopodite is short and the inner branch a small rudiment. In the female (Fig. 5) the modification has not proceeded so far. The endopodite is here the shorter and has no secondary branch. In the very young forms (first larvæ) these appendages appear to be nearly alike in both sexes (Pl. XXII, Fig. 5).

The uropods or sixth pair of pleopods hardly require special notice (Pl. IV). The endopodite, much the smaller division, is an oval plate, and on its upper side there is a roughened median ridge. The free edges of the plates are fringed with long and closely set plumose setæ.

V.—VARIATIONS FROM THE SPECIFIC TYPE.

We are now ready to consider the remarkable variations which this species undergoes. The form just described was taken as typical, and the largest adults invariably belong to it.

(1) Variety *Longicarpus*: This is the widest departure from the first form or type and is very commonly met with in the brown sponges already noticed. Probably more than 90 per cent of the

individuals found in them belong to this variety. The color variations of this form have already been given in section I.

The rostrum is sometimes wanting, as in the individual from which Fig. 11, Pl. XXII, was drawn. This variation has been noticed in other species and is interesting, since the absence of the rostrum is a constant character in a closely related series of forms, which are placed by Dana in a separate genus (*Betæus*). These variations indicate that the uniform presence or absence of a rostrum is a *specific* and not a generic character, as has already been shown by Kingsley (29). The structural points of difference between the *longicarpus* and the other form lie chiefly in the antennæ and first pair of walking legs. These may be seen by a comparison of Figs. 11, 13, 18, Pl. XXII, and Fig. 2, Pl. XXIV, with Figs. 4, 8, Pl. XXIII, and Fig. 3, Pl. XXIV.

In the first pair of antennæ the aural spine (Fig. 11, Pl. XXII) is scarcely more than half the length of the first segment of the stem. It is blunt and somewhat ovate in shape, as seen from above.

(2) In the other form (var. *brevicarpus*) the aural spine (Fig. 4, Pl. XXIII) has a different shape, and is relatively nearly twice as long. In this case it extends beyond the first segment to two-thirds the length of the second. The second or outer antenna of the *longicarpus* is armed with two spines at its base (Fig. 11, Pl. XXII); an inferior and outer basal spine, and a slightly longer one, the *squamous spine*, articulated to the joint carrying the latter. There is no scale. The basal spine is rather more than one-half the length of the antennal stalk. There may be present a small tubercle on the upper surface of the segment bearing the basal spine, near the articulation.

In variety *brevicarpus* (Fig. 8, Pl. XXIII) the squamous spine is stout and reaches nearly to the end of the antennal stalk. There also springs from its inner and proximal margin an elongate plate or scale, the inner free edge of which is fringed with plumose setæ; scale not quite as long as spine. The inferior basal spine not one-half the length of the squamous spine. There is a rounded or pointed tubercle over basal spine near the joint.

The small chela of the first pair of thoracic legs of the *longicarpus* (Fig. 2, Pl. XXIV) is short and broad. The finger ends in two or three horny teeth or prongs, which interlock those of the opposing thumb. The dactyle bears on its outer surface a tuft of peculiar hairs. The latter are finely serrate and have bent or hooked tips. The carpus is relatively very long, quite as long as the palmar portion of the propodus.

In the *brevicarpus* the small chela is long and somewhat narrower (Fig. 3, Pl. XXIV). Tips of fingers usually simple, but sometimes notched; the peculiar tuft of hairs is wanting. Carpus relatively short; about one-third the length of the palm.

The large chela of the *longicarpus* may also differ noticeably from the *brevicarpus* type. (Compare Fig. 8, Pl. XXIV with the figures on Pl. IV.) Fig. 8 represents a common form of this appendage. The propodus is long, cylindrical, slightly twisted, very smooth, and polished; ends above dactyle in a short spine and below in a rudimentary thumb with claw-like tip. Dactyle overreaches propodus, and its inner margin is not concave, or but slightly so.

These two forms, differing in the particulars just mentioned, would doubtless be considered as two distinct species if only these facts were known. A prolonged study, however, of a large number of individuals, collected both in sponges and from porous rocks on a number of reefs, has resulted in the discovery of a complete series of intermediate links. These connecting forms suggest a number of important questions relating to the causes and significance of variation.

By far the greater number of individuals of this species have the characteristics of the two varieties just described, but about five per cent of the collection made at different points near Nassau present intermediate characters.*

More fully stated, the noticeable points of variation are as follows: (1) The relative length of the antennular stalk and aural spine; (2) the lengths of the antennal spines relative to each other and to the peduncle of the antenna; the presence or absence of a squame or scale; (3) the character of the dactyle and propodus of the small chela of the first pair of pereiopods; (4) the length of the carpus of the small cheliped; (5) the general shape and character of the large

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* While the species live, as a rule, in the interior of the green and brown sponges, a few undersized individuals may be found, by careful searching, among the loose blocks of porous coral which are scattered over the reef, and it frequently happens that these individuals possess intermediate characters between the two varieties just described.

claw. (1) With respect to the first point, we meet with a perfectly graduated series between the two extremes (Figs. 11, 18, Pl. XXII, Figs. 4, Pl. XXIII). (2) The same is true of the relative lengths of the antennal spines, the scale, and peduncle (Figs. 11, 13, 14, Pl. XXII). In Fig. 11 there is no evident scale and the spines are nearly equal. In Fig. 14 the spines are markedly unequal, and there is a rudimentary scale. In Fig. 13 this scale is further developed. (3) Great variation is seen in the small chela. The fingers of this claw may each end in two or three prongs, or one in two, the other in three, or the tips of the fingers may be simple or merely notched. The tuft of peculiar setæ on the dactyle may be reduced or wanting. (4) Various stages between the long and short carpus are observed, and (5) slight variations not easily described are constantly seen in the relative size, shape, and other characters of the large chela.

These variations are shown in a general way in Table I. (For detailed measurement, v. Table II.) The fifteen cases here recorded were selected from upward of seventy-five, in a large number of which the variable parts were drawn for more careful comparisons.

TABLE I.—*Showing variations in Alpheus saulcyi and the intermediate stages between the varieties brevicarpus and longicarpus.*

No.	Sex.	Habitat.	Length.	Aural spine.	Squamous spine.
			mm.		
1	♂	Green sponge.........	29.7	Extends ⅔ length 2d segment of antennular stalk.	Extends nearly to end of antennular stalk.
2	♀	....do	42	To ½ l. 2d segment.........	Do.
3	♂	Brown sponge........	9	......do	Do.
4	♂	Green sponge.........	9.5	......do	Do.
5	♀	Rocks; Dix Pt. reef..	17	⅓ l. 2d segment.............	Extends nearly to end of antennal stalk.
6	♀	....do	10.4	......do	Not nearly to end of antennal stalk.
7	♀	....do	11.6	l. of 1st segment..........	Do.
8	♂	Rocks; Hog Id. reef..	10	Over ½ l. of 1st segment	⅗ l. antennal stalk.
9	♂	....do	10	Nearly to end 1st segment..	More than ⅗ antennal stalk.
10	♂	Rocks; Green Key reef.	9.5	¾ l. 1st segment.............	Nearly to end antennal stalk.
11	♂	Brown sponge	17.5	Nearly to end 1st segment..	⅗ antennal stalk.
12	♂	....do	13	......do	More than ½ antennal stalk.
13	♂	Rocks; Dix Pt. reef..	9.5	½ 1st segment.............	Do.
14	♂	Brown sponge	5.5	......do	⅔ l. antennal stalk.
15	♀	Reef rocks...........	11	Nearly to end 1st segment..	¼ l. antennal stalk.

No.	Inferior basal spine.	Squame or scale.	Carpus of small chela.	Fingers of small chela.	Remarks.
1	½ length squamous spine.	Scale as long as squamous spine.	Short	Tips simple; no tuft on dactyle.	Type of var. *brevicarpus.*
2	Less than ½ l. squamous spine.	....do	...do	Tips simple; no tuft.	v. drawing, Pl. IV.
3	....do	Scale nearly as long as squamous spine.	...do	....do	Claws dull red.
4	....do	Scale somewhat shorter than squamous spine.	...do	....do	
5	Nearly ½ l. squamous spine.	Scale not quite l. squamous spine.	Long......	Tips simple; rudimentary tuft.	Combines characters of both varieties.
6	....do	Small and rudimentary.	...do	Prongs; tuft on dactyle.	
7	⅓ l. squamous spine.	....do			
8	¼ l. squamous spine.	Rudiment	Short	Tips simple; no tuft.	v. Fig. 13, Pl. XXII.
9	....	....do	Long......	Prongs and tuft....	v. Fig. 14, Pl. XXII, (outer antennæ from above).
10	More than ½ l. squamous spine.	Rudiment (hardly visible).	...do	Propodus ends in prongs.	Dactyle missing.
11	....	Rudiment	...do	Prongs and tuft....	Claws reddish orange.
12	....	No scale	...do	....do	
13	....	....do	...do	....do	Type of var. *longicarpus.*
14	Nearly as long as squamous spine.	....do	...do	....do	Rostrum wanting.
15	....do	....do	...do	....do	Claws bright blue; dactyle of small chela extends 1mm beyond propodus.

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In Nos. 1 to 4 we find little variation from the *brevicarpus* form, which we consider as nearest to the type of the species. From No. 5 to No. 15 the departure from this type is increasingly evident, and in Nos. 12 to 15 we recognize the widest divergence in the varity *longicarpus*.

No. 5 is an interesting case, since it combines the characters of both varieties. The aural spine is rather blunt and extends to one third the length of the second segment of the antennular stalk. The inferior basal spine is rather less than one-half the length of squamous spine; upper basal spine a rudimentary knob. The squamous spine has a well-developed squame; nearly equals length of antennal peduncle. The "finger" and "thumb" of small chela end in simple, sharply pointed hooks. There is an inconspicuous tuft of setæ on the dactyle. The *carpus is long.* (See Table II.)

No. 8 is also an interesting variation. The antennæ are intermediate in character, between the extremes of the table, while the small chela is of the *brevicarpus* type. There is a rudimentary antennal scale. The tips of the small chela are simple. There is no tuft, and the carpus is short.

In No. 9, which is of the same sex, the same length, and from the same locality as No. 8, the small chela has the characters of the variety *longicarpus.* Nos. 5 to 12, in the middle of the table, show in one way or another intermediate characters between the extremes, Nos. 1 to 4 and Nos. 12 to 15.

VI.—MEASUREMENTS IN MILLIMETERS.

TABLE II.

[Locality: Nassau, N. P., Bahama Islands.]

Habitat	Green sponge.	Green sponge.	Rocks: Dix Pt. Reef.	Rocks: Green Key Reef.	Rocks: Green Key Reef.	Brown sponge.	Rocks: Dix Pt. Reef.
Sex	♀	♂	♀	♂	♀	♀	♀
Number in Table I	2	1		10	6		
Length (tip of rostrum to end of telson)	42	29.7	16	9.5	10.4	11	21
Length of carapax, including rostrum	15	11	7	....	4.4	4.5	8
Greatest width of carapax	11	......	4	....	2.3	2.1	5
Greatest depth of body	11	......	4	....	3	......	......
Distance between ocular spines	2.4	1.7	......	....	....	......	......
Breadth of second abdominal somite	15						
Depth of abdomen (with ova)	15	......	......				
Length of terga of abdominal somites in median line:							
First tergum	2	1.3	......	....	....	......	......
Second	6.2	2.8	......	....	....	......	......
Third	5.1	3	......	....	....	......	......
Fourth	4.1	3.3	......	....	....	......	......
Fifth	4	2.6	......	....	....	......	......
Sixth	3.8	2.6	......	....	....	......	......
Length of telson	5.5	4	......	....	....	......	......
Breadth of telson at base	4	3.2	......	....	....	......	......
Breadth of telson at tip	2	2	......	....	....	......	......
Length of antennular stalk	6	5.2	2	1.8	1.8	1.9	3.3
Length of antennular segments:							
First	3	2.2	0.9	0.9	....	1	2
Second	2	2	......	....	....	......	......
Third	1	1	......	....	....	......	......
Breadth of first antennular segment	1.1	1	......	....	....	......	......
Length of antennular or aural spine	4	3.7	1	0.7	0.7	0.7	2.3
Width of same at base	1	......	......	....	....	......	......
Length of exopodite of antennule	6	7	......	2	....	1.8	......
Length of endopodite of antennule	9	10	......	3	....	2.7	......
Length of antennal stalk	6.5	5.5	......	1.5	1.5	1.5	2.8
Length of long segment of same	4.6	4.7	1.6	....	....	......	......
Greatest width of long segment	1.2	1.0	......	....	....	......	......
Length of squamous spine	4.7	4	1.4	1	1.2	0.9	2.1
Length of "squame"	5	4	......	....	0.1	......	1.9
Width of spine and scale at base	1.9	1.7	......	....	....	......	......
Length of inferior basal spine	2.2	2	0.9	0.8	0.7	0.8	......
Length of superior basal spur	0.3	0.2	......	....	....	......	......
Width of basal segment	1.1	......	......	....	....	......	......
Length of same to articulation of squamous spine	2.0	......	......	....	....	......	......
Length of flagellum	16	15	......	3+	....	5.8	7

TABLE II—Continued.

[Locality: Nassau, N. P., Bahama Islands.]

Habitat	Green sponge.	Green sponge.	Rocks: Dix Pt. Reef.	Rocks: Green Key Reef.	Rocks: Green Key Reef.	Brown sponge.	Rocks: Dix Pt. Reef.
Sex	♀	♂	♀	♂	♀	♀	♀
Number in Table I	2	1	......	10	6		
Length of propodus of large chela	15	16	......	5.7	4.5	6	7.7
Length of same to spine at base of dactyle	11	11	5.1	4.4	3.4	4.4	......
Greatest width of same	5.5	6.1	......	2.5	2	2.4	3
Greatest depth of same	4	1.6	......	......	1.4	2	2
Width of same at spine, at base of dactyle	4.6	5	......	2	......	......	......
Length of "thumb" of propodus	5.2	6.5	......	......	......	......	......
Length of dactyle	4	6	2	2	1	2	......
Width of same, over tooth	3	3	......	1	......	......	......
Length of carpus of large cheliped, on upper median line	2.8	2.4	1	0.8	0.6	......	......
Length of meros of same	5.5	5.3	3	2.5	2.0	2.0	......
Greatest width of meros of same	3	2.6	1.7	......	......	1.5	......
Length of propodus of small cheliped	6.7	6	2.2	2	4.5	2	......
Length of same to articulation of dactyle	4	3.1	1.8	1.8	3.4	1.3	......
Greatest width of same	2.4	2	0.9	0.8	2	1	......
Greatest depth of same	1.8	......	......	......	1.4	......	......
Length of dactyle of same	3	3	1	......	1	......	......
Width of dactyle of same	1	0.9	......	......	......	......	......
Length of carpus of same	2.3	2	1.9	1.5	0.6	1	......
Length of meros of same	6	5	3	......	2	2	......
Greatest width of meros of same	2.7	2.5	0.8	......	......	......	......
Length of carpus of second pereiopod	7	5.5	......	1.8	1.7	1.7	......
Length of first segment of carpus of same	4	......	......	0.8	......	......	......
Length of fifth segment of carpus of same	1	......	......	0.6	......	......	......
Length of second, third, and fourth segments of carpus of same	2	......	......	......	......	......	......
Length of propodus of same	2.2	2	......	1	1	1	......
Length of meros of same	5.1	......	......	......	......	......	......
Length of propodus of third pereiopod	5	4.6	......	......	......	......	......
Length of carpus of same	2.8	2.7	......	......	......	......	......
Length of meros of same	6.2	5.8	......	......	......	......	......
Length of protopodite of third pleopod	6	1.9	......	......	......	......	......
Width of same	1.2	1.5	......	......	......	......	......
Length of endopodite of same	8	3.5	......	......	......	......	......
Greatest breadth of endopodite of same	2	1.6	......	......	......	......	......
Length of exopodite of uropod	5.8	4	......	......	......	......	......
Breadth of same	4.2	3.7	......	......	......	......	......
Length of endopodite of uropod	5	3.7	......	......	......	......	......
Breadth of same	3.5	2.9	......	......	......	......	......

VII.—THE CAUSES AND SIGNIFICANCE OF VARIATION IN ALPHEUS SAULCYI.

If we consider Nos. 1 or 2 of Table I as representing the nearest approach to the mean of the species, Nos. 5 to 15 must stand for individuals which have fluctuated farthest from the mean.

The individuals given in the table were chosen without reference to sex, yet it appears that nearly two-thirds of the number are males. In examining a larger collection of these aberrant forms I find a still greater percentage of males. There can be little doubt that in those cases the males are in the excess, although I have not tested this point carefully. It is also evident from observation and detailed measurements that the average size of these abnormal individuals is less than one-half that of the brevicarpus type. The brown sponges teem with a population of under-sized forms, nearly all of which are aberrant, and none of those which were examined exceeded the length of 17.5mm, which is considerably less than the average for the type.

How far are these variations individualistic and how far are they confined to the race or species as a whole? In other words, is the individual plastic, departing from the standard of the species and becoming different at different periods of its life, or do individuals deviate from the mean of the species, each along its own line? Further, are the variations congenital? While we

are not prepared to answer these questions as fully as we could wish, yet the facts are sufficient to throw some light upon the subject.

We have abundant evidence that there is considerable fluctuation in the life of the individual, as regards the number, color, and shape of pigment cells for instance. In all larvæ of these prawns the external antennæ have a well developed scale, and it is thus clear that this organ may degenerate and apparently disappear, to be reconstructed again at a later period. The variety *longicarpus* (No. 15, Table I) has no "squame," although it is present in the young (Fig. 7, Pl. XXII), and the cases in which the organ is seen in various stages of development (Figs. 13, 14, Pl. XXII) support and illustrate this conclusion. This, however, is not a rule with the species as a whole, as it is in the somewhat analogous case of the loss and subsequent reconstruction of the last two pairs of thoracic legs in the larvæ of Stenopus and Sergestes.

The question as to how far the characters which distinguish such forms as Nos. 1 and 15, Table I, are congenital can only be answered by a careful study of their development. My attention was not directed to this subject while at the seashore, and in this connection some interesting experiments remain to be performed. The evidence we have goes to show that the young in any given case share the peculiarities of the mother, and this is probably true of such details as the right and left handed condition of the large chelipeds. The following examples illustrate this fact: (1) The adult female in this case has the characters of No. 15, Table I. The antennular or aural spine is nearly three-fourths the length of the first antennular segment. The aural spine has a corresponding length in the larvæ of this prawn at the time of hatching. In the adult the fingers of the small chela end in prongs; there is a tuft of peculiar setæ on the dactyle. In the first larva the fingers of the small chela also end in prongs, and there is a tuft of rudimentary setæ on the dactyle. In the adult the carpus of the small cheliped is relatively very long. In the first larva the carpus of this appendage is about one-third the length of the propodus (relatively a little shorter than in the adult). Fig. 11, Pl. XXII, may be taken to represent the mother (rostrum here wanting), and Fig. 17 the young. The small chela of the mother is shown in Fig. 2, Pl. XXIV, that of the young in Fig. 15, Pl. XXII. Another case exactly like this was observed, where the embryo was taken from the abdomen of the female. (2) The adult in this case has the characteristics of No. 2, Table I (var. *brevicarpus*) (Pl. IV, Figs. 1, 2). The larvæ are shown in Pl. XXI, Figs. 1, 2, 3, 8. The aural spine, at first short, is nearly as long as the first antennular segment when the larva is a week old (Fig. 10, Pl. XXII). In both the parent and young the carpus of the small cheliped is relatively short. The fingers of the small chela end in simple tips; there is no tuft on the dactyle (see Fig. 16, Pl. XXII).

These facts indicate that the young share the peculiarities of the parent, but exactly how far the individual may depart from this standard in its own life, or how strictly the law of inheritance applies in all cases, my observations do not warrant a decisive answer. A few experiments could be easily made upon this Alpheus which would throw light on some interesting questions in heredity. The females with ova are easily obtained; the young are readily hatched and kept alive in glass dishes until they have reached the adult state.

In this species the change of environment, due to the adoption of life in sponges, has probably acted as a direct stimulus to variation. These animals tend to vary most along certain definite lines, as, for instance, the relative lengths of the antennular segments and aural spine vary much, while those of the segments of the carpus of the second pair of thoracic legs are practically invariable. Homologous parts vary alike, unless specially differentiated in different ways, as in the chelipeds. There is no diversity of life between males and females, and both sexes vary alike, but aberrant males are probably the more common.

The occurrence of large numbers of individuals showing variations of the same kind, but of different degree, render it plausible at least that the same variations may occur in a large number of individuals simultaneously, but the reason why this or that part has varied most is wholly obscure.

The aberrant forms (variety *longicarpus*) which have adapted themselves to life in the brown sponge thrive and produce young which, in the early stages certainly, share in the peculiarities of the parent. The variety *brevicarpus* is similarly adapted to its environment and its young resemble

it. Has natural selection, then, acted so far as to differentiate the species in more than one direction? There are some facts which favor the view that it has done so, but before the question can be definitely settled we must determine more precisely how far intermediate or aberrant forms represent phases of the individual and of the race. It is not probable that we are here dealing with the hybrids between two originally distinct species.

PART SECOND.

THE DEVELOPMENT OF ALPHEUS.

I. STRUCTURE OF THE LARVA.

(Pl. XLIX, Fig. 174. Pl. LIII, Fig. 196. Pls. LIV–LVII.)

These studies in the embryology of Alpheus begin with the growth of the ovarian egg and the early phases of segmentation and extend to the larval and adult periods. In order that the progress of development may be followed in the light of the structure which the embryo finally attains, we will start with a general survey of the anatomy of the first larva of *Alpheus saulcyi*. A fuller description of the histology and histogenesis of the tissues will be given in the parts which treat of the different organs in detail.

A profile view of the larva as it appears while still inclosed by the eggshell and of one immediately after hatching is seen in Pl. XXI, Figs. 1 and 5, and the brief and insignificant metamorphosis which is required to provide it with the adult characters are illustrated and described in a separate paper (Pls. XXI–XXIV).

Most noteworthy are the large, stalked, compound eyes, the segmented abdomen provided with its full number of appendages, the short, stumpy antennæ, and the swollen chelæ or pincers of the first pair of thoracic legs. At this stage this Alpheus is a *larva*, but in a restricted sense, since many adult characteristics are present. It is a larva, with preparations for immediately assuming the adult state. Some of the *larval* peculiarities are the spatulate telson, the biramous or schizopodal pereiopods (first to fourth pair, inclusive), the rudimentary pleopods, the unabsorbed food yolk, and the uncovered, stalked eyes.

The structural details are now very great, so that it is often impossible to interpret the parts seen in a single section, and it is only by comparing sections made in different planes that the relations of the organs can be successfully made out.

In Fig. 196 (Pl. LIII) the plane of section is nearly vertical and median throughout, except for the posterior half of the abdomen. The supra-œsophageal ganglion, which is usually spoken of as "the brain" (*s. o. g.*), is a complex organ, composed of internal, medullary masses (*punktsubstanz balls*), and cellular tissue which completely invests them. It is made up of the fused ganglia of at least two segments, those of the first and second antennæ. This fusion is complete from the early stages of development, and the relations of the parts are now extremely complex. They are best illustrated by a comparison of the series of transverse sections (Pls. LIV, LV, Figs. 211–219) with those made in a horizontal plane (Pl. LVII, Figs. 238–243), and it will be seen that there are four pairs of fibrous masses in the brain, intimately connected together.

These compact and finely granular masses in the interior of the ganglia of invertebrates were described by Leydig twenty-five years ago under the name of *Punktsubstanz* and later by Dietl (1876) as *Marksubstanz*. As Krieger remarks, the latter name is bad, since it confuses this tissue with the spinal marrow of vertebrates, with which it has nothing to do. It is essentially a *felt* of very fine fibers. We will therefore speak of it as the *Punktsubstanz*, or, to use a more descriptive term, the *fibrous substance* of the ganglia.

The first pair of these, the *anterior or optic fibrous masses* (Pl. LV, Figs. 212–215), are the largest. They are completely fused on the middle line and form a single compact mass, which is slightly constricted laterally (Pl. LVII, Fig. 242, *of.*) and which is divided in front (Pl. LIV, Figs. 210, 211), where it gives off two diverging stems of fibrous tissue (sometimes called *optic nerves*) to the optic ganglia in the stalks of the compound eyes (see also Pl. LVII, Fig. 240 *of.*).

Next in point of size are a pair of large *lateral balls,* which appear kidney-shaped in transverse section (Pl. LV, Fig. 216, *l. f.*). Each is virtually segmented at the lower surface into two lobes (Pl. LVII, Fig. 242, *l. f.*). These lobes are closely united to each other, and by a pedicel or stalk of fibers to the lower posterior extremity of the anterior, optic mass. A third pair of fibrous masses (Pl. LV, Figs. 215, 216, *af.*) fuse with the anterior mass at the same point. Each of these balls is also bilobed, and from them issue the fibers of the antennular nerves. (Pl. LVII, Fig. 243, *n. au.*, also Pl. LV, Figs. 212–214, *a. o., nau.*) The nerve of the first pair of antennæ consists of cells and fibers, which pass to a mass of deeply staining cells (*a. o.*), *the ear,* and to the tissues of the antennular stalk. The fourth pair of fibrous masses (Pl. LV, Figs. 217, 218, *gf.*, also Pl. LVII, Fig. 243) are intimately associated with the last and with the common bridge of tissue (Pl. LV, Fig. 216, *of.*) which unites them all. From these arise the fibrous elements of the antennal nerves, which supply the green gland and the tissues of the appendage (Fig. 216, *n. ag.*). From this same region (Fig. 218, *fo.*) the commissures which surround the œsophagus and unite the brain to the ventral nerve cord also originate (Fig. 220). These commissural bands meet immediately behind and below the œsophagus, where they fuse (Pl. LV, Figs. 222, *œm.*) and join the ventral chain of ganglia. This last consists of the ganglia of the remaining eighteen segments of the body. Each ganglion is double and is made up of two fibrous balls, united by a transverse commissure, and of a thick envelope of nerve cells. Longitudinal commissures of cells and nerve fibers unite the successive ganglia, which form a double chain. These relations are well shown in Fig. 196 and by the horizontal section (Pl. LVII, Fig. 243). The first six thoracic ganglia are very closely crowded together (Fig. 196, *g.* 4–9) and form what is usually known as the *infra œsophageal ganglion* (ganglia of mandibles, first and second maxillæ, and first, second, and third maxillipeds). The next five ganglia, *g.* 10–14, which are less closely crowded than the preceding, belong to the five pairs of thoracic legs and their segments. The fiber balls of each ganglion are pear-shaped masses, disposed vertically, with the large end of the pear turned toward the base of the appendage. The abdominal ganglia are more widely separated and the longitudinal commissures are consequently more marked (Fig. 196, *g.* 15–20; see also the series of transverse sections, Pls. LV, LVI). The nerves, always difficult to distinguish, owing to the close similarity of their cells to those of the surrounding ectoderm, are best exemplified in the case of the antennular and antennal nerves already mentioned.

The relations and course of the fibers, which are very complicated, are partially indicated in some of the sections. There is a marked transverse commissure of fibers in the anterior half of the large optic swelling (Fig. 213), and at its posterior extremity, where it fuses with the lateral and antennal masses (Pl. LIII, Fig. 198, *gf.*).

The optic stalks or lobes, bearing the compound eyes (Pl. LIV, Figs. 209, 210, and Pl. LVII, Figs. 239–242), consist of an irregular series of fibrous masses, in shape of a distorted letter L. The angle of the letter L is continuous with the fibrous substance of the brain, while its shorter limb proceeds to the compound eye and its longer forms a large swelling in the upper part of the stalk. There is a nauplius eye (Pl. LIII, Fig. 197; Pl. LIV, Figs. 209, 210, *oc.*) borne on a median papilla, which projects downward between the eye stalks. The details of the structure of the eyes are given in Section IX.

The alimentary tract of the larva is a somewhat complicated structure, and the relations of its parts are best understood by reference to sections taken in more than one plane. We can recognize five well-defined portions: the œsophagus, the masticatory stomach, the midgut, the hindgut or intestine, and the appendages of the midgut. These are shown in a semidiagrammatic way in the cut (Fig. 2), and the longitudinal section (Pl. LIII, Fig. 196) and series of transverse and horizontal sections (Pls. LV–LVII) illustrate the structures in more detail.

It is interesting at this point to compare the larva shown in Fig. 196 with the longitudinal section of an advanced embryo (Pl. XLVIII, Fig. 168). In both we recognize the foregut, a tube bent on itself, consisting of the œsophagus and masticatory stomach (*m. s.*). In the embryo the latter is closed on the side of the food yolk. In both we also see a vertically directed fold of endoderm (*f.*, overlying mg^3 in Fig. 196) and behind this the large lumen of the hindgut, which gradually tapers into that of the narrow, tubular intestine. Between this fold on the one hand and the stomach on the other we find in the embryo an enormous space filled with yolk, which is partially walled in

with endodermal epithelium near the point where it communicates with the cavity of the gut. This in the larva corresponds to the midgut (Fig. 196, *mg.*) and its diverticula.

The œsophagus (Figs. 196, 218–220) is a straight, vertical tube, with very thick walls, which are thrown into longitudinal folds. There is an anterior and posterior fold and two lateral ones, which give to the lumen of the œsophagus the shape of the letter X when seen in transverse section (Pl. LVII, Figs. 241, 242). The walls of the masticatory stomach resemble those of the œsophagus, and the folds of the latter are continuous with the valvular structures of this region. The lateral and median thickenings (Pl. LV, Fig. 221, *p. v.*) at the point where this portion of the stomach passes into the midgut may be regarded as a rudimentary pyloric valve. The pouches formed between the median ventral fold (Fig. 221) and the lateral folds (*p. v.*) correspond to the gastrolith sacs in the crayfish embryo (54), but no gastroliths are found in Alpheus.

The midgut appears in the longitudinal section (Fig. 196, *mg.*) as a short, restricted cavity. It is, however, a spacious chamber, as we see by examining a series of sections made in other planes (Pls. LV–LVII). It consists of seven parts or divisions: a dorsal, unpaired, median division (*mg.* in all the figures), and, opening from this, a pair of anterior lobes (*mg.*^{1}), a pair of posterior (*mg.*^{3}) and a pair of ventral lobes (*mg.*^{2}). All these parts are lined with a peculiar columnar epithelium, composed of endoderm cells, derived primarily from the wandering cells, excepting a part of the median and the anterior divisions, where the endodermal wall is absent or only imperfectly formed. The epithelium of the midgut passes imperceptibly into that of the intestine, since the cavity of the hindgut is in communication with the food yolk from the very early stages of the embryo, and since also the endoderm is formed very gradually and first appears in the region where the hind gut communicates with the yolk. On the other hand, the demarcation between the wall of the masticatory stomach (of ectodermal origin) and that of the midgut (Fig. 196) is most pronounced. Correlated with this distinction is the fact that the foregut is a blind sac and completely cut off from communication with the yolk until very late in embryonic life (Pl. XLVIII, Fig. 168). The anterior lobes contain the remnant of unabsorbed yolk (Figs. 218, 237, *y.*), and in cases where the lining epithelium is unformed, the food yolk is in contact with the brain. These lobes are separated by a median vertical partition (*mp.*), composed of connective tissue and muscle cells, which suspend this portion of the digestive tract to the anterior dorsal wall of the body. In a very late embryo which is about ready to hatch we find that the partition separating the anterior lobes is incomplete. The dorsal half of it consists of a downward-growing fold of endoderm cells, with a mesodermic core. The ventral and lateral walls of these diverticula are devoid of epithelium, so that the endoderm extends itself most rapidly forward, on the dorsal median line, and thence spreads to the ventral floor.

The posterior lobes (*mg.*^{3}) are the first to develop (see Pl LI, Fig. 185, *mg.*^{3}). They lie to one side of and below the hindgut (Pl. LVI, Figs. 226–230, *mg*^{3}., *gg.*$^{1-3}$). Up to this stage their position is never dorsal to other parts of the digestive tract. It is from these lobes that the gastric gland or so-called "liver" arises. Each lobe is simple until a short time before the embryo hatches, but in the newly born larva it is divided into three lobules. This division is effected in this manner: The lower median part of the primary lobe (Fig. 228, *gg.*^{1}) is constricted off by the growth of a fold from the side next to the hindgut, downwards and outwards, to form a secondary lobule (*gg.*^{2}). By the constriction of the upper portion in the same way the primary lobe becomes divided into three pockets. The relations of the posterior division of the midgut to the unpaired central portion is best shown in a horizontal section (Figs. 236–238). It seems quite probable that a part of the epithelial lining belonging to the enlarged section of the hindgut is endodermal in its origin, but just how much it is impossible to say.

The ventral lobes (Fig. 224, *mg.*^{2}) are ventro-lateral diverticula from the central portion of the midgut and are completely lined with columnar epithelium.

An examination of the structure of a young Alpheus of this species, ten days old, throws much light on the anatomy of the larva just considered. The alimentary tract has at this time essentially its adult structure. The gastric glands open into it by short ducts at a point just behind the masticatory stomach. They consist of three pairs of lobes or cæca. One pair, corresponding to the posterior division of the midgut (Fig. 226, *mg.*^{3}), is imperfectly divided into three lobules, as in the early larva. They extend backward, below and to one side of the gut. The two remaining

pairs pass forward on either side of the masticatory stomach to a point about on a level with the first maxillary segment. The ventral is the larger and longer of these, and two lobules are constricted off from it near its extremity. They correspond to the ventral lobes of the midgut (*mg.*[2] cut, Fig. 2). The dorsal pair represent the anterior lobes (*mg.*[1]), which are now entirely withdrawn from the head region, and naturally contain no food yolk. The gastric cæca are all filled with a coagulable fluid which stains feebly in carmine. The gastric epithelium for a short distance behind the point where glands communicate with the stomach has marked histological peculiarities. The internal absorbent surface is increased by folds which nearly obscure the lumen of the tube. The cells are columnar and resemble the glandular cells of the liver and probably have the same origin as the latter. In the masticatory stomach there is a strainer of hairs developed on the ventral and lateral walls which are greatly thickened, as we saw in the larva. The dorsal wall is thin, but there is a large valvular fold on the ventral side.

The vascular system of the adult is already outlined in the larva in all its essential characteristics. The walls of the blood vessels are exceedingly delicate, so that it is not easy to ascertain their distribution by means of sections alone. The heart (Pl. LIII, Fig. 196, H.) is a short tubular chamber, flattened between the dorsal body wall and the enlarged section of the hind gut. It is suspended in the pericardial sinus (*p. s.*) to the body wall and surrounding organs by means of strands of connective tissue (alæ-cordis). The walls of the heart are quite thin, and its cavity is partially divided into three compartments by the growth downward from its roof of two sheets of mesoderm cells (Pl. LVI, Fig. 231, and Pl. LI, Fig. 186).

Of the several arteries which lead from the heart, three, and possibly five, can be distinguished. Posteriorly the heart is continuous with the large *superior abdominal artery*, which traverses the abdomen close to the dorsal wall of the intestine (Figs. 196, 232, 235, *a. s. a.*). Near its origin from the heart, the sternal artery (Fig. 196 shows a trace of this vessel between ganglia 12 and 13, to the left of *pr.*) is given off, and passes directly downward to the ventral nervous system, which it penetrates at a point between the third and fourth thoracic ganglia. This is continued backward under the nervous system and forms the *inferior abdominal artery* (Figs. 229–234, *a. i. a.*) Anteriorly the heart gives off the unpaired *ophthalmic artery* (Figs. 196, 215–229, *op, a. op.*), which runs forward to the region of the eyes and brain. It is not an ophthalmic artery, strictly speaking, but from the first, supplies arterial blood to the brain and anterior cephalic region generally. In Figs. 215, 216, it is seen cut in partial longitudinal section, where it evidently communicates with the blood space surrounding this part of the brain. The antennal arteries can not be clearly distinguished in sections, but in a much earlier stage trains of cells are seen at the surface of the egg passing forward on either side of the middle line toward the eye stalks, which possibly represent the antennal vessels.

Besides the sinuses already mentioned, there is a large sternal sinus (Fig. 196, *sts. s.*). This occupies the extensive space between the thoracic ganglia and the alimentary tract and "liver," and, like all other similar spaces, is more or less completely filled with serum and blood corpuscles.

Five pairs of gills are present at this stage. They are developed from simple pouches or folds of the skin on the bases of the thoracic appendages (Figs. 193, 230–233, *br*[2-5]). The outer surface of this primary fold soon becomes divided into a number of secondary folds or gill plates, and in a larva which has moulted twice and is twenty-four hours old, the branchia has the structure shown in Fig. 195. The adult gill is precisely similar to this, except that it has a greater number of plates and more definite branchial vessels. In the early larval stages the skin and especially the branchiostegites (Fig. 193, *bg.*) probably serve as important respiratory organs.

In respect to its muscular system the first larva appears to differ but little from the adult. The flexor and extensor muscles of the abdomen are most prominent (Fig. 196, *mu. f., mu. e.*). The former consists of a double rope of fibers, fused completely together and very much twisted. They extend from the sides of the thorax to the terminal telson (Fig. 227–235, *mu. f.*). The extensor muscles (*mu. e.*) are smaller, but otherwise similar to the latter, both in origin and extent. They lie above or to the sides of the digestive tract. Their attachment to the carapace is shown in Figs. 227, 228.

The next most prominent muscles are the adductors of the mandibles and great chelæ. The former consists of a large band of fibers which pass from one side of the body to the other directly

over the nervous system (Fig. 221, *ad. m.*). Closely associated with it are the muscles of the maxillæ. The large flat tendon to which the adductor muscle of the forceps is attached, is well developed at the time of hatching. It is formed by the infolding of a sheet of ectoderm cells at the point of articulation of the fingers of the claws, and in a plane at right angles to their plane of action. The outer ends of the cells of this infolded sheet now oppose each other and secrete the chitinous tendon, while to their morphologically *inner* ends the muscle fibers are attached.

The connective tissues invest the organs and seem to bind them together and to suspend them to the outer ectodermal wall of the body, but in some cases the ectoderm of the surface is apparently replaced by mesoderm cells, and often muscle fibers appear to be attached to the tergum of the somite (Fig. 196). This may be explained by the intimate fusion of the ectoblast and mesoblast at these points.

The green gland (Pl. LIII, Fig. 198, *ag.*) at the base of the second antenna is a well-defined structure. It consists of a blind tube, which passes up close to the brain as far as the anterior sacs of the midgut, and of a solid, disc, shaped body. The walls of the tube are composed of a single layer of large cubical cells. These thin out at the lower end, and to the outer wall is applied the solid nodular body. Neither at this stage nor at any previous one have I been able to detect an opening to the exterior.

In the adult the tubular portion of the gland grows to very great length, coiling itself in all the available space in the anterior region of the body in front of the mandibles. It surrounds the brain and œsophagus and passes down to the labrum and into the eyestalks. The solid almond shaped body (probably the end-sac) becomes a spongy mass of tissue. Its function is plainly different from that of the epithelium which forms the wall of the tube and to which the secretive product of the gland is due.

The reproductive organs, or what I regard as such, are difficult to find, owing to their very rudimentary condition. They consist of a small cluster of large cells on either side of the middle line between the digestive tract and the anterior end of the heart (Stage X, Fig. 173, R. O.).

With this sketch of the structure of the larva we are ready to trace the history of development from the earliest stages and to ascertain the manifold changes through which the unicellular egg with its great store of yolk passes, before it attains to the wonderful complexity of the larval and adult forms.

II.—THE ORIGIN OF OVARIAN EGGS IN ALPHEUS, HOMARUS, AND PALINURUS.

(a) *Alpheus.*—The ovaries of Alpheus are paired cylindrical bodies which extend between the alimentary tract and dorsal blood vessels, from just behind the eyes to the end of the third or fourth abdominal somite. Owing to the transparency of the skin in this species (*A. saulcyi*) they are extremely conspicuous, giving to the female an intense green or yellow hue, according to the color of the egg (Pl. IV). The oviducts open in the usual way by means of a slit-like valve on the basal joint of the third pereiopods.

In Pl. XXVI, Fig. 11, the condition of the adult ovary is shown, as it appears two or three days after the eggs then carried on the abdominal appendages had been laid. The ovarian ova are ripe by the time the young are ready to leave the shell, and the new ova are laid in a few hours after the hatching of the larval brood. Thus there is a constant succession of young, and females are not commonly found without either attached or large ovarian eggs. The breeding season of this species extends, as we have seen, throughout the entire year.

The structure of the ovary is quite simple (Fig. 11). It is essentially a sac lined with germinal epithelium. The external layer of the sac (O. W.) is muscular and contains numerous nuclei. Between the epithelium and fibrous coat there is a wide space filled with blood. This may be unnaturally large in the preparation owing to the disturbing effects of the reagents employed, but it is not wholly abnormal. The germinal epithelium consists, for the most part, of a single layer of large cubical cells. The nuclei are large and granular, and the cell outlines are often distinct. The function of these epithelial cells is twofold: (1) They give rise to ova; (2) They form the epithelium of the egg follicle.

There is no germogen or polynuclear mass of protoplasm from which the ova are developed, but the eggs appear to originate directly from epithelial cells. The new eggs begin to develop,

while the ovarian lobe is yet crowded with ripe ova ready to be laid, on the ovarian wall next the middle line of the body. The process seems to be as follows: The nuclei of the cells of the germinal epithelium increase in size along a certain tract. The cells grow rapidly and are slowly dehisced or pressed into the cavity of the sac. Each is surrounded by a coat of follicle cells. This is formed by the ingrowth of the germinal epithelium about the egg. Sometimes several ova occupy a common pouch (Ger.) which is separated from the rest of the ovary by sheets of follicular tissue (F. E.), but eventually each egg has a covering of its own. Between very young ova (e) no larger than the epithelial cell, and the maturer egg (e^1) every stage can be traced. The yolk appears very early as a fine granular deposit in the protoplasm of the cell.

In this species the development is nearly direct, there being no zoöal stage, and the egg contains more than nine times as much yolk as the egg of *Alpheus minus*, in which the first larva is a zoöa-like form. The materials for the yolk must be derived directly from the blood, and in this form the germinal epithelium is bathed with the blood current. Where there is an enormous food yolk blood must be supplied to the developing ova in more than the usual quantity. This is often accomplished by reëntrant blood sinuses which penetrate all parts of the ovarian stroma, as in the lobster (*Homarus*) and in the cephalopods, which are precocious in development and consequently deposit a great store of yolk in the egg. In the latter the follicular epithelium is folded in a remarkable manner about the egg to increase its nutritive surface.

The germinal vesicle (Fig. 11, G. V.) is filled with coarse chromatin grains, and in the early phases grows relatively faster than the rest of the egg. In the egg, (e,^{1} to the left) which is $\frac{1}{300}$ inch in diameter, the diameter of the germinal vesicle is one-half that of the entire egg. The chromatin grains increase in size until there are formed, as in an egg like the last, six or more large masses of chromatin, or nucleoli. The older eggs are spherical; their food yolk is often vacuolated, as in later stages, and they are invested by a single membrane, the chorion, which is a chitenous secretion of the follicular cells.

In the ripe ovary of this Alpheus the mature eggs fill the ovarian sac, except at the lower portion next the middle line, where, as already stated, the young ova first make their appearance. These mature eggs are closely crowded and irregular in shape, and their bulk greatly distends the body of the prawn. The chorion is now fully formed and closely invests the vitellus. The yolk is in the form of spherules, usually fused and always vacuolated in preparations which have been subjected to alcohol and turpentine. In the ripe egg the nucleus was not seen, but it is quite probable that careful sectioning would show that it lay at the surface, as is the case with the ripe ovarian egg of the lobster, which is often left in the ovary, after the bulk of the eggs are laid. We thus conclude that the extrusion of polar cells may be internal, that is, may take place within the ovary, as is sometimes, if not always, the case with *Homarus*.

(b) *The Lobster* (*Homarus americanus*).—The ovaries of the lobster consist of two lobes or rods of tissue, united by a short transverse bar. When filled with eggs their color is a dark olive green, except in young females, where the color of the immature ovary is variable. Each lobe is composed of an outer wall, which is a felt of muscle and connective tissue fibers with very small nuclei, and of a loose framework of germinal epithelium, which penetrates all parts of the lobe. The latter is a syncytium and consists of a matrix in which great numbers of small nuclei are embedded. These nuclei, with surrounding protoplasm, give rise (1) to ova and (2) to cells of the egg follicle.

The growth of the ovarian egg from the epithelial nucleus is illustrated in Pl. xxv, Figs. 3, 6. Fig. 6 is from a section through the posterior end of an ovarian lobe of a lobster obtained from the Baltimore markets in January. Fig. 3 shows the central portion of this section greatly enlarged. The diameter of the entire section is about twice that of the part represented in Fig. 6, and the oldest eggs lie at the periphery. The germogens, the centers of dispersion of new eggs, lie nearly in the long axis of the lobe. We can therefore trace in a single good section at this stage the development of the egg through every stage, from the indifferent nuclei of the ovarian stroma to the large peripheral ova. The ovary is supplied with blood by means of sinuses which penetrate to all its parts (Bl. S.). The sinuses are definite reëntrant channels with thin membranous walls.

The ovarian tissue (Ct. S.) consists of a fibrous matrix in which numerous oval granular nuclei are embedded. The process of the conversion of the epithelial cells into eggs is shown in Fig. 3. The epithelial nucleus (O, O^2) swells out, becomes spherical, and its chromatin has the charac-

teristic granular appearance of the germinal vesicle of the young egg. The first trace of the yolk (O^3, O^4, O^5) appears in the outer granular layer which surrounds the germinal vesicle. This layer represents primarily the cell protoplasm, in which the yolk is formed. The cell takes on a definite shape and is very early invested with a follicular coat (F. C.). In an egg a little older (O^7) the nucleolus has appeared, and in still older eggs (Fig. 6, O, O^1) a delicate chorion (Ch.) can be seen. This is secreted by the cells of the follicular envelope (F. C.). The growing eggs pass out from the central to the peripheral parts of the lobe in the sheets of stroma between the blood sinuses. Distinct yolk spherules are very early seen (O^7) and are of uniform size, but in maturer eggs (Fig. 6, O, O^1) the germinal vesicle is sometimes surrounded by a central layer of small spherules and a peripheral layer of larger ones. The germinal vesicle is centrally situated and always contains a single excentric nucleolus, besides stellate masses in the chromatin reticulum.*

(c) *The Spiny Lobster* (Palinurus).—In the spiny or rock lobster from the Bahamas the ova originate exactly as in Homarus, and the structure of the ovary is essentially the same. There are several nucleoli, as in Alpheus. The ovary is not nearly so richly supplied with blood sinuses as in the cases just considered. This is perhaps correlated with the fact that the amount of yolk

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* Since the above account was written I have been able to study the structure of the ovary more thoroughly, and the subjoined notes are largely extracted from a preliminary notice on "The Reproductive Organs and Early Stages of Development of the American Lobster." (23.)

The structure of the mature ovary is somewhat peculiar. The free, unextruded eggs fill the lumen of the ovarian lobes. The lobe or tube itself consists of the proper ovarian tissue and the outer muscular wall, which is very thick. The stroma is characterized by the presence of *gland-like structures*, blood sinuses, and immature ova. The glands are in close relation with the growing eggs. They are plaited or folded structures, and consist of a single layer of columnar cells, the boundaries of which are indistinct. The lumen of the fold usually contains a granular residue, but often yolk and degenerating nuclei. It seems possible that these structures are comparable to *yolk glands,* and that their function is to supply the growing ova at this stage with a part of their massive food yolk. Three days after the extrusion of the eggs the glandular cæca have much thicker walls; the rapidly dividing cells are smaller, and their nuclei lie at various levels. In another ovary of about the same age the glands are relatively very large. The columnar cells are greatly elongated, their nuclei lie at the deeper or outer ends of the cells, and the lumen of the gland is often completely obscured. The gland forms a kind of egg tube, abutting upon and partly inclosing the growing egg. The columnar cells stop short at the sides of the egg, so that the glandular cæcum resembles a narrow bag with an egg pushed into its mouth. The glandular cells are directly continuous with those of the follicle. The axial portion of this ovarian lobe is composed of hollow spaces, blood sinuses, and loose stroma, in which very young eggs occur. Degenerating cells occur not only in the stroma, but probably in the developing ova also. In *Peripatus Novæ Zealandiæ* the yolk is described by Lilian Sheldon as arising not only from the egg protoplasm, but also from the follicle cells (57).

When ten to fifteen days have elapsed after egg-laying (eggs in egg-nauplius stage), the gland-like bodies have almost wholly disappeared. The walls of the cæca are shrunken and crumpled, and the latter have been crowded to the extreme periphery of the ovary. The ovary now contains a solid core of immature eggs, stroma, and bloodvessels. This is continuous with radial sheets of similar tissue which extend from the center toward the periphery. The outer and more mature masses of ova are thus divided into more or less continuous, longitudinal bands.

At a still later period (eggs with eye pigment, four to five weeks' old) the glands are present merely as shriveled remnants. Later still (lobster taken August 21; egg embryos in a late stage) there is no trace of gland-like structures. In the ovary of a lobster (taken June 30), with eggs about to hatch, the condition is similar to the last. It is now about eleven months since the eggs were laid, yet the diameter of the largest ovarian ova is only about one-half that of the mature eggs. The ovarian wall is thinner than in previous stages, and in the axis of the lobe there are still sheets of very small, immature ova.

It seems that the bodies which have been described as probable yolk glands are present in the peripheral parts of the ovaries only during the limited period of from two to three weeks after the eggs are laid, and when the organs are recovering from the changes which follow this event. Their structure is quite unlike that of bloodvessels or sinuses with which they are intricately associated, and their relation to the growing eggs seems to imply that they have some function to perform in the nourishment of the peripheral ova. Their short existence, on the other hand, might lead us to suspect that they were more or less rudimentary structures, or that they were concerned with the secretion of the gluey substance with which the eggs are coated at the time they are laid. Their true function, however, remains to be determined.

Ovaries which I have examined, taken in summer (July) from lobsters ("paper shells") which have recently moulted and which do not carry eggs, present very thin walls, and the largest ovum measures in diameter about one-half that of the mature egg. These lobsters have probably hatched a brood the present season and have afterwards moulted. (Compare the ovary of the lobster taken June 30 above.)

Some allowance is to be made for individual difference, but the slow growth of the ovarian egg, which we have traced from the summer when eggs were laid to the following summer when these eggs were hatched, is very noteworthy, and shows conclusively that the lobster is not an annual breeder.

in each egg is very small, although the number of eggs produced by this animal is enormous. At Nassau, Palinurus begins to spawn in June.

(d) *Comparison.*—Ishikawa describes very fully the ovaries and ovigenesis of the prawn *Atyephyra compressa* and concludes that the ovum "originates from the inner lining of the ovary and is at the beginning a cell with a nucleus and one, two, or rarely three nucleoli." The mature egg, according to this observer, has two membranes, one of which is due to the "hardening of the peripheral protoplasm of the egg," while the other (secondary egg-membrane) is secreted by the epithelial cells of the oviduct and added at the time the eggs are laid.

There seems to be an error here in regard to the origin of the chorion. In the Decapod Crustacea it is the rule that the chorion it secreted gradually during the growth of the egg by the cells of the egg follicle. The large glandular cells found in the oviducts of Atyephyra possibly secrete the viscid fluid by which the eggs are attached to the swimmerets, yet this point needs comfirmation.

The chorion was found in the ovarian egg of Pagurus by Mayer (39), who says:

Das Eierstocksei von Pagurus ist in der ersten Zeit seines Bestehens eine echte Zelle mit Protoplasma, Kern und Kern-Körperchen. Später findet eine Einlagerung von Deutoplasma und die Bildung einer Hülle aus Chitin statt. Endlich wird der Kern unsichtbar; das Ei stellt dann eine Cytode vor.

Das fertige Ei verlässt den Leib des Krebses ohne Kern und mit einer Hülle versehen.

This description answers for Alpheus in all essential points.

The ripe egg of the crayfish (*Astacus fluviatilis*) is inclosed by a single envelope, the chorion. According to Ludwig and Waldeyer it is not known whether this is a product of the egg or of the follicle cells. Huxley (26) merely states that " a structureless *vitelline membrane* is formed between the vitellus and the cells which line the ovisac." The ovisacs burst and the ova pass through the ovary into the oviduct. When laid, the eggs "are invested by a viscous, transparent substance which attaches them to the swimmerets of the female and then sets." Here as in other forms the chorion is clearly the secretion product of the ovisac.

In *Cranyon vulgaris* Kingsley (31) finds that the late ovarian ova resemble the newly laid eggs. There is a thin structureless envelope (chorion), but no trace of an inner vitelline membrane.

Ludwig's general statement that the egg cells of all Arthropods are surrounded by a vitelline membrane (Dotterhaut), the product of the egg itself, is certainly erroneous. He divides the egg membranes into *primary egg membranes*, those which are derived from the protoplasm of the egg itself or from its follicle cells, and *secondary egg membranes*, those formed by the wall of the oviduct or otherwise. Balfour, following Van Beneden, restricts the term *vitelline membrane* to structures derived from the protoplasm of the ovum, and *chorion* to those formed by the cells of the follicle or oviduct. In the category of secondary structures would fall also those secreted by special glands, found, according to Ludwig, in Trombidium, Chilopoda, and nearly all Crustacea, and the winter eggs of Daphnia and Tardigrada, which is due to a moult or direct separation of epithelium from the body of the mother.

In speaking of the vitelline membrane Van Beneden and Bessels, in their monograph on the formation of the blastoderm (60), thus define it:

Nous entendons la membrane vitelline dans le sens où M. Claparède l'a si nettement définie dans son travail sur les vers Nématodes : C'est la couche externe du protoplasma de l'œuf, qui, ayant acquis une densité plus grande que la masse sous-jacente, se sépare de celle-ci par un contour net et tranché. Elle est à l'œuf ce que la membrane cellulaire est à la cellule ; elle se forme de la même manière.

According to this view the ovum is morphologically a cell, the vitelline membrane is the cell wall.

The origin and growth of the egg in Amphipods (*Gammarus locusta*) agrees quite closely with what takes place in Alpheus and Homarus. According to Van Beneden and Bessels (60) the young ova are at first protoplasmic cells, the nucleus of which becomes the germinal vesicle. The ovarian egg is a cell without a membrane, and in the cell protoplasm refringent vesicles are developed which form the yolk elements. According to these authors the mature ovarian egg consists of a viscous, finely granular, and contractile liquid, which represents the primitive cell protoplasm and holds in suspension the germinal vesicle, and, secondly, of nutritive yolk elements (called by them *deutoplasm* because of secondary origin), which are also suspended in the protoplasm of the egg.

In insects it appears that a chorion is always present in ovarian eggs, while, on the other hand, arachnids possess a vitelline membrane and the eggshell is secreted in the oviduct.

There is no simple rule to express the appearance of egg membranes in a diversified group like the Arthropods, and, considering that these structures are purely secondary to the cell and expensive products however formed, this is what we should expect. Their function is chiefly protective, and where a chorion is present in the ovary a yolk membrane is not developed, but the latter is present, as in spiders, when the shell is a later product. Erdl (15) describes three egg-membranes for the lobster, but it is clear, as Mayer has already shown, that the inner, delicate membrane which has been described for the decapod egg, is a secretion product of the blastoderm.

III. SEGMENTATION OF THE EGG OF ALPHEUS MINUS.

In the small green Alpheus of the southern coast we have a peculiar modification of the usual process of segmentation, which seems to be anomalous.

The fertile egg is pervaded with a remarkably fine reticulum, which incloses yolk spherules of minute and uniform size. The nucleus is central, or nearly so,* and consists of an ill-defined mass of protoplasm, in which a fine chromatin network is suspended. In the next phase (Pl. XXVI, Fig. 14) the nucleus is elongated and about to divide. Division appears to be direct and irregular. At a somewhat later stage the phenomena of the most interest occur (Figs. 12, 13). Each product of the first nucleus has developed a swarm of nuclear bodies (S. S.), which seem to arise by fragmentation. These bodies take the form of spherical nuclei in clear masses of protoplasm. The yolk frequently has a tendency to segment about the nuclear masses, in the same way that it divides about a single nucleus to form a yolk pyramid. This yolk segmentation seems to be normal, but it is very irregular. In one case there were two large segments, which nearly divided the egg in two, besides several smaller ones. Nuclear matter consists either of small particles or of indefinite reticulated masses, resembling the first nucleus (Fig. 14). Clear areas are sometimes found with nuclei which appear to be breaking down. About eight nuclear swarms or clusters are present in the stage shown in Figs. 12, 13. The nuclei vary in size from refringent particles to bodies of ordinary nuclear appearance.

Figs. 25 and 26 represent two sections of one of the clear areas in the same egg from which Fig. 12 was drawn. This clear field has several degenerating nuclei near its border. The largest one (S. C.) is included in both sections. A small chromatin mass with indistinct body lies next it (S. C.²), and other similar bodies occur in different sections. The cell S. C. contains two chromatin balls, and in Fig. 26 (the next section but one in the series) this body appears to be discharging through its broken-down wall numerous minute elements (S.) into the clear field. In Fig. 22 a small protoplasmic area occurs, in which a single nucleus lies. This body is granular and contains a large chromatin ball. Figs. 5 and 23 are also from the same egg. Here we see structures similar to the cell just mentioned. They are surrounded by yolk and consist of a delicate reticulum in which usually one large nucleolus is suspended, besides great numbers of small chromatin particles.

Various stages of growth are here represented, and it might appear at first sight that we have a case of endogenous cell formation. I see no reason to suppose that the eggs examined are abnormal, and I conclude that we rather have in this species a remarkable modification of the usual indirect cell division, attended by an equally remarkable degeneration of nuclear material.

In the last stage obtained (Fig. 29) the whole egg is filled with several hundred very large elements, which are descended more or less directly from some of the nuclear bodies just considered, but the intermediate stages have not been traced. This probably corresponds to stage VI of *A. saulcyi*, at the period just before invagination, but it is quite unlike anything which I have seen in other species. The yolk is now irregularly segmented into blocks or balls, but probably not with reference to these cells.

This case is interesting when we compare it with the degeneration of cells to be described in another section, and from a cytological point of view it deserves careful study.

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* In single sections the nucleus is strictly central, but whether it is so with respect to the entire egg it is not easy to determine. Minot states that the egg nucleus is always eccentric.—*Am. Naturalist*, Vol. XXIII, 1889.

IV.—THE DEVELOPMENT OF THE EMBRYO.

STAGE I.—SEGMENTATION TO FORMATION OF THE BLASTODERM.

These observations relate to *Alpheus heterochelis* of the Southern States, to a Bahaman form which hatches as a zoëa but which otherwise resembles this species very closely, and to *Alpheus saulcyi*, also the from Bahamas, which has large eggs and a nearly direct development. Except where it is necessary to mention specific differences, these three species will be treated as one form.

In June two Alphei (*A. saulcyi*) laid eggs in an aquarium, but the ova were in each case unfertilized, and for the most part failed to adhere to the swimmerets. One of these eggs, hardened at an interval of five hours after it was laid, is shown in section on Pl. XXVII, Fig. 17. I regard the nucleus of this egg as the female pronucleus. It consists of clear protoplasm, which stains feebly and sends out processes on all sides into the yolk, and of an indefinite chromatin network suspended in it. The massive yolk is composed of corpuscles of uniform size, excepting at the periphery where they are much smaller. Numerous small lacunæ occur, representing parts of the yolk which were soluble in the reagents employed. The chorion, or inner egg-membrane, is transparent, tough, and very distensible. It frequently splits into thin layers when subjected to the hardening and embedding process, thus showing the manner in which it is formed in the egg-follicle. It thus appears that the unfertilized egg of Alpheus is incapable of segmentation.

The first segmentation nucleus has been observed in a few cases. That shown in Fig. 16 is possibly preparing for division. It possesses a fine reticulum; it is lenticular in shape, and granular in appearance, and is surrounded by protoplasm which spreads into the yolk. The once divided nucleus and the next phase with four cells were not obtained in Alpheus, but the latter was seen in an allied prawn (*Pontonia domestica*), and is shown in Fig. 27. One of the three cells present is in the aster stage of karyokinesis and has a well-marked equatorial plate. The third segmentation phase is illustrated in Figs. 9, 28, and 30. In the section through the entire egg, three of the eight cells present are met with, and one of these (x) is shown with greater detail in Fig. 30. A cell in process of division is represented in Fig. 28. In another egg with eight cells present, two are undergoing division in different planes. As before, the cells consist of a chromatin network of various shapes surrounded by a clear protoplasmic body, which sends out processes between the surrounding yolk spheres. It is important to notice that the products of the segmentation of the first nucleus pass gradually and uniformly to the surface of the egg. At this stage they have not reached the surface but are visible through the egg shell. The yolk in these specimens consists of spherules or angular blocks (Fig. 28, Y. S.), which are largest in the center of the egg, and contain very few vacuoles.

The fourth phase of segmentation is attended by the cleavage of the superficial parts of the yolk (Fig. 10) around the nuclei, thus giving rise to sixteen blastomeres or partial yolk pyramids. The division of the yolk proceeds but a short distance below the level of the nuclei, so that all the yolk-pyramids open by their inner ends into the common yolk mass which fills the segmentation cavity of the egg. The base of the pyramid, which abuts on the surface is polygonal in shape, and at its middle point some distance below the surface, the nucleus is seen with its investments of protoplasm. The nucleus is large and granular, and the protoplasm which surrounds it reaches out on all sides into the yolk. We may look upon the yolk pyramid as a cell in the strict morphological sense, its protoplasm being concentrated about the nucleus. The blastoderm or primitive egg envelope arises through the multiplication and consequent reduction in size of these huge yolk elements. The surface has then the usual appearance of a fine mosaic of hexagonal plates or cells, the nuclei and surrounding protoplasm of which lie at the surface.

The fifth segmentation phase is shown in Figs. 15 and 31. The septum between the pyramids extends farther into the yolk, while the nuclei are slightly nearer the surface, and the long axis of each is parallel with it. This particular egg was taken in a period of "rest," but in others the nuclei are in karyokinesis, the division being always radial or in a plane at right angles to a surface tangent.

The segmenting egg of *Hippa talpoides* is shown in Fig. 1 (32-cell stage), and a section of a later phase in Fig. 4. The egg appears to have undergone a total segmentation when seen from the surface, but this is not quite so marked as represented in the sketch. The yolk pyramids

(Fig. 4, Y. P.) agree with those in Alpheus and are probably formed in a similar way. In *Palæmonetes vulgaris* the history of segmentation appears to be essentially the same. The nucleus and base of one of the yolk pyramids of this form is shown in Fig. 24. Here we see that the perinuclear protoplasm has a rayed appearance, being produced in all directions into very delicate threads which ramify among the yolk spherules. Some of these threads moreover unite with a thin septum (Sep.) which forms the boundary wall between two adjacent yolk pyramids.

Segmentation proceeds with a regular rhythm up to the fifth stage, but beyond this it soon becomes irregular. A blastula is thus formed, consisting of a single layer of cells or *blastoderm*, and the inclosed central yolk. All the nuclei reach the surface and take part in forming the blastoderm, so that all the protoplasm of the egg which is at first central or internal, comes gradually to assume in the course of segmentation an external position with respect to the food yolk. The blastodermic cell is the direct descendant of the yolk pyramid. It is improbable that the yolk contains any active protoplasm, excepting that which radiates from the nuclei, and which is descended from the perinuclear protoplasm of the first segmentation nucleus.

STAGE II.—THE BLASTODERM AND INVAGINATION.

The prawn when discovered with eggs in the fifth stage of segmentation (Fig. 15) was kept in an aquarium, and the ova were preserved at intervals of several hours. Thus it has been possible to follow the changes which take place between segmentation and invagination with considerable detail.

The egg represented in Fig. 47 is about 15 hours older than last described (Fig. 15). Cell division, which is now irregular, has become accelerated over a part of the egg so that a germinal area or disk (G. D.) representing the future embryo is formed. The side of the egg shown in Fig. 47 corresponds to that occupied by the germinal disk. In reverse view there are much fewer nuclei. The egg has thus lost its radial symmetry and become two sided. Invagination soon follows this stage at a certain point in the germinal area (G. D.). The superficial cells of the blastoderm (Fig. 48) are about one-third their former size, but they still have the characteristics of the yolk pyramids. The cell is polygonal in surface views; the nucleus is surrounded by yolk and the cleavage planes between adjacent cells (Fig. 38, Sep.) are still present.

This stage is characterized by the passage of large numbers of cells from the surface to the central parts of the egg just before the invagination takes place. This process is well illustrated by a series of consecutive sections (Figs. 38–44) taken from the same egg. In all these sections the cleavage of the yolk can still be seen. Many of the blastoderm cells (Fig. 39, a.) are in different phases of division, the dividing plane being always perpendicular to a surface tangent. It is probable, therefore, that the nuclei with their perinuclear protoplasm, leave the yolk pyramid and pass by amœboid movement into the interior. It is, therefore, evident that while morphologically the yolk pyramid is a cell, the elements which pass into the egg have also the value of cells in a physiological sense. Six nuclei are met with in Fig. 38, one of which has wandered some distance from the surface. In the next (Fig. 39) two cells (a. a^1.) are in the aster phase of division; one (a^2) has passed just below the surface, and another (a^3) is near the center of the egg. These cells (a, a^2, a^3,) are sectioned again in the following figure (Fig. 40). Various phases of the process of migration* are seen in other members of this series. In an enlarged portion of a similar section (Fig. 37) several cells are met with, some at the surface just beneath the shell, and others at some distance below it. The protoplasm about the nucleus has no definite bounds, and is often filled with fine particles of food yolk. It is thus evident that these cells feed essentially like amœbæ, by taking the food directly into the protoplasm of the cell.

The critical stage at which cells begin to pass from the superficial to the central parts of the yolk was obtained in an egg just thirteen hours older than the fifth segmentation phase, shown in Fig. 15. There are about a dozen yolk cells in this egg, and one of these is in karyokinesis. The remainder lie very near the surface, but for the most part are separated from it by a thin layer of yolk spheres. It is thus clear that the migration of cells to the central parts of the egg begins

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* In the lobster the primary yolk cells arise by delamination, and as suggested in Section V, this is possibly true of Alpheus.

before all the protoplasm, that is, the nuclei and perinuclear protoplasm of the yolk pyramids, has reached the surface. In the slightly older phase, shown in Pl. xxx, Fig. 46, all the protoplasm which does not pass inward is strictly superficial. The yolk has the same appearance as in previous stages, and, as already noticed, the cleavage planes (Sep.) between yolk pyramids are still met with. Very soon, however, the central portion of the yolk segments into balls or angular blocks (Fig. 46, Y. B.), apparently with reference to these wandering cells. A section through the germinal disk of an egg seven and one-half hours older than that shown in Fig. 47 is given in Fig. 57. The cells in the area of the germinal disk are quite closely crowded, and the superficial segmentation of the yolk is still apparent. We now have a primitive epiblast, or external layer of cells, and a primitive hypoblast, composed of yolk cells which have migrated from the blastoderm.

The invagination stage immediately follows that last described (Pl. xxxi). A slight depression occurs at a point on one side of the germinal disk, where the cells are multiplying most rapidly, and numerous cells pass downward into the yolk. The invagination is nearly solid, and the segmentation cavity is still filled with the great mass of yolk and with primitive hypoblast. In the crayfish (*Astacus fluviatilis*) the invaginate cavity becomes a closed chamber within the yolk (54), and this is eventually converted into the midgut, but in most decapods the pit is very small and the mesenteron is formed independently at a later period. A line drawn through the pit and the middle of the germinal disk marks the long axis of the embryo, and the point of ingrowth is at the posterior end.

.   The structure of the embryo is illustrated by a series of transverse sections (Pl. xxxi). The cells in the center of the egg represent the primitive hypoblast or yolk cells. The nuclei are large and granular, and sometimes occupy the center of a yolk ball. In Fig. 49 the posterior edge of the embryo is sectioned, and the three following sections (Figs. 50–53) pass through the region corresponding to the invaginate area (Ig.). Fig. 52 represents the entire section, of which Fig. 51 is a part. The pyramidal cells, which form the floor of the depression, contain at their peripheral ends no unabsorbed yolk, but at the deeper ends of the cell, below the level of the nucleus, the cell boundaries are lost, and the protoplasm of the cell blends off into the yolk and ingulfs its finely divided particles (Fig. 50). Numerous cells (Figs. 52–54, b, b¹⁵) have already wandered from the point of invagination into the egg and a considerable distance forward under the germinal disk (Fig. 54, G. D.). These cells are more or less intimately united by pseudopodal extensions of the protoplasm. A coarse reticulum is thus formed, the meshes of which are filled with yolk. In front of the invaginate cells, the germinal disk (Fig. 55, G. D.) is still one cell thick. At the close of the invagination stage the primitive hypoblast has received a considerable accession of wandering cells. This stage is usually described as the "egg-gastrula," in accordance with the theory that it represents an ancestral condition, and that the cavity formed at the surface is the remnant of the primitive digestive tract. The discovery of delamination, the actual separation of the inner ends of the cells of the blastula by karyokinesis before any invagination occurs, as I have described in the lobster, and the occurrence of this or of multipolar emigration in Alpheus, together with the fact that in the typical decapod the invagination has no direct relation to the digestive tract or to to the mouth and anus, point to the view already expressed in a preliminary paper upon the lobster (23), that the invagination stage has no reference to an ancestral invaginate gastrula. It seems to me more probable that the egg with primary yolk cells corresponds to the cœlenterate planula stage, and that these yolk cells, which originate from the blastula and which partially or entirely degenerate, represent the remains of a primitive hypoblast. According to this view the invagination is a secondary process, which became so indelibly impressed upon the ancestors of the Decapods that it has remained in the ontogeny of present forms. The conditions which are found in the crayfish can not be regarded as in any sense general or typical.

STAGE III.—OPTIC DISKS AND VENTRAL PLATE FORMED.

This stage (Fig. 58) is characterized by a thickening of epiblast which gives rise to the thoracic-abdominal or ventral plate in front of and around the point of ingrowth, by the simultaneous spreading of invaginate cells below the surface, and by the appearance of the optic disks (O. D.),

two patches of ectoblast on either side of the middle line in front of the ventral plate. When the living egg is examined by reflected light these structures appear as misty white patches separate from each other. (See Fig. 2.)

The principal cell mass is the thoracic-abdominal plate (Fig. 58, Ab. P.), from which the thoracic-abdominal process is developed. The position of the pit (Ig.) is faintly marked by the arrangement of the cells at that point. The optic disks are due to the rapid multiplication of epiblastic cells around definite centers. Each is joined to the ventral plate by a lateral band or cord of cells (L. Cd.), on which the appendages are subsequently budded off. A transverse cord (T. Cd.) soon bridges over the space between the optic disks, thus inclosing a triangular area, which corresponds largely to the sternal region of the adult. The extension of the invaginate cells below the surface is only partially indicated by the shaded nuclei. They advance forward and backward from the point of ingrowth, but principally upward, that is, toward the center of the egg, along the lines joining the optic disks to the ventral plate (Figs. 59, 60). The embryo covers nearly one hemisphere of the egg. It is V-shaped, but the angle between the arms of the V varies much in different eggs. There is a marked contraction of the embryo which takes place immediately after this phase, that is, the area of the surface occupied by the embryo becomes appreciably smaller. A similar contraction of the embryo has been observed in Astacus (54) and Crangon (31). With the extension of the epidermis there has been a corresponding activity among the wandering cells. Their relations are well shown by sections through the entire egg (Figs. 56, 59, 60), in which we can still distinguish the primary yolk cells (P. Y. C.) from the cells derived from the invagination (S. Y. C.). The cells of the first have large, granular nuclei and send out processes into the yolk. The others are smaller and are probably multiplying more rapidly. It soon becomes impossible to find any distinction between these wandering cells. The yolk is irregularly segmented into balls (Figs. 60, 63, Y. B.), inside of which the migrating cells are usually found. The epiblastic cells of the surface, which are the direct descendants of the yolk pyramids, have definite boundaries, but some of the cells of the ventral plate (Pl. IX, Figs. 61, 63) tend to form a syncytium, as already seen, while the wandering cells are independent, free-moving elements.

The lateral section (Fig. 56) passes through the outer edge of the ventral plate, and the next toward the middle line (Fig. 60) encounters a sheet of wandering cells. We see at a glance that the migrating cells pervade the greater part of the egg, and that they pass out in all directions from the region of the ventral plate (Ab. P.). Fig. 59 represents a median longitudinal section through the embryo and entire egg, and Fig. 63 a part of a section highly magnified through the ventral plate and region of ingrowth. The cells immediately below the surface (S. Y. C.) are characterized by large and very granular nuclei, which stain with much less intensity than the superficial epiblast. This shows that they are multiplying rapidly, and the finely divided yolk in their neighborhood shows also that the cell protoplasm is rapidly absorbing food. A series of transverse sections of this embryo is given in Pl. XXXIII. The plane of section in Fig. 61 is oblique and passes in a posterior direction. In Fig. 62 the lateral cords (L. Cd.) are crossed and numerous wandering cells are encountered, while anterior to this (Figs. 68, 69) the optic disks are cut. The optic disks (Figs. 64–67) consist of a single layer of epiblast. Their cells are flat and polygonal, cell boundaries are distinct, and the long axis of the oval nucleus is parallel with the surface. When the cell divides this position is reversed, the plane of division being perpendicular to a tangent at the surface. From the optic disk the eye and its ganglia are developed.

STAGE IV.—THICKENING OF THE OPTIC DISKS AND RUDIMENTS OF THE APPENDAGES.

An embryo a few hours older than the last described is shown in Fig. 72. On the thickened cords of cells (L. Cd.) uniting the optic disks to the ventral plate the traces of two pairs of appendages can be made out—the first pair of antennae A (1.), and, close to the ventral plate, the mandibles (Md.). Some of the central cells (C. M.) of the optic disk have large, granular nuclei. These mark the area of most active cell division, and form an ingrowth or thickening, which is the rudiment of the optic ganglion.

Glancing at a series of longitudinal sections through this egg (Figs. 70–71, 73–75), we notice

several important changes since the last stage. The ventral plate is more extensive and the wandering cells are more numerous. The primary and secondary wandering cells can no longer be distinguished, but all the cells within the yolk are similar in character. They have large, granular nuclei, and multiply by ordinary karyokinesis (Fig. 75, Y. C²). Some pass forward underneath the embryo (Fig. 74, Y. C.) and to other parts of the egg. In Fig. 71 two yolk elements are found near the lateral cord, and in Fig. 70 one is seen just under the optic disk. In Fig. 75 the section is median and corresponds closely with the similar longitudinal section of the last stage (Fig. 59.). The transverse cord (T. Cd.) is seen to consist of a single layer of flat epiblastic cells.

The structure of the ventral plate is shown in detail in Fig. 85, which is a section just in front of the point of invagination. This illustrates the character of the syncytium beneath the surface of the plate and the fine degree of fragmentation which the yolk suffers in the presence of the cell protoplasm. At the surface, the cell walls are quite distinct, as already seen, but as soon as the cells pass below it, the protoplasm extends itself in pseudopodia-like processes and incloses particles of yolk. Under these favorable conditions of nourishment these elements, which must be regarded as the mother cells of the mesoderm and the endoderm, multiply rapidly and spread to all parts of the egg. If this section is compared with that of the invaginate stage (Fig. 54), and with a similar section of Stage III (Fig. 61), it is easy to understand the relations of the ventral plate to the wandering cells, and the way in which the thickening of the plate is brought about. At the second stage comparatively few cells take part in the invagination, and the most of these pass directly into the yolk. But, almost simultaneously with this migration of cells there occurs a migration of cells from the surface of the ventral plate. Thus this becomes thickened and cells continue to be supplied to the yolk. This thickening of the plate is possibly due to cell division in both planes; that is, to delamination and emigration. (Compare cells EC, EC¹⁻³, Fig. 85.)

The process by which the optic disk becomes thickened at this stage is quite similar, although there is no true invagination concerned in it. This is shown by a series of connective sections (Figs. 76–83) passing through the entire disk. The anterior rim of the disk is cut in Fig. 76, and in Fig. 83 the rudiment of the first antenna. This thickening is mainly the result of the migration of epiblastic cells from the surface. After leaving the surface, the cell wall usually becomes indefinite. The relations of the optic disks to the entire egg are seen in Fig. 84. The central yolk is segmented as shown in Fig. 74, and a yolk cell usually lies within the segment.

STAGE V.—RUDIMENTS OF THREE PAIRS OF APPENDAGES—CELL DEGENERATION.

The embryo represented in Fig. 93 is, approximately, three days old (temperature at Nassau 78–80° F.). It occupies nearly one entire hemisphere of the egg, the opposite side of which is covered with flat epithelial cells like those seen at the periphery of the figure. The shape of the embryo proper is nearly that of an equilateral triangle, one angle of which corresponds to the ventral plate, and the other two to the optic disks. A line drawn through the first of these angles and the middle of the opposite side would therefore correspond with the longitudinal median axis of the embryo.

The rudiments of the second pair of antennæ, A (II), have now appeared, and we therefore have present at this stage buds of three pairs of appendages, namely, the first and second pairs of antennæ and the mandibles. All are developed nearly simultaneously, but the second pair of antennæ seem to lag a little behind the rest. In respect to the order of appearance of these appendages, allied species of Crustacea differ slightly. The central parts of the ventral plate (Ab. P.) and optic disks (C. M.) are areas of rapid cell division, and are characterized by the presence of large granular nuclei and by the irregular arrangement of the cells. In all other parts of the egg the superficial cells form a uniform stratum one cell deep. This irregularity is due to the gradual migration from the surface of individual cells in these three places. The first pair of antennæ are closely associated with the optic disks, and the mandibles abut against the ventral plate on either side of the middle line. The appendages start on the lateral cords from definite centers of cell division, and the cells tend to assume a radial and concentric arrangement around each center.

The space between the optic disks is now completely bridged over by a sheet of closely

crowded cells (T. Cd.), and the backward extension of this, and the approximation of the lateral cords has quite closed over the central or sternal region of this part of the embryo (St. A.). Cell outlines are very distinct at the surface in preparations, and they are sometimes well defined in cells which have passed from the surface to parts below it, in both the region of the optic disk and that of the ventral plate (Fig. 80, Ec.), but elements closely associated with yolk are usually amœboid. The nucleus of the epiblastic or epithelial cell on the confines of the embryo, or on the extra-embryonic surface of the egg, has the shape of a flattened, round, or oval disk. Epiblastic nuclei in the appendages and other parts of the embryo, where there is rapid cell division, are angular in consequence of crowding, and deep-lying nuclei are generally spherical.

The arrangement of the embryonic cells of the superficial epiblast in beautiful curves and rings around definite centers—orthogonic systems of curves—is not nearly so pronounced as in the embryo crayfish (*Astacus fluviatilis*), according to the delineations of Reichenbach and Winter. Reichenbach states that in the crayfish the superficial embryonic cells multiply about a given center, like that of the "head fold" (optic disk), or "thoracic abdominal rudiment," according to definite laws. This was discovered by Sachs in the growing tips of plants. According to Sachs, Reichenbach, and others, the cell nuclei always divide in one of two opposite planes; that is, they either separate along a radius drawn from a given center, thus giving rise to radial strings of cells, or in a plane at right angles to this, producing new strings. Thus there is developed about the initial cell a series of concentric circles and radiating lines of cells. The positions of the equatorial plates of dividing nuclei, which some eggs of Alpheus show in abundance, do not indicate the prevalence of such a law in the earlier stages. The early embryo of Alpheus is much less diffuse than in the crayfish, and the different cell groups soon impinge on each other, and their relations are disturbed.

Several transitional stages between the last two embryos figured (Figs. 72 and 93) will now be examined. The first is represented by three longitudinal sections (Pl. XXXVI, Figs. 88–90), and is about seventy hours old. It is from the same prawn as the segmented egg shown in Pl. XXVII, Fig. 15. These sections give some interesting facts with reference to the rôle of the wandering cells. The first (Fig. 88), which is nearly median, cuts the ventral plate and below it the cells which are migrating from it into the yolk. A continuous layer of cells extends anteriorly to the transverse cord (T. Cd.). In this region a wandering, mesoblastic cell (Y. C.) is nearly in contact with the superficial epiblast. The next section touches the outer edge of the ventral plate (Fig. 89), which is marked by large granular nuclei, and crosses the lateral cord and rudiments of the appendages (A. I, A. II, Md.). The folds of the latter arise through the ingrowth of superficial cells. Here another cell (Y. C.[1]) is close to the outer surface of embryo; another (Y. C.[2]) is in a distant part of the egg and is in the aster stage of karyokinesis; others still (Y. C.[3]) have wandered in a diametrically opposite direction. In Fig. 90 we see still more of these wandering cells, in this instance, chiefly above the embryo.

In the middle of the optic disk some of the large granular cells visible from the surface (Fig. 93, C. M.), are met with, and one of them (Fig. 90, Ec. dotted line extended) has just passed below it.

Figs. 86 and 87 are parts of longitudinal sections of an embryo six hours older than the last. The first exposes the optic disk (O. D.) and gives evidence of the further increase of the latter by the emigration of cells from the surface, and it is quite probable that some of the wandering, mesoblastic cells (Y. C.) have already attached themselves to it. (Compare Fig. 90.) In the next (Fig. 87) the inner edge of the optic disk (O. D.) and the outer border of the ventral plate (Ab. P.) are involved. Here the epiblast consists for the most part of a single layer of cells. Two large wandering elements (Y. C.[1]) are in contact with the surface cells of the embryo in the neighborhood of the appendages.

Fig. 91 is from an embryo twelve hours older than the last. The plane of section passes obliquely through the optic disk, cutting the anterior half of one (to the left) and the posterior part of the other. A study of this section and of the series to which it belongs, shows us beyond a doubt what is the fate of large numbers of wandering cells, present at this time. As has been already shown by preceding figures (see Figs. 73, 88, and others), the cell mass constituting the thoracic-abdominal plate is now the principal source of the wandering yolk elements, and, as has been also shown, they migrate into all parts of the egg, multiply by karyokinesis, and settle

upon the optic disks, the bases of the appendages, and other parts of the embryo. They also pass to the extra-embryonic surface of the egg. In Fig. 91 one of these wandering cells (Y. C.) is approaching the surface, while another (Y. C.[1]) nearly touches it; and in Pl. xxix, Fig. 34, which represents a portion of a section from a later series (Fig. 106) greatly enlarged, we find two yolk elements (Y. C.) quite at the surface. They are triangular in outline, one of the flattened sides being applied to the surface of the egg. Histologically their nuclei are more granular and stain with less intensity than the nucleus of the ordinary epiblastic cell (Ep.), which appears spindle-shaped in vertical section. But between a cell like that seen in Fig. 91 (Y. C.[1]), where the long axis of the nucleus is at right angles to the surface, or cells like those shown in Fig. 34, where the nucleus is flattened against it and the ordinary epiblastic cell, a variety of transitional phases can be found. This is most clearly illustrated in the next stage.

The egg already described (Fig. 93) shows some important changes. The structure of the optic disks and ventral plate is readily seen in the transverse (Figs. 92, 94, 95) and lateral longitudinal sections (Figs. 96, 97). The optic disk, which in stage iii consisted of a single stratum of cells, (Fig. 69), is now a thick cell-mass two-thirds the size of the ventral plate. In it we still distinguish a small area of cells with large granular nuclei (Fig. 93, C. M.), which, as we see in Figs. 96, 97, C. M., O. D., is clearly differentiated. It occupies a position just without (or external with respect to the longitudinal median axis) the center of the disk. The nuclei of surrounding cells are not more than half their size. These large cells do not all lie at the surface, but form a solid mass extending into the yolk. The evidence of karyokinetic figures shows that these cells are dividing, and usually in planes perpendicular to the surface. This results in the crowding of the cells, and also in their migration from the surface to parts below it.

In Fig. 90 there is a cell (ec.) whose nucleus has sunk below the level of the surrounding cells, but the cell protoplasm still reaches up to the surface. Such cases render one cautious in pronouncing positively upon the emigration of cells, but sections like that given in Fig. 94, and the fact that cell divisions seem to be for the most part in one plane, convince me that the thickening is partly, if not largely, due to this cause. In Fig. 95, a large cell, the polar star of which is just below the surface, is delaminating. Cases of this kind were rarely noticed, but were observed at a later stage (Pl. xxxix, Fig. 102, ec.). That wandering cells attach themselves to the optic disk, there is little doubt. They can be traced in all stages of progress from the region of the ventral plate to the neighborhood of the disk (Fig. 90, Y. C.) until they finally come in contact with it.

The thickening of the optic disk described in Stage iii (Pl. xxxiii, Fig. 69), is therefore effected: (1) partly, perhaps largely, by emigration of cells from the surface; (2) partly by delamination; (3) by the accession of wandering cells; (4) by the indirect cell division of the elements constituting the deeper part of the disk.

Chromatin grains make their appearance somewhat abruptly at this stage (Fig. 96, S.[1-2]) and they serve to explain in some degree the peculiar granular nature of nuclei in earlier stages. They originate by the degeneration of cells in the ventral plate and in other parts of the embryo, and probably correspond to what Reichenbach has called in the crayfish "secondary mesoderm cells." Their history has been fully traced and will be discussed in Section vi.

The structure of the ventral plate (Fig. 92) resembles that of an earlier stage (Fig. 85) with the difference that the nuclei are considerably larger and contain from one to several large sporelike masses of chromatin. This cell mass has not increased in bulk at a rate corresponding with the growth of other parts, since elements are being continually subtracted from it and added to the yolk. This loss on the part of the ventral plate is made good not only by cell divisions, but also by continued emigration from the surface (Fig. 98, Ab.).

An embryo six hours older than the last is represented by three longitudinal sections (Figs. 98–100). The optic disks resemble in size and general shape the three pairs of rudimentary limbs. The abdominal fold is not yet formed and the labrum is undeveloped. The stomodæum (Fig. 98, Std.) is just making its appearance as a slight invagination of epiblast on the middle line between the first pair of antennæ. The number of chromatin balls (S) and degenerating cells (S. C.) has greatly increased. We see them in all parts of the embryo. Sporelike nucleoli are seen in cells of the epiblast and are confined to no part of the embryo, but they are most characteristic of the ventral plate and optic disks.

In Fig. 98 several independent chromatin balls (S) are seen in the yolk, and the granular cells of the ventral plate are very marked. A large nucleus of one of the cells (ec.), which contains several sporelike bodies, is very irregular in shape, owing to the pressure to which it is subjected, and it has evidently been crowded down from a level nearer the surface. The cell protoplasm, however, shows that it still belongs to the surface tier of cells. This is also true of the small lenticular nucleus next it on its anterior side. Just anterior to this cell is another (Ee.¹) which is in the act of dividing in the usual way. It seems probable that had this division been effected one or more of the adjacent cells must have been crowded quite below the surface. It is difficult, however, to always determine whether cells whose nuclei are a considerable distance below the surface do not send up stands of protoplasm to meet it. We find in the ventral plate, independent cells multiplying by karyokinesis, and, as evidences of delamination in this region are rare or altogether wanting, we are convinced that, as in the case of the optic disks, this thickening is largely due to the migration of cells from the surface.

There is at this stage a fairly well-defined sheet of cells (Figs. 99, 100, Mes.) extending forward from the ventral plate on either side. The nuclei are oval or elongated, and their long axes are parallel with the surface, that is, at right angles to the major axes of the superficial epiblast cells. This layer of cells is most marked at the bases of the appendages (Fig. 100, Mes.) and extends from the optic disk on either side to the ventral plate. The question of the origin of these cells is not difficult. They are wandering cells which have settled down on these parts of the embryo. They form a part of the future mesoblastic tissues; exactly what part they play will be discussed later on. They multiply by indirect division and extend into the folds of the appendages, while some, on the other hand, degenerate.

STAGE VI.—THE EGG-NAUPLIUS.

The fully developed egg-nauplius is represented in Fig. 111, but before this condition is reached there are several intermediate stages to be considered. A series of longitudinal sections (Pl. XXXIX, Figs. 101–105) illustrates the structure of an embryo twelve and a half hours older than the one last described. The thoracic-abdominal fold (Fig. 104, Ab.) can now be recognized, and the stomodæum (Fig. 105, Std.) has the form of a straight, narrow tube, between the buds of the first and second pairs of antennæ. The space between these two structures is filled with yolk fragments, among which are scattered, numerous chromatin particles (S) and cells derived from the thoracic-abdominal fold. The epiblast of the sternal region (Fig. 105, 98, St. A.) is no longer a simple layer, but is slightly thickened. This thickening seems to be partly due to rapid cell division in one plane. The cell nuclei are elongated or wedge-shaped and stand perpendicular to the surface. As will be seen later it is also due to the accession of wandering, mesoblastic cells.

The stomodæum is a relatively long straight tube with very slight lumen, and is surrounded with chromatin grains and scattered cells. It is formed at a considerable distance in front of the point of invagination, and one to two days earlier than the proctodæum.

The thoracic-abdominal fold seems to arise by the sinking down of the epiblast along a definite line. There is thus formed a narrow transverse pocket (Fig. 106, Ab. C.), which is quite deep and perpendicular with the surface. Numerous cells continue to pass from the thoracic-abdominal fold to various parts of the embryo, and to join the sheets of cells (Fig. 103, Mes.) already mentioned. In Fig. 103 the four segments of the embryo are well shown. This section crosses the optic disc (O. G.), the buds of the three appendages, and the edge of the thoracic-abdominal fold. The sheet of mesoblastic cells (Mes.) is most marked opposite the folds of the appendages.

The optic disks are now large masses of cells united by a transverse cord which is thickened slightly on the middle line. In Fig. 102, three cells are met in karyokinesis, one in the abdominal area and two side by side in the optic disks. The former exemplifies the common method of cell division, while the latter is a good example of the less common delamination. As has been already seen, karyokinetic figures of dividing cells are commonly met with in Alpheus at all stages, excepting the species *Alpheus minor*, where the division is at first probably direct. I have seen nuclear figures at the yolk segmentation stage of *Crangon*, also in *Hippa*, *Pontonia* and *Homarus*, and Reichenbach found them in abundance in *Astacus*. Indirect cell division is undoubtedly the rule in

the developing eggs of the Crustacea and probably of all the Metazoa.   Since we often study only the rapidly achieved result, the phases of nuclear division may be easily missed.

Fig. 106 is a median longitudinal section of an embryo preserved a few hours later than the last. This shows the thoracic-abdominal fold and cleft (Ab. Ab. C.) previously referred to. The sternal area between the latter and the stomodæum now lies next the egg shell, but soon changes its position (Fig. 125, St. A.), owing to the forward growth of the thoracic-abdominal fold. The labrum, here undeveloped, soon grows backward toward the latter, helping to bend the œsophageal tube and probably slightly altering the position of the mouth (Fig. 125).

The proctodæum arises as a solid invagination of the epiblast, at a considerable distance behind the abdominal cleft (Fig. 106, Pd.), in a stage intermediate between the embryos represented by Figs. 105, 106.   A transverse section through the point of invagination is shown in Fig. 126, Pd.

The relation of the embryo to the rest of the egg can be seen in Fig. 108, which belongs to the same species as Fig. 106.   Besides the shell, which is unnaturally distended, the egg is surrounded by a delicate embryonic membrane (Mb.).   This membrane is secreted early by the superficial epiblast, as shown by the fact that it does not conform with the thoracic-abdominal fold.

Wandering cells (Fig. 108, Y. C.) become gradually less abundant, but still continue to pass to the outer surface of the egg next the epiblast.   The transition from the wandering, amœboid cell to the flattened mesoblast cell, lying close to the surface, can be best followed at this stage.

The fully developed egg-nauplius (Fig. 111) is about a week old.   Embryos from the same prawn vary slightly in size and in the degree of development, and also in the general character of the cells.   In some, the cells are larger and fewer in number, in others they are smaller and much more numerous.   The embryo is usually at one pole of the oblong egg.   That represented in Fig. 111 is about one-eightieth inch long, and if the entire end of the egg were shown the drawing would be nearly twice as large.

The relation of the embryo to the whole egg can be determined from Fig. 127, where the plane of section is through the long axis of the egg, but through the short axis of the embryo.   In the course of development the egg increases appreciably in size and also changes its shape, at first being spherical, but gradually becoming oblong.   At this period the long axis of the embryo (using this term to apply to the more obvious embryonic tissues of the egg) is parallel with the short axis of the egg, while in the course of growth the embryo spreads over one side of the egg, until its long axis coincides with that of the latter.

The optic disks have become large oval masses of cells which project from the surface, and may now, for the first time, be appropriately called *lobes*.   They represent the eye and eyestalk. The blocks of cells (S. O. G.) in intimate relation with the optic lobes are the ganglia of the antennæ, and represent a large part of the future brain.   The appendages are all simple, but a bud soon grows out from the posterior sides of the second pair of antennæ.

The right antenna is already bifid near its tip.   A little later it has the appearance shown in Figs. 109 and 110.   Rudiments of the first pair of maxillæ (Mx. I.) are also present.   The ganglia of the second pair of antennæ are developed in close union with the ganglia of the antennules. Together they form the supra-œsophageal ganglion or "brain."   The stomodæum (Std.) appears from the surface as a distinct mass of cells extending behind the labrum (Lb.).

The thoracic abdominal fold, at first vertical to the surface, bends up and grows forward toward the labrum, and a shallow groove which marks the median notch of the telson plate (Fig. 110) is formed at its extremity.   The anus passes forward (backward in a morphological sense) from its dorsal position through the median notch until, at a considerably later period, it comes to lie on the ventral side of the fold near its apex.   The mass of cells (H.) behind the anus probably represents the heart.   Near the mandibles and maxillæ, cells are seen with large granular nuclei. These are cells which have migrated from the yolk to this part of the embryo.   Nuclei of epithelial cells are sprinkled over the entire surface of the egg, but increase in number as we approach the embryo.

The section through the entire egg (Fig. 127) shows some of the general characteristics of the egg-nauplius.   The thoracic abdominal fold is here cut on a level with the anus, and lies in a wide shallow groove.   The yolk is composed of irregular blocks, only a few of which are represented, and contains numerous wandering cells.   Some of these (Y. C.²) are settling down on the ventral nervous

plate, while others (Y. C. Y. C.[1]) have wandered far and wide through the yolk. The embryo is raised considerably above the general surface of the egg and the shell more closely invests the egg than shown in the drawing. The embryonic membrane is not represented.

Fig. 125 is a nearly median longitudinal section, and shows the relations of the thoracic-abdominal fold, the œsophagus, and the ventral or sternal surface between them. The loose and irregular arrangement of cells immediately below the surface is most marked, and also the granular nature of the nuclei which is such a constant character. Numerous degenerating cells (S. S. C.) are seen near the œsophagus, and amœbiform cells can be traced from the thoracic abdominal fold to the surface immediately behind it.

The structure of this embryo is illustrated more completely by a series of transverse sections (Figs. 114–124), the first two of which (Pl. XLI, Figs. 114, 115) traverse the optic lobes, and the third cuts the brain. The central mass of large cells which was noticed in the optic disks can no longer be distinguished. The lobe (O. L.) is composed of similar cells with granular nuclei, the superficial tier being somewhat the larger and columnar. In the brain the central cells are smaller and stain more intensely than those at the surface (Fig. 116, S. O. G.). Wandering cells (Y. C.) can be traced in their passage from the yolk to the optic lobes, brain, ventral nervous plate, and other parts of the embryo. Between the lateral halves of the brain there is a shallow median furrow (Fig. 116, M. F.). This is continued backward into the much broader and deeper depression in which the convex ventral side of the abdomen fits (Pl. XLII, M. F.). The three following sections (Figs. 117–119) pass through the œsophagus, and the ventral nerve thickening immediately behind it.

About the œsophagus (Fig. 117, Std.) numerous chromatin balls (S., S. C.) are seen in the yolk, and a mass of cells (Mes.) is met with at the base of the appendage and within its fold. These elements are derived from the wandering cells and must be regarded as mesoblast. The fold of the appendage consists essentially of a single layer of cells. Those elements which enter it undoubtedly go to form the musculature of the limb while the cells of somewhat similar appearance, which are derived from the ectoblast, represent the ganglia and nerves. On either side of the œsophagus the yolk has undergone important physical and chemical changes. The yolk spheres or blocks are full of vacuoles and have a corroded and granular appearance, while in contact with the embryonic cells there is a residue of small refractive granules. These vary considerably in size, and some of them stain lightly in hæmatoxylin and represent the last stages in the degeneration of chromatin. The eroded and altered yolk (A. Y. S.) is represented in many of the sections. Between the œsophagus and bases of the antennæ the yolk is absorbed, leaving a protoplasmic reticulum (Fig. 117, Ret.).

In Fig. 118 the mass of cells representing the mandibular ganglion (Md. G.) is sectioned, and in the following figure, the mandibles themselves (Fig. 119, Md.). Numerous cells, both in this and the following sections, are seen in the course of their migration from the yolk to join the ventral nerve-thickening. The latter, which is the rudiment of the nervous system, is at this stage scarcely thickened at all, on the middle line, below the level of the mandibles. Thus in Fig. 121 the buds of the first maxillæ (Mx. I.) are united by the primitive layer of epiblast. To this a single migrating cell has attached itself on the middle line. Migrating mesoblast cells (Mes.) also pass into the fold of the appendage, and others (Fig. 120, Mes.) take up a position against the epiblast of the body wall. The nuclei of the latter stain intensely and become flat, spindle shape in section, and probably represent the nuclei of muscle cells.

The structure of the abdomen at this stage is shown in Figs. 120–123. The body wall of the dorsal side consists of a single layer of columnar epiblast, while the ventral wall is thickened. The hind gut (Fig. 122, Hg.) is a tube, the wall of which consists of a single layer of cells. It is laterally compressed so that the lumen is hardly appreciable. The intervening cells (Mu.) largely represent the rudimentary flexor and extensor muscles of the abdomen. A comparison of Figs. 123 and 125 shows that cells extend from the thoracic-abdominal fold on all sides into the yolk.

The cells at the surface in Fig. 124 have come mainly from the yolk (H.) and are in the position where the heart is subsequently developed. Cells approaching the surface in this region are very clearly shown in Fig. 125 (Y. C., Y. C.[1]), which is a section through a somewhat younger embryo.

The wandering cells, as we have seen, abound in the parts of the yolk nearest the embryo. The

nuclei have the usual characteristics—irregular shape and granular contents. They are surrounded by a small irregular body of protoplasm which does not readily stain and which is often difficult to observe. In Pl. XXIX, Fig. 33, several of these wandering cells are seen greatly enlarged. Sometimes, as here, the perinuclear protoplasm appears to join that of neighboring cells, but in most cases there appears to be no such connection between them.

The endoderm, though not represented in the drawings, makes its appearance as a distinct cell layer at this time. In an embryo a few hours older than that represented in Fig. 125 the endoderm has the form of a narrow sheet of rather large cells, between the yolk and the rudimentary heart, near the body wall. In the space corresponding to the heart, blood corpuscles can already be detected, besides scattered mesoblastic cells. Both the latter and the entoblast are derived from the wandering cells which come out of the yolk.

STAGE VII.—RUDIMENTS OF SEVEN PAIRS OF APPENDAGES.

Fig. 110 represents a phase intermediate between the egg-nauplius (Fig. 111) and the present stage (Fig. 130), and is of special interest for the light which it throws on the history of the wandering cells. The structure of this embryo is illustrated by Pl. XLIV, and Figs. 136, 137, 144, 145. Fig. 137, which represents a section just behind the base of the first antenna (A. I.), may be compared with Fig. 117. Numerous yolk elements are found in the vicinity of the œsophagus, where, as will be seen (Fig. 134, Mu.), they become speedily converted into muscle cells and somatic mesoblast. In Fig. 136 several wandering cells attached to the body wall, have all the characteristics of blood corpuscles, a deep staining granular nucleus, and a clear irregular cell body. The blood cell and muscle cell are both derived from wandering mesoblastic cells, and in the early stages of their metamorphosis they resemble each other, so that it is not always possible to distinguish them. Undoubted blood cells, however, have already made their appearance.

Figs. 144, 145 show that the yolk is pervaded by a great number of cells. These originated in the way described, chiefly by migration from the ventral plate and thoracic-abdominal fold, and also by subsequent multiplication in the yolk. At this period some of the cells migrate to the pole of the egg opposite the embryo and apparently assist in forming a conspicuous dorsal plate (Dp.). In this embryo they have not quite reached the surface. A structure is eventually formed which reminds one of the "dorsal organs" of various Crustacea. This and the wandering cells will receive further consideration later on.

The embryo of Stage VII is represented in Fig. 130, Pl. XLIV. Figs. 111, 109, 110, and 130 form a consecutive series of embryos, each but a few hours older than the preceding. In the first (Fig. 111) the optic lobes, first and second pair of antennæ, and mandibles are all simple appendages, and are quite similar in general appearance. The abdomen and part of the thorax are represented by a simple fold, the thoracic-abdominal fold. In the second embryo (Fig. 109) the parts are more compact and the second pair of antennæ are forked at their tips. In the third phase (Fig. 110) the optic lobes and abdomen exhibit the most rapid growth. The former are drawn closer together and arch outward from the middle line. The anus is dorsal. The abdomen extends forward until it nearly meets the labrum and has a slight groove or depression at its extremity. All the appendages have assumed a more oblique position with respect to the long axis of the body, and the second antennæ are now the largest.

In the fourth phase (Fig. 130) we see the same changes carried still further. The optic lobes are large convex disks which join each other on the middle line and are intimately united to the brain. The anus is terminal. On at least the first pair of antennæ hairs are developed, although there is not perhaps so marked a contrast between the first and second antennæ in this respect as would appear from the figure. The first and second maxillæ and the first and second maxillipeds are present as rudimentary buds.

The general structure of the embryo (Figs. 129, 131) agrees with that of preceding stage. The embryonic tissues consist of cells of various sizes and shapes, from quite large cells down to particles no larger than the balls of chromatin which are suspended within the nucleus, and from the spherical to the lens-shaped, spindle-shaped, and wedge-shaped forms. Generally all the nuclei agree in containing coarse grains of chromatin or nucleoli. These vary much in size and number in different nuclei according to the condition of the cell. In degenerating nuclei, the chromatin residue is aggregated into fewer and larger masses.

Wandering cells are now scattered throughout the entire egg. They occur in abundance both in proximity to the embryo proper and on the sides of the body walls, and especially in the region immediately behind the thoracic-abdominal fold.

Fig. 131 is a median longitudinal section through an embryo like that shown in Fig. 130. The outer or superficial cells are generally columnar and have distinct boundaries. Their nuclei are spherical, elongate, or wedge-shaped. They divide in both planes, but most commonly in the plane perpendicular to the surface. When we compare this section with the similar one (Fig. 125) of the preceding stage the most striking difference is the great increase in the length of the thoracic-abdominal fold and the ventral thickening of the nervous system. Some of the cells of the latter next the yolk (Mes.) are flattened and spindle-shaped. They have recently come from the yolk and joined the nervous system, and it is possible that these and similar cells represent primitive connective tissue envelopes.

In a more lateral section (Fig. 129) the optic lobe is seen to consist of two portions, a superficial layer of large cells (O. E.) and a deeper layer (G. L.). The first is continuous with the general epiblast over the surface of the body. Its cells multiply in both planes, and some of them pass below to join the deeper layer. The cells of the latter multiply by the usual mitosis and also receive accessions from the yolk. The plane of section passes through the equatorial plate of one of these dividing cells. Some of the cells next the yolk (Mes.) are flattened like those just described in the ventral nervous thickening, but this condition appears to be somewhat transitory. The outer layer of the optic lobe may be regarded as a *retinogen*, since from it, or from a layer corresponding to it, the visual apparatus of the eye is developed, while from the deeper layer or *gangliogen* the optic ganglia of the eyestalk are formed.

A comparison of the transverse sections (Figs. 128, 132–135) with corresponding sections of the previous stage (Figs. 115, 117, 121, 124) shows some interesting changes. The brain is larger and more compact, and some of the cells next the yolk are flattened (Fig. 132, Mes.) and bear a resemblance to muscle or connective tissue cells. They originate from the cells marked Ct. S. in Fig. 116, and come from the yolk. Like the cells already mentioned in the optic lobes and ventral nervous system, they seem to represent a rudimentary perineurium, but, as a well-developed covering of the nervous system is not present until a considerably later stage, they are probably transitory. Fig. 134 corresponds closely with Fig. 117. It shows the section of the œsophagus and of the ganglia of the second antennæ. In the younger stage the ganglion (seen to the left in Fig. 117, at the base of the appendage) is a small, loose mass of cells associated with the surface epiblast, while in the older embryo it is in contact with the wall of the œsophagus, is more compact, and its cells are somewhat differentiated. The central nuclei are smaller and stain most intensely. The œsophagus (Std.) is suspended to the body walls by rudimentary muscles (Mu.), the cells of which are much elongated. They are derived from migrating mesoblastic cells like those seen in the earlier stage (Fig. 117, S. C.), or like the one shown in this figure to the left of the œsophagus. Fig. 137, which is from a stage intermediate between the two just considered, gives additional evidence of this rôle of the wandering cells. Fig. 128 furnishes a very interesting comparison with Fig. 121. In the latter, cells abound in the yolk adjoining the rudiment of the ventral nervous system, which is represented by the primitive epiblast on the middle line. In the older stage scattered mesoblast cells are greatly reduced in number and the ventral thickening is very marked. Cells of recent derivation from the yolk (Mes.) at the base of the appendage can also be distinguished.

In Fig. 133, as in Fig. 124, the plane of section is just behind the thoracic-abdominal fold. Here we recognize a tier or plate of tall, columnar cells (End.), the nuclei of which lie at the deeper ends of the cells or on the side away from the yolk. In the presence of these bodies the food yolk (Fig. 135, A. Y. S.) is absorbed or converted into a granular residue. This layer represents the *entoblast* or the epithelium of the mesenteron already described. Numerous wandering cells are encountered (Figs. 124, Mes.; 135, Y. C.), which take up a peripheral position, and from the first are closely associated with the epithelium of the hindgut. They unite the mesenteron to the hindgut, and it is impossible to say exactly where the one begins and the other ends. Between this entoblastic plate and the surface epiblast (Ect.) numerous cells are interpolated (Figs. 133, 135, Mes.), which are undoubted mesoblast. They are directly continuous with the layer of mesoblast (Fig.

128, *Mu.*) which extends throughout the abdomen between the hindgut and body wall. Mesoblast cells derived from the yolk (Fig. 129, *Mu.*) are also seen underneath the epiblast on either side of the body. The nuclei of these cells stain very deeply, and the cell protoplasm is prolonged into a short fiber or forms an irregular body. In the latter case the cells have the appearance of blood corpuscles.

The heart originates in the mesoblast (Fig. 135, *Mes.*), between the entoblast and outer wall of the body, just behind the thoracic-abdominal flexure.

At this time fibrous substance (punktsubstanz) is first seen in the brain. It appears as two small masses joined by a transverse commissure, in a plane just anterior to the roots of the first antennæ. It is distinctly fibrous and apparently originates from the protoplasm of surrounding cells.

STAGE VIII.—SEGMENTATION OF THE NERVOUS SYSTEM—AT LEAST EIGHT PAIRS OF APPEN-
DAGES PRESENT.

We have two longitudinal sections (Figs. 138, 139) to illustrate this stage. If we compare the latter figure with the corresponding one of the previous stage (Fig. 131) we see at a glance that a long step forward has been taken in development. Between these, I have obtained one intermediate phase, which is a trifle older than the embryo given in Pl. XLIV, and can be best described by showing in what respects it differs from it.

The rudiment from which the nervous system is formed (Stage VII) is a plate of cells extending from the optic lobes to the apex of the abdomen. Anteriorly in the brain (Fig. 132) it is very thick, but gradually thins out as it is followed backward, until it consists of a single layer of epiblast at the very tip of the abdomen. In the phase intermediate between Stages VII and VIII the portion of nervous thickening between the œsophagus, which passes through it, and the thoracic-abdominal fold is partially segmented into cell masses, the primitive ganglia.

The cells of this ectoblastic thickening may be roughly divided into a surface layer, the nuclei of which are large and contain diffuse granules of chromatin, and a deep cell mass with smaller nuclei which stain more intensely. Similarly in the optic lobe we find a thick pad of uniform, deeply stained cells (gangliogen) next the yolk, and separated from this a well-marked surface layer (retinogen) of larger cells. The superficial, epiblastic cells on the inner or ventral side of the thoracic-abdominal fold are large and columnar. The nuclei are very much elongated and closely crowded together, and lie at all levels. This implies rapid cell division in this layer in a plane perpendicular to the surface, and as a result of this, the thickening of the ectoblastic plate in this region, such as we see in the next phase (Fig. 139).

Near the apex of the abdomen there is a transverse zone of very large cells, and the smaller superficial cells adjoining it are arranged in parallel lines. Something resembling this was noticed in Stage VI (Pl. XLII, Fig. 120, *B. Z.*). It corresponds to the budding zone (*Knospungszone*) which Reichenbach figures and describes in the crayfish. He detects it in a very early stage (Stage E, embryo with rudiments of the mandibles, corresponding nearly to Stage V of this paper), and finds that it consists of a transverse zone of cells containing large nuclei at the extremity of the abdomen, below the notch of the telson. From it the segments following the mandibular segment are gradually budded off.

The present stage is characterized by the segmentation of the nervous system and the great development of the optic lobes. The ventral nerve plate is blocked out by lateral constrictions into its component ganglia. There is also a median vertical ingrowth or constriction which tends to divide the plate into a double cord. It is, however, discontinuous at the middle of each block, so that the ventral nervous system consists of a double chain of ganglia, each pair of which are united by a transverse commissure or band of cells, and each ganglion is similarly joined to the one behind or in front of it. Distinct commissures pass from the brain around the œsophagus and unite the former to the ventral nerve chain. The first pair of post-oral ganglia contain two masses of fibrous substance united by transverse fibers as in the brain. The ganglia following these also contain punktsubstanz. It is developed as a small isolated mass on the dorsal side of each ganglion, toward the middle line. As development proceeds these masses increase in size and are gradually united by transverse commissures in each pair of ganglia (Pl. XLVI, Figs. 150, 151, *Pk.*).

A mass of fibrous or granular substance appears in each optic lobe in the gangliogen next the brain. Fibers pass from it to the punktsubstanz of the brain, which sends fibers down to the

circum-œsophageal commissures to the first post-oral ganglia. The fibrous masses unite on either side of the ventral chain to form a double longitudinal commissure. Thus at an early stage the optic lobes, brain, and ventral nervous system are intimately connected by fibrous tissue.

All the segments of the body are now marked off as seen in Fig. 139. The first post-oral segment is the mandibular (g. IV), and following it are the segments of the maxillæ the maxillipeds and the first pereiopod. The second thoracic ganglion lies in the angle made by the thoracic-abdominal flexure. The third, fourth, and fifth thoracic, and the six abdominal segments constitute the thoracic-abdominal fold.

In the superficial parts of the brain large elements are met with which multiply by mitosis, but have a distinct histological character. They consist of a large spherical nucleus containing a diffuse chromatin network, and a granular cell body without definite wall. They are the ganglion cells, which are abundant in all later stages.

The optic lobe consists of two sharply distinguished parts already mentioned, the *retinal* and *ganglionic* portions. The retinogen which forms the eye is a superficial disk of cells resting like a cap on the other part of the lobe, thickest on the outer side of the lobe and rapidly thinning out toward the middle line to a single layer of cells. The nuclei are elongated and wedge-shaped, and cell division takes place commonly in a plane perpendicular to the surface, corresponding to the long axis of the vertical nucleus. The gangliogen consists of a deeper portion next the brain, containing a ball of fibrous tissue, and a part next the retinogen or eye rudiment. Below the thickest portion of the eye the cells have large nuclei, which show a tendency to arrange themselves in rows radiating from the deeper half of the lobe. These large, clearer cells also extend down to the food yolk, and in lateral longitudinal sections (Fig. 138) form the inner stratum of the lobe. The cells which lie between them and the eye, here one cell thick, are smaller and stain intensely (v. Section IX).

The heart (Fig. 139, *H*) is now a broad and greatly flattened chamber between the body wall and endoderm (*End*). It extends forward a considerable distance between the epiblast and yolk, and is continued backward into the superior abdominal artery (*A. a. s.*). It is filled with serum and blood corpuscles.

The endoderm is a more conspicuous layer (*End.*), and the wandering cells are reduced in numbers. They are still seen in all parts of the egg, approaching the body wall, the nervous system, the endoderm plate, and other parts of the embryo (Fig. 139, *y. c.*).

STAGE IX.—EMBRYO WITH EYE PIGMENT FORMING.

A sketch of the embryo at the time when eye pigment has already formed is shown in Pl. XLVII, Fig. 158. The optic lobes are huge pear-shaped masses meeting on the middle line in front and arching outward and backward on either side of the brain. The ocular pigment appears as a thin, dark-brown crescent near the outer surface of the lobe. Pigment is first formed at the posterior end of the lobe nearest the base of the antennules, and spreads upward over its larger convex end. The brain is constricted into two portions corresponding to the antennular and antennal segments.

The segments of the abdomen are faintly marked off at the surface, and the telson plate which overlaps the mouth, is deeply forked at its extremity. (Compare with spatulate telson of the first larva, Pl. XXI, Fig. 9.) The plumose setæ which garnish the posterior edge of the telson are now represented by short stumps.

The first pair of antennæ are stout, simple appendages, tipped with setæ and folded backward along the sides of the body. The second pair of antennæ just inside of the latter, are biramous. They are also hairy at the tips, and the embryonic membranes surround them like the fingers of a glove.

The present stage is illustrated by Pls. XLVI and XLVII. The drawings are made from different embryos, all of which are of the same age, excepting those represented by Figs. 152, 158, 159, and 161, which are a trifle more advanced.

In the first series (Pl. XLVI, Figs. 146–151) the pigment cells are just forming in the eye. They are first developed in the thickest part of the retinogen next the food yolk. A single section, like

Fig. 146, shows the complete history of development of the retinal layer from its one-celled condition toward the median line (already seen at an earlier stage, Fig. 136, Stage VII) to the point farthest from the middle line, where pigment is formed. The fibrous nerve tissue of the gangliogen now consists of three masses, a ball nearest the brain, which is the first to appear, and two smaller masses between it and the retinogen. Huge ganglion cells (gc.) are of frequent occurrence, especially at the surface of the eye stalk next the brain. (The details of the development of the eye are reserved for a special section.)

The brain at this time (Figs. 146–148) differs from that of the previous stage chiefly in point of size. It is composed of nerve cells and large ganglion cells (gc.), which occur chiefly near the outer surface, and central fibrous tissue. It rests against the food yolk, and in the living embryo it is bathed with a current of blood (B. S.). The fibrous tissue of the brain has the form of a letter H with a wide and short transverse bar. In front of the transverse commissure (Fig. 147, Tc.) the fibrous substance is prolonged on either side into the optic lobes; behind, it extends down to the ventral nerve cord, on the inner side of the œsophageal ring (Fig. 148, ocm.).

The ventral nervous system, like the brain, is bathed with blood, which fills a large sinus between it and the yolk. This communicates with extensive blood sinuses extending along the sides of the body (Figs. 148–154, B. S.). In some cases the food yolk, usually in an altered or finely divided state, is in close contact with the nerve chain (Fig. 157). Cells extremely flattened and spindle-shaped in section, are found in small numbers closely applied to the nervous system (Figs. 152, 157, pr.), and forming a rudimentary perineurium. In most cases they are undoubtedly isolated cells, and do not constitute a membrane. They originate from the wandering cells and correspond to cells similar in shape and origin which appear between the yolk and nervous system at a much earlier period (Stage VII, Fig. 131, Mes.). The brain and ventral cord are not as yet differentiated from the superficial epiblast, but anteriorly, flattened epiblastic cells begin to appear between the nerve cells and cuticle. Ganglion cells (Fig. 150) also make their appearance in the cord, commonly at either side, close to the surface.

There is direct continuity of fibrous substance in the optic lobes, the brain, and the ventral cord as far back as the abdominal ganglia. In the latter this substance has not been developed. In each single ganglion there is a ball of this tissue which is united to its fellow in the same segment by a transverse commissure (Fig. 151), and to the preceding and following ganglion by longitudinal commissures. It is as a rule completely inclosed by the ganglion cells, but is separated from the yolk or blood sinus often by a unicellular layer (Fig. 150), and in the antennular and antennal segments of the brain (Figs. 147, 148) the cells next the yolk are discontinuous. In the circumœsophageal cords the fibrous tissue also is without a cellular cortex on its inner or central side (Fig. 149, fs.). With slight changes these relations are maintained in the hatched larva (see Pl., LV., Figs. 220–222). The foregut is at this time a tube with definite walls and wide lumen (Figs. 148, 152, fg.). At about its middle it is bent abruptly backward on itself in an acute angle. The first portion, leading from the mouth to the angle, is the œsophagus and is directed forward; the hinder blind end of the tube lies in nearly a horizontal plane, and represents the masticatory stomach. The walls of the foregut consist of a single layer of columnar cells with large nuclei. They end abruptly next the yolk, but the cavity of the tube is screened from the latter by a thin membrane of flattened cells. A sheet of elongated or spindle-shaped cells surrounds the wall of the foregut and extends over the nervous system (Figs. 148, 149, Mes.), while just below the œsophagus and behind the mouth a bundle of elongated cells grows over the nerve cords to the roots of the mandibles representing the adductor muscles, which become so prominent in later stages. These relations are easily deciphered in the structure of an earlier embryo (Stage VII, Fig. 134), where we have already seen muscle and connective tissue elements, derived from the wandering cells, extending from the œsophagus to the epiblast of the body wall.

Wandering cells also pass into the blood sinuses from all parts of the egg, and become converted into blood cells and connective tissue elements. In Fig. 148 we see two such cells on the edge of the blood stream, and in Fig. 152, (yc.) several of these bodies are in contact with the blood current on the side of the egg opposite the embryo. The relations of the epiblast, wandering cells and blood corpuscles in this part of the egg are seen in detail in Fig. 161, where a single large wandering cell is already half submerged in the blood. The various other drawings illustrating this stage (Figs. 154, 155, 160, yc.) point to a similar fate for a portion of the wandering

cells. This subject of the rôle of the wandering cells in Alpheus is one of the most difficult and at the same time the most interesting which has been met with in the study of its life history, and a full discussion of it is reserved for another part of this paper (Section VII).

A new structure, the carapace (Figs. 148–151, 160, *cp.*), is seen for the first time at this period. It takes the form of a lateral longitudinal outgrowth of ectoderm on either side of the body in the region of the thorax. These longitudinal folds represent the branchiostegites, which form the outer wall of the branchial cavity. In Fig. 160 the structure of the rudimentary carapace and the way in which it originates is very clearly shown. The epiblast cells at the surface multiply and the cell protoplasm is prolonged downward into long strands or spindles. Meantime the ectoblast is pushed outward along definite lines and the spindles of one side of this fold unite with those of the side opposite, thus forming a framework of transverse beams or pillars. Blood enters the fold, which thus becomes a respiratory organ. This structure is essentially maintained up to larval life (v. Fig. 195).

The hindgut or intestine (Figs. 150, 157, *Hg.*) has a considerably larger lumen than in the preceding stage, but its histology is essentially the same. The walls are composed of a single tier of large columnar cells. The cell protoplasm is granular, and projects into the lumen of the tube, and the cell wall is usually distinct. There is an outer investment of mesoblast as in earlier stages, which is closely associated with the surrounding cells of the developing abdominal muscles (Figs. 150, 160, *mu. f.*). The muscle fibre appears as an outgrowth of the cell protoplasm of the muscle cell. The nucleus elongates until it becomes rod-shaped. The fiber is homogeneous, nonstriated and stains feebly in borax carmine, but not at all in hæmotoxylon. The intestine communicates with the midgut or the cavity which contains the great mass of food yolk, and with the exterior by the anus, which is on the under side of the telson plate opposite the labrum.

Fig. 157 shows the continuity of the epithelia of the hind and midguts, and illustrates in a very satisfactory manner the origin of the endoderm. Histologically the entoblastic cells resemble those of the adjoining epiblast, and it is impossible to draw a sharp line between them. The endoderm cells are vesiculated, have less definite boundaries, and extend pseudopodia-like processes into the yolk. The endoderm begins near the point marked *vac.* Fig. 157. Here the lumen of the tube enlarges, and the endoderm extends forward over the flexure of the nerve cord and upward over the sides of the body. Posteriorly it is separated from the body wall by the blood sinus which represents the heart and its arteries (*H*). The yolk next the endoderm is eroded and granulated. The formation of the endoderm thus begins near the abdominal flexure, in the egg-nauplius stage, at the point where the hindgut communicates with the cavity of the mesenteron, and advances gradually forward on all sides. It is composed of cells (Fig.157, *y. c.*) which migrate from the yolk and assume an extreme peripheral position with respect to it. They eventually acquire cell walls, unite and inclose the yolk which they continue to feed upon, apparently by first producing chemical changes in it and then absorbing its particles. In the early stages the mother cells of the endoderm and mesoderm can not be distinguished with certainty. However, since the endoderm originates as a distinct epithelial layer behind the ventral plate, and thence spreads forwards, slowly walling in the mesenteron, it is obvious that the bulk of the anteriorly wandering cells are mesoblast.

The extensive blood sinuses which are now present have already been mentioned. In the angle between the optic lobes in front, there is a large blood space (Fig. 152, *b. s.*), and blood passes from the heart upward and forward nearly around the egg in a thin irregular stream between the skin and food yolk. Mesoblast cells grow forward from the abdominal region and line the outer sides of the endodermal wall, and extend upward to a thin sheet between the yolk and the epiblast. Endodermal cells coming from the yolk attach themselves to this layer. The pulsatile chamber of the heart is not a very definite structure at this stage. It lies above the endoderm, nearly opposite the angle of the thoracic-abdominal fold. Its walls are delicate, and appear in sections as thin strands of mesoderm cells. The nuclei are elongated and the cell protoplasm is produced into long processes. The pericardial space surrounding it is filled with blood.

In Stage VII (Figs. 144, 145, *Dp.*) we noticed an extraordinary migration of wandering cells to the pole of the egg opposite the embryo. These cells eventually reach the surface and reinforcing the primitive epiblast, give rise to a conspicuous dorsal plate, which is shown in Fig. 153 (*Dp.*). This is from an embryo intermediate between Stages VIII and IX, in which eye-pigment

is not yet formed. The plate is slightly thickened at its center, where there is an inconspicuous pit marking the point of ingrowth. As the invaginated cells pass into the yolk they degenerate, giving rise to spore-like particles which spread in incredible numbers through a large part of the egg. Some of the wandering cells in this region doubtless degenerate before reaching the surface. A part of a similar section is shown in more detail in Pl. v, Fig. 36. The particles vary considerably in size, stain uniformly and intensely and the yolk about them is granular or finely divided.

At a corresponding stage in the lobster (*Homarus americanus*), I have observed a large diffuse patch of cells which probably answers to the structure just described. In this case the embryo rests on the side of the oblong egg and the cell plate is at one end of it, at a point about 90° behind the embryo. This position seems to be quite constant, while in Alpheus the plate is nearly opposite the embryo, at the stage when it is most conspicuous.

STAGE X.—EMBRYO WITH EYE-PIGMENT STRONGLY DEVELOPED AND THE POSTERIOR LOBES OF THE GASTRIC GLAND FORMING.

All the thoracic limbs and the sixth pair of abdominal appendages are present in a rudimentary condition. The abdomen has grown forward until the tip of the telson now extends beyond the optic lobes. The embryonic telson is fringed with seven pairs of setæ, and resembles the larval telson, except that the median notch is deeper. Seen from the exterior the eye-pigment has the form of an oval disk.

The longitudinal section, Pl. XLVIII, Fig. 168, shows most of the important changes which have occurred since the last stage. These chiefly concern the eye, the nervous system, and the midgut.

The ectodermal pigment cells (retinular cells) of the retinogen have spread inward until they cover its whole inner convex surface (Pl. XLVIII, Fig. 167). Near the outer surface of the eye the crystalline cone mother cells (*cc*) can be recognized, and between the eye and the ganglia of the optic lobe there is a narrow space which communicates freely with the blood sinus (*B. S.*) on the outer side of the lobe. Wandering cells are frequently seen near this blood sinus, and in the space between the eye and ganglia flattened cells also occur, which find their way in thither from the yolk. In the optic lobe another fibrous mass has developed near the eye (Fig. 164-7). In horizontal section (Pl. XLVII, Fig. 159) the relations of the fibrous tissue of the brain and optic lobes is clearly shown. In each lobe there is a chain of four fibrous masses united by a stalk of fibers to the anterior or optic swelling of the brain (*of*).

The structure of the brain (Figs. 159, 169, 170) begins to approach in complexity that of the larva, which was described in the first section of Part II of this paper. The lateral fiber-balls, so conspicuous in the later stages have now appeared (Fig. 159 and Pl. XLIX, Fig. 174, *lf*.). They are developed in close union with the large central fibrous mass, which supplies the optic lobes, and probably belong primarily to the antennular segment. Below this and nearer the middle line there is a less definite fibrous center (*qf.*) which supplies the antennal segment. With this, the œsophageal commissures are directly continuous (Figs. 171, 174 *ocm.*).

The complete chain of ventral ganglia can be seen in Fig. 168. This section is not perfectly median, but cuts a fiber-ball of each ganglion. The skin or hypodermis is now differentiated from the nerve elements and consists of a thin layer of flat cells. The fibrous masses of the ganglionic chain are also imperfectly surrounded by peculiar cells, the nuclei of which are spindle-shaped in section. These also occur in the brain, and in either case must be regarded as metamorphosed ectoderm cells, or more probably as intrusive mesoblast. A transverse section of the nerve cord in the thoracic region is shown in Fig. 172, and corresponds very nearly in plane of section with Fig. 151 of the last stage. The fusion of the ganglia is now more complete, and the fibrous balls and commissure are relatively larger. (Compare with this, Fig. 176, a section of the thoracic ganglion of the larva.) In the abdominal ganglia the fibrous elements have essentially the same relations, but lie at a deeper level, being separated from the adjoining tissues by at most a single layer of nerve cells. In Fig. 168 we see that the yolk comes in close relations with the nerve cord behind the œsophagus to the endodermal fold (*f*) near the point of union of the mesenteron and hindgut. Wandering cells approach the cord and become flattened against it, as already observed in much earlier stages.

The two divisions of the foregut, œsophagus, and masticatory stomach, have the relations already described. The wall consists of a single layer of tall columnar cells. In the masticatory division the wall has begun to thicken next the yolk screen, its cells being cuneiform, and the nuclei elongated and crowded below the surface. From the anterior wall, muscle or connective tissue cells extend forward under the brain.
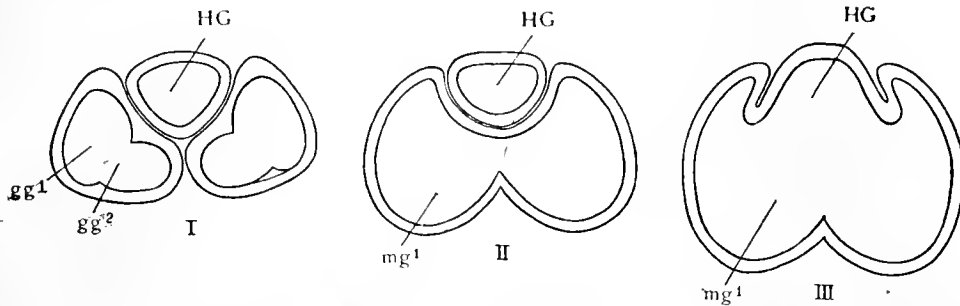
FIG. 1.—Diagrams of transverse sections through the alimentary tract of an embryo of *Alpheus sauleyi* which is nearly ready to hatch, to show the origin of the gastric gland from the postero-lateral lobes of the midgut. Section I cuts the hindgut and lobes of the "liver," Section III the hindgut where it merges into the mesenteron. *gg¹*, *gg²*, Secondary lobules of *mg¹*; *HG*, hindgut; *mg¹*, postero-lateral lobes of midgut.

The development of the mesenteron can be understood by reference to Figs. 162–165, 168, and 185. The endodermal epithelium spreads by the division of its own cells and by accession of cells from the yolk, both forward over the nervous system and upward against the sides of the body. This is shown in the series of horizontal sections (Fig. 162–165). Fig. 168 which is from an embryo a little more advanced, shows that the endoderm is rising from the nervous cord near its point of flexure, into a transverse vertical fold. Simultaneously with the upward growth of this ventral fold, two dorsal longitudinal folds grow downward, and finally unite with the ventral fold and with each other, thus constricting off from the alimentary tract two lateral pouches, the primary lobes of the "liver." The folds grow forward and the constriction proceeds gradually with the growth of the embryo. This process is illustrated by the diagrams (Fig. 1) which were drawn from an embryo near the point of hatching. The histology of the endoderm as shown in Fig. 173, is essentially the same as in the previous stage. The cells are prismatic, and the nucleus spherical, and, as in all stages, filled with numerous nucleoli or chromatin balls. The cell walls are very delicate and the protoplasm often contains large vacuoles.
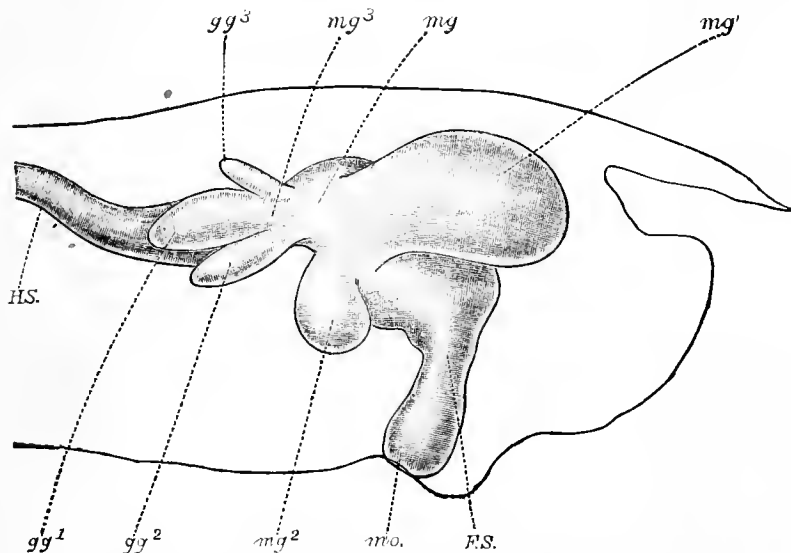
FIG. 2.—Semidiagrammatic representation of the alimentary tract and its appendages in the first larva of *Alpheus sauleyi*. The middle line of the body is also shown. *FS*, foregut; *gg 1–3*, secondary lobules of postero-lateral lobe of midgut; *HS*, hindgut; *mg*, midgut; *mg 1–3*, anterior, lateral, and postero-lateral divisions of midgut; *mo*, mouth.

Wandering cells still occur in all parts of the yolk, though in far less abundance than in earlier stages. We find numbers of them moving toward the periphery, or next the body wall to take part in forming the endoderm. The epiblast is conspicuous in Fig. 168 just in front of the optic lobes. This corresponds in position with the dorsal plate (Fig. 153 *dp.*), and is probably a remnant of it. The small clusters of cells beneath it and the degenerative products which occur near them, probably also represent the remains of the great swarm of degenerating chromatin particles which was formerly present in this region. A blood space (Fig. 168,) now extends over the dorsal side of the egg between the epiblast and the yolk, from the heart to the optic lobes and region of the head.

Anteriorly we can distinguish in transverse section three vessels—a median impaired one, which answers to the ophthalmic artery, and a pair of lateral vessels, the antennary arteries. The vascular walls are extremely delicate and contain flattened cells, the nuclei of which in longitudinal sections appear almost linear. Seen from the surface of the egg the blood vessels have the appearance of two bands of tissue, passing backward from near the point of union of the optic lobes. Between and at either side of the optic lobes, and beneath and to each side of the brain, we find blood spaces packed with corpuscles (Figs. 166–169, *B. S.*) It is not possible, in most cases, to distinguish at this phase true sinuses (veins) from arteries. The structure of the heart is shown in Figs. 164 and 168 (*H.*), and is essentially the same as in Stage IX.

In Fig. 173 there is a small solid cluster of peculiar cells (*R. O.*) on either side of the alimentary tract, between it and the heart. This I regard as the rudiment of the reproductive organ. The cells are clearly differentiated from the surrounding cells. The nuclei are very large, spherical, and stain lightly and diffusely. They are enveloped in a capsule of mesoderm cells, like those forming the walls of the heart, and they originate from similar elements. In Stage IX (Fig. 157) these cell masses were first recognized. They are then distinct from the surrounding elements, and the nucleus contains a very delicate reticulum. Each cell cluster is so small that unless the sections are uniform and complete it is very easily overlooked. The muscles have developed in various parts of the body (Figs. 168, 171, 172, *mu., mu. f., mu. e., g. m. a.*), but most striking at this stage are the great flexor and extensor muscles of the abdomen.

The green gland (Fig. 170, *A. G.*) is another organ which we now meet with for the first time. It is an irregular tube, closed at both ends, and lies at the base of the second antenna, extending up a short way between the body wall and brain. In the previous stage all the tissue at the root of this appendage is very loose and reticular, and no lumen can be seen. I have been unable to detect any opening of the gland to the exterior, nor should we expect to find any, since, as we have already seen in Section I, there is none in the larva. It must be regarded as a mesodermic structure.

STAGE XI.—EMBRYO OF ALPHEUS HETEROCHELIS NEARLY READY TO HATCH.

The later stages (Stages VI–X) have had reference to a single species of Alpheus, namely, *Alpheus saulcyi*, the larva of which is described in the first section. The embryo of *Alpheus heterochelis* at about the time of hatching is considerably less advanced than the embryo of the first species at a similar period, and will serve in many respects as a convenient connecting link between the larva described in Section I and the last stage. The embryo of *Alpheus heterochelis* is represented by a longitudinal vertical section and by a series of transverse ones (Pls. L, LI). The longitudinal sections of Stage X, of this stage, and of the larva (Figs. 168, 180, 196), form a very interesting series for comparative study.

The eye and the ganglia of the eye stalk (Figs. 177–179, 187) have become highly specialized, and closely resemble the adult organs. The brain is larger, but shows no new structures which have not already been noticed. The entire nervous system is more compact, and is completely separated from the skin. The foregut is larger than in the previous stage, and the walls of the masticatory stomach have become very much thickened. It is screened from the yolk by a membrane composed of large cells, which extend backward over the nerve cord. A double band of muscles (Figs. 168, 180, *g. m. a.*) passes upward from the anterior wall of the masticatory stomach and from the brain, to the body wall. These will be referred to the anterior gastric muscles.

The mesenteron (*mg.*) is very largely reduced in size and is filled with a granular coagulum, and, anteriorly next the head, with vesiculated and eroded remnants of yolk. The endoderm lines all but the anterior third of this cavity, extending farther forward on the dorsal wall. A few wandering cells are still present in the peripheral parts of the cavity next the advancing edge of the endoderm. Those elements, represented in Fig. 182, prove to be endoderm cells mechanically detached from the wall of the mesenteron. The primary lobes of the midgut ("liver") are larger but otherwise similar to those described in Stage x. The endoderm cells are greatly vesiculated, and the cell protoplasm has often a striated appearance.

The heart (Figs. 180, 186, *H*.) has undergone very considerable changes since the period represented by Figs. 164, 168. It is no longer dorso-ventrally flattened, but in transverse section it is triangular in appearance. One side of the triangle is toward the intestine and one apex next the body wall. Its suspension in the pericardium is very delicate. The ectoderm cells send down spindle-shaped processes (Fig. 186), the *Ectoderm pfeiler* of Reichenbach, and to these, mesodermal elements become attached. The cavity of the heart is imperfectly divided by lateral partitions into three longitudinal compartments. In Fig. 186 the partitions are imperfect and represented on each side by a single rudimentary muscle fiber. The walls and partitions of the heart are composed of delicate muscle fibers, which are distinctly striated. In the abdominal muscles, striations can also be made out.

STAGE XII.—THE FIRST LARVA.

We now reach the stage with which this paper began, the first larva of *Alpheus saulcyi*. The histological structure of the zoëa in the species with a regular metamorphosis differs only in minor particulars from the larva already described. The organs are all very much smaller, and the cells are relatively larger and less compact. The mesenteron is about half filled with the unaltered and unabsorbed food yolk. Wandering cells are almost entirely absent, and the endodermal walls are nearly complete. The partition between the masticatory stomach and the midgut is absorbed and communication between them is established.

The anterior and median lateral divisions of the midgut are present, but the posterior lateral lobes are represented only by spaces not as yet walled in by endoderm. There is a slight dorsal median fold of endodermal cells. In the larva of the same species three days' old the posterior lateral lobes are formed, but are very small.

STAGE XIII.—ALPHEUS TEN DAYS OLD.

In the first twenty-four hours the larva moults twice, but the histological changes in this period are not of a very extensive character. The organs which experience the most rapid growth are the gills (Pl. LIII, Fig. 195.). These have now acquired the folds or plates for increasing the respiratory surface, and are more efficient as breathing organs.

The fibrous tissue of the brain is relatively greater in bulk, and the tracts of fibers are more numerous and more complicated. The eye stalks are much shorter, and the optic ganglia and anterior parts of the brain are drawn closer together.

In a larva four days old (Pl. XXI, Fig. 3) the eyes are completely covered by the carapace. The ganglia of the eye stalks and brain are intimately fused together. The nervous system and all the tissues have undergone greater or less histological changes. These can be more conveniently considered in a still older larva.

The period of metamorphosis, strictly speaking, is passed in about twenty-four hours after the time of hatching. The structure of an Alpheus ten days old, which had spent its entire life in an aquarium will now be briefly considered. It is sexually immature and some of the organs, like the "liver" and green gland, are less complicated, but otherwise the structure is essentially that of the adult form.

When we compare the brain of the first larva with that of the ten days old and the adult fully grown form, we find the same parts present in all. In the last two the fibrous tissue is relatively much greater in bulk, and differentiation of the fibers and fibrous tracts has advanced much farther. The brain consists of the same fibrous masses surrounded with a thinner cortex of nerve and ganglion cells.

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The anterior or optic enlargement is continuous on each side with the ganglia of the eye stalks. Its two halves are united by transverse fibers. The lateral enlargement is markedly kidney-shaped, and from its hilus there issues a complex system of fibers. A great part of these fibers issue from the ganglion cells inclosing the lateral ball, pass out in a bundle to the middle of the brain, and thence up to the optic ganglia, apparently without crossing. The fibrous substance of the lateral enlargement has a pyramidal structure—that is, its tissue is permeated with pyramidal blocks of a denser substance which stains faintly with carmine. The apices of these pyramids point toward the center of the ball. Below the lateral enlargement and nearer the middle line there is the antennular mass from which the auditory nerve issues. This is bilobed and has the same general relations as in the first larva (Pl. LV, Fig. 216, *lf.*). The antennal enlargement, which is closely connected with the latter, is now a much more conspicuous mass than in the earlier stage. From it issue the antennal nerve and the œsophageal commissures.

The alimentary tract has undergone very important changes, of which mention was made in Section I. What corresponds to the foregut of the larva comprises that portion of the tract from the mouth to the duct of the gastric glands. It is divisible into a straight and vertical portion, the œsophagus proper and a masticatory stomach. The latter consists of two parts, an anterior section continuous with the œsophagus, and probably corresponding with the gastric mill, and a pyloric portion or strainer. In transverse section the cardiac section appears circular and the walls are rather thin and slightly folded. As this passes into the pyloric division the floor of the tract rises into a broad tongue-shaped process, which is surmounted by a particular strainer of hairs. This median fold is continuous throughout the pyloric division, where it narrows into a crest. The lateral walls, which are greatly thickened and studded with hairs, approach each other so that only a small lumen is left, through which the food is strained as it passes over the network of hairs. These two sections of the stomach correspond to portions of the tract marked *Ms.*, Fig. 196. They are of epiblastic origin, and in passing to the midgut the epithelium suddenly changes as it does in the larva.

The ducts of the three glands unite on each side and thus form two common ducts. The epithelia of the gastric cæca of the ducts and midgut are directly continuous and pass gradually into each other. They consist of a delicate layer of connective tissue which forms a capsular investment and the large columnar cells already described. In the "liver" many of these cells are in the process of active secretion, and as a result of this activity the lumen of the gland is filled with a coagulated liquid. The secreting cell at this period swells out to two or three times its former size and has the form of a distended bladder projecting into the cavity of the gland. The contents of the cell consist of a light granular fluid and when the cell breaks down this is discharged into the lumen of the gland.

Just how much of the wall of the alimentary tract behind the glandular ducts is of endodermic origin it is impossible to say, since from the first there is no sharp morphological boundary between the hindgut and mesenteron. But it is certain that only a very small portion of it can arise in this way, and that the endoderm of the larva goes mainly, if not exclusively, to form the lining of the gastric cæca.

The heart is very much compressed from above downward as in the adult. The walls of blood vessels consist of a single layer of cells which secrete a homogeneous limiting membrane. As in the early larva, the heart and pericardium are screened from the digestive tract and other organs by a horizontal membrane. The reproductive organs are still in the rudimentary condition already described.

V.—NOTES ON THE SEGMENTATION OF CRUSTACEA.*

Under this head I will add a few notes upon the segmentation of the egg of a number of Decapods, which have been studied chiefly for the sake of comparison with Alpheus.

Alpheus saulcyi and *A. heterochelis* are both typical examples of centrolecithal segmentation with the formation of yolk pyramids. They possess a massive food yolk and hatch as mysis-like

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* The concluding sections of this memoir were written after the lapse of a long interval, during which time it was not possible to refer to my earlier manuscript. This will account for any unnecessary reiteration of facts, or for any inconsistencies in statement which I have failed to eliminate.

larvæ.   On the other hand, the Bahaman variety of *Alpheus heterochelis* and *Alpheus minor* (from Beaufort, North Carolina) agree in having a relatively smaller yolk and in hatching as zœa-like forms.   They differ, however, in their segmentation, the first species agreeing in this respect with *A. saulcyi*, while in *A. minor* yolk pyramids are generally absent and the segmentation is irregular. The yolk in *A. heterochelis* of Beaufort is about nine times as voluminous as that of the Bahaman *heterochelis*.   The segmentation, however, has remained unaltered.   The peculiarities which we find in the early stages of *A. minor* can not therefore be laid to the door of the yolk alone, but must be regarded as a comparatively recent modification of the yolk pyramid type.   While the type of segmentation may be very persistent and uniform, it is subject to profound change, not only in closely allied species, but, as has been shown in a few instances, within the species itself.

In the Decapod egg we have, as a result of segmentation, a great central yolk-mass which is either undivided or imperfectly divided, and which completely fills and obliterates the segmentation cavity, and a surrounding layer of cells, the blastoderm.   More fully stated the process is as follows: The segmentation nucleus divides first at a point near the center of the egg.   The daughter cells separate widely, and a second division follows.   With subsequent divisions the cells approach nearer the surface.   The yolk may share in these early divisions but often does not, until eight or sixteen cells are formed (third or fourth segmentation stage).   When there is no progressive segmentation of the yolk in the early phases, the yolk segments appear either gradually and on one side of the egg, or make their appearance simultaneously in relation to all the nuclei present.   Segmentation is always rythmical.   During one phase (period of "rest") the segments shrink away from the surface and flatten out in the usual way, while at the beginning of the period which follows (period of "activity") they swell and stand out prominently.   The division of the yolk often appears total in surface views, while in reality it is not.   The constrictions marking off the segments may be nearly superficial, or they may extend deep into the yolk.   Cell division is usually indirect.   The only exception to this rule which I have observed is *Alpheus minor* (see p. 397).   With each division the protoplasm approaches nearer the surface of the egg, and the segments become more pyramidal in shape.   These are the "yolk pyramids" which were first described in the crayfish by Rathke in 1829.   The bases of the pyramids form the surface of the egg and their apices fuse in the central yolk mass.   The nucleus, surrounded by a rayed body of protoplasm, lies near the base.   By repeated division the pyramids become smaller; the cleavage planes of adjoining segments become less distinct and the protoplasm draws nearer and nearer the surface.   Before, however, any of the protoplasm is flush with the surface, certain of the cells divide horizontally, that is delaminate, and one of the products of each division migrates into the yolk below.   The surface of the egg is now covered with a single layer of small polygonal cells, and the pyramidal structure of the peripheral yolk has nearly disappeared.   The greater part of the protoplasm of the egg is thus at the extreme outer ends of the reduced yolk pyramids, while the lesser body of it is represented by the migrating yolk cells.

The invagination stage soon follows, and the large numbers of cells which now become migratory (in Alpheus penetrating to all parts of the egg), joining the primary yolk cells, represent mesoblast and entoblast.   The process above described will be found to apply, I believe, to the majority, if not to all Decapods.   Differences in detail may be expected in the time of appearance of yolk segmentation and the degree to which this is carried.   This account differs from that usually given in recognizing delamination, following close upon the latter phases of segmentation, or the origin of cells, from the blastosphere before the invagination appears.   This regularly occurring in such typical forms as Alpheus and Homarus argues strongly for its presence in allied species where it has possibly been overlooked.

Stenopus hispidus.—I have described and figured the segmentation of Stenopus in a paper on the life history of this form.   In one egg which I sectioned before the beginning of yolk segmentation, a single cell, probably the male pronucleus, is seen at the surface, while another cell, the female pronucleus, lies near the center.   A single polar body was also present, just beneath the shell, near the first nucleus.   I saw no evidence of yolk segmentation until the third phase of division was reached.   The yolk then became constricted at the surface into eight blastomeres.   The superficial furrows are quite deep during active periods, giving to the egg the appearance of total cleavage. This egg now resembles that of Penæus as figured by Haeckel, but in the latter form yolk segments

appear at an earlier phase. The cleavage of the yolk is wholly, or almost wholly, confined to the surface furrows, dividing planes rarely extending into the yolk below. My material was not adequate for determining whether invagination was preceded by delamination or not, but seems to render it highly probable that a delamination does not occur.

My observations on *Pontonia domestica, Palæmonetes vulgaris*, and *Hippa talpoides* are very fragmentary. In Pontonia I have one stage (Fig. 27) with three cells, one of which is dividing with no sign of yolk division, and another with sixteen nuclei and corresponding yolk pyramids. Here the conditions are precisely like those in *Alpheus saulcyi* at a similar stage, and probably the segmentation of the two is similiar. In *Palæmonetes* Faxon (17), relying wholly upon surface views, states that segmentation of the egg begins in two planes almost simultaneously. These planes are at right angles to each other and pass through the long and short axes of the egg. Whether this follows close upon the first division of the nucleus I have not determined. I have an egg with two nuclei near the center of the undivided yolk, and a stage with thirty-two yolk pyramids. This egg also agrees closely with that of *Alpheus saulcyi* at the same stage. The nuclei are not quite at the extreme surface of the yolk. In the next phase when sixty-four pyramids are present the protoplasm abuts on the surface (Fig. 24) of the egg. All the protoplasm is distributed to the yolk pyramids and no delamination has taken place.

With reference to Hippa I can only add the note that yolk pyramids normally occur, and in the 64-cell stage (Figs. 1, 4) the lines of cleavage between adjacent segments are very distinct and extend nearly to the center of the egg. At this stage all the protoplasm is apparently concentrated in these cells. Yolk pyramids similar in surface views to those of Hippa occur in *Callinectes hastatus, Platyonychus ocellatus*, and *Libinia canaliculata*.

Crangon vulgaris.—Kingsley (31) describes the segmentation of Crangon as follows:

> With the first segmentation the protoplasm begins to leave its central position and seek the surface of the egg; before the second division is completed it has reached the surface, leaving the yolk in the center. * * * After the second protoplasmic segmentation is effected the first segmentation furrows appear, the one following close upon the other. The first to appear corresponds in its direction to the first nuclear division; the second is at right angles to it. * * * In Crangon, so far as I have been able to see, amœboid cells reach the surface and take part in the formation of the blastoderm before the process of gastrulation begins. In that form no yolk pyramids occur.

Of cell division he says:

> In the process of cell division I have never seen any traces of karyokinesis; the division seems to be direct, and affects first the nucleus and next the protoplasm. * * * In fact I do not recall a single statement of karyokinesis being witnessed in decapod segmentation excepting in Astacus.

On Pl. I he gives a drawing (Fig. 3) of an egg with "about sixteen segmentation spheres." Fig. 4 of the same plate represents a section of the egg shown in Fig. 3 and has six nuclei, five of which are even with the surface, while one is near the center of the egg. The yolk spherules appear to be fused, owing possibly to the disturbing effect of the reagents employed. This central cell, according to Kingsley, represents a portion of the egg protoplasm which is belated in its passage to the surface, but it divides and gives rise to cells which eventually reach the surface at a certain point which marks the germinal area. Thus all the nuclei take part in the formation of the blastoderm, and the migration of the belated cells is completed before the "gastrula" invagination occurs. I have made no observations on the very earliest phases of segmentation of Crangon, but I have several eggs sectioned at the sixteen-cell stage, which ought therefore to correspond with Fig. 4 of Kingsley's paper, but, on the contrary, they show a somewhat different condition of things. There are just sixteen nuclei present, all of which are peripheral or nearly so, and each nucleus forms the center of a yolk pyramid, the cleavage planes of which are very marked and extend more than half way to the center of the egg. Fig. 15, Pl. XXVII, of the segmented egg of Alpheus, although belonging to a later phase, will fairly represent the condition of things which we find in Crangon. None of the nuclei are tangent to the surface, but between them and the surface there is still a considerable layer of yolk. Each is surrounded by a large mass of protoplasm, which stains lightly with hæmotoxylon, and has the characteristic rayed appearance. One of these nuclei is in the equatorial plate or metakinetic stage of division, and may be represented very nearly by Fig. 28, which shows a dividing cell in the egg of Alpheus at the same period. As already stated, the central yolk mass does not contain a single nucleus. The yolk is in the usual form of

large spherules on angular blocks, which are abundantly perforated with round lacunæ. Crangon agrees essentially at this stage with at least three other species, namely, with *Alpheus saulcyi, Pontonia domestica,* and *Stenopus hispidus.*

It is probable that Figs. 3 and 4 of Kingsley's paper do not correspond, the latter representing the older egg, that is, older than the sixteen-cell stage. In the segmenting eggs of Homarus there is a striking individual variation, which finds expression chiefly in the external characters of segmentation, but I have never observed this in any related forms, and can not say to what extent it occurs. Judging from analogy, I think it will be found that as a rule all the protoplasm in the egg of *Crangon vulgaris* reaches, or very nearly reaches, the surface, as in *Homarus* and *Alpheus saulcyi,* and that toward the close of the yolk-pyramid stage delamination occurs and some of it wanders back into the depths of the yolk. If this is true, the "belated" cell near the center of Fig. 4 of Kingsley's paper may represent some of the protoplasm which has taken this roundabout journey.

[While this memoir was in press a paper has appeared by W. F. R. Weldon, on "The Formation of the Germ-layers in Crangon vulgaris." (*Quart. Jour. Mic. Sci.,* Vol. XXXIII, pt. 3, March, 1892). He makes no mention of the budding of cells from the blastoderm before invagination, nor of the presence of migrating cells at a later period not derived from the invaginate cells or ventral plate, hence it is probable that in *Crangon* primary yolk cells do not occur. In this case the suggestion just offered does not let us out of the difficulty.] I have not succeeded in obtaining the segmenting eggs of Callianassa for comparison with the early stages of *Callianassa mediterranea,* described by Mereschkowski (40). It seems to me, however, that the diagrams in Mereschkowski's paper are misleading, and that the process of segmentation in Callianassa, instead of being peculiar as one might infer, is essentially typical. According to this observer's account the "blastoderm" arises without yolk segmentation. Nuclear division is at first central, and the resulting cells, sixteen in number, pass gradually to the surface and form a deep layer of protoplasm inclosing the yolk. This layer, at first raised into hillocks corresponding to the nuclei, finally segments into sixteen parts around the latter. These segments are formed simultaneously over the egg, but the yolk is not involved. The cells multiply rapidly and form a layer of tall prismatic elements, which gradually flatten out as division proceeds, into ordinary blastoderm cells.

If there is any analogy between this egg and that of related forms the broad "protoplasmic" layer is really the protoplasm plus the peripheral yolk. It would be remarkable in any case if a segmenting egg could acquire such a mass of protoplasm, not to speak of the suddenness with which the acquisition is made. That this layer, comprising more than one-half the contents of the egg, is largely yolk is indicated by the fact that the nuclei which occur in it are represented as surrounded by a protoplasmic reticulum as normally occurs. If this is true, the *prismatic cells* are *yolk pyramids,* and their line of separation from the central yolk is purely imaginary.

Ishikawa found, in his studies upon a Japanese prawn, *Atyephyra compressa* (27), that the egg underwent at first a total and regular segmentation. At the end of the fourth phase the yolk is centralized and the protoplasm surrounds it, and in the next stage, after thirty-two blastomeres have been formed, the central end of each separates off to form a yolk segment. The yolk segments, which fill the center of the egg and correspond to the common yolk mass with which the apices of the yolk pyramids blend in other Decapods, are of unequal size and contain nuclei which do not take part in the "blastoderm." These nuclei probably correspond to the delaminated cells of Homarus and Alpheus. In the latter they appear at the close of segmentation. It is quite probable that the time at which these cells are budded off may vary considerably in different species.

In *Eupagurus prideauxii* (39) Mayer found that the protoplasm segmented first in the center of the egg, as in other forms, until eight nuclei were present. When this stage is reached the yolk now segments not simultaneously into eight blastomeres, as in the case with the Isopod *Asellus aquaticus,* but according to its inherited primitive manner, first into two, then into four and eight spherules. Segmentation of the yolk is thus at first total, but after the fourth phase the spheres unite in a central yolk core as in other forms.

In *Alpheus saulcyi* I did not find any eggs which showed a progressive segmentation of the yolk between the stages represented in Figs. 9 and 10, and hence I infer, as already stated, that the segmentation of the yolk is there a simultaneous process for each of the sixteen segments

involved. This remark also applies to Stenopus, where eight blastomeres or yolk pyramids appear at the beginning of the third phase. In Homarus there is less uniformity in the appearance of the superficial segments, since the cells do not migrate to all parts of the surface at a uniform rate.

Lereboullet (36) described the early stages of the segmenting egg of the crayfish *Astacus fluviatilis* in 1862. His account, though somewhat vague and unsatisfactory owing to the technical difficulties under which he labored, is confirmed in essential particulars by a later observer, Skimkewitch (56), who has given a short description, without figures, of the process in the Russian crayfish *Astacus leptodactylus*. His account is briefly as follows: The cleavage nucleus with its protoplasm passes from the center to the surface of the egg and undergoes segmentation. The resulting nuclei, the exact number of which is not given, then diffuse over the surface of the egg and the yolk segments around them. The cleavage planes between adjacent pyramids, at first extend only half way to the center of the egg and never quite reach it. There remains at the close of the segmentation a small mass of undivided yolk ("*dotterkern*") lying in the center of the ovum.

According to these observations then, Astacus offers us an example of *centrolecithal* segmentation in the most exact sense of the term. It seems to me quite probable that this migration of the protoplasm may be only apparent, and that the segmentation may proceed much as it does in the lobster.

Brooks, in his memoir on *Lucifer* (8), gives an account of a segmentation which differs in some particulars from that of any macrouran which has been studied. The Lucifer egg undergoes a total and perfectly regular segmentation, and in the first stages may be compared with Eupagurus. In Lucifer, however, a segmentation cavity is formed, which can be clearly seen when sixteen spherules are present. At this time one pole of the egg becomes flattened, and one of the spherules in the area, which has become differentiated by the possession of food yolk, is gradually invaginated into the segmentation cavity. Meantime the invaginated cell divides; other changes ensue which lead to the infolding of more cells and the formation of a two-layered embryo, the "gastrula." Brooks thinks that the yolk-bearing cell represents a yolk pyramid, and that after a longitudinal division each half divides transversely or delaminates, and that the other two inner cells contain the yolk, while the outer products remain at the surface and form a part of the "blastoderm" (or endodermic invagination). This last point, however, was not settled. In Brooks's view the segmentation in Lucifer is a secondary modification of the yolk pyramid type, and this has been brought about "by the gradual reduction of the amount of food material and its restriction, at last, to a single one of the cells of the segmenting egg." He says that, while Lucifer is undoubtedly a very primitive Malacostracan, it can hardly be regarded as a primitive Crustacean; and since we meet with abundant examples of centrolecithal segmentation both above and below Lucifer, we can not regard the Lucifer egg as ancestral or as the unmodified descendant of an ancestral type of egg. "We must, therefore, believe that the egg of Lucifer has been simplified by the loss of the greater part of its food yolk."

It is to be regretted that Professor Brooks did not find material sufficiently abundant to warrant the sacrifice of some of the segmenting eggs for sections; for until this is done we can not be certain of the origin and relations of the mesoblast and entoblast in this extremely interesting species. A careful study of the subject both in Lucifer and Sergestes would form a very valuable and much needed contribution.*

It seems to me quite probable that we have in Lucifer a repetition of what occurs in Homarus and Alpheus, and that the yolk-bearing cell corresponds to the inwandering or delaminated cells, which occur in the lobster at the close of segmentation. In each case they arise by transverse division from the superficial cells of the blastophere. In each case, also, they appear just before invagination, and migrate into the segmentation cavity. The differences are that in the lobster, for instance, the segmentation cavity is already filled with yolk; the centripetal cells are numerous, and they do not necessarily come from that point on the surface which corresponds to the point of invagination or ingrowth. As to the comparative history of the two cells in the two cases little

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* Since this was written Professor Brooks has announced in his report of the work of the marine laboratory of the Johns Hopkins University, that he has recently obtained the eggs of *Lucifer* in abundance at Jamaica, and is now engaged in studying its embryology.

can be said. Brooks thought that in Lucifer they represented the food yolk, although this was not settled. In Alpheus these cells are later joined by great numbers of wandering cells at the invagination period, and out of this common stock, so far as we can determine, both mesoblastic and entoblastic organs are developed. In Homarus, on the other hand, the invaginate cells unquestionably degenerate.

The eggs of *Scyllarus* and *Palinurus* have not been thoroughly studied, so far as I am aware. Dorhn (14), however, has figured the eggs of *Scyllarus arctus* in late stages of yolk segmentation, and in surface view they resemble, at this time, the ordinary Decapod type. We have as yet no knowledge of the segmentation of the Stomatopods.

The relations of the different varieties of segmentation which are met with among the Decapods, may be expressed by the following table:

Segmentation of the Decapod egg.

I. Total: regular: segmentation cavity present.
- (I). *Lucifer typus.*
- Segmentation of yolk at first total, afterwards partial.
  - (1) *Palæmon.*
  - (2) *Eupagurus prideanii.*
  - (3) *Atyephyra compressa.*

II. Partial: centrolecithal (yolk pyramids): segmentation cavity filled with yolk.
- (II). Segmentation of yolk.
  - Regular.
    - (1) *Penæus.*
    - (2) *Crangon.*
    - (3) *Stenopus hispidus.*
    - (4) *Alpheus saulcyi.*
    - (5) *Pontonia domestica.*
    - (6) *Hippa talpoides.*
    - (7) *Palæmonetes vulgaris.*
    - (8) *Callianassa mediterranea.*
  - Irregular.
    - (1) *Homarus americanus* (yolk segmentation at first irregular, but later regular or nearly so).
    - (2) *Alpheus minor.*

Of the Thoracostraca, the Schizopods undoubtedly depart widest from the common decapodal type of segmentation. Nusbaum (45) thus describes the process in *Mysis Chameleo*: The protoplasm—that is, the segmentation nucleus, with its protoplasmic body—retreats to a point at the surface of the egg. The nucleus then suffers division, and the protoplasm becomes differentiated into an outer striated zone containing a single nucleus, and an inner granular zone with one or more nuclei. The single external nucleus divides and gives rise to a small blastodermic disk, formed of a single layer of hexagonal cells. From the internal nuclei and protoplasm a small number of nuclei are produced under the blastodermic disk. The free cells below the disk are the products (1) of the nuclei and formative protoplasm of the deeper layer, and (2) of the cells of the upper layer or blastodermic disk. While a solid accumulation of cells is thus being formed below the disk, the superficial cells gradually extend on all sides and inclose the egg. The thickened disk marks the *ventral* side of the embryo. It divides into a median, caudal, or *abdominal plate*, and two lateral plates, the *ventral bands*. Yolk cells which were not present up to this stage, now arise by migration from the abdominal plate.

The segmentation of the Schizopod is especially interesting, since it agrees so closely with that described in certain Isopods and Myriapods, and resembles also the segmentation of Arachnids.

Bobretyky's observations on *Oniscus* (5) need to be repeated, and especially in the early stages. According to this observer the earliest phase of segmentation was characterized by the anomalous withdrawal of the egg protoplasm to the surface, where it accumulated in a distinct body, and underwent segmentation. A disk of large columnar cells was thus formed, marking the ventral surface of the embryo. The cells spread with the thickening of the disk, until they inclose the entire egg. The superficial cells form ectoblast, the rest entoblast and mesoblast.

Morgan (41) has described a form of segmentation in *Pycnogonids* which resembles that of the Decapod. Here the invagination (which leads to the formation of the stomodæum) is preceded by the delamination of endoderm cells from the blastosphere, very much as in Alpheus, if we may regard the yolk cells as primitive endoderm.

In *Agelæna*, Locy (37) found the unsegmented egg to contain a central nucleus and protoplasm, united by a fine network to a peripheral protoplasmic layer, the blastema. The nucleus divides, and its products pass gradually into the blastema, which is used up in forming the blastoderm.

Bruce (10) speaking first of Bobretyky's work, thus describes the formation of the blastoderm in Lepidoptera:

In the earliest stages he found four amœbiform cells in the yolk, situated in pairs at opposite ends of the egg. Later the blastoderm is formed by a multiplication of these cells; according to Bobretyky it is not formed simultaneously over the entire surface of the egg, but is laid down first at one or more points on the surface. This type of segmentation can not strictly be called entolecithal, inasmuch as the cells are not, in the earliest stages of segmentation, at the surface inclosing the yolk. All the primitive undifferentiated cells do not, according to Bobretyky, reach the surface to form the blastoderm, but some remain centrally located as yolk cells after the formation of the blastoderm. The earliest stages of segmentation observed in *Thyridopteryx* showed several amœbiform cells in the yolk in each cross section.

In *Thyridopteryx* the blastoderm is first formed in a given area on the surface, afterward completely inclosing the egg, but in this particular closely related insects seem to differ.

Heider's recent observations on *Hydrophilus* (24) show that numerous nuclei which originate from segmentation, do not reach the surface to enter into the "Keimhautblastem," but remain in the yolk as yolk cells.

The segmenting egg of *Julus terrestris* is described by Heathcote (19) as a syncytium. Segmentation is at first central, and the resulting nuclei are united by strands of protoplasm. Upon reaching the surface they spread themselves over it to form a blastoderm. The blastodermic cells are united to each other by strings of protoplasm, and to the cells of the yolk. The entire egg is thus pervaded by a network of protoplasm. The yolk cells are regarded as entoblast, and give rise to the "keel" or thickened blastodermic plate. This stage, characterized by a thickened blastodermic disk, keel, or cumulus, probably corresponds to a similar stage which is met with in Schizopods, Isopods, Myriapods, to the primitive cumulus in Arachnids and the ventral plate which suffers invagination in some insects. Possibly it corresponds also to the invagination plus the thickened ventral plate of Alpheus and Homarus.

Possibly we have in Astacus and Homarus an approach to the mesoblastic type of segmentation, such as is found in Mysis. This would be reached in Astacus if the protoplasm (which according Skimkewitch passes at once to the surface) should in the course of division build up a disk, instead of diffusing itself over the egg. A similar result would be achieved in Homarus if the belated cells should not reach the surface at all, and if those which are first to appear should not diffuse over the egg, but segment to form a thickened plate.

Balfour says, in speaking of forms like Penæus:

It is probable that *not* all the nuclei which result from the division of the first segmentation nucleus become concerned in the formation of the superficial blastoderm, but that some remain in the interior of the ovum to become the nuclei of the yolk spheres.—(*Comp. Embryology*, Vol. I, p. 113.)

This, I think, is an error, and that what is true of a number of forms, as Alpheus, Crangon, Homarus, probably expresses the rule for the Decapods, that all the egg protoplasm enters into the peripheral cell layer. Exceptions to the rule may, however, occur.

The use of the term *centrolecithal* to express the relations of the protoplasm and the yolk in the egg of Arthropods is not beyond criticism, but the strict application of a single term is clearly impossible. The ground of any objection is sufficiently covered by Balfour, in emphasizing the fact that *it is the centrolecithal condition which is eventually attained.* He says:

As might be anticipated on the analogy of the types already described, the concentration of the food yolk at the centre of the ovum does not always take place before segmentation, but is sometimes deferred till even the later stages of this process.—(*Comp. Embryology*, Vol. I, p. 110.)

In most cases the protoplasmic segmentation is at first *central*, or, as Kingsley points out, ectolecithal, and then, after passing through the intermediate stage, it is finally centrolecithal.

The question as to whether the products of the segmentation nucleus before the yolk is involved, are to be regarded as independent *cells* was raised by Balfour, who, in reference to Bobretyky's work on the embryology of insects, says:

He regards the nuclei surrounded by protoplasm, which are produced by the primitive segmentation nucleus, as so many distinct cells. These cells are supposed to move about freely in the yolk, which acts as a kind of intercel-

lular medium. This view does not commend itself to me. It is opposed to my own observations on similar nuclei in the Spiders. It does not fit in with our knowledge of the nature of the ovum, and can not be reconciled with the segmentation of such types as Spiders, or even Enpagurus, with which the segmentation in insects is undoubtedly closely related.—(*Comp. Embryology*, Vol. 1, p. 119.)

This discussion seems to have arisen from a confusion of the morphological and physiological significance of the cell. The segmentation of the nucleus and its surrounding protoplasm is plainly the only important phenomenon, and the segmentatior of the yolk is not merely a secondary process, but in many cases a wholly unnecessary one, as we see in the early phases of many Decapods. In these cases the individuality of the yolk pyramid is temporarily sacrificed or subordinated to that of the true cell, which is surrounded by unsegmented yolk. Later, when the yolk has become divided, the yolk segment or pyramid is gradually reduced until we get the superficial, embryonic cell, with more or less definite boundaries. All the elements of the egg, whether superficial or amœboid, are clearly to be regarded as cells in a fundamental, physiological sense, as shown by the part which they play in the development of the embryo.

SECONDARY SEGMENTATION OF THE YOLK.

There are traces of a *secondary segmentation* of the yolk in Alpheus during the second, third, and fourth stages; that is, from the period of invagination to the outlining of the primary append- ages. The yolk spheres arrange themselves in spherical clusters or balls, so characteristic of the early development of nearly all the Arthropods. The yolk ball contains at least one yolk nucleus with perinuclear protoplasm and corresponds to a yolk pyramid, being a *cell* in the same sense as the latter. Various phases of this secondary segmentation may be seen by glancing over Pls. XXX– XXXV In one egg, which I sectioned just prior to invagination (Fig. 46), there appears a segmen- tation of the yolk around the central nuclei.

Bobretzky attributes a morphological value to the secondary segmentation of the yolk in Arthropods, supposing it to be connected with the spreading and final establishment of the ento- blast. The secondary yolk pyramids or giant endoderm cells, which form the lining of the midgut of the embryo crayfish, he compared with the *Dotterballen* of Oniscus and Palæmon. In Palæmon the food yolk breaks up into round or polygonal pieces soon after the blastoderm is formed, while in Oniscus certain cells pass into the yolk from the keel or germinal eminence and gorge them- selves with the yolk substance until they form large balls, which represent the endoderm (Darm- drüsenzellen). It is stated, however, by Nusbaum (44) that a part of the endoderm of Oniscus which gives rise to the gastric gland arises from primitive mesoblast, and in insects the endoderm is formed independently of the yolk cells. The history of the yolk cells and of the wandering cells will be discussed in another section.

VI.—CELL DEGENERATION.

The rapid and often extensive breaking up and final disappearance of embryonic cells in the course of Arthropod development is a very remarkable phenomenon, and strange to say, it has almost escaped attention up to the present time among the Decapod Crustacea. A study of this subject in Alpheus, Astacus, and Homarus has convinced me that the peculiar bodies described as secondary mesoderm cells in the crayfish (54) correspond to the degenerating, sporelike par- ticles which characterize similar stages in the development of both Alpheus and Homarus.

In some early notes on the development of Alpheus I called these nuclear fragments "spores" (22), but the term is inappropriate if we are dealing with cells in the process of dissolution, as is undoubtedly the case. The anomalous "secondary cells," which have been a sort of outstanding puzzle to embryologists, receive, in my opinion, a more reasonable explanation on the ground that they represent degenerating elements. This view is supported by a comparative study of embry- onic growth in other Arthropods.

Alpheus.—Degenerating cells are present in *Alpheus sauleyi* in considerable numbers when the nauplius appendages are budding and increase for a short time beyond this period. They continue in greater or less quantity until six to eight pairs of postoral appendages are formed, when they disappear from the embryo almost completely. They vary in size from small refringent particles to spherical masses as large as ordinary nuclei, or even larger. Many nuclei, instead of having the normal appearance, in which the chromatin has the form of a coil or a reticulum with stellate

nodules in its meshes, begin to show retrogressive tendencies. They sometimes appear swollen out to an unusual size, and their chromatin is aggregated into a single large ball, which may become vesicular and strongly refractive. The chromatin ball is sometimes of large size, central in position, and stained intensely, suggesting strongly the nucleus of a blood cell, or it may stain so faintly as to be hardly recognizable. Again, it may be eccentric and attended by one or more smaller balls, or the nuclear body may be filled with numerous coarse grains. These bodies then recall yeast cells in process of producing ascospores. As in the yeast cell, the wall of the nuclear body seems in many cases to break down and thus set free into the yolk the naked, spore-like masses of degenerating chromatin.

In Figs. 21 and 32 (Pls. XXVII, XXIX), taken from the egg-nauplius embryo, we see various stages of this process. Around the stomodæum, and within or near the pockets of the antennæ and mandibles, there are large numbers of these pseudo-spores. Some are small chromatin balls (s), which combine actively with hæmotoxylon, while others stain feebly or are quite unaffected by the dye, and resemble straw-colored particles of vesiculated and altered food yolk. Below and to either side of the stomodæum there is a granular residue (Fig. 118, A. Y. S.), composed of yolk and nuclear matter in various stages of chemical degeneration.

The ordinary nucleus in the resting condition is generally characterized by the presence of balls, nodules, or granules of various sizes, which represent chromatin constituents of the nucleus. Under high powers these usually appear as stellate masses suspended in the nuclear reticulum. A number of representative nuclei are shown in Fig. 18. They are all drawn to scale and are taken from the egg-nauplius series under review. It is so plain that it is hardly necessary to state it, that the nuclear fragments in these bodies, c, f, or h for instance, correspond to similar fragments which occur free in the yolk. The larger nodule in the nucleus f resembles figure b, except that the latter is surrounded by an outer light zone. This zone is often very large and not as sharply defined as in the drawing. Again, figure c resembles figure b, except that the outer light zone is larger in c and the chromatin or stainable residue has nearly disappeared. I regard the bodies b and c as masses of degenerating chromatin which have escaped from a disrupted nucleus or cell. In c the retrogressive changes are furthest advanced. Finally, when the chromatin or stainable matter has been completely disorganized, there is left a vesiculated mass which stains very feebly or not at all, and resembles yolk (Figs. 102, 107, A. Y. S.). Nearly every drawing of the egg-nauplius stage shows one or more bodies resembling b in Fig. 18 (see Fig. 21, s, s^2, and Fig. 32, s^1). In many cases the outer light zone is cloudy, as already stated, and the element resembles a spherule of yolk with a ball of chromatin imprisoned in it. These bodies bear a certain resemblance to blood cells, but this resemblance is probably transitory, and after a careful study of a great many stages I can find no direct evidence that they are ever reorganized into new tissue. The blood cell of the adult is shown in Fig. 19 and that of an embryo in Fig. 35. In each case it consists of a deeply staining granular nucleus and a clear cell body. The nucleus corresponds to the apparently naked yolk nucleus (Fig. 35, Mes.; Fig. 18, etc.) and the cell body to the perinuclear protoplasm, which is present, though often of small quantity, in the wandering cells. As we have already shown, it is probable that the blood cell (Fig. 35, B. C.) is derived directly from the wandering cell (Mes.), and that the characteristic appearance of the cell protoplasm is a rapid acquisition.

Degenerating nuclei may be seen by glancing over the plates (Pls. XXXVII–XXXIX and XLI–XLIV), but it is unnecessary to refer to these in detail.

The dorsal plate or dorsal organ (?) furnishes a most striking instance of the degeneration of cells (Pl. XXIX, Fig. 36; Pl. XLVI, Fig. 153). Its cells seem to originate from the ectoblast, with accessions possibly from the wandering cells. After the slight ingrowth, which takes place in the middle of the plate, many of the cells pass into the depths of the egg and break up into meteoric clouds of small deeply staining particles.

To sum up the previous remarks which relate to the appearance of these bodies in Alpheus, degenerating cells are first seen in Stage IV, and in the following egg-nauplius stage they are abundant. In Stage VII (Pl. XLIV, Fig. 131) they are still present, and in Stage VIII there is a fresh irruption of degenerating products into the yolk, arising from the centripetal cells of the dorsal plate. At a slightly later period they have almost wholly disappeared. Even as late as in the tenth stage a few chromatin granules can be seen in the region of the dorsal plate.

CELL DEGENERATION AND AMITOSIS IN ALPHEUS MINOR.

In the segmentation of *Alpheus minor* there are numerous cases which illustrate the fragmentation and apparent degeneration of nuclei. A nuclear body sometimes seems to be breaking down and discharging a large number of sporelike balls or grains of chromatin (Fig. 26, Pl. XXVIII, *S. C.*). This probably represents an element in process of dissolution. If this be true, the clear area is similar to the plasmalike mass shown in Fig. 13, in which the nuclear bodies have disappeared from view. Clear areas are sometimes seen containing only minute particles of nearly dissolved chromatin. The large swollen bodies, like those shown in Fig. 23, each with a single, often minute, ball of chromatin, certainly remind us of somewhat analogous structures which can be seen at a later stage in the crayfish.

The egg sectioned in Fig. 12, Pl. XXVI, contains eight large nuclear nests or shells. The nuclear masses are seen to be very irregular in size, and in some instances the nuclei are unquestionably breaking down. In other cases the egg contains a smaller number of large, very irregular masses of nuclear material, consisting of a fine network, with chromatin granules in suspension. These nuclear masses sometimes appear to be constricting into two parts. The swarm of small nuclei, like that shown in Fig. 13, I interpret, as already stated, as arising by a kind of budding of the large nuclear mass and the subsequent constricting off of the buds.

It is very interesting to find that in this case, possibly the only case of amitotic cell division in the segmentation of the ovum yet recorded, the indirect division of the nuclei is followed to some extent by a degeneration of these bodies. This lends some weight to the view that indirect division is connected with the senescence of nuclei.*

The nuclei of the large endoderm cells lining the mesenteron in the crayfish appear to divide directly, and in this case the process is again followed by dissolution. In may, however, prove that we have here a case of multiple karyokinesis, similar to that which I have recently observed in the superficial cells of the lobster embryo, where nests containing from four to sixteen closely packed nuclei are very characteristic of certain early stages.

CELL DEGENERATION IN ASTACUS AND HOMARUS.

Homarus americanus.—I find certain bodies in the lobster essentially similar to those which characterize the Alpheus embryo. If a longitudinal section of the egg nauplius of Homarus be compared with Fig. 125, which represents a similar section of a similar stage of *Alpheus saulcyi*, we find not a few chromatin balls, but a meteoric swarm of granulated bodies and naked chromatin grains coextensive with the embryo, and reaching a considerable distance into the yolk amid the scattered mesodermic cells, but perhaps most abundant, as in Alpheus, in the neighborhood of the stomodæum. A long nebulous train of yolk spherules and granules extends forward a considerable distance in front of the mouth, and is especially marked in front of the optic disks. The labrum and the folds of the appendages which contain yolk abound in these peculiar granulated bodies. In less number they occur in connection with the endoderm cells, which have at this stage extended through a greater portion of the egg and form a series of irregular sacs filled with yolk. These yolk masses, with their surrounding sheet or advancing column of cells, correspond to the endoderm sac of the crayfish. In the latter the peculiar cell bodies also occur.

If one now examines very thin sections under high powers, we find that the granules and the granulated bodies correspond in general to the structures we have found in Alpheus. The chromatin grains appear sometimes as naked masses in the yolk; sometimes they possess a distinct protoplasmic body. The degenerating chromatin stains either very intensely or faintly and is often vesiculated; that is, it appears as a hollow shell. Under favorable conditions it is easy to demonstrate the fact that these bodies surround particles of yolk, and occasionally they have a crescentic shape, when it can be clearly seen that they are enwrapping a yolk spherule. This vitellophilus

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* While this memoir was in press a paper was received on *Amitosis in the Embryonal Envelopes of the Scorpion*, by H. P. Johnson, (Bulletin of the Museum of Comparative Zoölogy, Vol. XXII, No. 3). Only two instances of direct cell division in the embryo of Arthropods are recorded: that found by Carnoy in the ventral plate of *Hydrophilus piceus* and the case which Wheeler has described for the blastoderm of *Blatta germanica*. Mr. Johnson finds that degeneration does not always follow upon indirect cell division, as in the case of amitosis in the testicular cells of certain Isopods.

characteristic is certainly not so apparent in Alpheus, yet I believe that in this form it is present in some stages, though in a less marked degree.

Astacus (?)—I have studied several critical stages in the development of the crayfish, critical at least so far as the appearance of degenerative products is concerned, with an eye to comparison with Alpheus and Homarus.* The youngest set of embryos corresponds nearly to Reichenbach's stage E, but differs from it in some details. Rudiments of five pairs of appendages are present, the two maxillæ being seen between the mandibles and the thoracic-abdominal process. None of the appendages, however, are folded. The mouth is seen on a line between the first and second pair of antennæ.

The bodies which Reichenbach calls "secondary mesoderm" occur in abundance in or near the wall of the endoderm sac next the embryo. They also abound in the yolk under the ectoderm, and are most numerous in the area extending from the optic invaginations to the mouth or slightly behind it. In this respect they recall the distribution of similar bodies in Alpheus and Homarus.

I wish to call attention to the fact that at this stage none of my sections show a cavity in the endoderm sac, as is represented by Reichenbach (compare Taf. VIII, 54), and the endodermal yolk segments or pyramids do not always possess completed walls. To what extent this appearance is normal, and to what extent due to the action of reagents, I can not at present say. These eggs were treated with hot water and corrosive sublimate. The endodermal nucleus is surrounded by a thin layer of protoplasm, which works its way amid the yolk so as to practically surround a pyramidal mass. This strongly recalls the serpentine manner in which the endoderm cells creep through the yolk in Homarus. Whether these cells in Astacus are simply migrating in a column or sheet, spreading gradually towards the periphery of the egg, as in the lobster, cannot be decided from the material at my command, but it is a point of considerable interest in its morphological bearings. The endodermal cells probably multiply indirectly, but I saw no nuclear figures in my sections, and they appear also to divide directly, independently of the yolk pyramids as Reichenbach has described, giving rise to the chromatin balls and granulated elements (compare Fig. 20) but, as pointed out above, this appearance may be very deceitful. This process is most marked in the endodermic area noticed above, underlying the anterior half of the embryo. Here we see great numbers of the bodies of varying size, both within and without the domain of the endoderm cells. They closely resemble the vitellophagous elements which I have described for the lobster, and possibly they attack the yolk in a similar way. Where they are thickest the yolk is comminuted and shows traces of profound chemical change. In the midst of the altered yolk one can discover very faint outlines of vesicular bodies which exhibit but slight reaction to the stain. These I regard as degenerated cells.

The next stage of Astacus which I have studied corresponds nearly to Reichenbach's stage G. Eight pairs of appendages are present, and there are rudiments of a ninth pair. The first and second maxillæ appear as distinct buds, while the third pair of maxillipeds is represented by a proliferating cell area only. The extremity of the abdomen is not bifid.

In the central part of the endodermal sac there is a coagulable fluid which comes in close relation with the posterior end of the embryo. The endodermal cells laterally have quite or nearly reached the ectoderm, while dorsally they fall a little short of the surface. The yolk within the confines of the endoderm has an irregular, pyramidal, or radial cleavage. Centrally the yolk blends with the serum-like fluid, in which occasional granules or balls of chromatin may be found. Small spherical elements (like those represented in Fig. 18, a, b, c, or k, k,[1] Fig. 20), containing a single chromatin ball or several balls, occur not only in the yolk underneath the ectoderm and in the vicinity of the endodermal nuclei, *but also in the central yolk of the endoderm sac*, at various levels below the endodermal nuclei. This is a point of some interest in connection with the fate of these bodies. They wander not only peripherally but centrally. Rarely we meet one which is three or four times the average size, having a small chromatin spherule in its center. In later stages they are present in far less numbers.

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* For the opportunity of studying the crayfish development at this time I am indebted to the kindness of my friend, Dr. William Patten, who sent me a number of important stages collected at Milwaukee.

Reichenbach thus summarizes his observations on the "sekundäre Mesodermzellen:"

Die fraglichen Elemente sind als Zellen zu deuten, deren Kerne nicht immer die Beschaffenheit gewöhnlicher Zellkerne haben, dieselbe aber früher oder später erlangen (Fig. 20, m, m², Plate XXVII). Sie nehmen ihren Ursprung innerhalb derjenigen Entodermzellen, welche die ventrale Wand des Urdarmsäckchens zusammensetzen durch eine näher zu erforschende Art endogener Zellbildung, bei welcher die in der Mehrzahl in den Elementen des Entoderms vorhandenen Kerne eine wichtige Rolle zu spielen scheinen. In den dem Stadium D vorangehenden Entwicklungsperioden hat jede Entodermzelle meist nur einen Kern; dies trifft auch noch zum Theil für Stadium D zu. Bald vermehren sich aber die Entodermkerne ganz erheblich und endlich beginnen die sekundären Mesodermzellen aufzutreten. Wenn eine grössere Zahl der sekundären Mesodermzellen in den Entodermelementen liegen, so scheint das Kernmaterial verbraucht zu sein. Es wandern nun aller Wahrscheinlichkeit nach diese Zellen, deren Kerne anscheinend noch in der Metamorphose sich befinden, aus dem Entoderm aus und begeben sich unter die Embryonalanlage. Die betreffenden Contouren des Entoderms lassen oft noch Spuren dieser Wanderung erkennen. Ob sie wirklich aktiv auswandern oder auch ausgestossen werden, ist nicht festzustellen gewesen. Sie begeben sich nun unter die übrigen Mesodermzellen und sind bald nicht mehr von ihnen zu unterscheiden. Aus diesem Grund führte ich für sie den Namen "sekundäre Mesodermzellen" ein, während die älteren Urmesodermzellen als primäre bezeichnet werden. Da die letzteren die Tendenz zeigen, zu kompakteren Massen zu verwachsen, so darf man wohl vermuten, dass die sekundären Mesodermzellen die Blutzellen liefern werden (54, p. 36).

It is interesting to notice that in Alpheus, Astacus, and Homarus degenerating cells appear in greatest force at about the egg-nauplius stage, and from that time on their numbers begin to wane. In Astacus, Reichenbach first noticed the "sekundäre Mesodermzellen" in stage D (that is, when the optic disks, the thoracic-abdominal plate, and the mandibles are outlined), which nearly corresponds to Stage IV of Alpheus. In stage D the bodies in question are most abundant under the optic disks (Kopflappen) and in the region of the upper lip, but become more generally distributed in the egg-nauplius.

According to Reichenbach, "gastrulation" takes place after the optic disks are formed, but unfortunately his paper is incomplete at a very important period, namely, from the late yolk-pyramid stage of segmentation, when the protoplasm is at the surface, to the time when an embryonic disk or plate (Entodermhügel or Entodermscheibe) has been formed. It is impossible, therefore, to follow the history of the so-called "white yolk elements." He says of the latter:

Sie bestehen aus protoplasmatischer, feinkörniger Substanz und enthalten vacuolenartige Einschlüsse, die ihnen ein schaumiges Aussehen geben; ich habe sie als weisse Dotterelemente bezeichnet. Sie liegen entweder dicht unter dem Blastoderm oder im Centrum des kugligen Eies und verschwinden sehr bald (Op. cit., p. 7).

According to my view these bodies correspond to the vesiculated elements (m, Fig. 20), and both represent cells in process of dissolution. If Figs. 18 and 20 are compared (the latter being a copy of Reichenbach's Fig. 67) we will find a striking correspondence between these peculiar cell products in both Astacus and Alpheus, a correspondence which is even more marked when the comparison is made with the lobster.

Reichenbach emphasizes the statement that naked balls of nuclear material never occur free in the yolk outside the endodermal sac. In this yolk they always have a "cell body" as K, Fig. 20. It is an easy matter, however, to distinguish naked masses of chromatin, minute spherules, or smaller granules in the yolk of both the lobster and Alpheus.

My studies of the lobster are not yet completed, but from the observations which have already been made I draw the following conclusions: In Alpheus, the lobster, and the crayfish similar bodies make their appearance at nearly similar times and play a similar rôle. They are derived from all three layers of the germ, and in Alpheus minor degenerative products make their appearance in the segmentation stages. They tend to break up and ingest the yolk and to produce in it a chemical change, possibly in order that it may be more easily assimilated by the other embryonic cells. Having performed this task they degenerate; they are converted into a substance resembling yolk and function as nutrition. That any play a formative rôle, giving rise to blood cells for instance, as Reichenbach supposes, there is no direct evidence. The vitellophagous function seems to be in abeyance in Alpheus, but in all cases the yolk is comminuted and chemically changed in the neighborhood of these bodies. Nusbaum (45), following Morin, believes that the "white yolk elements" arise from the segmentation nucleus and migrate to the surface of the egg; that they give rise to the "secondary mesoderm," which are taken up along with the yolk by the amœboid, endodermal cells. This is reversing the account, and, in so far as the origin of the "secondary mesoderm" is concerned, it is not supported, so far as I am aware, by a single observation.

Ishikawa (27) finds in Atyephyra after the close of the invagination stage, certain proto-plasmic elements under the ectoblast, which he thinks may correspond with the " white yolk ele-ments " just referred to, and he also identifies " secondary mesoderm cells," but does not trace their origin or function.   They are " small granules," easily stained by logwood solution, and some are of considerable size and have a clear cell outline.   "These are mostly aggregated in the cephalic region between the involutions of the ectoderm cells, but are also found in all places."   In time of appearance and in their position, he says they seem to correspond to the " secondary meso-derm cells" of Astacus.   This short notice with his figures leaves little doubt that these bodies are similar to those just described in Alpheus and Homarus.   Fig. 62 of his paper represents a longitu-dinal median section of the egg-nauplius, and may be compared with the same stage of Alpheus (Figs. 104, 105), with respect to the general character and appearance of the degenerating cells.

I have noticed similar nuclear fragments in the egg-nauplius of a crab (Fig. 113, Pl. XL), and Lebedinski (34) has described "secondary mesoderm " in the embryo of the Mediterranean sea crab, *Eriphia spinifrons*. According to this observer they are found in all stages from the "gastrula" on, to the egg-nauplius; they are derived from ectoderm, and probably give rise to blood cells. In the stage with one pair of maxillipeds these elements are in active proliferation :

Man findet, die Zellen desselben bieten verschiedene Momente und Zustände des Zerfallens dar ; dieses Zerfallen der Zellen steht in genauen Zusammenhänge mit der Entstehung der Blutkörper.

He further says :

Ueber die Bildung des Blutes kann ich nichts bestimmtes mittheilen. Im Stadium des ersten Paars kieferfüsschen sind die ersten Blutkörperchen vorhanden, welche zum ersten Mal im Bereiche des Herzens vorkommen, wo sich auch am frühesten das sekundäre Mesoderm rückzubilden beginnt.

From these quotations it appears that the " secondary mesoderm " shows signs of degenera-tion, and its conversion into blood cells is an unverified inference.   It seems more probable that the structures in question correspond with similar bodies already noticed in Alpheus, Homarus, and other Decapods, and that in all cases they have to do primarily with the dissolution and not with the construction of cells.

Wheeler (67) in his careful paper on the development of the Cockroach and Potato beetle (*Blatta germanica* and *Doryphora decemlineata*) describes an interesting case of the decomposition of nuclei, which bears a close analogy to what takes place in Alpheus and probably also in Astacus.   In Doryphora two masses of endoderm are found, one under the stomodæum the other under the caudal plate.   At both these places numerous cells which originate in the endoderm pass into the adjacent yolk and disappear.   The process of dissolution is described as follows :

The karyochylema becomes vacuolated, probably with substances absorbed from without, to judge of the larger size of some of these nuclei, while the chromatin ceases to present the threadlike coil and becomes compacted into irregular masses between the vacuoles. Finally the vacuoles fuse and the masses of chromatin, formally numerous, agglomerate to form one or two large irregular masses which usually apply themselves to the wall of the clearly vesic-ular nucleus   *   *   *   In the last stages seen the masses of chromatin lie between the yolk bodies, all other portions of the nucleus having disappeared.   They still take the deep red stain, but finally become comminuted and disappear in the intervitelline protoplasm.

The vesiculated elements recall similar bodies which appear in Reichenbach's plates.   Thus the element *t*, Fig. 88 of Wheeler's paper, where the chromatin is applied to the walls of the nucleus, strikingly resembles nucleus *i*, Fig. 20 (see this paper), where the chromatin is similarly disposed around the wall of a vacuole.

Bruce (10) figures certain yolk cells undergoing what he considered to be endogenous cell division in an advanced embryo of a spider, and compared it with the endogenous cell division which Reichenbach describes as taking place in the endoderm cells of Astacus.

The disintegration which has been attributed to the leucocytes of the mammalian blood affords an interesting comparison with the phenomena which have been described for the Arthropod embryo.   Howell's careful observations (25) support the view that the multinucleated leucocytes are disintegrating cells.   " The leucoblasts enter the lymph stream, and eventually reach the blood as unicellular leucocytes."   Here they undergo changes, acquire amœboid movements, while the nuclei elongate, become constricted, and finally fragmented.   " The multinuclear stage   *   *   * is probably followed by a complete dissolution of the cell."   Howell adopts the highly reasonable

view that the nuclear fragments persist for a while in the circulation as the blood plates, and considers it probable that the latter take some part in forming the paraglobulin of the blood. If the blood plate is then a degenerate body, it may be compared to the spore-like masses of chromatin, which are discharged from the disrupted cells in the lobster or crayfish embryo.

VII.—THE ORIGIN AND HISTORY OF WANDERING CELLS IN ALPHEUS.

The wandering cells in Alpheus have a triple origin, from the blastosphere, from the invagination, and from the thoracic-abdominal plate. Those which arise from the blastula at the close of segmentation are, perhaps, the representatives of a primitive endoderm. Following the invagination, a thick pad of cells is formed, the ventral or thoracic-abdominal plate. From this plate a general migration of cells occurs on all sides into the yolk (Pls. XXXII–XXXV). While there is a great tendency to migrate to parts underlying the embryonic area, the cells nevertheless wander to all parts of the egg, even to those most remote from the embryo. The first of these wandering bodies which originate from the blastosphere have been called "primary yolk cells." The latter classes may be called "wandering cells." Since these classes can not be distinguished after a certain period, I refer to all cells which move about in the yolk and have no direct connection with the thoracic-abdominal plate, and the parts of the embryo in front of it as *wandering cells*. I have been somewhat at a loss to find a suitable term for these bodies, since there are obvious objections to the use of "yolk cells" or "yolk nucleus." Where these terms have been employed in the present paper, they must be understood to refer to the wandering cells which have been defined above. The term "embryonic nuclei" is used for convenience merely to discriminate the remaining nuclei of the egg from those of the wandering cells.

The object immediately in view is to determine the fate of these wandering cells, to ascertain what formative rôle they play while the mesoderm, and more particularly the endoderm, are being differentiated into definite cell layers. In the following account, cells which have parted all connection with the thoracic-abdominal plate and have entered the yolk are enumerated as wandering cells. In an earlier part of this paper I gave an account of the origin and supposed fate of the wandering cells, the general conclusion being that in the early stages (Stages III–V) they pass from the yolk to the embryo and to the extra-embryonic parts* of the egg, and contribute to both mesoblastic and entoblastic structures.

A number of friends to whom I showed my sections objected to this interpretation on the ground that these wandering cells could be regarded with equal probability as originating, in some measure at least, in the opposite way, that is, as budding from superficial cells not concerned with the thoracic-abdominal plate, and migrating into the yolk. A careful study of successive stages would not support this idea, but the objection could not be satisfactorily answered, and neither view could be readily proved. I therefore undertook a renewed and more precise study of the wandering cells in Alpheus, and I think that their fate has been definitely settled.

The number of wandering cells which occur in the yolk, and the number of "embryonic cells" (that is, all the other cells of the egg) have been enumerated in five different stages, including seven different embryos, from the period of delamination at the close of primary yolk segmentation to the early egg-nauplius condition (Stages II–V.) This covers the most important period so far as the wandering cells are concerned. The rate of increase of both wandering cells and embryonic cells has also been determined for the successive stages, and the data are given in Table I.

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* There is a certain convenience in thus referring to the embryo proper and to the less differentiated regions, while it is understood that all the cells constitute the embryo.

TABLE I.—*Showing the number of nuclei in yolk, and the number of other "embryonic nuclei," and the relative increase and decrease in these bodies from the close of yolk-segmentation to the egg-nauplius period.*

Stage.	Number of nuclei in yolk.	Increase in number of nuclei in yolk.	Decrease in number of nuclei in yolk.	Number of "embryonic nuclei."	Increase in number of "embryonic nuclei."	Total number of nuclei of egg.	Total increase in nuclei of egg.	Increase per cent of nuclei in yolk.	Decrease per cent of nuclei in yolk.	Increase per cent of "embryonic nuclei."
II. Delamination (Figs. 38–45, 46, Pl. XXX)	*34	......	—	284	......	318	......	......	......	
II. Invagination (a) Figs. 49–55, Pl. XXXI	*37	3	......	421	137	458	140	8	......	32½
(b) Figs. 49–55, Pl. XXXI	*37	3	......	430	146	467	149	8	......	34
III. Optic disks (Pls. XXXII, XXXIII)	199	162	......	†736	306	935	468	81	......	42
IV. First antennæ, mandibles (Pls. XXXIV, XXXV)	240	41	......	†915	179	1,155	220	17	......	20
V. Early egg-nauplius (a) Figs. 34, Pl. XXIX; 101–105, 107, Pl. XXXIX	199	......	41	†2,989	2,074	3,188	2,033	......	21	69
(b) Figs. 34, Pl. XXIX; 101–105, 107, Pl. XXXIX	128	......	112	†2,230	1,315	2,358	1,203	......	87½	59

* Primary yolk cells.
† Number obtained by method described below.

The distribution of the wandering cells and of the embryonic nuclei is also illustrated by a series of curves, constructed in the following manner: Each vertical row of the smaller squares corresponds to a section of the ovum (Sections Nos. 1, 2, 3, etc.), while each square in this row represents a single nucleus. The number of nuclei in a section is shown by the number on the line where the curve makes a bend or intersects the middle of the lower side of a square (nuclei Nos. 1, 2, 3, etc.). Thus where the descending line of the curve in Fig. 5 stops in section No. 2, making an angle in the fifth vertical square, counting from the upper base line, this implies that in the second section of the egg, corresponding to this vertical area, there were five nuclei which did not appear in the following or preceding section.

The number of nuclei were determined in the following way: Camera-lucida drawings were made of every section of a given series on thin paper and each nucleus was marked. Then, by superimposing upon each drawing the drawing of the section immediately following, every nucleus new to that section could be determined in the early stages with absolute certainty. The number of primary yolk cells and wandering cells were thus counted in all stages. In the older embryos (see numbers marked with dagger in Table I, Stage III–V) where this method became impracticable with reference to the total number of embryonic nuclei, their number was estimated in a different manner. The nuclei appearing in each section were counted and the total number of nuclear sections was thus obtained for the whole series. Then the percentage which the actual number of nuclei in the egg bore to the total number which appear in sections could be determined approximately by the method described above applied to a number of lateral sections, that is, by actual count of nuclei in a favorable part of the series. The percentage which the actual number of wandering cells bears to the total number appearing in section could be exactly determined and compared with the former estimated percentage. The percentage which involved the wandering cells was in the average of all stages a trifle the smaller, showing that the yolk cells were, on the average, a little larger than the other embryonic nuclei. In Stage II before invagination the superficial nuclei are the larger, while after invagination the difference is at first very slight indeed. In Stages III and IV the wandering cells are markedly the largest in the egg, while in Stage V they either equal or fall slightly below the size of the other embryonic nuclei.

This method presupposes a perfect series of sections of uniform thickness. These conditions were approximately fulfilled. The egg ($\frac{1}{2}$mm, or $\frac{1}{50}$ inch in diameter) was cut, on the average, into 57 sections, each section being $\frac{1}{114}$mm in thickness. The size of the egg, neither too small nor too large, rendered this species (called throughout this paper the Bahaman variety of *Alpheus heterochelis*) most favorable for study so far as technical difficulties were involved.

STAGE II.—*Close of yolk segmentation—Formation of yolk cells, followed by invagination.*—A surface view of this egg is given in Fig. 47, Pl. XXX. The curve (Fig. 5 of text) shows that the blastodermic cells are distributed very uniformly. In other words the embryonic area is not as yet marked off. The distribution of the primary yolk nuclei, of which there are exactly thirty-four, is shown in the constructed figure (Fig. 3), which represents the egg as it would appear if the yolk were transparent and the nuclei opaque. The distribution of these nuclei through the egg is given more completely by the curve (Fig. 4). The only questions which need detain us in this stage are, how do the primary yolk cells arise and from what part of the surface do they come? Karyo-kinetic figures, which abound among the surface nuclei, ought to furnish an immediate answer to the first question. In this egg no less than sixteen nuclei are met in various phases of division, fifteen of these belonging to the superficies and one to the central portion of the yolk. Clusters of two and rarely of three nuclei also occur at the surface, showing that cell division is active. In every case the cleavage is radial or perpendicular to the surface, and in no instance have I seen an unambiguous case of delamination (v. Pl. XXX). It is possible, however,
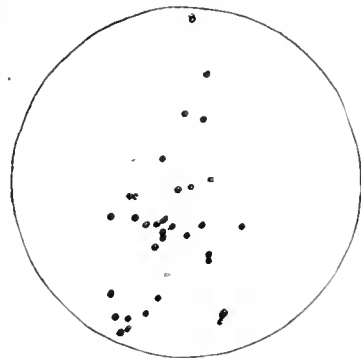
FIG. 3.—Diagram of egg in delamination stage, constructed from serial sections, showing all the primary yolk cells. For details, see Table I. Stage II (Delamination).
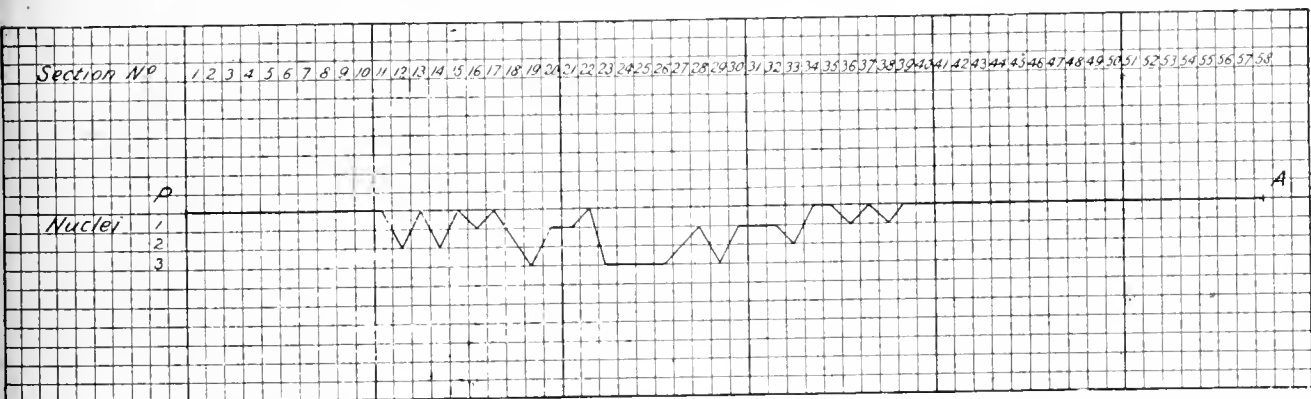
FIG. 4.—Curve constructed from serial sections, showing the distribution of the primary yolk nuclei in the egg represented by Fig. 3. For further details, compare Table I, Stage II (Delamination). A = Anterior; P = Posterior.
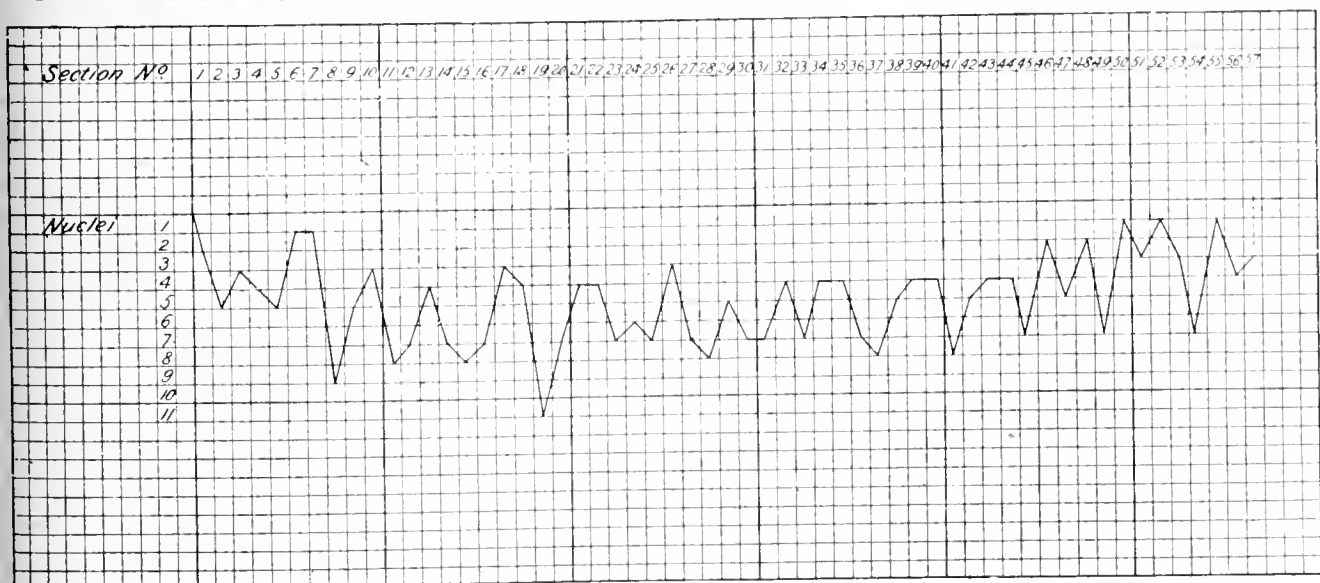
FIG. 5.—Curve showing the distribution of nuclei at the surface (that is, nuclei of the embryonic cells, exclusive of primary yolk cells) of the egg represented by Figs. 3 and 4. For details, see Table I, Stage II (Delamination).

that the primary yolk cells are formed in this way rather than by emigration, and that my failure to detect the actual process is due to the fact that I did not section exactly the right stage, the egg shown in Figs. 38–45 being a trifle too old. In Homarus the primary yolk cells arise by delamination, as I have already shown in a preliminary paper in the development of this form (23, Fig. 5).

Sections of this stage show conclusively that the primary yolk nuclei do not come from any one point on the surface, but that the majority of them may come from a restricted area of the egg. In Fig. 3 about two-thirds of the nuclei present are confined to the lower (ventral ?) surface of the egg. They are in various degrees of progress from the surface toward the central parts, which the majority have already reached.

FIG. 6.—Diagram of egg in invagination stage, constructed from serial sections, to show all the primary yolk nuclei present. For details of this egg, see Table I (II, a). Invagination. In point of invagination, nearly in the plane of the paper.

The formation of primary yolk cells is followed by the invagination and ingrowth of certain cells at the surface. The histology of the embryo at this phase is given in Pl. XXXI, and Fig. 6 (of text) is constructed from the entire series of sections to show all the primary yolk nuclei present. The plane of the paper (supposing the drawing to represent a sphere) nearly passes through the point of invagination (in.).

In order to test the accuracy of the method, two eggs of this stage were studied (a, II and b, II of Table I), and the results show a remarkable agreement. Thus there are exactly thirty-seven primary yolk nuclei in each egg, and the total difference in the number of embryonic nuclei in the two eggs is only nine. Curves were constructed to show the number and distribution of yolk nuclei and embryonic nuclei in both eggs, and the two are introduced here because of the striking similarity. Figs. 7 and 8 are constructed from the egg seen in Fig. 6 (II, a, of Table I). Figs. 10 and 9 represent corresponding curves constructed from the second egg (II, b). The two sets of curves tell exactly the same story in each case, and it is not necessary to dwell upon it.
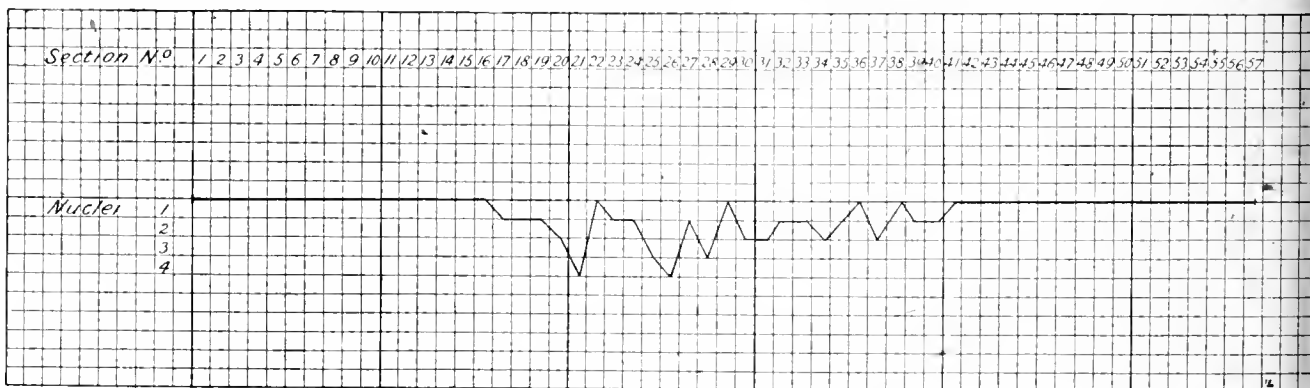
FIG. 7.—Curve constructed from serial sections, showing the distribution of the primary yolk nuclei in the egg represented by Fig. 6. (See Table I, Invagination stage, II, a.)

The bulk of the primary yolk nuclei are placed near the center. Of the thirty-seven nuclei in a, II, twenty-two are in the ventral (?) hemisphere of the egg, and fifteen in the dorsal. In egg b, II, twenty-one nuclei are situated in the ventral half and sixteen in the dorsal. Thus these yolk nuclei incline toward the ventral side of the egg, and hence, as already inferred, are probably derived in great measure from that part which corresponds to the embryonic area.

The curves showing the relations of the embryonic nuclei (Figs. 8 and 10) read from end to end of the embryo (posterior to anterior), the sections being transverse to the longitudinal axis. The greatest depression naturally occurs in the region of the thoracic-abdominal or ventral plate (Ab. P.), near the center of which is the point of invagination. In front of this there is a more extensive, but less depressed portion, corresponding to the embryonic area (E. A.). The number of cells entering into the ventral plate at this time are shown in Table II.
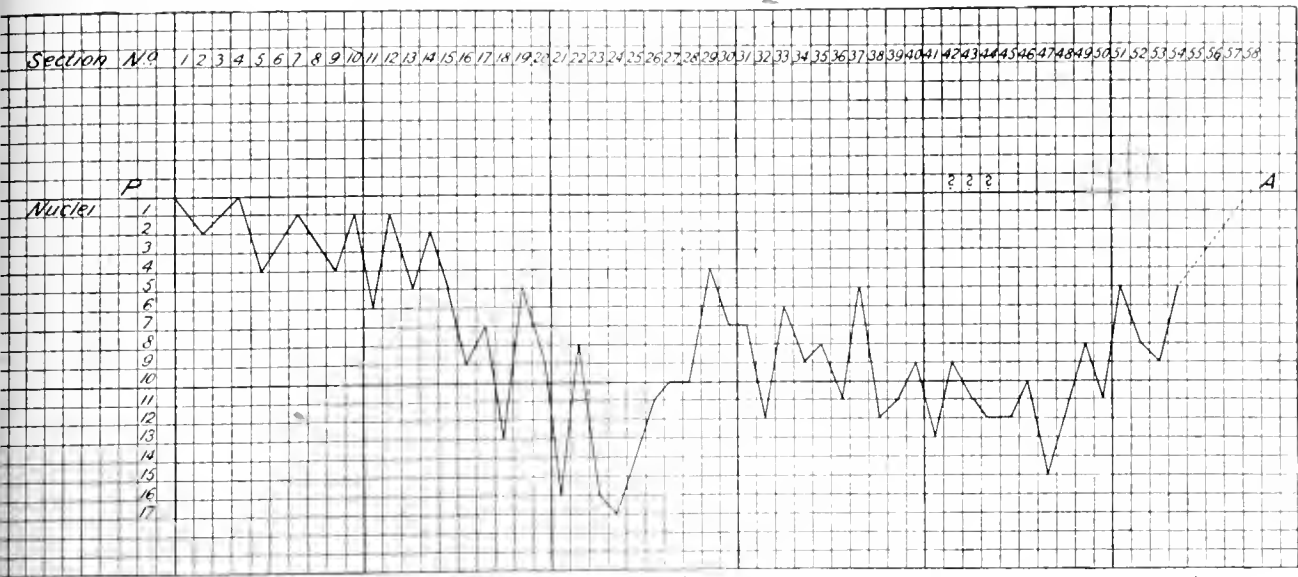
Fig. 8.—Curve showing distribution of all nuclei, exclusive of primary yolk nuclei, in the same egg as represented by Figs. 6 and 7. (See Table 1, Invagination stage, II, a.) A, Anterior; P, Posterior; Abp, Ventral plate; EA, Embryonic area.
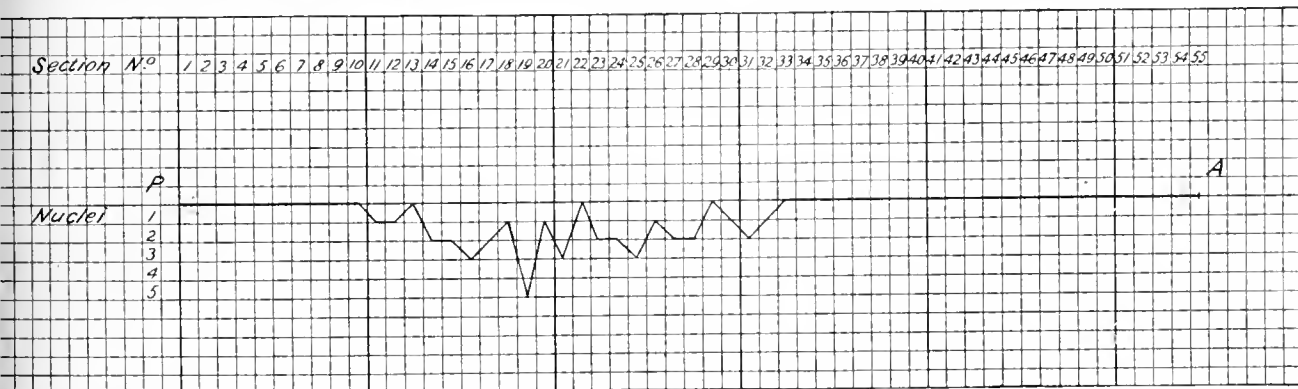
Fig. 9.—Curve showing the distribution of the primary yolk nuclei in the invagination stage, egg No. II, b, Table 1. (Compare with Fig. 7.)
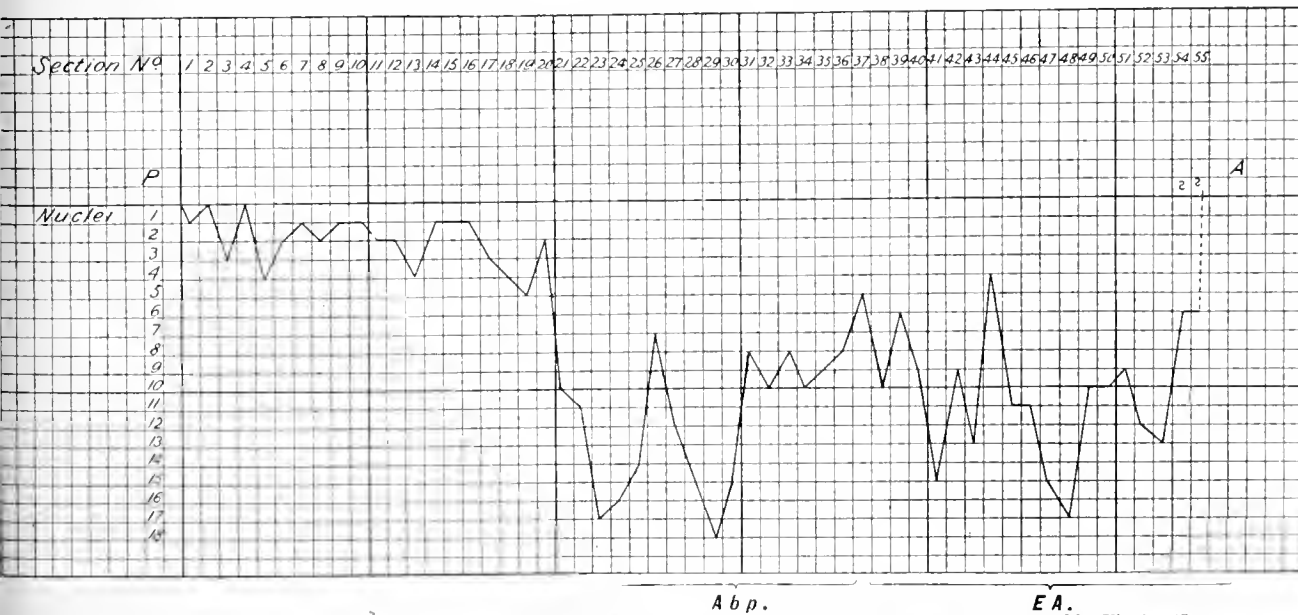
Fig. 10.—Curve showing distribution of all nuclei, exclusive of primary yolk nuclei, in the same egg as represented by Fig. 9. (See II, b, Table 1, and compare with Fig. 8.) A, Anterior; P, Posterior; Abp, Ventral plate; EA, Embryonic area.

TABLE II.

Stage.	Nuclei at surface of Ab. P.	Nuclei in Ab. P., below surface.	Total number of nuclei in Ab. P.	Primary yolk nuclei.	Remaining embryonic nuclei.	Total number of nuclei of egg.
a, II	56	60	116	37	305	458
b, II	52	48	100	37	330	467

Of the forty-eight to sixty cells which appear below in surface at this time in the ingrowing cell mass, a large number (twenty in b, II) are parting company with their fellows and beginning to migrate into the yolk. So that at this stage the primary yolk cells receive their first recruits from the ventral plate.

STAGE III.—*Optic disks and thoracic-abdominal or ventral plate.*—Wandering cells now become a very marked characteristic of the Alpheus egg (Pls. XXXII, XXXIII). We see by Table I that the total number of yolk nuclei has come up to 199, an increase of 81 per cent against an increase of only 42 per cent on the part of the other embryonic cells. In other words, the wandering cells have increased nearly twice as rapidly as the other nuclei of the egg. It is, perhaps, hardly necessary to point out that this rapid gain is due to at least four possible causes: (1) to the multiplication of primary yolk cells, probably the least important; (2) to the irruption into the yolk of invaginate cells, or cells derived from these, the most important source; and (3) to the multiplication of the latter in the yolk itself; and (4) to migration from the ventral plate, which is formed by a thickening about the point of invagination.

The curve showing the distribution of wandering cells at this stage (which is not figured) is nearly bilaterally symmetrical. The greatest depression is in the region of the thoracic-abdominal plate, while on either side of this there is a marked drop in the curve, answering to nuclei which underlie the optic disks and the parts behind them. (Compare Fig. 11 of text.)

A considerable number of cells have migrated to points near the surface both behind the ventral plate, to either side of it, and immediately in front of it (see Figs. 56, 58, 59, 60). A very few have wandered out to points just beneath the optic disks. Quite a number have started in the direction of the dorsal surface of the egg, but none have reached it.

STAGE IV.—*Rudiments of First Antennæ and Mandibles.*—This is the most interesting stage in some respects (see Pls. XXXIV, XXXV), since it is critical so far as the fate of the wandering cells is concerned.
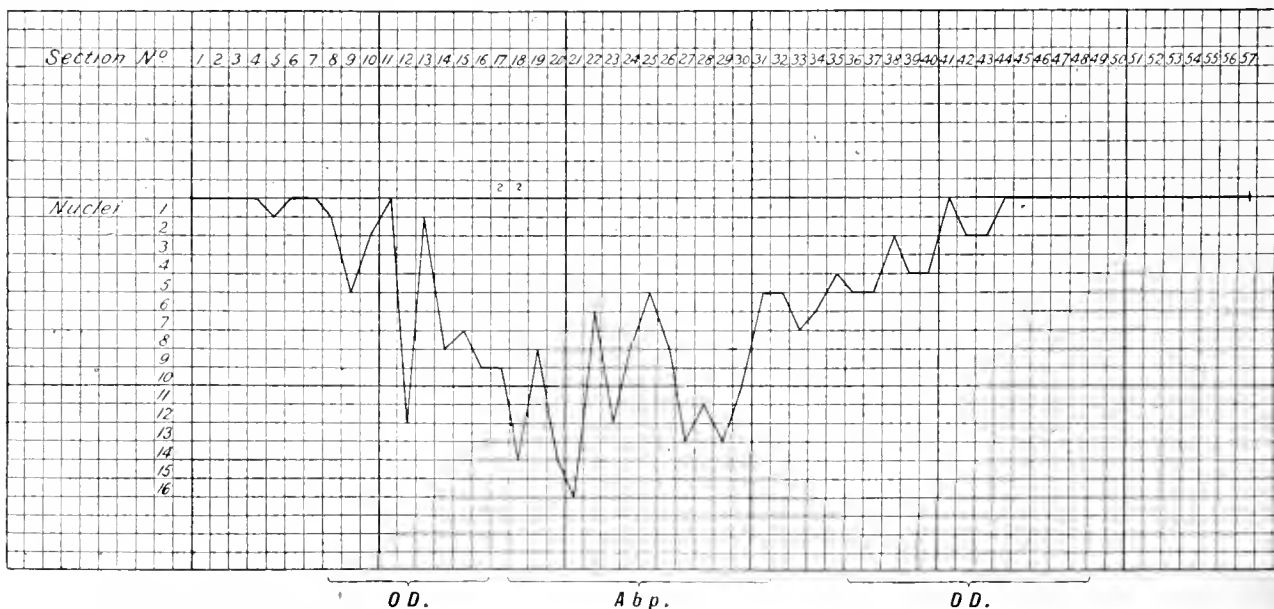
FIG. 11.—Curve showing the distribution of wandering cells in Stage IV, rudiments of first antennæ and mandibles present. (Compare Pl. XXXIV, and for numerical details, see Table I, Stage IV.) *Abp*, region of ventral plate; *O D*, Region of optic discs.

Table I shows the remarkable fact that the percentage of increase of wandering cells, which in Stage III was twice as great as that of other embryonic nuclei, has now dropped until it is actually less than the latter. This means that the wandering cells are multiplying less rapidly or that their numbers are being depleted. The relative increase of yolk nuclei from Stage II to III, and from Stage III to IV, namely, 81 per cent and 17 per cent (showing a marked falling off), is not specially significant, since these numbers depend largely upon the age of the embryo or time which elapses between successive stages. But this element does not enter into the relation which exists between the relative increase of wandering and embryonic cells in the same egg, expressed by 81 per cent and 41 per cent, respectively, in Stage III and by 17 per cent and 20 per cent in Stage IV.

The curve constructed from Stage IV (Fig. 11) shows the wandering cells much more widely diffused through the egg than at any earlier period. The thoracic-abdominal plate is no longer sharply marked off from adjacent parts, and a considerable number of nuclei underlie the optic disks.

In this egg there are thirty-seven nuclei in various phases of karyokinesis (Figs. 70, 75); two belong to the yolk, three to the deeper cells of the thoracic-abdominal plate, and the rest to the surface cells of the embryo. In the optic-disk region a very few cells appear to be delaminating; the rest are cases of radial division. Cell disintegration has not yet become a disturbing factor in the enumeration of cells. There are but two nuclei in the egg, one in the yolk, the other in the deeper part of the ventral plate, which show any traces of dissolution.

The above facts lead to the conclusion that the wandering cells are being rapidly depleted at this time, that they leave the yolk in considerable numbers and attach themselves to the growing embryo and to the extra-embryonic surface of the egg. They thus warrant our interpretation of a cell like yc, Fig. 70, or yc^1, Fig. 71, as a migrant from the yolk. While the wandering cells are being rapidly depleted, it does not of course follow that they never receive *any* recruits from *any* part of the egg without the limits of the ventral plate, and it requires no very elaborate calculation to show that wandering cells are making early contributions to the mesoblast, but the study of individual sections and the facts brought out in Table 1, prove beyond a doubt that the only cells which enter the yolk, up to this time, arise from one of the three sources already named, the blastoderm, the invagination, and the ventral plate.

STAGE V.—*Egg-Nauplius.*—The early egg-nauplius stage is represented by two individuals, one (V. *a*, Table I) cut in transverse and the other (V. *b*) in longitudinal vertical planes. Respecting the wandering cells we now notice: (1) that their numbers have markedly decreased; (2) that they are far more widely and evenly distributed; and (3) that many are close upon or in contact with the embryo or with the general surface of the egg.

In egg V, *b* (Table I) the number of yolk cells is only one hundred and twenty-eight, considerably less than are present in Stage III, a decrease of 87 per cent, while in the other egg the decrease is 21 per cent. On the other hand, the rate of increase of embryonic nuclei is greater than at any previous stage, 59 per cent in one egg and 69 per cent in the other. That this is not explained by a large interval of time existing between Stages IV and V is shown by the fact that during the period (Stage IV and Stage V, *b*, Table I) the total number of nuclei of the egg has scarcely more than doubled, while the percentage of increase of embryonic nuclei has more than trebled. Between Stages II, *a*, and III, on the other hand, the number of nuclei has nearly doubled, while the percentage of increase of embryonic nuclei has risen from $32\frac{1}{2}$ to only 42.

How is this very rapid increase in embryonic nuclei and coördinate decrease in wandering cells explained in the egg-nauplius stage? The conclusion reached in Stage IV applies here also, with a certain restriction. The problem is now not a simple one, since perturbations caused by the disintegration of nuclei appear to some extent in this stage. The diminution in the number of wandering cells is now due to two causes, to cell disintegration and to the gradual subtraction of cells from the yolk by emigration. Disintegration of cells occurs both in the yolk and in parts of the embryo. It is perhaps most marked near the line of contact of the yolk with the embryo. Yet the embryonic cells are meantime making a rapid net gain.

We are thus warranted in our conclusion that the wandering cells, which spread far and wide through the egg, play a formative rôle in development, to a large extent at least. This conclusion is rendered certain by the changes which ensue between Stages II and IV, already noticed. The

percentage of increase of wandering cells between Stages II and III is double that of the embryonic cells. Between Stages III and IV the increase per cent of wandering cells is less than that of the embryonic cells, and up to this time cell disintegration is ruled out as a disturbing factor.
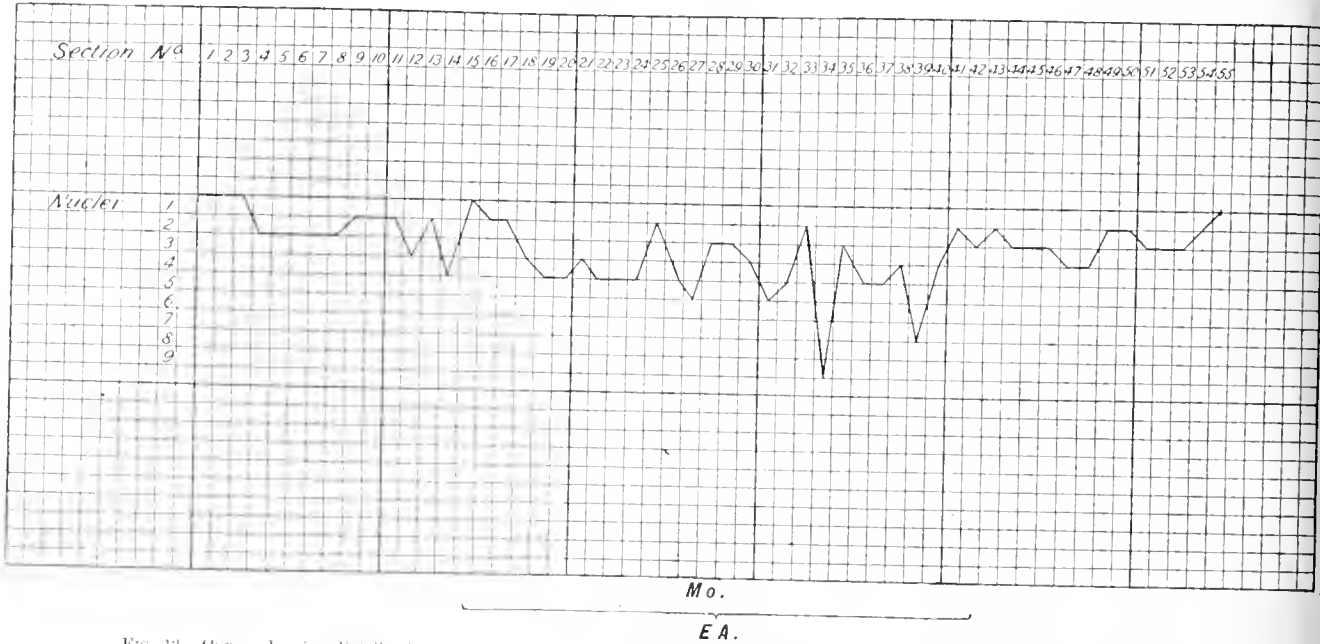
Fig. 12.—Curve showing distribution of wandering cells in Stage V (Early egg-nauplius). (Compare Fig. 11, and for details see Table I, Stage, II b.) E A, Embryonic area; Mo, Mouth.

The second fact which was pointed out as characteristic of this stage, the distribution of the yolk nuclei commensurate with that of the yolk itself, also points to the conclusion already reached. This is well shown by two curves (Figs. 12, 13). In curve 13, which is constructed from a series
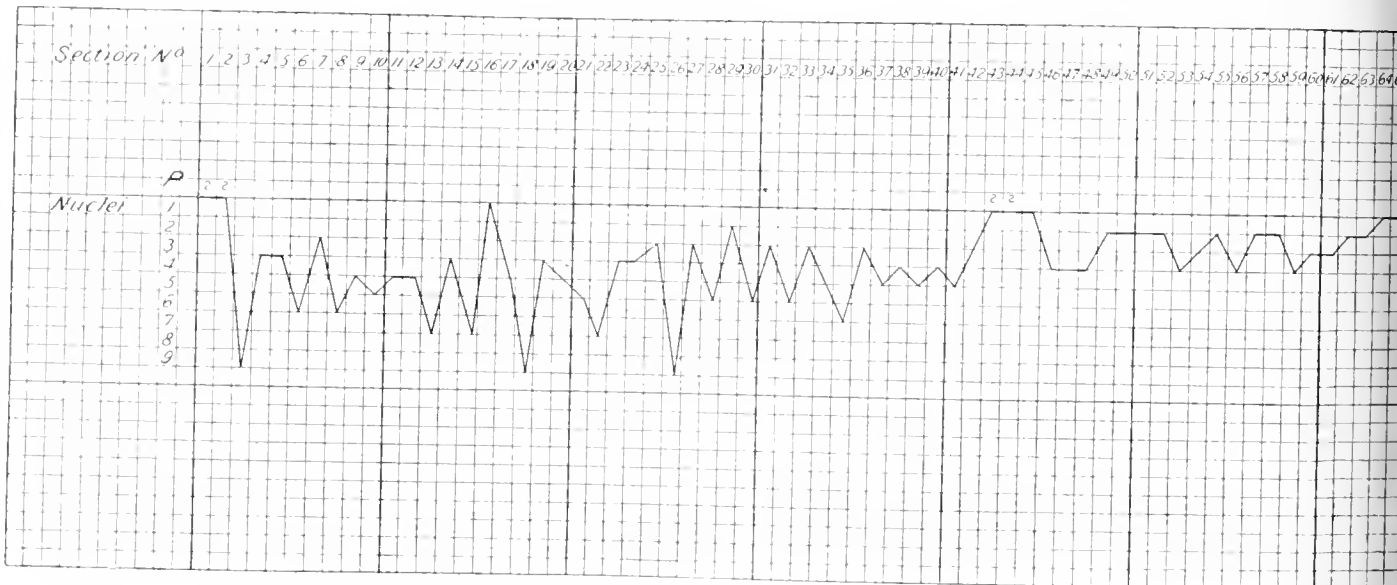
Fig. 13.—Curve showing the distribution of wandering cells in Stage V. a. (V. Table I.) A, Anterior; P. Posterior.

of transverse sections, we see that wandering cells are most abundant in the thoracic-abdominal fold region and in that which answers to the future heart. We also notice the forward extension of migratory cells beyond the anterior edge of the optic lobes. In cut 12 the lateral extension of the nuclei on either side the embryo is well shown. The mouth is involved in section No. 28,

and the embryonic area is included between sections 14 and 41. The marked peripheral distribution of the migratory cells is very significant. There seems to be a general movement of these bodies to all parts of the superficies.

What is the ultimate fate of those cells which wander out to the surface of the egg? Fig. 34, Pl. XXIX, represents part of a section of the extra-embryonic surface at this stage. Here is undoubted ectoblast (Ep.), and cells (Y. C.), which have undoubtedly come from the yolk, are pressing against the surface. In a single egg one may meet with twenty or more such cells, as well as with cells in various degrees of proximity to the surface. Do these cells (Fig. 34, Y. C.) eventually contribute to the mesoblast or ectoblast of the embryo? This question can not be answered by direct observation, since it is clearly impossible to follow the fate of the individual cells. From all the evidence which I have gathered I conclude that the wandering cells give rise to mesoblast—muscles of body wall, connective tissue, and blood corpuscles, and, later, to the definitive entoblast lining of the midgut. The part which the primary yolk cells play can not be decided, nor can it be determined whether degeneration is more characteristic of these elements than of the invaginate wandering cells.

In a lobster's egg at the delamination stage, equivalent to Stage II, Table I, I find 213 nuclei present. Eleven of these belong to the yolk. Upwards of twenty, two of which are yolk cells, are in process of division. Of the eighteen superficial or peripheral cells which are in karyokinesis, two are dividing horizontally or delaminating. In the lobster the primary yolk cells degenerate, in part if not wholly, at a very early stage, as already stated.

In the egg-nauplius phase it was noticed that wandering cells settle down upon the ectoblastic bands out of which the nervous system is subsequently developed (Fig. 127, Y. C.). In this case also it is impossible to ascertain with certainty the fate of such cells. They might form ectoblast or mesoblast, but it is more probable that they contribute to the latter layer only.

It is evident that the history of the wandering cells is largely the history of the mesoblast and entoblast. The mesoblast,[*] where it has been studied in Decapods, as in Astacus, is found (54) to originate in certain swollen cells in or near the anterior margin of the "blastopore" or pit. From this primary mesoderm cells are budded off, which extend forward in a more or less continuous sheet over the ectoderm. It is possible that in Alpheus the wandering cells may serve as a means of a precocious development of the mesoblast and entoblast. In connection with this idea, it is interesting to recall the fact that in high temperatures of the tropics the developmental stages are passed very rapidly. At Woods Holl, Mass., the late egg-nauplius of the lobster, *Homarus americanus*, is from fourteen to sixteen days old, while a similar stage is reached by *Alpheus saulcyi* at Nassau, N. P., in about seven days.

VIII.—THE DEVELOPMENT OF THE NERVOUS SYSTEM.

The nervous system can be referred back in the embryo to an early stage (Figs. 58, 62, 68), when V-shaped ectoblastic thickenings unite the optic disks to the thoracic-abdominal plate. The intervening space is gradually encroached upon until the optic disks are completely bridged by a dense sheet of ectoderm. There is an apparent concrescence of the limbs of the V, and in the egg-nauplius (Pls. XLI, XLII) these thickenings form a pair of more or less closely united cords, which are separated on the middle line by a median longitudinal furrow. The shallow furrow is formed by the swellings of ectoderm which correspond to the future ganglia, and extends from the supracœsophageal ganglia to the segment of the first maxillæ.

The nervous system of the egg-nauplius is not differentiated from the general integument, and the ectoderm is still a single layer on the middle line in the maxillary region (Fig. 121), while at the base of the first pair of antennæ (Fig. 116) it has the appearance of an elliptical plate in transverse section.

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[*] Weldon, whose paper on the germinal layers in Crangon has been referred to, says truly that the difference between invaginated cells is not sufficient to enable one to say that certain cells are endoderm and that others are mesoderm, but he designates as endoderm all cells which are derived from the invagination, and restricts the origin of the mesoderm to the lower layer cells of the ventral plate. Judging from the evidence which has thus far been presented, the cells which he has marked endoderm, lying against the embryo and near the folds of the appendages, are in my opinion to be interpreted as mesoblast. The thoracic-abdominal thickening is composed of a pair of concave "neuro-muscular" or ventral plates, which correspond to the single plate described in Alpheus.

The antennular ganglion is in close union with the optic ganglion and unites also with the antennal ganglion which lies along the sides of the stomodæum, extending slightly behind it.

The histological differentiation of the nervous elements is not very considerable at this stage. In the ectoblastic thickenings, out of which the nervous system is formed, we can distinguish three kinds of cells: (1) the superficial cells, (2) the central cells, and (3) the accessory cells which come from the yolk. These are best seen in a section of the antennular ganglion (Fig. 116). The outer cells (1), which form the integument, possess very large granular nuclei. Some of these, on either side of the middle line, can be distinguished beyond doubt as the nuclei of those large ganglion cells so characteristic of later stages (see Figs. 146, 147, 169, 170, 191, *g. c.*). They possess a more or less definite cell body of a round or oval contour. In preparations this is fine-grained and, like the nucleus, stains but feebly. The weak stain of the nucleus is due to its very fine and loose chromatin reticulum. Karyokinetic figures attest to the multiplication of these cells (Fig. 191), and it is highly probable that they give rise to similar cells which occur in both larva and adult. But what is remarkable in the earlier stages is their enormous size and their peripheral position. Reichenbach calls attention to similar cells in the embryo crayfish, which also arise from the outer layer of ectoderm cells and for a long time help to form the outer wall of the body. It is hardly probable, however, that these cells are relatively more highly differentiated in respect to their ultimate function than any of the surrounding cells which take part in the nervous system. The central cells (2) are the ordinary ganglion cells of the cortex which inclose the fibrous masses. They have smaller and less regular nuclei, which stain very heavily. Cell boundaries are entirely effaced, and the cell protoplasm is reduced to a minimum. The accessory cells (3) rest on the dorsal surface of the thickening, and represent indifferent or wandering cells derived from the yolk (Fig. 116, *cts.*, Pl. XLI, *mes.*). I am not prepared to say that any of the ultimate nervous cells are derived from this source, but I am certain that cells migrate from the yolk and attach themselves to the ectoblastic thickening out of which the nervous system is formed, and that they multiply by indirect division. It is probable that the connective tissue sheaths of the nervous system may be due, to some extent at least, to such cells. The ectoblastic thickening is increased by the radial division of superficial cells and by the horizontal division of the deeper cells.

In the larval and adult stages the large balls of fibrous substance, particularly those of the brain, are surrounded by a delicate cell layer or internal envelope. The nuclei are small and spindle-shaped and form an exceedingly thin sheet. It is possible that this represents intrusive mesoblast, derived from the yolk. Reichenbach states very positively that in Astacus connective tissue cells are squeezed into the fiber balls and eventually surround them. I have no positive evidence to show that the cells in question are not of ectodermic origin, but the behavior of the wandering yolk cells renders it probable that they should rather be referred to the mesoblast of the embryo.

The Punct-substanz of Leydig or fibrous substance is not present at this time, unless it is represented by a very delicate reticulum in the midst of the nerve cells of the ganglia of the first antennæ on their dorsal surface next to the yolk. Degenerating cells (Fig. 114 s[1]) occur in abundance close upon the optic ganglia and the ventral ectodermal thickening.

It may be interesting to notice that the structure of the antennular ganglion (Fig. 116) is similar to that of the optic lobe. In either case there is a peripheral tier of cells possessing large granular nuclei, an inner layer with smaller nuclei, and an imperfect layer of investing cells.

Passing to Stage VII (Pl. XLIV) we find the nervous system still very rudimentary. The superficial cells, particularly in the region of the optic lobes and the antennæ, have large nuclei, which can be seen in the act of division, dividing both longitudinally, thus increasing the superficial area of the plate, and also tangentially, in this way adding to its thickness. The very intimate union of the optic ganglion (Fig. 132 *G. L.*) with the antennular ganglion (*S. O. G.*) is still very noticeable, and the delicate investment of these parts on the side of the yolk (*mes.*) is more marked.

Punct-substanz has definitely appeared in the supra-œsophageal ganglion where there is a marked transverse commissure, and can even be distinguished in the œsophageal commissures. It forms a very delicate protoplasmic reticulum, and there can be no doubt that the fibrous substance of this part of the nervous system arises as an outgrowth from the protoplasm of ectoderm cells.

The paired structure of the ectodermal plate is well shown in the antennular ganglion on a level with the transverse commissures, or even in front of this, where paired masses, with small, deeply dyed nuclei, are separated by a median sheet of much larger and clearer cells. This may possibly correspond to the mittelstrang, referred to again.

Shortly after this (Fig. 139) the ganglia are blocked off by a series of superficial constrictions. At least seventeen such ganglionic segments can be counted, beginning with the optic and supra-œsophageal ganglia and passing to the last abdominal segments. The ganglionic blocks are formed rapidly from the front backward. The ganglia of the first antennæ are now the most conspicuous part of the nervous system, unless we accept the large optic ganglia. There is a broad, transverse, fibrous commissure in the antennular segment, which is still more prominent at a little later period (Pl. XLVI), when eye pigment is forming. From this commissure longitudinal rods extend forwards and unite the brain with the optic ganglia, while similar rods grow backward and form the fibrous axis of the circum-œsophageal commissures.

The plane of section in Fig. 148 passes just in front of the œsophagus and through the roots of the first pair of antennæ (A 1), which should appear in the drawing as continuous with the integument. The ganglionic cells, which are directed toward the appendages, represent the antennular nerves, and are more apparent in the following section. The antennular ganglion is both preoral and preantennal, lying in front of the first pair of antennæ, which it supplies with nerves.

The brain and ventral nerve cord are now plainly separated from the hypodermis, and are bathed throughout their extent with blood plasma, in which numerous blood corpuscles are seen floating at every point. Giant ganglion cells have become most conspicuous in the optic region and at the periphery of the brain next the hypodermis.

The brain is partially divided in front next the optic ganglion by a delicate membrane, which forms a median superficial partition between its two halves. This is continuous, with a delicate envelope, which in some cases can be detected about the brain, and is like that which covers the optic ganglion and nervous system generally. A similar non-cellular membrane at this time divides the retina from the optic ganglion, and is continuous with the cuticular sheath of the latter. The intercepting retinal membrane is directly continuous with the delicate basement membrane of the hypodermis. The cuticular sheaths of the nervous system are present in the embryo (Figs. 157, 168 pr.), the larva (Figs. 175, 176), and the adult. It may not seem easy to harmonize this account with the view already taken that the wandering cells attach themselves to the nervous rudiments and form a delicate investment to them (Figs. 129, 131 mes.). Such is plainly the fate of some of the wandering cells, but the number of cells is probably too small to form a continuous structure, and it is possible that the delicate membrane secreted by the ectoblast may serve as an accession to that formed by mesoblast.

With respect to insects, Wheeler (67) concludes that in Doryphora the "outer neurilemma" is ectodermic rather than mesodermic in origin, since—

Shortly after the separation of the nerve cord from the integumentary ectoderm, it sheds from its surface a delicate chitenous cuticle simultaneously with the shedding of the first integumentary cuticle. This cuticle, which is separated from the surface of the outer neurilemma, and even from the surfaces of the main neural trunks, is afterwards absorbed.

At the time when the nervous system has completely separated from the integument there is a slight ingrowth of ectoderm cells along the midventral line, most pronounced between the ganglia, and the appearance of a corresponding constriction on the side next the yolk. In transverse section the nerve cord is somewhat hourglass-shaped. This may be due to a mechanical necessity, arising from a more rapid development of the nerve cells in the lateral masses than in the other parts.

Ectoblast cells derived from the integument appear to be infolded between ganglia (see Fig. 157—a thin sheet of cells, with spindle-shaped nuclei bending in between the last thoracic and first abdominal ganglion, in the lower right hand portion of the figure), but these infoldings may be somewhat deceitful, since they are straightened, to some extent at least, with the growth of the abdomen (Fig. 168, abg. I). On the ventral surface of the thoracic region (Fig. 168) spindle-shaped nuclei are seen wedged between the nerve cords on the middle line. It is not, however, certain that these cells are ectoblastic, since the sternal blood sinus is already formed, to which

blood cells have penetrated, and here eventually the sternal artery is developed. While the evidence is not conclusive, we have only to decide between the former conclusion—that the intrusive tissue is derived from the wandering cells, and is to be referred to mesoblast, or the view that it represents differentiated ectoblast.

A general account of the structure of the nervous system of the larva is given in the first section. Further than this the details of development have not been followed.

In comparing this account with that given by Reichenbach for the crayfish, *Astacus fluviatilis*, there are numerous particulars in which there is no agreement, while in some important matters we are in accord.

I find in Alpheus the oral invagination occurring on a line drawn between the bases of the antennular buds, and I have a great many preparations of the eggs of the lobster, *Homarus americanus*, which show the earliest traces of the stomodæum. Before the first antennæ are folded, when they are distinguished as dense patches of cells, some eggs show the primitive mouth as a minute circular pit, lying nearly on a line drawn between the centers of these proliferating cell areas, but, so far as my observation goes, never distinctly in front of them.

The relative positions of the mouth and first pair of antennæ shift very rapidly during the early period of their growth, which precedes the fully developed egg-nauplius condition. The pit elongates and becomes a transverse furrow, and by the time the first pair of antennæ are clearly marked off as rounded buds, and before the second pair are raised into folds, the mouth is still on a line with the first of these appendages. When the second antennæ are elevated into folds the mouth is behind the buds of the first pair, or on a line between their posterior edges.

Reichenbach (taf. II, Fig. 7a, Lb.) describes and figures a cell thickening between the "Kopflappen" of the crayfish embryo (Stage E), which he considers the beginning of the labrum. His sections show that below this point a mass of ectodermic cells occurs, which is interpreted as the "Vordarmkeim." The mouth is not represented as appearing until the following egg-nauplius stage (Stage F. Compare Fig. 66 and p. 100, § 7, "Der Vorderdarm"), when it occupies a position exactly comparable with that observed in the lobster. I therefore can not agree with Kingsley in saying that Reichenbach "has all the appendages at first distinctly postoral." While the position of the Crustacean appendages may have been primitively postoral, it may be questioned if in the higher Crustacea the first antennæ ever arise behind the mouth invagination.

Kingsley describes the position of the mouth in Crangon as distinctly postoral, but an inspection of figure 11 of his paper, leaves some doubt as to whether he is not mistaken in this particular. A single rudimentary appendage, marked as the first antenna, is represented as occupying nearly the entire space between the optic disk and thoracic abdominal fold. This does not agree with my own preparations,* and since in Alpheus, Homarus, and Astacus the mouth does not appear until a dense stratum of cells carpets the intermediate space between the optic disks and lateral cords, there is some difficulty in interpreting the cluster of cells marked *m*, in Kingsley's paper, as the invagination of the mouth.†

In Alpheus, Homarus, Astacus, and probably in Decapods generally, the ganglion of the first antenna cannot be said to be postoral, but its development begins nearly on a line with the invagination of the primitive mouth. The ganglion of the second antenna is developed behind the primitive mouth, but gradually shifts forward with its appendage until it comes to lie, in the larva, considerably in front of the mouth. In this movement, the ganglion however outstrips the appendage. The ganglia of these two appendages unite to form the brain or supra-œsophageal ganglion. The ganglion of the first pair of antennæ is constricted into two portions marked by an oblique, transverse line at the surface. The anterior of these parts Reichenbach calls the

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* I have preparations of the eggs of *Crangon vulgaris*, in various stages of development, from the segmentation onward. In one egg, which is somewhat more advanced than that of figure 10 (31), or than the Alpheus in Fig. 58 of this paper, the optic disks and ventral plate are dense patches of cells. On either side of the ventral plate and in close relation to it there is a marked area of cell proliferation which represents the mandible. In the space between this and the antenna the nuclei are more scattered, but the karyokinetic figures show the activity of cell division. In a late nauplius stage the stomodæum is on the middle line between the first and second antennæ, and the antennular ganglion is segmented into two parts on each side, as shown for Alpheus in Fig. 110.

† This criticism is supported by Weldon's observations on Crangon, who, with reference to this subject, says: "The first antennæ are evidently præoral from the very earliest period at which the mouth is visible." Op. cit.

"vordere Hirnanschwellung" and the posterior the "Seitenanschwellung," using the terms of Krieger and Dietl. These latter particulars accord with Reichenbach's description of the crayfish. I have not, however, found that in Alpheus, behind the level of the first pair of antennæ, the lateral parts (Seitenstränge) divided up into three sections. Reichenbach further states that in each segment a middle-strand invagination is found, while the ganglia of the fifth (first maxillary) segment has a prominent median string.

In Alpheus I find an undoubted median ingrowth of surface ectoblast between the two nerve cords. This in all probability corresponds to the mittelstrang, and, as already stated, it is most marked at a stage just before or at the time of the first appearance of the eye pigment, when the ganglia are separating from the integument. It is seen between the successive segments of the ventral nerve cord, where a single cell or string of several cells appears to be wedged between the two cords which are entirely separated (compare Figs. 151, 160). The nuclei of these cells are elongate and perpendicular with the surface. They are derived by delamination from the superficial ectoblast, as the karyokinetic figures of dividing cells clearly show. These ingrowths are most noticeable between the segments, and whether they form any part of the nervous system or not, I have been unable to determine. In insects the mittelstrang appears to take no part in the nervous system of the adult, but in the thoracic region it is converted into the chitenous furcæ.

According to Reichenbach the lower œsophageal ganglion in the crayfish is formed by the fusion of the ganglia of the fourth (mandibular) to the ninth (third maxillipedal) segments. This is probably true of Alpheus, as may be inferred from Fig. 196.

With reference to the commissures, Reichenbach states his belief that the transverse commissures originate in the unpaired fiber masses present in each ganglion, while the paired masses give rise to longitudinal commissures. In Alpheus there appear in successive segments behind the mouth a pair of punctsubstanz balls, one ball in each single ganglion. These extend forward and backward, uniting the ganglia into chains and forming the longitudinal commissures. A little later the transverse commissures are formed by bridging the cords between the points occupied by the fiber-substance balls in the several ganglia. All these stages can be observed in the embryo shown in Fig. 139, but all do not appear in the drawing.

The origin of the peripheral nervous system is beset with many difficulties. It is often impossible to distinguish developing nerves from rudimentary connective tissue and muscle, owing to the similarity of the nuclei of each. This is less true of muscles, which in some parts of the embryo, as in the carapace, are clearly distinguishable. In view of this, Reichenbach found it difficult to say whether the nerves were budded off from the central nervous system, from other ectoderm, or from wandering mesoderm cells. He thinks, however, that since many structures like the optic ganglion, the crystalline cone cells of the retina, etc., are early recognizable, the nervous system is generally in intimate connection with the other organs. So the appendages, the nervous system, and the nerves, which at first can not be distinguished from each other, are intimately connected from the start; so the eye and the ear are never separated from the central nervous system. The separation of the central nervous system from the skin takes place slowly, and the ectodermal thickenings in the early stages must conceal the rudiments of nerves and skin elements. It is difficult, he remarks, to understand the late connection of the midgut with the central nervous system and the scattered mesoderm cells which form the muscles, but he says, in conclusion:

Bei der Untersuchung der wunderbaren Entwicklungserscheinungen in der organischen Welt aber drängt sich bei tieferer Betrachtung immer wieder der Gedanke auf, dass man schon vom ersten Stadium an einem untrennbaren Ganzen gegenübersteht. (54, p. 80.)

This view of the intimate colonial relations of all the cells of the embryo can not be disputed, since it follows from the common descent of all the somatic cells from the ovum. But the relation which the embryonic cells bear to each other as the undifferentiated ectoblast to mesoblast must be of a very different nature from that which exists between muscle fiber and nerve in the differentiated state. It seems more probable that the union of the central nervous system with other organs by means of nerves is strictly a secondary one, and that the latter arise by budding, as in vertebrates, from the central ganglia. The only observations which I have made on the development of nerves (see section I) refer to those of the first and second antennæ (Pl. LV, Figs. 213–216, n. au., n. a. g.; Pl. LVII, Fig. 243, n. au.). The antennular nerve, which supplies

the ear, appears to arise as an outgrowth from the antennular fiber mass of the brain (Fig. 243, *af.*). It consists of a fibrous portion leading directly from the fiber mass of the brain and of somewhat flattened, or spindle-shaped nuclei, which penetrate the cortex of nervous cells and are undoubtedly proliferated from them. Possibly the internal sheath is continued over the growing nerve.

IX.—THE EYES.

The eyes in Decapods consist of a pair of lateral compound eyes, which in the larva are mounted upon long stalks, a condition usually retained in the adult, and of a median ocellus. In the Alpheus family the compound eyes are nearly sessile and are completely hooded by the carapace. In the larva, however, the eyes are both naked and possess long, movable peduncles (see the metamorphosis, Pl. XXI). In *Alpheus saulcyi* the optic stalks are reduced to a mere rudiment, and, though provided with muscles, they can possess but very slight power of movement. They meet on the middle line in front of the brain, over the roots of the first pair of antennæ. The compound eyes face forwards and outwards at an angle of 45° with the mesial plane of the body. A median papilla projects from below the lateral eyes, bearing the pigmented ocellus (Figs. 209, 210, of larva). Two small hairy tubercles, outgrowths of the integument, occur on the inner side of the optic stalk.

Spence Bate (3) says that since the Alphei are frequently found in ooze and muddy bottoms, he is inclined to think that they burrow more extensively than the common shrimp, and that the carapace has become modified to protect the eyes on this account. This may be true, but the Squillæ, on the other hand, in which the burrowing habit is more characteristic, have undergone no such modification.

THE MEDIAN EYE.

The median "nauplius" eye persists in the adult Alpheus, and is probably functional to some extent as a visual organ. This is represented in Fig. 18, Pl. XXII, where it is seen as a small conical papilla, lying between the basal joints of the antennules, and at the roots of the compound eyes, very close upon the brain. This is the first instance I have noticed of the persistence of the nauplius eye in the adult.

The general position of the median eye of the first larva of *Alpheus saulcyi* is seen in Figs. 209 and 210, and the minute structure in Fig. 197. The pigment takes the form of an inverted Greek capital upsilon (ʏ). There is no lens. A coaguable fluid is present, which is probably blood plasma. Besides muscle-fibers and pigment-secreting cells, and the integumentary epithelium, these ectodermic nerve end (?) cells, which abound toward the center of the papilla, are continuous backward into the cortical cells of the anterior fiber mass of the brain.

The first trace of the frontal eye which I have noticed occurs in the tenth stage (Fig. 168), when a small number of cells developing black pigment (probably ectodermic) can be seen near the surface, on the middle line, next the anterior extremity of the brain.*

GENERAL ANATOMY OF THE EYESTALK.

The visual apparatus of the compound eye of a Crustacean consists of three principal parts, the retina, the optic ganglion, and the optic nerve, uniting retina with ganglion, in addition to a peduncle of nerve fibers, which puts the optic ganglion in communication with the brain. These parts are contained in the eyestalk or opthalmite. The eyestalks are covered with a cuticle secreted by the ectoderm like that over the rest of the body. This cuticle, which in some prawns like Stenopus is hard and armed with spines, is converted at the distal, hemispherical surface of the stalk into a transparent cornea. The ectoderm or hypodermis secretes a well defined basement membrane. This is continuous with the basement membrane of the retina, pointing clearly to the fact which development proves, that the retina is a differentiated portion of the hypodermis. Below the basal membrane we meet with blood vessels or sinuses, muscles which control the movements of the eyestalk, glands, connective tissue, ganglion cells, and fibrous substance.

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* While this memoir was in press a short paper appeared in the *Quarterly Journal of Microscopical Science* (January, 1892), "*On the Nauplius Eye persisting in some Decapods,*" by Margaret Robinson. The median eye was observed in some eight different species of the Carididæ, including the genera Palæmon, Hippolyte, Virbius, Crangon, and Pandalus.

Alpheus in the only genus in which I have found glands in the eyestalk. These are most noticeable at the peripheral parts of the stalk between the basement membrane and the ganglia. They are in reality parts of the green gland, which sends outgrowths from the bases of the second antennæ into the antennules, the eyestalks, the labrum, and the whole front of the head, so as to completely envelope the brain. The histology of the glandular cœca is the same in all parts. They consist of a cubical epithelium, composed of very large cells, supported by a basement membrane.

Near the cœca of the antennal gland comes a layer of very loose connective tissue. This is specially abundant below the basement membrane of the retina. It forms a continuous sheath for the optic ganglion, and is reflected over the optic peduncle and brain.

By far the greater mass of tissues of the eyestalk belongs to the optic ganglion. This is composed of ganglion cells (Fig. 187), nerve fibers, and the peculiar fibrous tissue variously called "Punct-substanz" or "Ball-substanz," and "substance ponctuée." Viallanes, who has made very careful and detailed studies of the optic ganglia of Arthropods, uses the following terminology (61). He divides the optic ganglion into two parts, an external and an internal portion. The surface of the external region is covered by the limiting membrane of the eye. The external is united to the internal parts by a bundle of crossing fibers, the *external chiasma* (Fig. 178, Ch. Ex.). This, according to Viallanes, corresponds to the center of the corneal surface, and consequently to that of the limiting membrane of the eye. The internal portion between the external chiasma and the optic peduncle is composed of three principal masses of punct-substanz: (1) la masse médullaire externe, (2) la masse médullaire interne, (3) la masse médullaire terminale. The external medullary mass is united to the masse médullaire interne by an *internal chiasma*, while a fibrous peduncle joins the internal medullary mass to the masse médullaire terminale. The nerve fibers which pass between retina and ganglion, he calls the post, retinal fibers, and designates as "optic nerve" the peduncle by which the optic ganglion is united to the brain. The distal mass of punct-substanz is styled lame ganglionnaire,* which he divides into a nuclear layer (couche à noyaux), a molecular layer (couche moléculaire), and a cellular layer (couche à cellules ganglionnaires).

The punct-substanz of the optic ganglion is thus divided into four principal masses (Figs. 178, 209). Without adhering closely to the rather cumbrous terminology of Viallanes, the parts of the nervous system contained in the eyestalk between the brain and retina may be designated as follows: *Optic peduncle* (optic nerve of Viallanes and others); *proximal segment* (masse médullaire terminale); *internal middle segment* (masse médullaire interne); *external middle segment* (masse médullaire externe); *distal segment* (lame ganglionnaire); *optic nerve* (couche des fibers post-rétiniennes).

GENERAL STRUCTURE OF THE COMPOUND EYE.

The transparent cornea is the secreted product of a specialized layer of the hypodermis, which was designated by Patten as the "corneal hypodermis" and later as the "corneagen" (50, 51). Beneath this lie several strata of dioptic and sensory cells, separated from the ganglion by a basement membrane, which is continuous with that of the general hypodermis of the eyestalk. The ommateum, or eye proper (including those parts which intervene between the cornea and basal membrane), is formed by the repetition of a highly specialized unit, the eyelet or ommatidium. The size, number, and arrangement of the ommatidia is characteristic of species or genera, but is subject to considerable variation in different individuals, and the shape and arrangement of the ommatidia may be very irregular in different parts of the same eye. The ommatidia are differentiated clusters of ectoderm cells. There is a single ommatidium for each lens or corneal facet. The number of cells composing the ommatidium is very uniform in Decapods, Stomatopods, and Schizopods, so far at least, as the most essential cells are concerned. They are as follows: Cells of corneal hypodermis, 2; crystalline-cone cells, 4; outer pigmented retinular cells, 2; inner pigmented retinular cells, 7 (functional); Accessory pigmented cells—irregularly distributed, both above and below the basement membrane, probably of ectodermic origin.

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* The lame ganglionnaire is called "Retina ganglion" by Claus, who regards it as the true retina; "das aussere Ganglion opticum" by Carriere, and "periopticum" by Hickson.

STRUCTURE OF THE OMMATIDIUM.

Both a lack of time and of fresh material have prevented me from making as thorough a study of the structure of the ommatidium of Alpheus as I had wished. The following account is based entirely upon sections:

The corneal facet is strongly biconvex (Fig. 200), the convexity of the lower side being the greatest. Its shape is usually hexagonal, but may be tetragonal, or sometimes nearly circular (as in *A. heterochelis*). There are two corneal cells to each lens. A single ommatidium is shown in Fig. 200. As in all Decapods, the cone cells which underlie the corneagen are four in number. The four segments of the crystalline cone (Fig. 208), which are secreted on the inner sides of the latter cells, are always separated by delicate boundary lines. The cone is capped by a mass of protoplasm in which the nuclei of the cone cells lie, although it is not always easy to distinguish them. This cap appears to be raised into a slight elevation which touches the center of the lens.

Pigment cells invest the cone more or less completely according to the conditions under which the eye is examined. These are the retinular cells. In the larva, and probably in the adult also, there are two distal retinular cells (*pg.* e Pl. LIV), as Parker (48) designates them, and at least seven proximal retinular cells (*rtl.*). Parker discovered in Homarus and several allied forms a rudimentary eighth cell belonging to the proximal series. This is present I believe, in Alpheus, although my sections do not show it with the same clearness that it can be demonstrated in Palæmonetes. The seven proximal retinular cells secrete on their inner sides the rhabdom or rhabdomeres. A transverse section of the rhabdom gives the peculiar seven-pronged figure shown in the drawing (Fig. 205). The cells appear as fused in section, but possibly they would separate with readiness if macerated. Unfortunately I had no fresh material to experiment with. The proximal retinular cells appear to penetrate the basement membrane, and they are continuous below it with nerve fibrils. As to their distal ends, I have seen no evidence that they extend out to meet the cornea. The retinular cells abound in dark pigment.

The accessory pigment cells secrete a peculiar pigment which is glistening white in reflected light and is amber color in transmitted light. This may be similar to the pigment of certain cells which occur beneath the cuticle of the larva of Decapods in various parts of the body. It is not decolorized when subject to the prolonged action of weak solutions of nitric acid, while the black pigment is completely removed. What I once regarded as chitinous bodies (20–21) were fused masses of this pigment which had been treated with nitric acid. These cells penetrate the basement membrane, beneath which there is a considerable mass of both yellow and black pigment. The trains of cells which accompany nerve fibrils into the fibrous portions of the optic ganglia also contain granules of black pigment. The number of accessory pigment cells belonging to each ommatidium is indeterminate. They have the power of free movement or migration outward from the basement membrane and the power of retraction like the retinular cells. In Fig. 200 they are seen widely diffused, while there is a zone of black pigment cells (the pigment withdrawn by acid) enveloping nearly the entire cone and the distal end of the rhabdom. In an eye taken from a prawn which had just moulted, the yellow pigment was restricted to a narrow zone next the basement membrane. Outside of this belt the retinular cells were colorless nearly up to the proximal ends of the cones, while the cones themselves were draped in black.

ARRANGEMENT OF THE OMMATIDIA.

In *Alpheus saulcyi* the ommatidia are arranged in a hexagonal system, subject to variations in different parts of the eye.* In the central parts of the cornea the facets are symmetrical hexagons. On the lower side of the eye the rows are more irregular and individual facets tend to become square and rounded. Toward the outer side of the eye the facets are very nearly square, next to these they become irregular and rounded, and on the extreme outer edge the facets are sometimes hexagonal. There is probably considerable individual variation. I have examined the cornea in four other species of Alpheus, namely in *Alpheus heterochelis*, *A. minor*, *A. normani*, and a West Indian species closely allied to *A. heterochelis*. These cases afford some very interesting

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* For a study of the cornea, adults of the largest size were selected and the cuticle was cleaned by boiling in a concentrated solution of potassic hydrate.

facts in connection with the arrangement of ommatidia. In *Alpheus normani* the facets are generally symmetrical hexagons, two of the sides being quite short. These tend to run into squares or rounded areas at parts of the periphery. *Alpheus minor* has the facets in the lower part of the eye either of the hexagonal or some polygonal form, while in the upper and outer parts the facets are perfect squares. These blend on all sides into symmetrical hexagons. The first transition from the hexagon to the square is seen on the outer edges of this area where the individual facets become more and more rhomboidal, as the two opposite sides of the hexagon are more and more reduced. Finally these sides disappear and the facets become rectangular. The square facets of any given row now lie opposite to those of the adjoining rows. Four facets belonging to any two rows meet at a common point. In passing, however, from the area of square facets to the peripheral parts, the facets, though square, are out of line. Starting from a point where the facets of a given row are both tetragonal and opposite those of adjoining rows, and following the line over the hemispherical surface toward the periphery, the facets of this row soon tend to become alternate with those of the row next to it. A facet of the second row lies slightly in front of the corresponding facet of the first row. The facet of the third row lies a little in advance of this and so on until the hexagonal shape is gradually assumed.

In the Bahaman variety of *Alpheus heterochelis* the facets in the larval eye are markedly hexagonal. In the adult there is the same curious transition from the hexagon to the square as we have noticed in *Alpheus minor*, only it is here much more striking. In the peripheral parts of the eye, especially in the lower and inner portions, the facets are generally hexagonal. In the upper half of the eye between the center and periphery there is a small area of square facets. In *Alpheus heterochelis* the facets are characterized by much greater looseness of arrangement, there being large interlenticular spaces. The facets are squares with rounded corners. In some parts of the eye, as on the inner lower side, the facets of the adjoining rows lie opposite each other. In other parts they regularly alternate and show a tendency to become hexagonal. At the periphery the facets are widely separated and circular.*

The markings on the corneal lenses generally consist of a small central spot which is slightly elongated and strongly refracts the light. It appears in section to represent a slight depression. In the lobster, as first shown by Parker, there is a faint diagonal band which intersects a central hazy spot and divides the square into equal triangles. These diagonal bands are all parallel in adjoining rows. In *Alpheus saulcyi* the elongated spots, if continued across the lens, would form a series of similar diagonal lines, but none such as these could be detected. In *Alpheus heterochelis* the markings are very constant and peculiar. In the center of the lens there is a large irregular impression from which numerous rays extend on all sides. The latter do not always reach the periphery. They appear like grooves in the substance of the lens. In the older embryo (Fig. 194) the apex of the cone cells seems to touch the under side of the lens in certain parts of the eye. It is therefore possible that these cells remain in contact with the cornea and the interference thus caused gives rise to the spot. A similar explanation is offered by Parker to account for the conditions found in the lobster. The significance of the radiating lines seen in *Alpheus heterochelis* I have not determined.

In Homarus the facets are square and grouped with remarkable regularity up to the very edge of the cornea, excepting at a point on the upper side, where a peninsula of tough cuticle juts in from the surface of the stalk and interrupts the elliptical jet black area of the surface of the eye. About this process, particularly in front of it, the facets are hexagonal or irregular and very much smaller.

Parker (48) states that in the lobster " the ommatidia rearrange themselves between the times when the young animal is 1 inch and 8 inches long. During this period the ommatidia increase about ten times in length and about five times in breadth." I find that this rearrangement begins at a much earlier period, in fact in the older larval stages. My examination comprised the following stages: (1) Length 8–9ᵐᵐ (first larval stage); (2) length 11ᵐᵐ (fourth larva); (3) length 15.3ᵐᵐ (sixth larval stage); (4) length 49ᵐᵐ (lobster 1 year old).

* A similar transition of the square into the hexagonal facet in the same eye occurs in Astacus. See Howes' Biological Atlas, Fig. 111.

In the first larva of both *Homarus* and *Alpheus sauleyi* I find that the facets are not only hexagonal but tend also to be slightly rounded. In the larva 11^{mm} long the lenses tend to become square toward the center of the cornea, while at the periphery they are smaller and generally hexagonal. Occasionally, however (just in what part I did not ascertain), the peripheral facets tend strongly to the tetragonal arrangement. In the next case (larva 15.3^{mm} long) the facets in the outer parts of the eye are small and symmetrical hexagons. Toward the center they become larger, nearly square, and there is considerable interlenticular space.

In the yearling lobster the readjustment of the corneal lenses from the hexagonal to the tetragonal system has been effected over the greater portion of the eye, but the transition is still illustrated in a very beautiful manner. The cuticular ingrowth or peninsula, already referred to, seen at the upper surface, is hook-shaped, bending backward. In the open angle in front the retina is least differentiated. The corneal facets in this region are small and mostly hexagonal. Following the lines of facets as they curve outward and backward from this point over the convex surface of the eye, we see illustrated in a very striking way the passage of the hexagon into the square by the gradual reduction of the opposite sides. The sides which are sacrificed are the third and sixth, counting from the side which lies between two adjoining lenses of the same row. Over a considerable area the facets are not quite square and thus tend to alternate with those of adjoining rows. The gradual transition to the square is attended by a gradual increase in size. In the narrow angle behind the peninsula, the area of the hexagonal facets is smaller. In all other parts of the periphery the facets are square up to the very edge, as in the adult. The corneal lens in an 8-inch lobster has about twice the area of that of the lobster one year old (length nearly 2 inches).

After reviewing these details the difficult question arises: What is the significance of this remarkable change, and how is it effected?

Parker (48), who has made a careful study of the arrangement of the ommatidia in different Crustaceans, recognizes two plans on which these organs are grouped, the hexagonal and the tetragonal. He says that "in the Brachyura, as well as in three families of the Macrura, the Hippidæ, Paguridæ, and Thalassinidæ, the arrangement of the ommatidia is invariably hexagonal. In the remaining macrurous Decapods the ommatidia are grouped on the tetragonal plan." There are, however, exceptions to the latter statement, some of which are mentioned. He regards the change from the hexagonal to the tetragonal system as apparently due to the increase in size and the consequent crowding of the ommatidia, and reaches the conclusion from the various facts presented, that the hexagonal arrangement is phylogenetically the oldest. Upon this view we should expect to find the eyes of the most highly differentiated of the Crustacea arranged on the tetragonal system, whereas in points of fact the crabs, who are notorious for their great activity and keen powers of vision, permanently adopt the hexagonal arrangement. The lower Macrura adopt both methods, and in certain species of Alpheus, as *Alpheus minor*, which are active in habit and show no trace of degeneracy, the change is begun but not completed in the same retina. In order of time the hexagonal prism precedes the square prism and the conditions which determine the permanency of each of these systems in the adult life of the individual are undoubtedly inherited, but they do not appear to have a phylogenetic significance, at least I do not see the way clear to an explanation upon this ground.

Taking, for example, the lobster and the crab, in each case the larval eye represents, we must believe, the more generalized type, the adult eye the more specialized type. The larval eye of both Macrouran and Brachyouran has the hexagonal facet. We may safely conclude that this is a primitive arrangement. The adult crab, which has a more highly organized nervous system and keener senses, retains this primitive arrangement, while the lobster, whose senses are without doubt duller, departs from the type, and in the adult the facets of the cornea take on a permanent tetragonal shape. The conditions which we would naturally look for are thus reversed in these two forms.

We must assume that the change in the case of the lobster is a useful variation, that it is in some way subservient to keen vision, otherwise it could never, upon the theory of natural selection, have secured such a permanent characteristic footing. On the other hand we must believe that the hexagonal facet puts the eye of the crab into better harmony with its environment than the square facet would do, for if the eye had not been in harmony with external conditions it must

have varied and attained to a new structure during the course of the evolution of the Brachyoura from Macrouran ancestors.

Many crabs like the sand crab, *Ocypoda arenaria*, spend a good portion of time out of the water and their eyes are admirably adapted for vision in the air, as in the case of this species, which will detect any moving object, such as a man or a dog, a long distance off. We might thus hope to find a way of escape from the difficulty in the diversity of habits in the two forms, the lobster being exclusively an aquatic animal. But the primitive Crustacea must have all been aquatic, and the hermit crabs, some of which spend all or nearly all of their time in the water, agree with the Brachyoura in having a corneal membrane composed of hexagonal facets, not to speak of other Macrouran forms which are invariably aquatic, like Alpheus, in which the hexagonal system is retained or there is a transitional condition between the hexagon and the square in the eye of the adult.

We do not yet know the physical or physiological significance of these two kinds of facets, and possibly in this fact lies the root of the difficulty pointed out above.

The hexagonal arrangement is the natural one for tubes with elastic walls to assume when there is sufficient mutual pressure, and it is also the most economical arrangement, so far as wall space is concerned, for regular prisms of equal capacity. Next to this in point of economy of wall space comes the square prism, and next to this the triangular prism, where, as before, all available space is occupied. This last arrangement, however, is not regularly assumed.

If a given number of hexagonal prisms occupying a given space tend to increase in size, then they would tend also to assume another form less economical of wall space, such as the square prism. If the wall area of the hexagonal prism remains the same and the number of prisms increases in a given space, then each prism must be less economical of wall area and assume another form like that of the square prism.

If we may apply the same principles to the growing ommatidia, it is possible that crowding may have something to do with the change.

In the lobster the change from the hexagonal to the tetragonal system is attended by a growth of the ommatidium in all directions and by the addition of new ommatidia. If an outline drawing of the eye of the first larva of the lobster be compared with a similar one of the fifth larva, it will be seen that the convexity of the outer surface, that is, the area of the eye, has very greatly increased, whereas the diameter of the eye stalk has remained very nearly the same. During this period the change from the hexagon to the square has been begun. During this time the ommatidia have increased in length with the increasing convexity of the cornea, and they have also increased in sectional area and in actual number. It is a very noticeable fact also that in the lobster the eye stalk is compressed dorso-ventrally, so that the horizontal radius of curvature of the retinal surface is considerably greater than the vertical radius of curvature. Furthermore, the sides of the hexagonal facets which suffer reduction lie in a vertical plane, indicating a strain or pressure in a dorso-ventral direction.

In *Alpheus saulcyi* the relative increase in the convexity of the corneal cuticula is very slight in passing from the first larva (length, about 4^{mm}) to later stages, and the eye of an adult (13^{mm} long) is only about one-fourth larger than that of the larva at the time of hatching. Moreover, in Alpheus the convex surface of the eye is nearly a perfect hemisphere, the curvatures being the same in every plane.

If we examine the eyes of a crab in a similar way we find that the area of the surface of the retina increases less rapidly in passing from the zoëa to the megalops stage than in the case of the lobster in going from the first to the fourth larval forms. The comparison, however, is of little value since the lobster has an abbreviated development. The eye stalk of the adult crab presents a large retinal surface, but it preserves a nearly cylindrical form, although the radii of curvature of the retinal surface are very unequal. In the hermit crab (in a single species examined) the hexagonal arrangement is preserved, not, however, without indications of a tendency to become tetragonal, the hexagons becoming asymmetrical in certain parts of the eye. There is, however, the same compression of the eye stalk in a dorso-ventral plane as we see in the lobster.

It has seemed to me worth while to point out these facts as offering some suggestions to the problems under discussion, although I make no attempt at a mechanical explanation.

The primitive arrangement of the ommatidia was probably in the form of simple tubes or cylinders, with spaces between them and with rounded or indefinite facets. Mutual pressure among these tubular eyelets, arising from any cause, produces the hexagonal arrangement, the most economical method so far as wall space is concerned. Interferences such as have been suggested, as growth of individual ommatidia or increase in the number of ommatidia in the same area, thus admitting a method of arrangement less economical of wall space, or the great increase in length of the ommatidia and a relatively less increase in width, attended by a progressive change of the hexagons into squares (the apparent slipping of the rows of facets on one another), may enter as factors into this change, but they do not suffice to explain all the conditions. It will be understood, of course, that there are no changes in the individual facets, these remaining in the same shape until they are cast off in the moult. The changes which the individual ommatidia undergo are very gradual, and since the number of cells for each ommatidium is constant and determined at a very early period, excepting the accessory pigment cells, they must be attributed to the change in the size and relative positions of the cells themselves rather than to intussusception. It is possible that the change from the hexagon to the square is not produced in the same way in all cases and that the conditions of growth which bring about this result are far more complicated than would appear from the suggestions which have been made. A careful study of the arrangement of cells in the ommatidia of the eye of the young lobster during the period of transition would possibly throw some light upon this interesting subject.

THE DEVELOPMENT OF THE COMPOUND EYE.

Five years ago (20) I stated my conviction that the compound eye of Alpheus, and probably also of Palæmontes and of the large Isopod, *Ligea oceanica*, originated from a thickening of the superficial ectoblast. The development of the eye in Alpheus was more fully described in a preliminary notice (21). I will now recapitulate the main results, at the same time correcting such errors as I have detected.

In studying the development of the eye the following are some of the subjects which present themselves for investigation: The origin and structure of the optic disks; the separation of the optic disks into a ganglionic and retinal portion by an intercepting basement membrane; the differentiation of the retina into ommatidia or eyelets; the differentiation of the optic ganglion and the development of the optic nerve, by means of which the sensory end organs of the retina come in direct relation with the ganglion.

(1) *Origin of the Optic Disk.*—The optic disks (Fig. 58, Pl. XXXII) consist of large ectodermic areas or patches on either side of the middle line. They are centers of rapid cell division, united by means of the lateral cords, which are bands of proliferating cells, with the thoracic-abdominal plate.

So far as I am aware we have no account of the origin of the optic disk in any Decapod excepting Alpheus, Astacus (54), Crangon (30), and Homarus (47). Parker, in his careful studies on the eye of the lobster, was unable to obtain the earliest traces of the developing optic disk, and the accounts of Reichenbach and Kingsley differ very materially. I will therefore describe somewhat in detail the process by which the optic disk is produced in Alpheus.

The optic disks at the time when they consist of a single stratum of cells are shown in Figs. 58, 68, and 69. A series of four transverse sections through the central portion of the left optic disk is represented in Figs. 64–67. The posterior face of each section is presented, the series passing from the front backward.

Since it is from the optic disk that the eye and its ganglion are developed, the important inquiry which arises at this stage is, how is the change effected by which the disk passes from this single-layered to a many-layered condition like that seen in the egg nauplius (Figs. 107, 114)? If the eye represents a series of hypodermal pits, it would be reasonable to look for some trace of these infoldings in the embryo. If, on the other hand, the compound eye of the higher Crustacea represents a closed vesicle produced by a single invagination of the hypodermis, of the type seen in the prototracheate Peripatus, we should expect to find some trace of an involution at this stage. So the answer to this question may have an important bearing upon the phylogeny of the compound eye.

Cell boundaries are easily discernible at the surface, but it is evident that the nuclei do not

all lie at the same level.   Passing now to Stage IV (Fig. 72), we notice several important changes in the external appearance of the optic disks.   They have approached nearer the middle line; they have increased in area; their nuclei are more crowded; near the center of the disk and on the side of it toward the middle line (Fig. 72, *C. M.*) the nuclei are distinctly larger.   In interpreting these changes we must resort to sections and a careful study of dividing nuclei.   A complete series of consecutive transverse sections through the left optic disk at this critical stage is given in Pl. XXXV.   The last of the series cuts the rudiment of the first antenna.   Karyokinetic figures come to our aid in pointing out the way in which the growth of the disk is effected.   The nuclei divide either radially, the plane of division, clearly marked by the equatorial plate, being perpendicular to the surface, or horizontally, the plate being in this case parallel with the surface.   In a single disk at this stage there were eight cells undergoing radial division.   Of these, six were near the periphery, where the cells formed a single stratum, while two were near the center, where the disk was slightly thickened (Fig. 80, *C. M.*).   It is evident from this and similar cases that the increase in area of the disk is accomplished by radial cell division.   The same is true of all proliferating areas in the lateral cords, where the appendages are soon budded.

In the area marked *C. M.* (Fig. 80) the optic disk is no longer a single layer.   This thickening is due either to horizontal cell division, that is, delamination, or to emigration.   The appearances of emigration are often very deceitful, but I think we may safely conclude that the initial thickening of the optic disk in the proliferating area, marked *C. M.* (Figs. 80, 90), is due to emigration, that a solid ingrowth akin to invagination takes place at this point.   Thus the cell marked *ec* in Fig. 80 is distinctly below the surface.   The boundaries of the cell can be clearly seen.   The cell *ec* in Fig. 90 (dotted line should be extended), on the other hand, is clearly in contact with the surface by a slender protoplasmic process, while the nucleus lies at a much lower level.   I interpret the latter as a cell at the point of breaking all connection with the surface and migrating to a lower position.   In the first instance this has already been accomplished.

In the stages under discussion there are one or two cases out of a large number of sections involving the optic disks of several individuals, which probably indicate delamination in the peripheral parts.   At a later period (Figs. 102-107) the nuclear figures are conclusive.   In one instance (Fig. 102, *ec*.) two cells are seen delaminating side by side.   The thickening of the optic disk is thus due in part to delamination, and this process is probably supplemented by emigration, at least in the central area.   The central area represents in all probability the "optic invagination" of the crayfish, and is concerned solely with the production of the optic ganglion.   In Alpheus there is a proliferating area simply, but no superficial depression or invagination in the strict sense.

It is noticeable that in Stage III (Pl. XXXIII) wandering cells, or cells which travel through the yolk, have not appeared in the neighborhood of the optic disks.   In Stage IV (Fig. 70, *Y. C.*) they are not far away, and in later stages (Fig. 91) these cells are close upon the disks.   Some of them which enter this region, coming near to or uniting with the disks, undoubtedly degenerate (compare *Y. C.*, Fig. 94, *s–s¹*, Figs. 95, 96, 99, 100).   Some of the cells of the disks next the yolk elongate, and appear to form a somewhat transitory covering.   As already suggested, these bodies are probably derived from the wandering cells.

The various stages by which the disk, already described, is converted into a conspicuous lobular mass of cells in closest relation with the antennular ganglion such as we have in the egg-nauplius (Fig. 111, *O. L*), can be seen by reference to the plates (Pls. XXXVI–XL).

(2) *The Development of the Retina and Optic Ganglion.*—The next event of importance is the differentiation of the optic disk into ganglionic and retinal portions.   This is already begun in Stage VII.   A deeper layer from which the ganglion is developed (Figs. 129, 132, *G. L.*) is gradually separated from a superficial tier of cells with very large nuclei (*OE*).   This layer is the retinogen. The differentiation begins in the lateral lower halves of the optic disks and extends upwards and toward the middle line.   As the disk spreads outwards, and at the same time increases in thickness, it tends to overgrow the hypodermis and becomes raised into a lobe or fold.   The optic lobe (Figs. 136, 138) thus represents a thickening of the hypodermis.   It is covered next the yolk by a delicate basement membrane (*Bm.*), which is continuous with that of the surrounding hypodermis.

Wandering cells are seen in contact with this membrane (Fig. 136), but they probably do not share in its secretion, although they occur in the closest relations with it.

At a little later period (Fig. 138) the retinal portion is several cells thick on the outer edges of the lobe, while it is a single stratum in the sagittal section, shown in Fig. 138. The plane of section is near the center of the lobe. The deeper nuclei of the ganglion are large and clear, the outer are smaller and stain more intensely. This section can be clearly understood if compared with the transverse section, Fig. 146. We see that the optic ganglion is here divided into an external or distal part and an internal or proximal portion by a thin sheet of very large and clear ganglion cells. Parker (47) describes and figures an exactly similar structure in the lobster, and I fully agree with him in regarding this band of nuclei as representing similar bands, which Reichenbach (Taf. XII, Figs. 173, 174, A. W. I. W.) describes in the crayfish. In Reichenbach's plates these nuclei appear as a narrow fold, forming the lining of what is described as a secondary optic invagination.

Three punct-substanz masses have already appeared in the inner half of the optic ganglion, the external middle segment, which lies next to the band of large nuclei, and the internal middle and proximal segments. The proximal medullary mass is much the largest and is the first to be differentiated, although the others follow close upon it. The dividing nuclear band lasts but a short time, and in Stage 10 (Fig. 167) has disappeared. In front of it is developed the lame ganglionaire or distal segment of the optic ganglion. This has an outer convex surface which is concentric with the basal membrane and with the outer surface of the retina, and it is carpeted by a special layer of ectoderm cells. These appear in section as a single row of elongated nuclei.

In an early communication (20) I stated my belief that the punct-substanz arose from a metamorphosis of ganglion cells. This view was suggested by certain appearances presented by the large clear nuclei, more particularly by those of the dividing band in the optic glanglion (see Fig. 180). Kingsley (32) came to the same conclusion in regard to certain large clear nuclei in or near the distal segment of the optic ganglion of Crangon. In reviewing this subject more carefully I am convinced that this interpretation is erroneous. These large clear cells are in reality undergoing indirect cell division, as proved by the karyokinetic figures which are occasionally seen. Both the chromatin network and the chromosomes are exceedingly delicate, and when the section is in the plane of the equatorial plate an appearance is presented which under certain conditions of staining and preparation might easily be interpreted in favor of retrogressive metamorphosis. I conclude that the punct-substanz of the nervous centers is in all cases derived from the protoplasm of cells, not from cell nuclei.

In Stage IX when eye pigment first appears, the structure of the retina is very simple. By the transverse section (Fig. 146), we see that the retina consists of a thickened ectoderm plate, thickest in its deeper portions, thinning out toward the middle line at the surface. It has the shape of the half section of a concavo convex lens.

In Palæmonetes the structure of the eye is precisely similar at this stage. Fig. 189 gives a section of the eye of this prawn, on a line with the œsophagus behind the optic ganglion, where it is seen to rest against the yolk. The black pigment, though appearing to arise in connection with certain mesodermic cells (wandering cells from the yolk), it in reality belongs to deep ectoderm, and marks the retinular cells. The cell protoplasm bearing the pigment bodies grows outward (Fig. 146), and also pierces and extends some distance below the basement membrane (Figs. 191, 192). The latter is a delicate cuticular structure secreted by the ectoderm cells which lie along the line of division of retina and ganglion, and continuous with the basement membrane of the hypodermis. In some sections it appears to be duplex, a condition described for the eye of the lobster by Parker (47), in which the inner layer enfolds the optic ganglion. The wide open fissure which now exists between retina and ganglion (seen in transverse section at *an*, Fig. 136) is partially filled with yolk. There is not the slightest doubt that cells enter this fissure from the yolk (Mes. Figs. 146, 167, 189, 191, etc.), but what the fate of these wandering bodies is, I find it very difficult to decide. I think, however, that it can be stated definitely that none of these cells enter the retinogen. They must supply some of the pigment found in this region, or they may become converted into connective tissue. In Stage X (Fig. 167) the yellow accessory pigment cells are clearly differentiated, or at least the pigment which these bodies give rise to, is seen

in abundance around the retinular elements. This is without doubt ectodermic in origin. Some yellow pigment also occurs below the basement membrane. This may be ectodermic or mesodermic, but the great bulk, if not all the accessory pigment cells, which in the adult eye extend their processes through the basement membrane, are ectodermic in their origin.

At the edge of the retinal plate the cells become very much elongated (Figs. 146, 188), and finally can no longer be distinguished from the superficial ectoderm. The thickening of the retinal plate is due solely to emigration. This might be inferred by the interwedging of the nuclei (Figs. 188, 189), and it is proved in cases of cell division by the position of the equatorial plate, which is always perpendicular to the surface.*

A later stage in the development of the eye is illustrated by Figs. 190 and 191, which are anterior (superficial) and posterior (deep) transverse sections. In Fig. 190 we see the retina differentiated into cell clusters. Each cluster represents part of an ommatidium—the corneal hypodermis, the cone cells, and possibly the distal retinular cells. The lower stratum of small nuclei belongs to the proximal retinulæ and to the accessory pigment cells. In deeper section, Fig. 191, we distinguish the proximal retinulæ—black, rod-shaped bodies piercing the basal membrane. The nuclei lie at the distal extremity of the pigment. Between the pigmented parts of the retinular cells other nuclei occur, which possibly represent an eighth rudimentary retinular cell (rtl^1). At the surface of the eye there is a stratum of cells with elongated nuclei. These are the nuclei of the corneal cells and probably also of the distal retinulæ. Between this and the inner stratum of retinular nuclei, the nuclei of the cone cells are seen, and a granular substance which is probably the first trace of the peculiar secretion of these cells. In an older stage represented by the drawing (Fig. 192) we see all these parts in a higher degree of development, and the eye has grown out into a very prominent lobe. Fig. 167 is intermediate between this and Fig. 191. The central parts of this eye are the most highly developed, and as we pass to the periphery especially away from the middle line, the ommatidia are less and less developed, until they reach the condition of a single layer of undifferentiated ectoderm. Thus, in a single section (like Fig. 192), we have a sort of composite picture of the various stages through which the developing retina has passed.

A considerably older stage is reached in Fig. 194. The cells of the corneal hypodermis are quite large and have already secreted a cuticular lens. The nuclei of the cone-mother cells are also conspicuous.

Later still, when the embryo is nearly ready to hatch, the eye has undergone very slight change. Fig. 187 represents an oblique longitudinal section through the eye stalk of *Alpheus heterochelis*. The black pigment of the retinular cells has been removed by the action of the nitric acid. Irregular sheets and masses of yellow pigment occur both above and below the basement membrane. The conspicuous stratum of nuclei, in which the bases of the cone cells are embedded, belong to the proximal retinular cells. The nuclei (unrepresented) lie close to the surface between the corneal cells. The cone cells end distally in a conical cap of protoplasm, the apex of which touches, in some cases at least, the corneal facet. The proximal ends of the cone cells taper gradually and can not be traced below the pigment zone.

In the first larva of *Alpheus sauleyi* the structure of the eye is similar. This is illustrated in Figs. 201–204 and Fig. 209. In transverse section (Fig. 201) the corneal cells are crescent-shaped. The distal retinulæ lie in the same plane with the latter and have the peculiar arrangement shown in the drawing. They are grouped in pairs, so that each set of corneal cells is surrounded by six nuclei—two pairs of nuclei and two single nuclei. The two odd nuclei pertain to the ommatidium in question. The delicate membranes which appear to surround the corneal cells belong, in all probability, to the distal retinular cells.

The structure of the compound eye has become a favorite subject of research during the past five years, and the important study of the development of the faceted eye, about which very little was known when Balfour's "Comparative Embryology" appeared, has not been neglected; still much work needs yet to be done in this direction. The literature of this subject has been recently examined by Parker (48), and I will therefore add to this account only a few comparative notes.

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* Parker states that the corneal hypodermis arises in the lobster by simple delamination. (*Op. cit.*) I have never seen delaminating cells in any part of the retina of Alpheus or Palæmonetes.

The proliferating areas in the optic disks of Alpheus and Homarus are undoubtedly homologous, and probably correspond also to the optic invaginations described in Astacus by Reichenbach and in Crangon by Kingsley. I therefore agree with Parker (47) in interpreting the ingrowth or involution of ectoderm, whichever may occur in the developing disk, as concerned with the optic ganglion solely and not with the retina. Reichenbach describes the visual organs as originating from three factors: (1) an epidermal layer; (2) the optic invagination; (3) the optic or segmental ganglion. From the epidermal layer and outer wall of the optic invagination the retina arises, while the inner wall of the secondary invagination unites with the optic ganglion. An inspection of Reichenbach's Fig. 224 (54) shows, as Parker has pointed out, that in all probability Reichenbach has misinterpreted his sections, and that the entire retina is derived from the hypodermal layer. The layer of cells with elongated nuclei, which he has designated as rhabdom, clearly pertains to the optic ganglion, and probably represents the nuclear covering of the distal convex surface of the lame ganglionaire (Fig. 192 of this work).

Kingsley, in his third paper on Crangon, changes his interpretation of the invagination of the optic disk of Crangon, regarding this involution as concerned only with the optic ganglion. I am inclined to believe that a renewed study of this subject would show that the optic disk originates in Crangon precisely as it does in Alpheus. A series of sections through the thickening disk of Crangon has little to show which is not brought out by a similar series of Alpheus (Figs. 76–83), and no pit or hollow invagination is seen.

The independent origin of the optic ganglia lends some support to the view that they have a segmental value and are not merely outgrowths from the brain, that the eyestalk is a modified appendage containing its proper ganglia.

Watase's interesting views (63) concerning the origin of the ommatidium from a hypodermal pit do not receive the support we should expect from embryology. How much value is to be given to the embryological data in this case it is hard to say, but, seeing the persistence of the involutions in the eye of Limulus, we would expect to find a trace of similar infoldings in the developing eye of the lower Crustacea, provided their eyes are constructed upon the same type. Until greater evidence is furnished I am inclined to regard the "compound eye" not as an aggregate of simple eyes, as the name implies, each one of which is due to a hypodermal infolding, but rather, as Parker has suggested, to differentiated clusters of ectoderm cells originating from a single epithelial layer.

THE EYE UNDER THE INFLUENCE OF LIGHT AND DARKNESS.

In June, 1890, while enjoying the facilities for biological research afforded by the laboratory of the U. S. Fish Commission at Woods Holl, Mass., it occurred to me that some valuable experiments could be made by testing the effects of direct sunlight and total darkness upon the growth and behavior of the pigment cells of the compound eye of Crustacea. After finishing my experiments upon one form I learned of the experimental work of Exner* upon the eyes of the glowworm, *Lampyris splendidula*, of Hydrophilus, Dysticus, and Colymbetes, in which he records the same phenomenon in insects which I have observed in a Crustacean. Later a paper has also appeared, by Mademoiselle M. Stephanowska, on the histological arrangement of pigment in the eye of Arthropods. I have seen only an abstract of this work, from which I gather that it deals either largely or entirely with the eyes of insects. My experiments were made upon the common prawn, *Palæmonetes vulgaris*.

A dark chamber was constructed and rendered as absolutely light-proof as possible. Inside of this a small glass aquarium was so arranged that a stream of sea water could be kept running through it for any length of time. Three egg-bearing females were then placed in the aquarium and the chamber was sealed. The egg embryos were early nauplius stages. Females with eggs in a similar stage were also kept under observation in an aquarium exposed to the light. The general cast of color of the prawn taken in the light is some shade of light brown or brownish green. After spending eighteen days in the dark, the prawns were taken out and exposed to the moderately bright light of the laboratory. The eyes were jet black and appeared to have greatly

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* Since these notes were written I have received the completed work of Exner, *Die Physiologie der Facettirten Augen von Krebsen und Insecten*, in which the field of experiment is greatly enlarged.

swelled in size, and the body was bleached nearly white. *The peculiar appearance of the eyes was caused by the forward extension of the distal retinular cells, of which there is a single pair in each ommatidium.*

The eggs of some of the prawns were hatching, and the pigment of the zoëa was carefully compared with that of the first larva of Palæmonetes hatched in the light. Both the black pigment of the retinular cells and the yellowish green pigment of the accessory pigment cells of the eye and the large brown chromatophores in different parts of the body were of the same character, whether the embryo had developed in darkness or light.

Another prawn was kept in the dark thirty-eight days, and on exposure to the light it presented the same appearance. As in the other cases, as soon as light reached the eye the distal retinulæ began to retreat to a deeper level. At first the black pigment which characterizes these cells extends out to the cornea. After an exposure of two minutes to direct sunlight a slight transparent band is seen below the cornea. This light zone increases as the pigment continues its retreat until, in the course of three-quarters of an hour, the distal retinulæ ensheath only the lower ends of the cones.

In another experiment a prawn was left only about twenty-four hours in darkness. The same effects were produced in the eye, which assumed its former condition after being in the diffused light of the room twenty-five minutes. The distal retinular cells thus respond very promptly to the action of the light, and in the course of a few hours (the exact time needed was not determined), if excluded from the light, completely enshroud the proximal ends of the cone cells.

In the eye of Palæmonetes, taken in ordinary daylight, there are three distinctly marked strata of pigment between the basement membrane and the cornea, a proximal narrow stratum of yellowish brown pigment belonging to the accessory pigment cells; a wider and much lighter area peppered with dark granules, pertaining to the proximal retinular cells, the nuclei of which form a conspicuous belt or layer on a level with the distal extremity of the rhabdoms. Lying close upon the tier of retinular nuclei is a thin stratum of intensely black pigment, composed of the distal retinular cells. As stated above, there are two of these cells to each ommatidium, and they each send out a slender thread-like process, which extends in some cases as far forward as the corneal cuticula, where it is possibly attached. I have not detected any similar prolongations in the direction of the basement membrane. Below the level of the cone, which terminates abruptly in a convex proximal surface, the cone cells are prolonged into a long slender stalk consisting of protoplasm or of a refractive substance of a different nature from the cone. The cone cells are not apparently prolonged below the level of the retinular nuclei. The distal retinular cells thus surround the proximal ends of the cone cells.

In the eye exposed for thirty-eight days in the dark the distal retinular cells form a stratum about midway between the corneal cuticula and the layer of nuclei of the proximal retinular cells. The nuclei occupy a central position in this layer. Pigmented pseudopodia extend forward to the cornea, and occasionally a cell shows a slight inward prolongation. Had the eyes been preserved without bringing them into the light, even for a moment, the distal retinular cells would undoubtedly have occupied a still more peripheral position.

In the eye kept in the darkness for the same length of time and afterwards exposed to the light for five hours the distal retinular cells have retreated until they lie around the proximal ends of the cones. The nuclei of these cells lie immediately upon the nuclei of the proximal retinular cells, and it is interesting to notice the pigmented body of each cell folded on itself. In section the pigment takes the form of plaited black ribbons. When the eye is again stimulated by light the ribbon unfolds as the cell travels forward.

These cells are called by Exner the iris pigment, since they regulate the brightness of the retinal image in much the same way as the vertebrate iris does.

X.—SUMMARY.

In the review, including Sections V–IX of Part Second of this memoir, the principal embryological facts have been summarized, and it will now suffice to recapitulate only some of the more interesting results.

PART I.

Metamorphosis.—(1) The majority of the Alphei hatch as zoëa-like larvæ, while two species are known, *A. heterochelis* and *A. saulcyi*, in which the metamorphosis is abbreviated. This shortening of the metamorphosis appears to be directly related to the habits and environment of the species. *A. heterochelis* has one metamorphosis at Beaufort, North Carolina, a more abbreviated development at Key West, Florida, and, if we are right in considering the Bahaman form as a member of this species, at Nassau, New Providence, the metamorphosis is complete or unabbreviated. The Nassau form of *Alpheus saulcyi* either has the metamorphosis greatly abridged or it hatches with all the external characters and the instincts of the adult. When we inquire into the modes of life of these species we find the remarkable fact that the Nassau *Alpheus saulcyi* is a parasite or commensal, living in the pores of certain sponges, and the metamorphosis is completely absent or profoundly modified. The Floridian *Alpheus heterochelis* is a parasite in sponges, and has its metamorphosis greatly abridged. The Beaufort *heterochelis*, which must be regarded as descended from the Floridian stock, has its metamorphosis less abridged than in the latter case and it is nonparasitic. However, we still find it occasionally producing small eggs, indicating a tendency to revert to the old metamorphosis, long since abandoned. Even if we decide that the Nassau *heterochelis* has had a different genealogy from that of the Beaufort variety, we still have strong evidence to show that the metamorphosis of the species may change in accordance with a change in habits and environment.

Variation and Habits.—(2) *Alpheus heterochelis* of Beaufort presents an interesting variation in the structure of the small chela, which appears to be a sexual one.

(3) In many Macroura as well as Brachyoura, and especially in the Alpheus, one of the claws is enormously enlarged, often nearly equal in size to the rest of the body of the animal. This great chela may be either on the right or left side of the body, but it almost invariably follows that all the young of a brood have the large claw on the same side, indicating that this characteristic is inherited from the parents, and that where both of the latter have the right or left claw enlarged they give rise to right and left handed broods, respectively.

(4) *Alpheus saulcyi* presents very profound variations, and some of these varieties would undoubtedly be regarded as distinct species by systematic zoölogists if the intermediate forms were unknown. These forms are described and discussed in Sections V and VII of Part First.

Species living side by side show no tendency to commingle, and hence we conclude that the striking varieties which we are here met with are not the result of hybridism, but are confined to a single species. Two well marked varieties occur, which I have distinguished as *Alpheus saulcyi*, var. *brevicarpus*, and *A. saulcyi*, var. *longicarpus*. Between these forms every intermediate stage is found.

The color variations in this species are also exceptionally marked. In all respects the males appear to be more variable than the females. The structural peculiarities of the mother appear to a large extent in the offspring, and if the swamping effects of intercrossing should be eliminated it is likely that this species would soon become separated into at least two distinct forms.

It seems most probable that the change in habits or environment which this species has undergone, has acted as a direct stimulus to variation.

PART II.

Structure of the Larva of Alpheus saulcyi.—(5) The structure of the first larva of this Alpheus reaches a very high degree of complexity, which is but little exceeded by that of the mature adult form.

The green gland does not yet appear to have an external opening. The five pairs of gills present at this time are also rudimentary, and the reproductive organs are only represented by a small cluster of large cells on either side of the middle line, between the digestive tract and the anterior end of the heart. For the histological details, reference must be made to Section I of Part Second.

The Ovary and Ovarian Egg.—(6) The ovary consists of an external stroma of muscular and connective tissue and a lining epithelium. The ova arise from the lining epithelium, and each egg

is differentiated from a distinct epithelial cell, the nucleus of the cell becoming the nucleus or germinal vesicle of the egg. Some of the epithelial cells enwrap the developing ovum and form the follicle or pocket in which it is lodged. The chorion or inner egg membrane is the direct secretion product of the follicular cells.

(7) In Homarus and Palinurus the character of the germinal epithelium is somewhat different from that of Alpheus. The outline of individual cells is obscured and the germinal epithelium extends inward from the wall, in the form of radial sheets or folds, between which are reëntrant blood vessels. There are a number of germogenal areas corresponding to the folds in which the ova originate. During growth the eggs gradually pass from the center toward the periphery. In the germogen the cell outlines are obscured.*

(8) The yolk arises within the cell protoplasm, and in Homarus degenerating nuclei occur in the ovarian stroma, and it is probable that a certain number of nuclei degenerate and enter into the food yolk of the egg. In the lobster also some of the follicle cells develop into gland-like structures which characterize the mature ovary. They appear to have a direct relation to the growing eggs, but their true significance has not yet been ascertained. In about two weeks after the eggs have been extruded these structures have almost wholly disappeared.

(9) I have observed a single polar body in a section of the egg of Stenopus, in which the male and female pronuclei were present, and two polar bodies in the ripe unextruded egg of the lobster. In lobster's eggs also which failed of extrusion at the proper time, and which eventually degenerate in the ovary, I find that the nucleus is at the surface. It has the appearance of a female pronucleus. It is thus probable that the polar bodies are often, if not always, given off before the eggs are laid.†

Segmentation in Alpheus minor.—(10) The segmentation in *Alpheus minor* is in some respects anomalous, and the conclusion seems to be warranted that we have here a case of amitosis, unlike anything which has been hitherto described in Crustacea. Unfortunately my material is not at present sufficient to enable me to say in exactly what way the usual process of cell division has here been modified.

Delamination.—(11) The segmentation has been thoroughly reviewed in Section v, and it is unnecessary to repeat the details. I wish to call attention, however, to the fact that at the close of segmentation in the lobster some of the blastodermic cells delaminate and their products pass into the yolk. In *Alpheus saulcyi* a similar migration of cells from the superficial to the deeper parts of the egg occurs, but in this case it was not determined whether this migration was preceded by delamination or not. These cells appear to originate in greatest number over that side of the egg which corresponds in position to the embryonic area. It seems possible that these cells may represent a primitive endoderm, the function of which has been usurped. In the lobster they speedily degenerate.

Invagination Stage.—(12) The invagination stage, which soon follows, results in the admission of more cells into the yolk and in the formation of an organ called in this memoir the ventral or thoracic-abdominal plate. Cells also continue to pass into the yolk from the ventral plate. While cells are constantly being subtracted from the plate, it is constantly receiving new recruits from the surface, owing to the activity of cell division in this region. We thus have in Alpheus a multitude of migrating cells, derived originally from three sources: from the blastoderm, from the cells which are first invaginated, and from those which originate later from the ventral plate, after all trace of the superficial pit has disappeared.

Germ-layers.—(13) These migrating cells, which are collectively called "the wandering cells" in Section vii, spread to all parts of the egg. While it is perfectly obvious that these bodies represent mesodermic and endodermic tissues, it is not so easy to determine what particular cells give rise to this or that layer, nor is it easy to decide in many cases, from a superficial study, whether migrating cells may not be derived from the ectoderm in various parts of the embryo. This sub-

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*The structure of the ovary of the lobster has been recently described by Bumpus in a detailed paper upon the embryology of this species. He has called attention to the folded character of the ovarian epithelium, which is so marked in the young or immature ovary. (The Embryology of the American Lobster, by Hermon Carey Bumpus, *Journ. of Morphology*, Vol. v, No. 2, 1891.)

† Polar bodies have been recently described in the external eggs of the lobster by Bumpus. *Op. cit.*

ject is fully considered in Section VII, the general results being: (1) That it is not possible to decide what part the primary yolk cells play in Alpheus, for reasons which have been already considered; (2) that the great bulk of the cells which migrate forward from the area of invagination and attach themselves to the embryo, or proceed to the peripheral parts of the egg and take up a position at the surface, are undoubted mesoblastic elements; (3) that those cells which give rise to the endodermal epithelium in the egg nauplius are derived largely from cells which migrate in a posterior direction from the area of invagination; (4) that degeneration, followed by the death and dissolution of the chromatin and cell protoplasm, is characteristic of the wandering cells at about the beginning of the egg-nauplius period. The mesoblast has become a well-recognized layer before the endodermal epithelium has appeared.

(14) The egg, with centrally moving cells which have budded from the blastoderm, may be compared with the *planula* stage of Cœlenterates, and the internal cells may represent the primitive endoderm. According to this view, the invagination stage has no reference to an adult gastrula-like ancestor, but is a purely secondary condition, which became so impressed upon the ancestors of the present Decapods that it has remained in their ontogeny.

In the majority of Decapods which have been studied the invagination has no direct relation to the mouth or anus, or to the alimentary tract. The conditions which are present in the crayfish cannot be regarded as typical or primitive.

(15) In Alpheus and Homarus the primitive mouth arises on a line between the rudiments of the first pair of antennæ, but these appendages are never post-oral. The hind gut originates as a nearly solid ingrowth, apparently at a point considerably behind the position of the pit due to the first invagination, and is formed one or two days later than the mouth.

Cell dissolution.—(16) The degeneration of embryonic cells is treated at length in Section VI. It is remarkable that the early segmentation stages of *Alpheus minor* are attended with the degeneration of protoplasm. The chromatin residues remain for some time in the yolk, and eagerly react upon dyes, but gradually lose this power and eventually enter into the general nutrition.

(17) Degenerating cells appear in greatest force in Alpheus, Astacus, and Homarus at about the egg-nauplius stage, and from that time their numbers begin to wane. They appear in one instance before the differentiation of the germinal layers, and are not confined to any one layer at a later period, but in *Alpheus sauleyi* they are most characteristic of the wandering cells, which represent mesoderm and endoderm. The "secondary mesoderm cells" and "white-yolk elements" which have been described by Reichenbach, are to be regarded as degenerating cells. Degenerating cells also occur in connection with the "dorsal plate."

The Eyes.—(18) The details of the structure and development of the eyes and nervous system are fully reviewed in Sections VIII and IX.

The eyes and optic glanglia are derived from the optic disk, in the formation of which there is in Alpheus no proper invagination. The thickening of the disk is accomplished by emigration from the surface and by the delamination of superficial cells. An area of active cell division can be distinguished, which corresponds to the invaginate area of the optic disk of the crayfish. The cells which migrate from the center give rise to the rudiment of the optic ganglion. The disk grows out in the form of a lobe, and becomes differentiated into an outer retinal layer and an inner ganglionic layer. The eye proper is differentiated from the retinogen, which is primitively a single layer of ectodermic cells.

(19) I am inclined to regard the "compound eye" not as an aggregate of simple eyes, as its name implies, each of which is due to a hypodermal infolding, but rather as a collection of differentiated clusters of ectoderm cells, originating in a single epithelial layer.

(20) The absence of light has no appreciable effect on the development of the eye pigment, but in *Palæmonetes* the distal retinular cells respond very promptly to the action of light. If the light is excluded from the eye, these cells migrate outward and enshroud the proximal ends of the cones, sending out pseudopodal prolongations to the cornea. When the eye is again stimulated by light the pigment immediately retreats from the surface, and the cell takes the form of a plaited black ribbon, leaving the cones free.

ADELBERT COLLEGE,

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APPENDIX I.

THE LIFE HISTORY OF STENOPUS.

Since this paper was written Chun has described (Die pelagische Thierwelt in grösseren Meeresteefen, Bibliotheca Zoologica, I, 1888) a small transparent crustacean which he calls *Meiersia clarigna*. It occurs at the surface and also at various depths down to 600 M. A comparison of his description and figure (Taf. IV, Fig. 6) with the Stenopus larva shown in Pls. IX and X of this memoir shows that Chun's *Meiersia clarigna* is undoubtedly a Stenopus larva, a little older than the one shown in Pl. X. (W. K. B.)

It is suggested at the bottom of page 340 that the cement by which the eggs are fastened to the abdomen may possibly come from the oviducts. According to recent observations of Cano (*Mittheil Zool. Stat. Neapol.*, IX, 1891; abstract in *Journ. Roy. Mic. Soc.*, No. 83, 1891) this is derived from cement glands situated in Stenopus under the epidermis of the pleopods. It is thought by Cano that these glands, to which the secondary egg membrane is due, are modified glands of the appendages, and that the cement substance may serve as the medium through which spermatozoa reach the ova. In order to reach the eggs the sperm cells probably pass through pores in the chorion.

This paper was written in the summer of 1888, before I had seen the report of Spence Bate on the *Challenger* Macrura (Report on the Crustacea Macrura dredged by H. M. S. *Challenger* during the years 1873-76, Zoology, Vol. XXIV, p. 209, Pl. XXX, 1888). The *Challenger* brought home only two specimens of *Stenopus hispidus*, one from Kandavu, Fiji Islands, and one from Bermuda. Spence Bate says that Stenopus has been "chiefly recorded from the eastern seas and the shores of India by Desmarest, Milne-Edwards, and Sir Walter Eliott; from Japan by de Haan." It has been thought that *Squilla greenlandica* of Seba, which appears under several names, may be the same as *Stenopus hispidus*. "The genus," says Bate, "thus appears to inhabit regions so widely apart as Greenland in the north, the Bermudas and Mediterranean in the west, and the southern coasts of India and the Fiji Islands in the east. It has been found in the cold waters of the Arctic regions as well as in the warm shallow waters of the tropics, but, despite this cosmopolitan range, it has not been recorded as having existed in any geological formation."

While the conclusion that the Arctic form is a *Stenopus* may be correct, it seems highly improbable that it is specifically related to *Stenopus hispidus*. There is no evidence at least to show that this is the case.

Bate figures a late egg embryo of Stenopus (Fig. 40, p. 212), and erroneously concludes that the animal has a short metamorphosis and that it hatches as a "Megalopa." He also gives a drawing (Pl. XXIX, Fig. 2, v.) of the first larva of *Spongiola renusta* (a prawn which is placed by Bate in the family Stenopidæ). This is clearly not a zoea, but a *protozoea*, as is better shown by the sketch of the recently hatched larva (Fig. 42, p. 216) by von Willemoes Suhm, and the strong resemblance which it bears to the protozoea of *Stenopus hispidus* is very striking (compare with Pl. VII, Fig. 11, of this paper).

According to Bate the branchial formula of Stenopus was first elucidated by Huxley in his memoir on the classification of crayfishes (Proc. Zool. Soc., London, 1878). There are *six* pleurobranchiæ; *eleven* arthrobranchiæ, five of which are anterior and six posterior; *one* podobranchia, and *six* mastigobranchiæ, of which the first is the only efficient appendage.

Spence Bate states that after careful comparisons he failed to find specific differences between specimens from the Eastern and Western Hemispheres.

ERRATA.

As numerous errors have unavoidably occurred in this paper, I will correct the more important of them.

Page 341, line 8, for "Pl. VII" read Pl. X.
Page 341, line 13, for "Lesneur" read Lesneur.
Page 343, line 2, for "cells have spread more rapidly at a given point on the egg" read cells have increased more rapidly over a given area of the egg.
Page 343, over table for "Temperature 80° F.," read Temperature of air, 80° F.
Page 344, lines 11, 16, 31, 32, and 47, for "Fig. 10" read Fig. 11.
Page 344, line 18, for "largely developed" read highly developed.
Page 345, line 20, for "Fig. 10" read Fig. 11.
Page 345, line 30, for "Fig. 11" read Fig. 10.
Page 345, line 38, for "the first and second maxillipeds" read the second and third maxillipeds.
Page 346, line 31, for "larger than telson" read longer than telson.
Page 347, line 16, for "XII and Fig. 40" read XIII and Fig. 39.
Page 347, line 29, for "and 38" read and 39.
Page 347, lines 37 and 41, for "Pl. XI" read Pl. XII.
Page 347, line 40, for "Figs. 43, 45" read Figs. 43, 44.
Page 347, line 47, for "Fig. 47" read Fig. 46.
Page 348, line 15, omit "errinem......larve."
Page 348, for lines 32–34 read: Body nearly cylindrical; tergal surface covered with spines. Carapace with prominent laterally compressed rostrum and distinct cervical and branchio-cardiac grooves. Outer antennæ with long bristle-bordered scale bent under the inner antennæ toward the middle line. Second maxillipeds with setigerous lamina, attached to endopodite.
Page 348, line 46, for "a marked transverse fossa" read a marked cervical groove.
Page 348, last line, for "transverse furrow" read cervical or mandibular groove.
Page 349, line 17, for "Fig. 40" read Fig. 39.
Page 349, line 21, for "their inner borders which meet in the middle line" read the inner borders of the exopodites which meet in front.
Page 349, line 23, for "Fig. 39" read Fig. 38.
Page 349, line 25, for "Fig. 38" read Fig. 36.
Page 349, line 39, for "Fig. 48" read Fig. 45.
Page 349, seventh line from bottom, for "the great chelæ" read bearing the great chelæ.
Page 350, first line, for "Fig. 48" read Fig. 47.
Page 350, first and second lines, for "bearing a shorter proximal one below" read bearing a longer tooth and a shorter proximal one below.
Page 350, line 9, for "Fig. 41" read Fig. 40.
Page 350, table, tenth line from bottom, for "Length of chela" read Length of chela of same.
Page 352, line 10, for "hartschälig" read hertschalig.
Page 352, tenth line from bottom, for "Crustaces, Arachnidses" read Crustacés, Arachnides.

APPENDIX II.

PARASITIC FUNGUS IN THE EGG EMBRYOS OF ALPHEUS SAULCYI.

The remarkable parasite of *Alpheus saulcyi*, to which allusion was made in Part First of the Memoir on the development of Alpheus, is illustrated in Fig. 199, Pl. LIII. Although a large number of egg-bearing females were examined and their eggs were sectioned, only a single female (a small specimen, probably var. *longicarpus*, obtained from the "loggerhead sponge" at Abaco) was found to be infested with this singular parasite. We may therefore regard it as very rare under these conditions.

The sections of these embryos were very kindly examined by Professors Joseph Leidy and W. G. Farlow. In reference to them Dr. Farlow writes as follows:

The parasite is certainly of great interest. I cannot find any description of it in botanical literature, although it appears to be a fungus belonging to Chytridiaceæ.

The fungus has no mycelium, but is composed of single cells of various sizes. In a section like that shown in Fig. 199 nearly one hundred large cells or cysts can be counted, and it is seen that the peripheral parts of the embryo are packed with them. These embryos were alive, although the embryonic cells were considerably altered from their normal condition, where they came in contact with the parasitic growths and showed traces of degeneration.

The parasitic bodies are mainly (1) large naked cysts or encysted cells, and (2) very small spore-like bodies. The naked cyst ($c. s.$, Fig. 199) is a thick shell which has collapsed and curled up with the escape of its contents. It is yellowish and is unaffected by staining reagents. The surface of the cyst is covered with very uniform, short projections or tubercles, which refract the light in a characteristic way.

Other encysted cells contain a protoplasmic reticulum (cs^1), and there are very similar but smaller bodies which are either naked or possess but a slight cuticular wall. These encysted bodies just described possibly represent zoosporangia, and give rise to the myriads of minute spores which occur in close relation with them. The spores (Fig. 199, $sp.$, represented by small black dots) are minute, oval, and highly refractive. In the eye and other organs certain nuclei take up the stain very eagerly and refuse to part with it. These are probably the nuclei of embryonic cells which have undergone modification. Occasionally one of the cysts appears black (cs^2), which is due mostly, if not wholly, to refraction.

According to Goebel, reproduction in the *Chytridieæ* is effected by means of swarm spores. Resting cells occur, which germinate and become sporangia, producing large numbers of swarm spores. Some forms, like Chytridium, have no mycelium. Its single cells, which live on or within the host plant, after reaching their full size become zoosporangia. These give rise to swarm spores, which are liberated into the water. The *Chytridieæ* are described as parasites on other aquatic plants, Fungi, Algæ, and Phanerogams.

According to De Bary resting spores are known to occur in certain species. These develop directly into sporangia or produce them after a short intermediate stage, and appear to resemble the sporangia in size and in possessing a warty cellulose coat.

APPENDIX III.

Some early abstracts of this work (Alpheus: A Study in the Development of Crustacea) were included in the Introduction published in the Johns Hopkins University Circulars, No. 97, April, 1892. The part relating to the embryology of Alpheus was here printed in its unrevised form, and differs materially from the results of later studies which are given in this memoir.

While this work was in press it was thought best to change the name Alpheus minus of Say to the correct form, *Alpheus minor*. As some of the pages were stereotyped before this correction was made, both forms of the name appear.

ADELBERT COLLEGE,
        Cleveland, Ohio, May, 1892.

PLATE I.

Alpheus minor, drawn from life by W. K. Brooks. (Enlarged eight diameters.)

Dorsal view of a specimen of the gray variety of *Gonodactylus chiragra*, twice natural size.
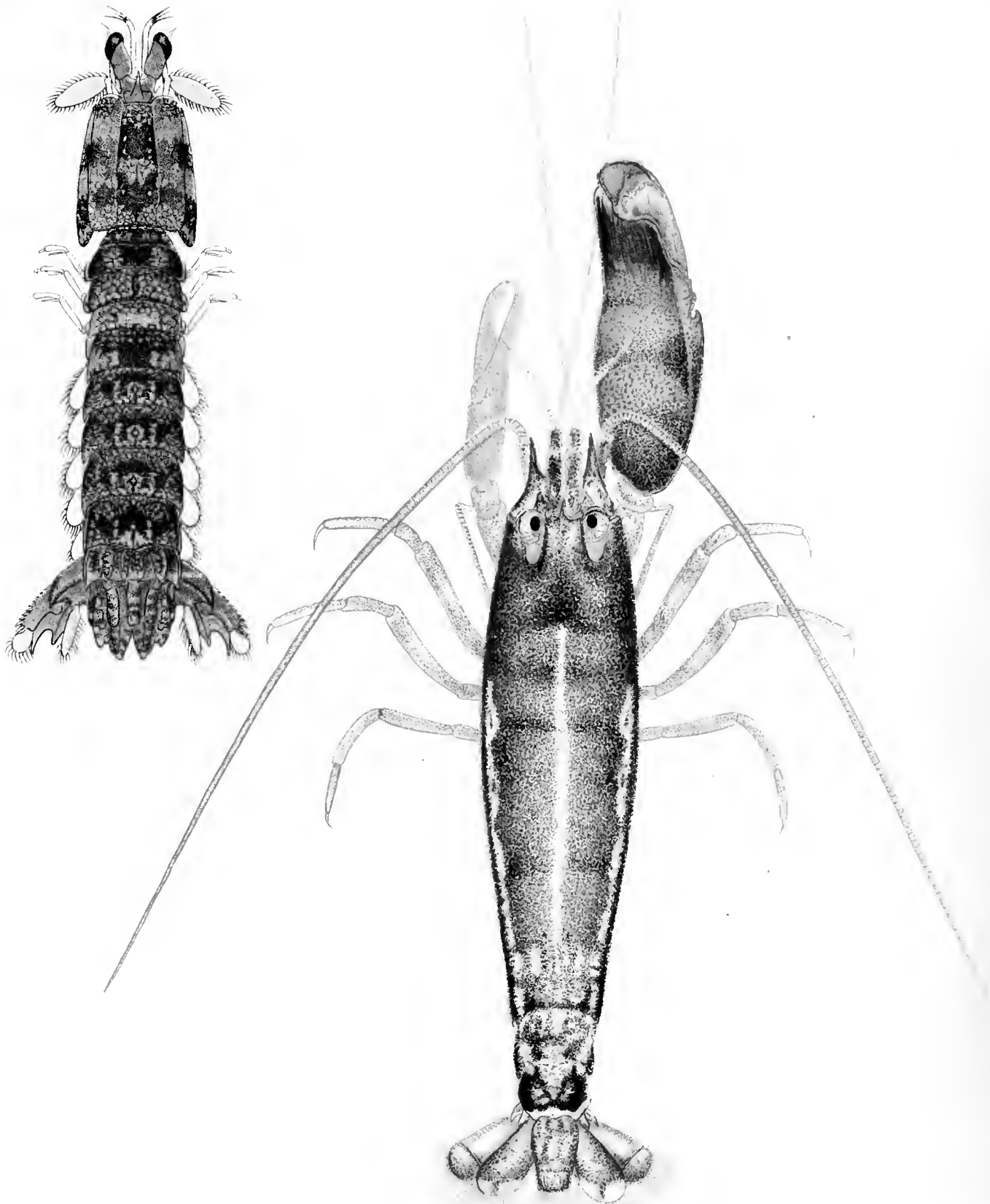
Plate I.

W. K. Brooks, del.

ALPHEUS MINUS AND GONODACTYLUS CHIRAGRA.

PLATE II.

Alpheus heterochelis, drawn from life by W. K. Brooks.　(Four times life-size.)

Plate II

ALPHEUS HETEROCHELIS.
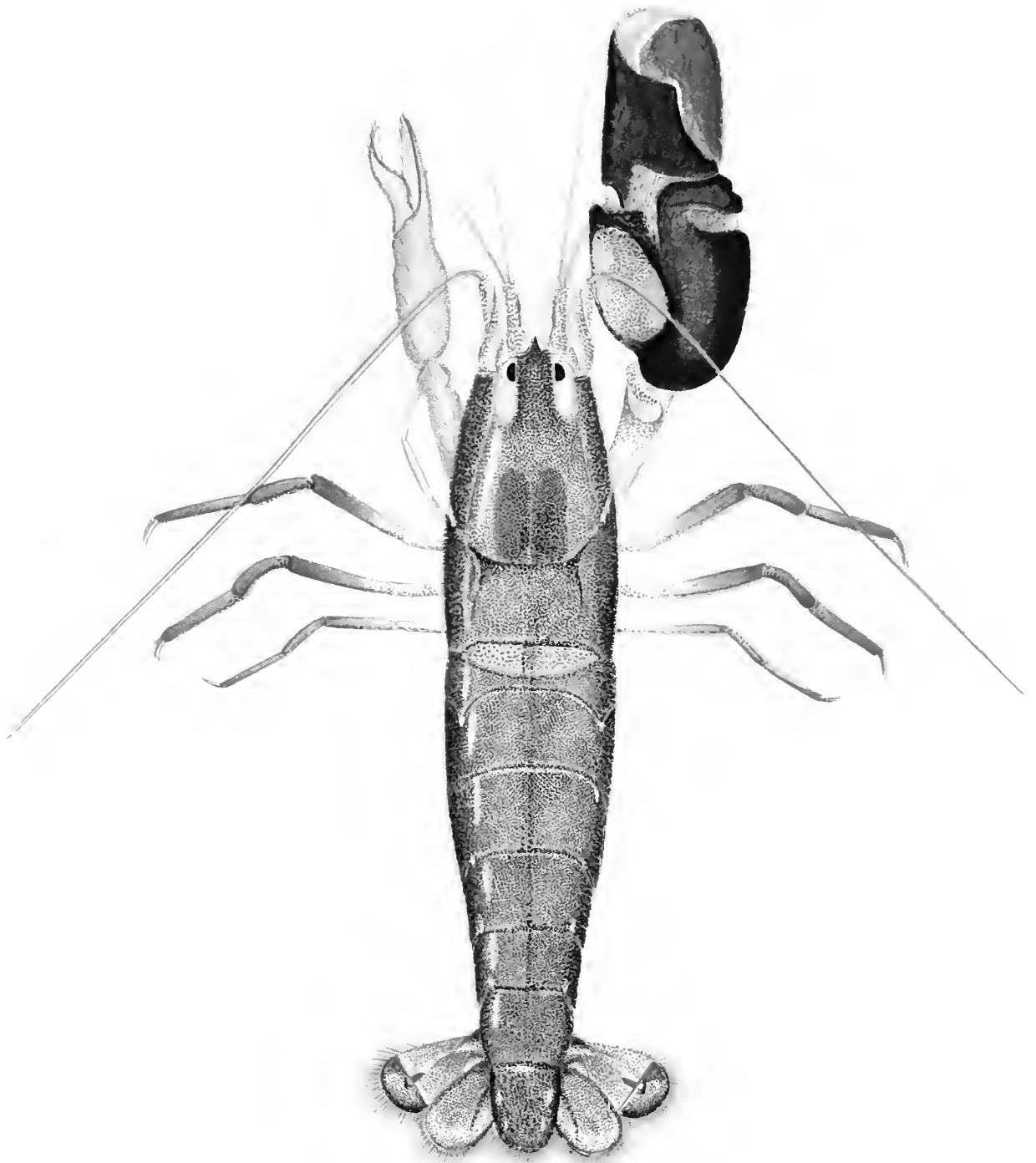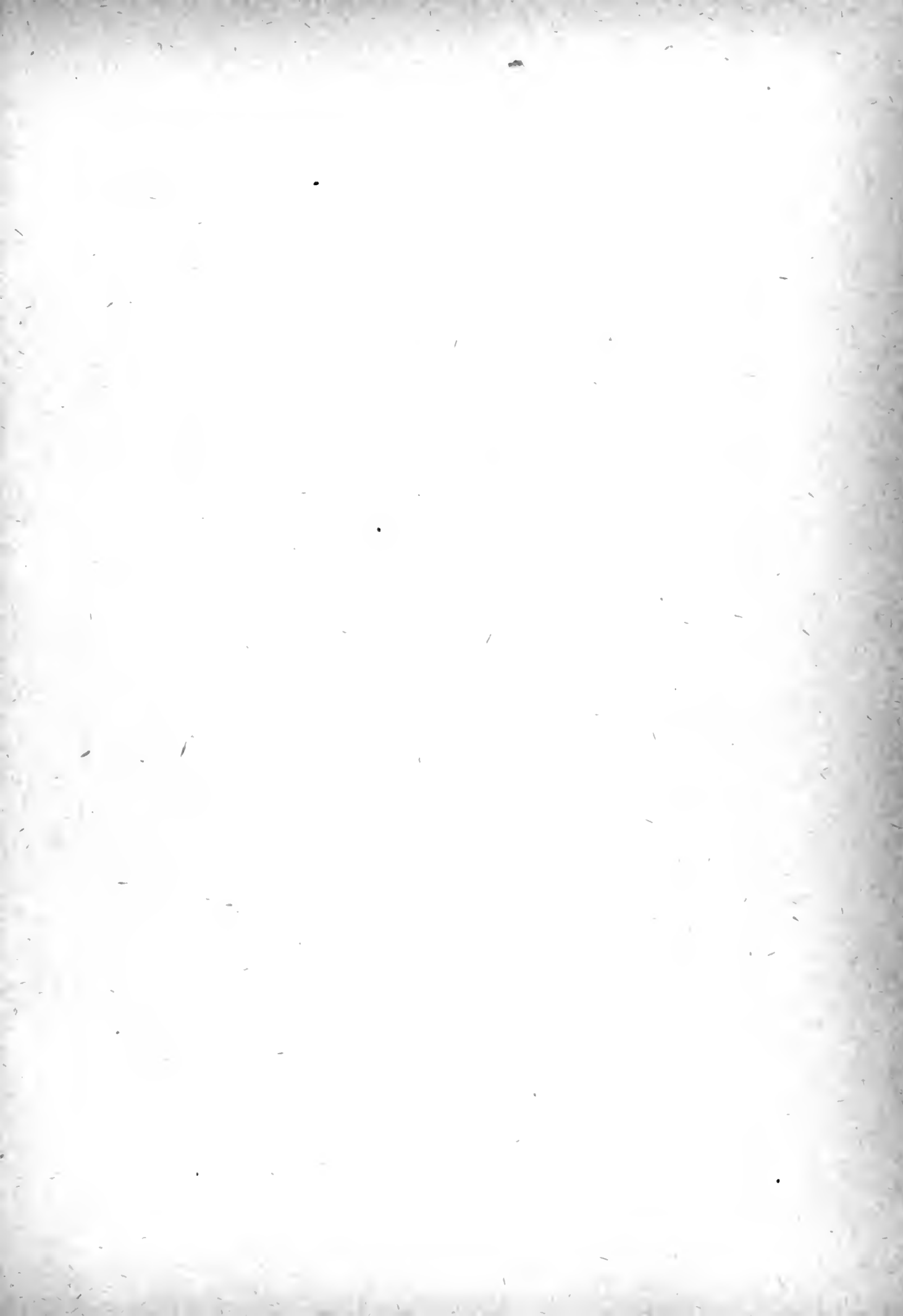
Plate III.

Gonodactylus chiragra, drawn by W. K. Brooks.

Adult female of the green variety, in her burrow, with eggs, twice natural size.
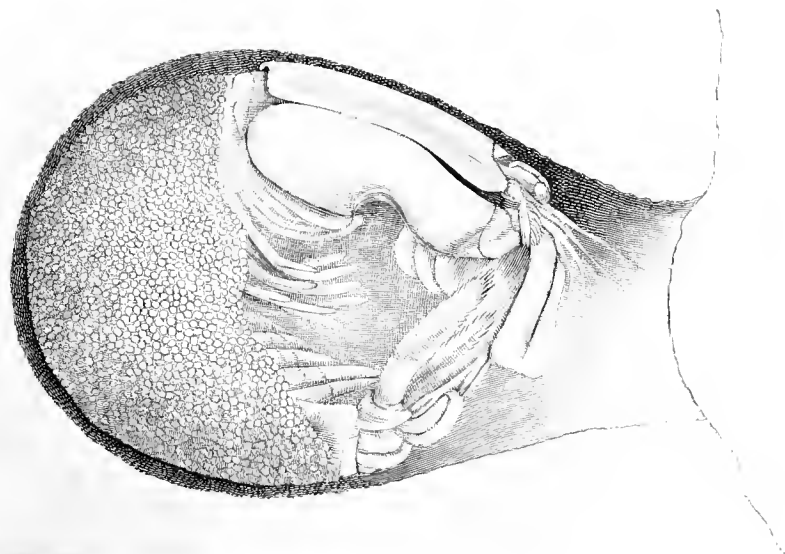
W. K. Brooks, del

GONODACTYLUS CHIRAGRA.

Plate IV.

Adult male and female of *Alpheus saulcyi*, var. *brevicarpus*, from Nassau, New Providence.

Fig. 1. Lateral view of female from green sponge. ×3½.

Fig. 2. Dorsal view of the same. ×3½. Parts only of the ovaries are visible in Fig. 2, while the eggs, which greatly distend the abdomen laterally, show plainly between the bases of the swimmerets. In Fig. 1 the small chela is bent downward, the position in which it is usually carried. In Fig. 2 the chelæ are represented in the attitude of defense. The dactyle of the left "hand," or large chela, is raised preparatory to striking.

Fig. 3. Small male. L = $\frac{10}{16}$ in. ×7½. Drawn under slight pressure, owing to which the antennal spines and the antennular exopodites have assumed an unnatural position. The posterior margin of the carapace is more correctly represented in Fig. 1.

Plate IV.

1.

2.

3.
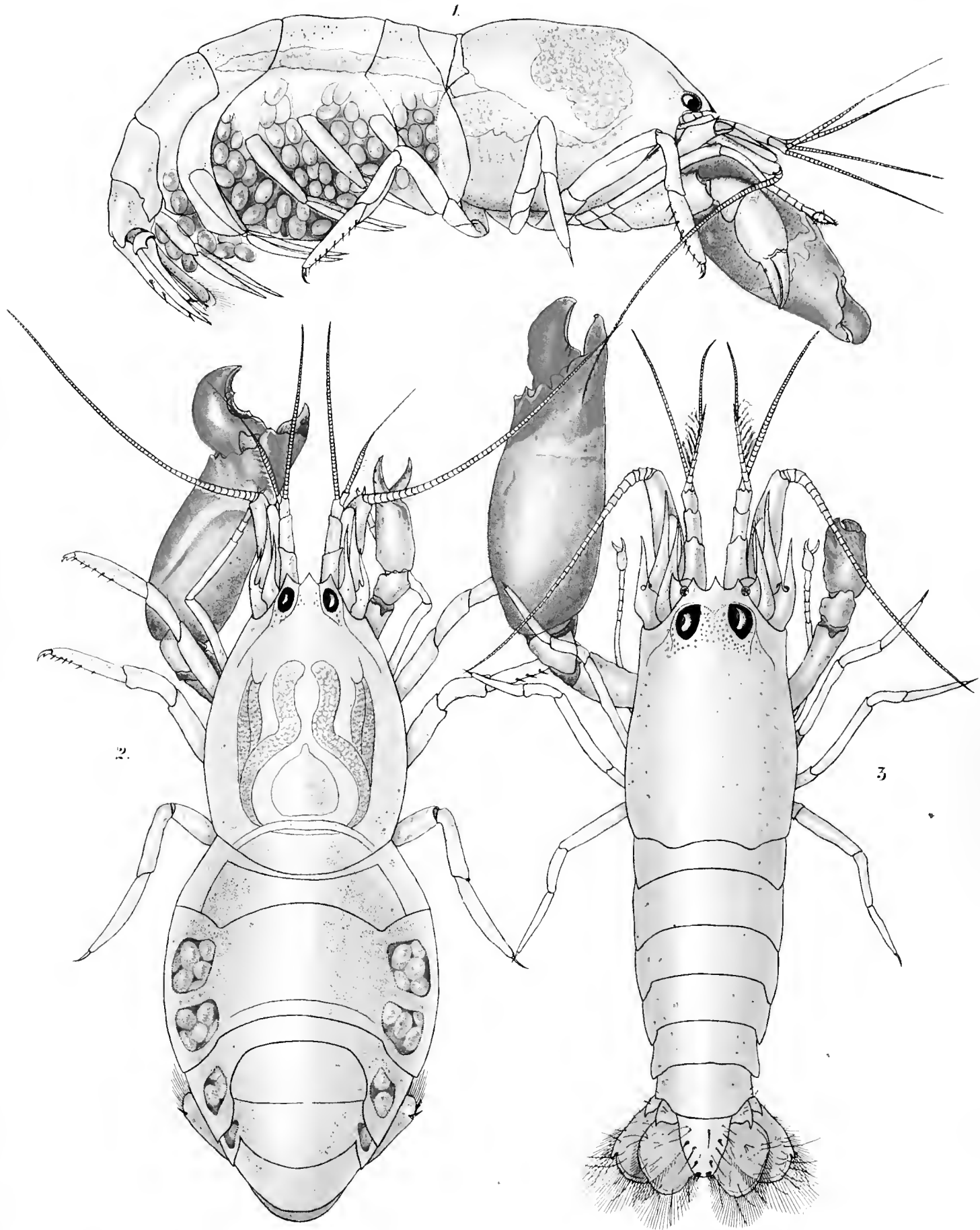
F.H.Herrick, del.

ALPHEUS SAULCYI, VAR. BREVICARPUS.

Plate V.

Dorsal view of the adult male *Stenopus hispidus*. Nassau, N. P., June, 1887.　L $= 1\frac{3}{4}$ in.　L. first antenna, exopodite $-3\frac{7}{8}$ in., endopodite $-3\frac{3}{8}$ in.　L. second antenna $= 4\frac{11}{16}$ in.　$\times 1\frac{3}{4}$.
Excepting the brilliant pigment bands the body and appendages are nearly white, and could be better represented against a black background.　The arching flagella of the antennæ are greatly foreshortened, and the spines and setæ are of necessity unduly emphasized in a pen and ink drawing.

Fig. 56.

STENOPUS HISPIDUS.
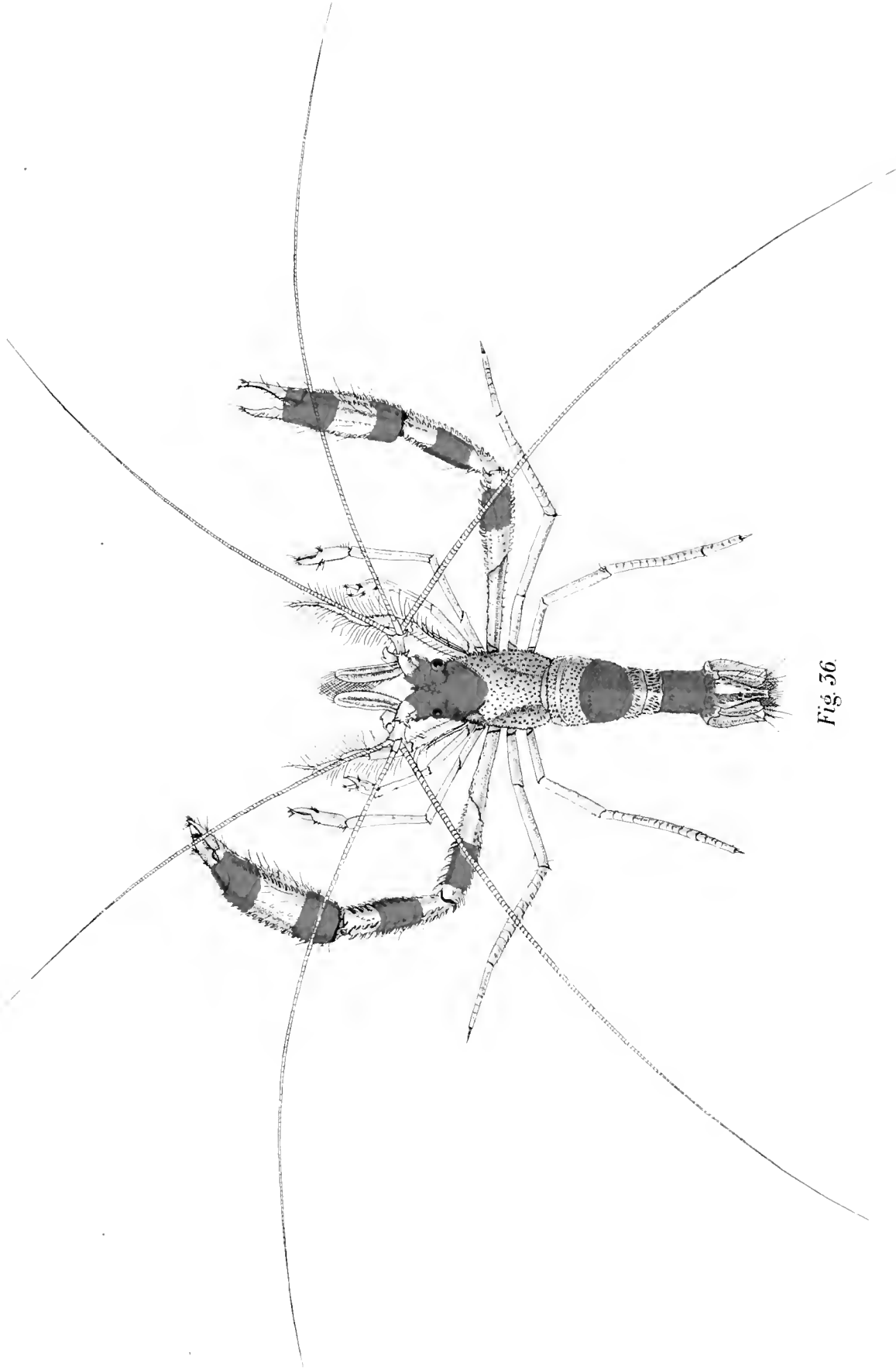
PLATE VI.

FIG. 1. Part of section of egg, showing the male pronucleus. The female pronucleus lies nearer the center of the egg, is less regular in outline and has less perinuclear protoplasm. A single polar body (not represented) is seen in this section. It lies close to the surface of the egg, beneath the membranes, not far from the male pronucleus. It appears as a small mass of chromatin, which stains quite as intensely as the nuclei. Egg about 6 hours old.   ×276.

FIG. 2. Section of egg with four nuclei, none of which are at the surface.   ×152.

FIG. 3. Part of same section, showing the nucleus and surrounding protoplasm and yolk.   ×276.

FIG. 4. Lateral section, cutting yolk segment on a level with the disk-shaped nucleus.   Compare Fig. 5 a.   Eight-cell stage.   Age about 12 hours.   ×276.

FIG. 5. Section through egg in eight-cell stage.   Compare Fig. 6.   Age about 15 hours.   ×152.

FIG. 6. Surface view of egg in the third segmentation or eight-cell stage. The egg membranes have been removed. The nuclei lie at a deeper level than they appear in the drawing.   Compare Fig. 5.   ×78.

FIG. 7. Section of egg in the fourth segmentation stage.   Sixteen cells.   ×152.

FIG. 8. Fifth segmentation stage.   Age, 19 hours.   Cells not yet at surface.   ×152.

FIG. 9. Invagination stage.   A solid ingrowth of blastodermic cells has taken place at *Ig*, where a slight pit is formed. The section cuts obliquely through the invaginate cells.   ×152.

REFERENCE LETTERS.

a, perinuclear protoplasm.
Ch, chitinous egg envelopes (removed, except in Fig. 5).
Ep, ectoblastic cell.
Ig, shallow pit of invagination.
y. c., yolk spherule.

Plate VI.

Fig.2.

Fig.1

Y.C.

Fig 3.

Fig.4

Fig.5. Ch.

a
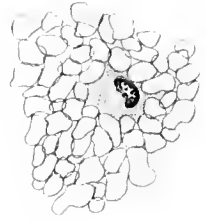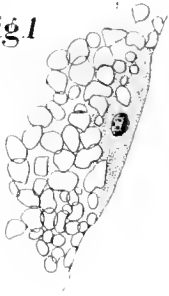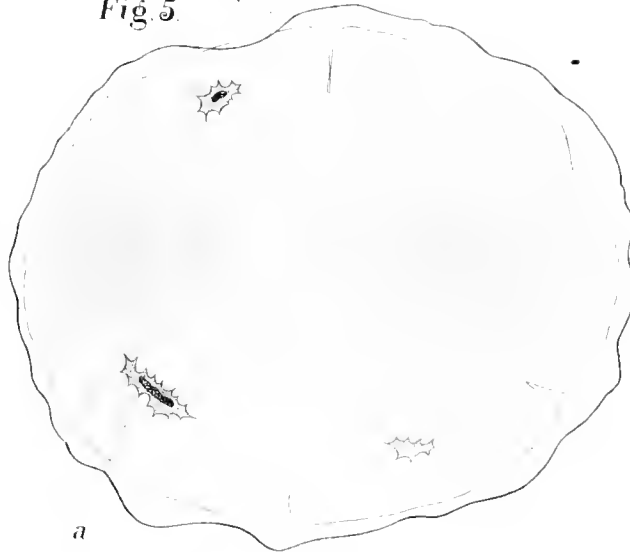
Fig.6.
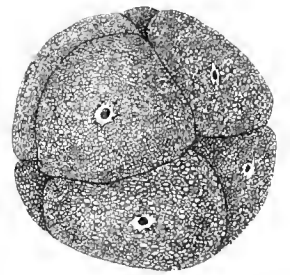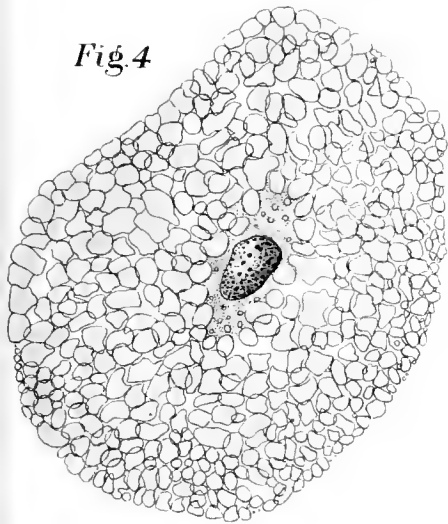
Fig.7.

Fig.8.

Fig.9.

Ig.

Ep.

STENOPUS HISPIDUS.
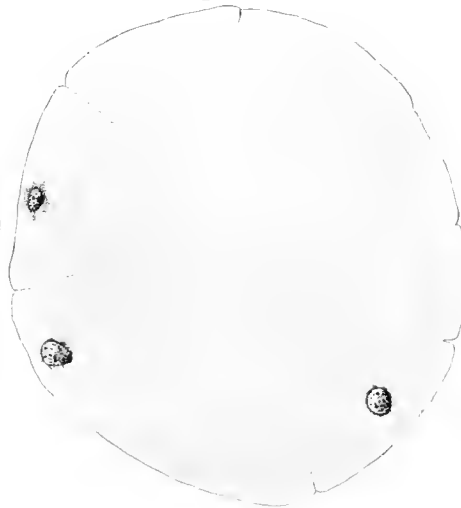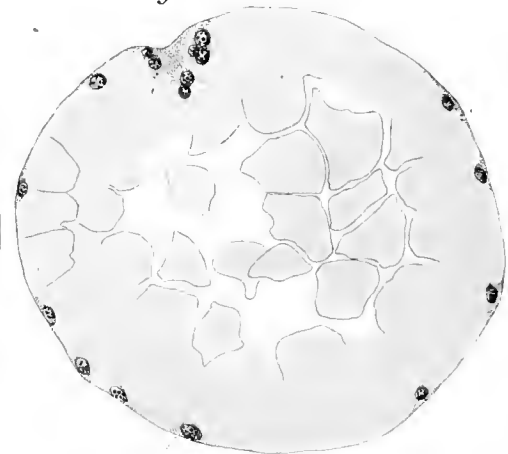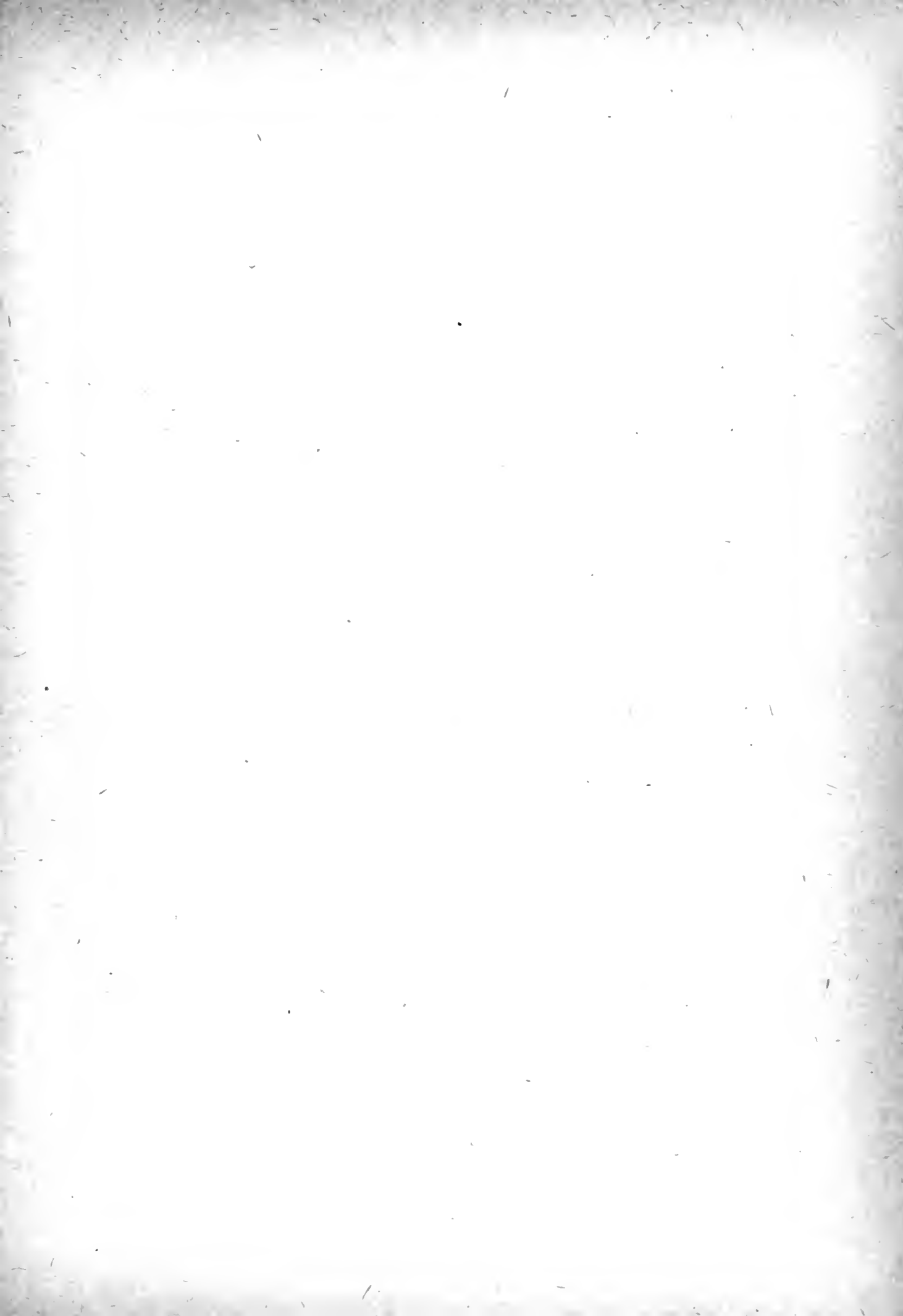
Plate VII.

Fig. 10. Left second maxilla of larva at the point of hatching, before the first molt. ×276. Compare with Figs. 25 and 21.

Fig. 11. First swimming larva, after the first molt, seen from below. Pigment cells, brown. $L = \frac{16}{100}$ in. (measured from tip of rostrum to median notch of telson). Length of rostrum = $\frac{5}{100}$ in. ×70.

Fig. 12. Right first maxilla of first larva, seen from the outer side. Setæ rudimentary. Compare Figs. 19, 25. ×276.

Fig. 13. Telson of larva before first molt, seen from below. Compare Fig. 11. The setæ are invaginated and covered with a loose cuticle. ×276.

Fig. 14. Right first maxilliped of larva on the point of hatching, seen from the outer side. Setæ invaginated. Compare Figs. 22, 25. ×276.

Fig. 15. Labrum and right mandible of larva, seen from above. ×276.

Fig. 16. Right third maxilliped of larva on the point of hatching, seen from the outer side. Compare Fig. 25. ×276.

REFERENCE LETTERS.

a, outermost spine in telson of larva at the point of hatching.

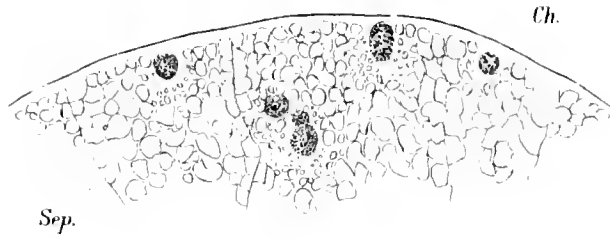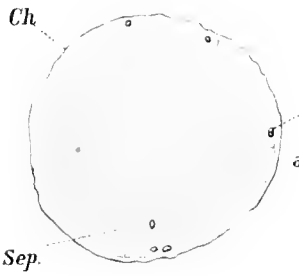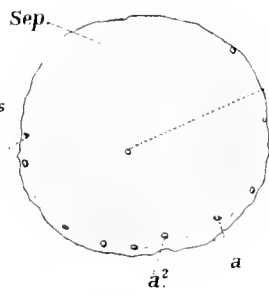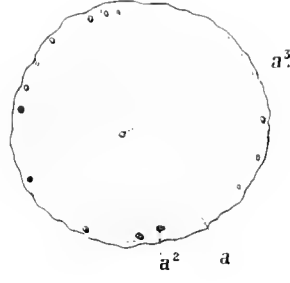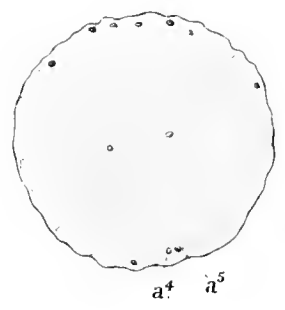*d*, equivalent of *a* in first locomotory larva.
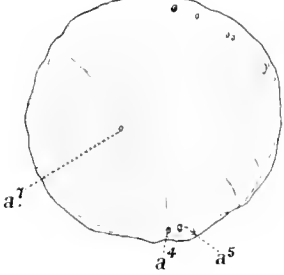
Lb, labrum.

Plate VI.
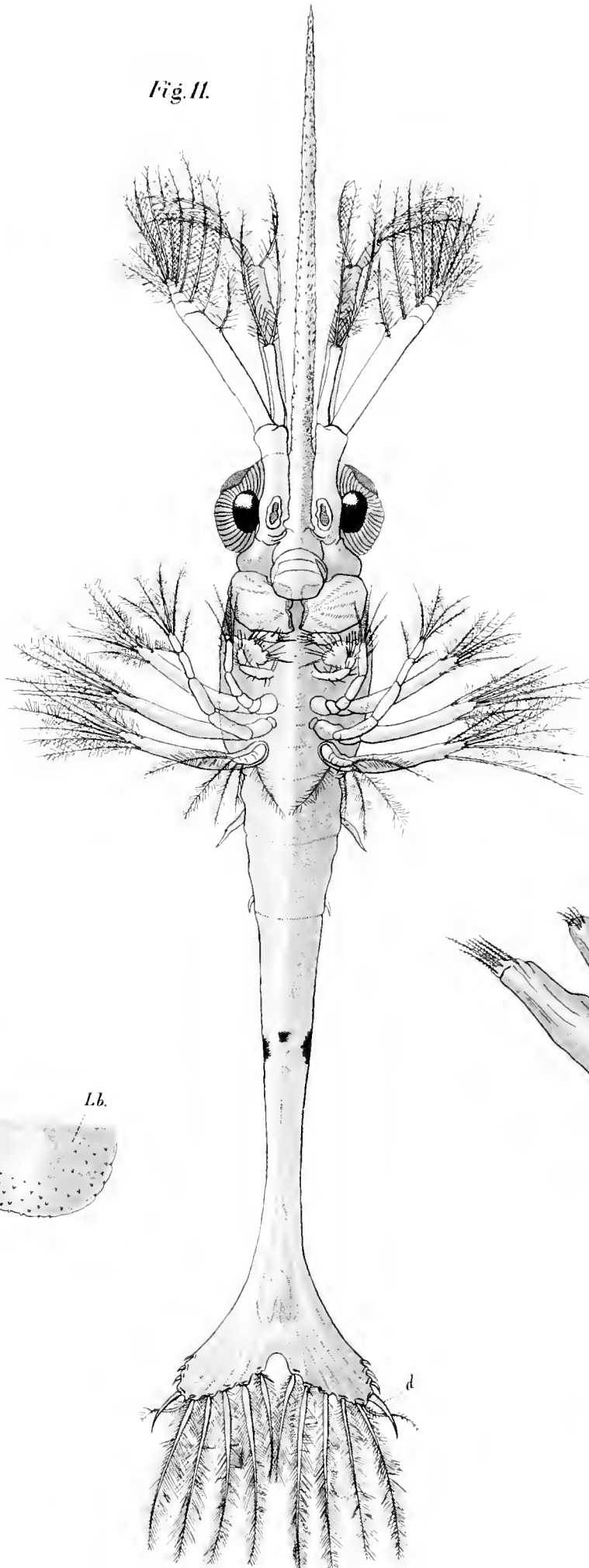
Fig. 10.
Fig. 11.
Fig. 12.
Fig. 13.
Fig. 14.
Fig. 15.
Fig. 16.

F. H. Herrick, del.

STENOPUS HISPIDUS.
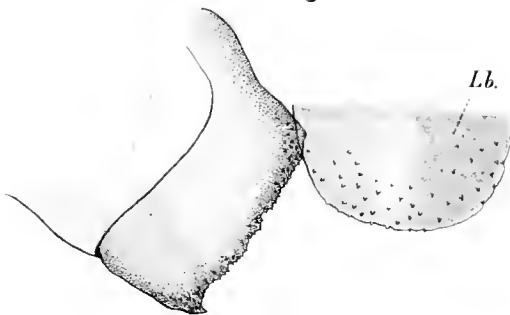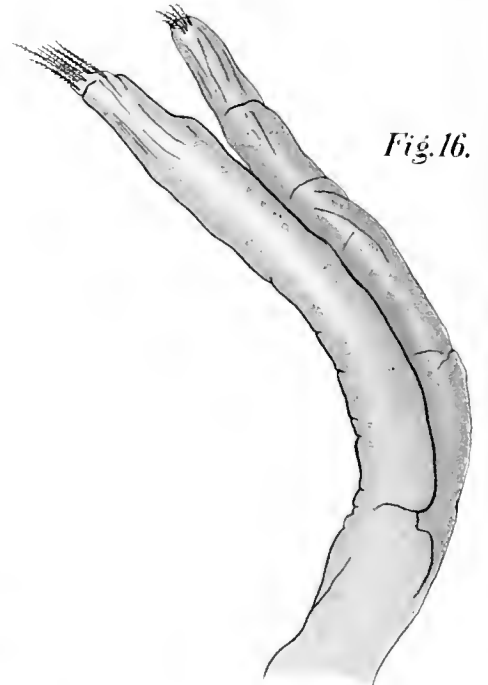
PLATE VIII.

FIG. 17. Second larva after second molt. L=$\frac{21}{100}$ in. ×70.
FIG. 18. Left mandible, outer side, of second larva. ×276.
FIG. 19. First maxilla of second larva. ×276.
FIG. 20. Telson of second larva, seen from below. ×70.
FIG. 21. Left second maxilla of second larva, seen from the outer side. ×276.
FIG. 22. Right first maxilliped of second larva, seen from the outer side. ×276.

REFERENCE LETTERS.

g g, gastric gland.
. . . . the dotted line in Fig. 20 points to the outer spine, the equivalent of *d*, Fig. 11.

Plate VIII

Fig.18.

g g.
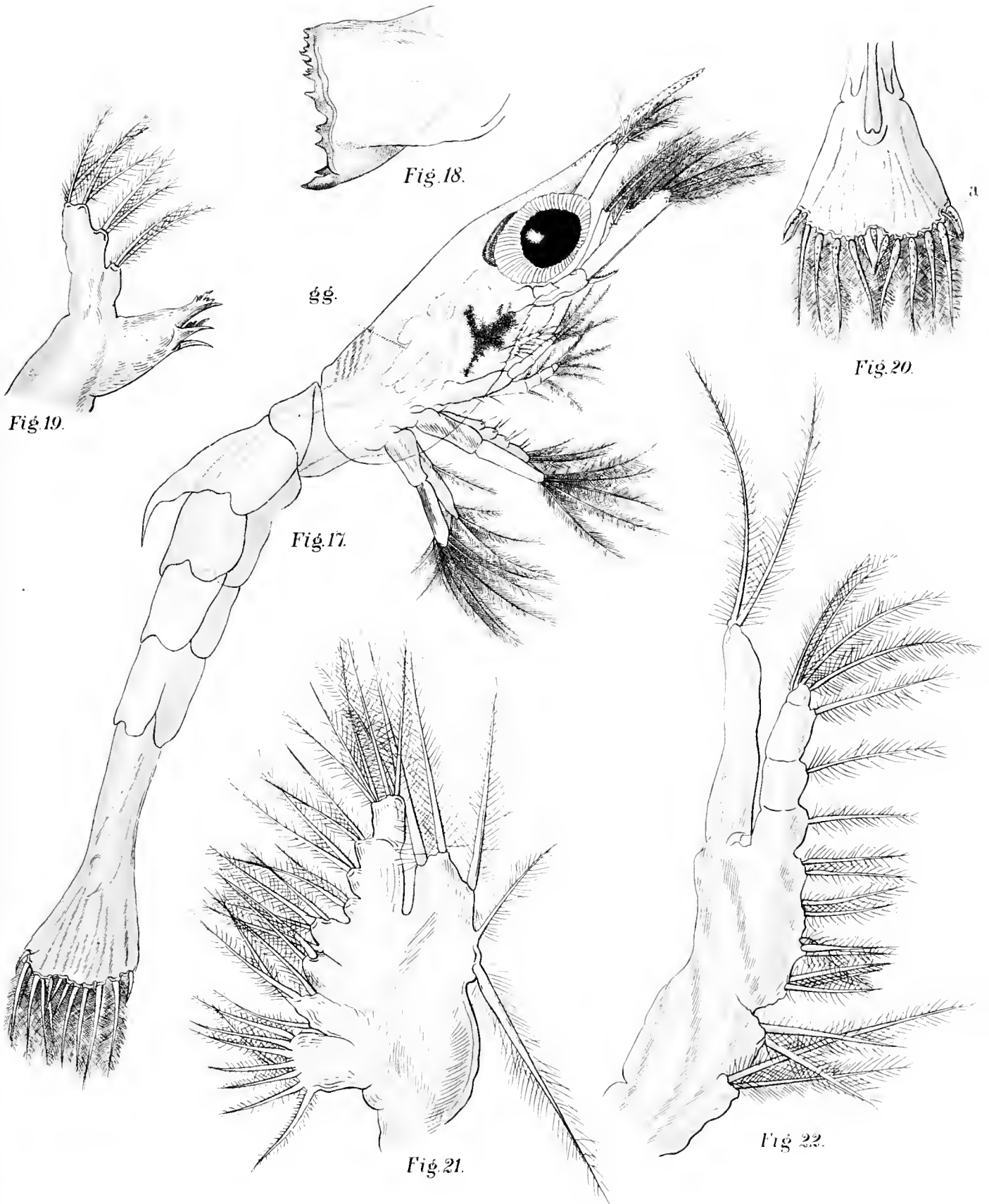
Fig.19.

Fig.20.

Fig.17.

Fig.21.

Fig 22.

STENOPUS HISPIDUS.

Plate IX.

Advanced pelagic larva of Stenopus hispidus, from Beaufort, North Carolina, drawn from life by W. K. Brooks.

Plate IX

Figure 23.

STENOPUS
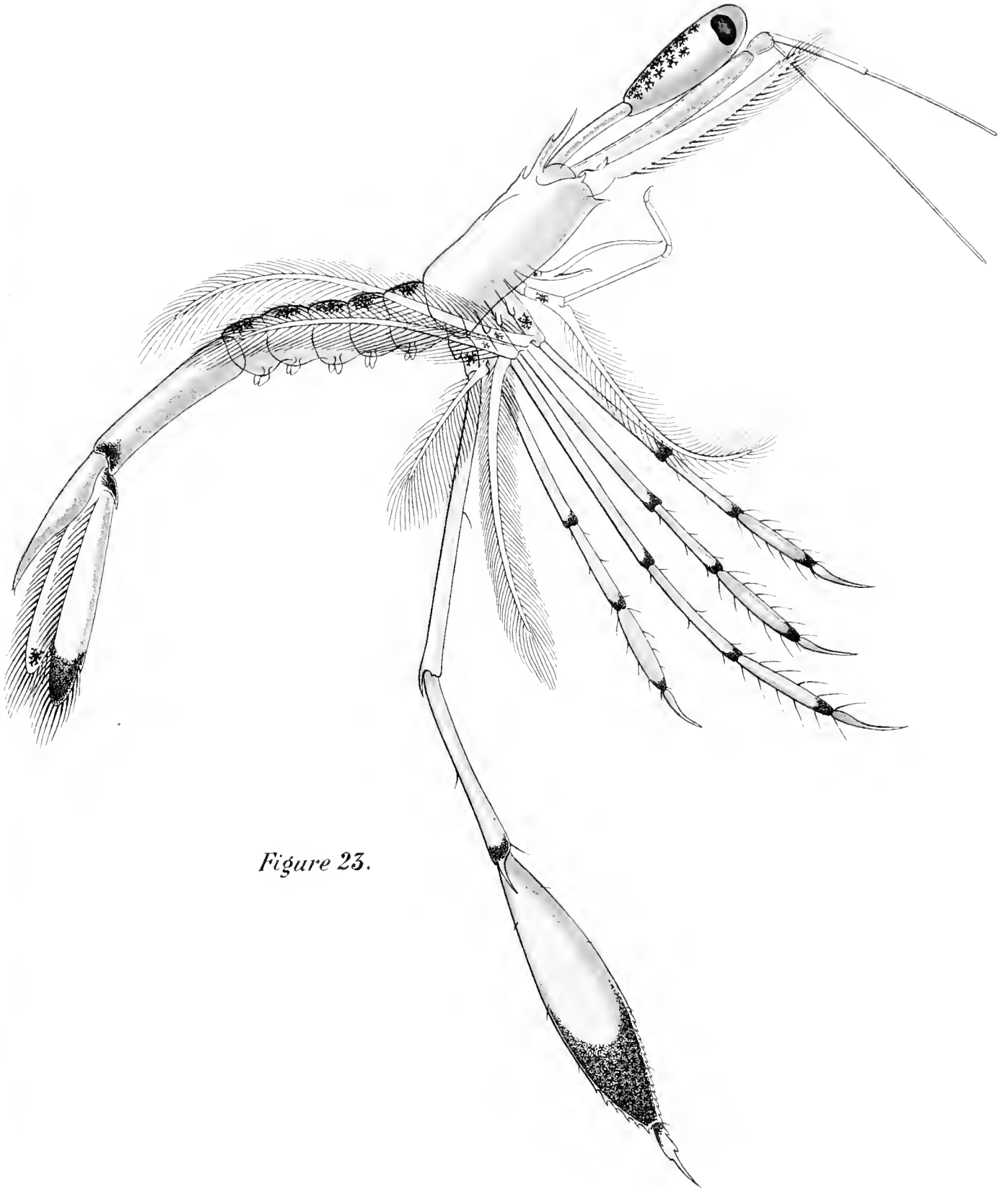
PLATE X.

Dorsal view of a larva like the one shown in Plate IX, drawn from life by W. K. Brooks.

Plate X.

Figure 24.

STENOPUS
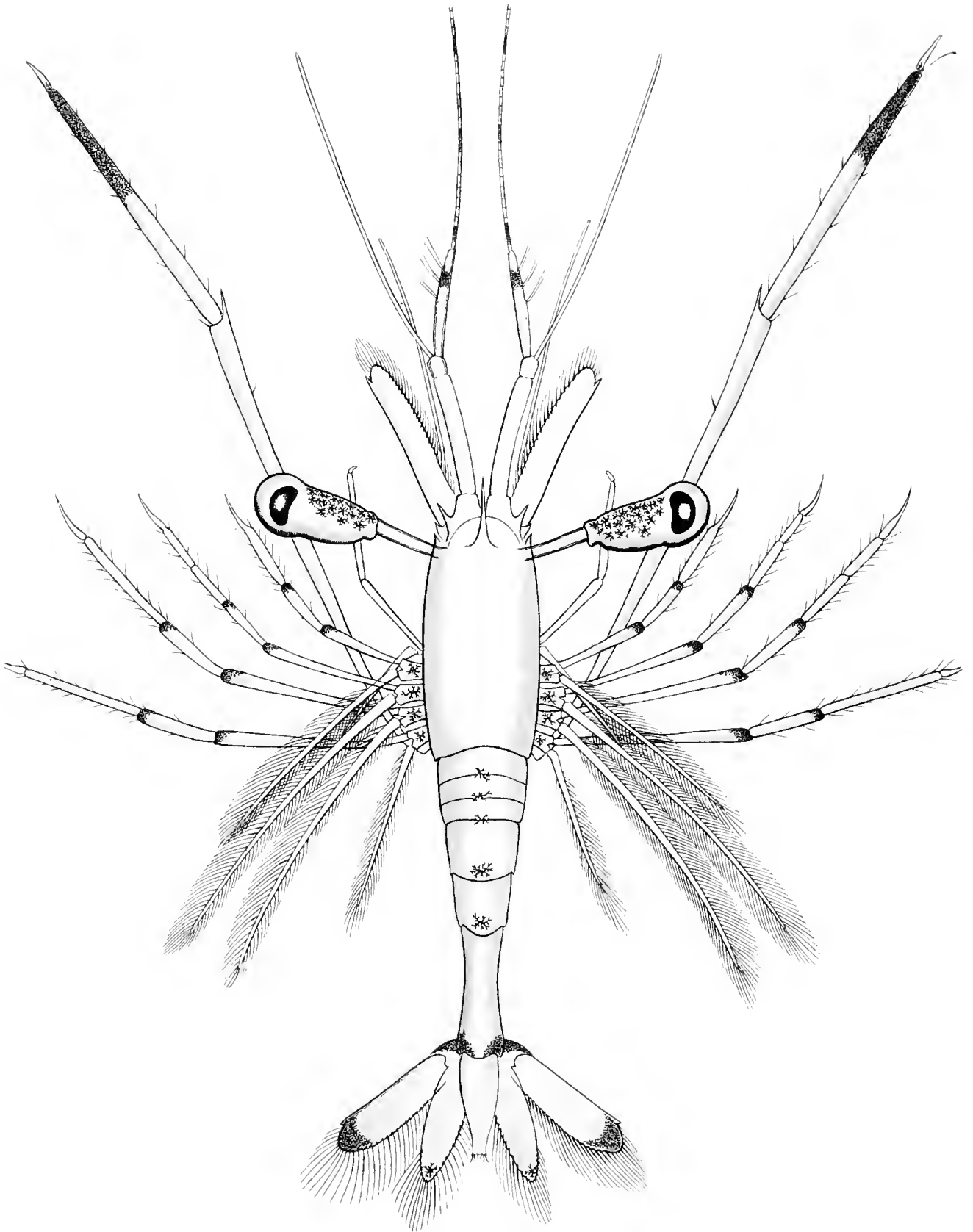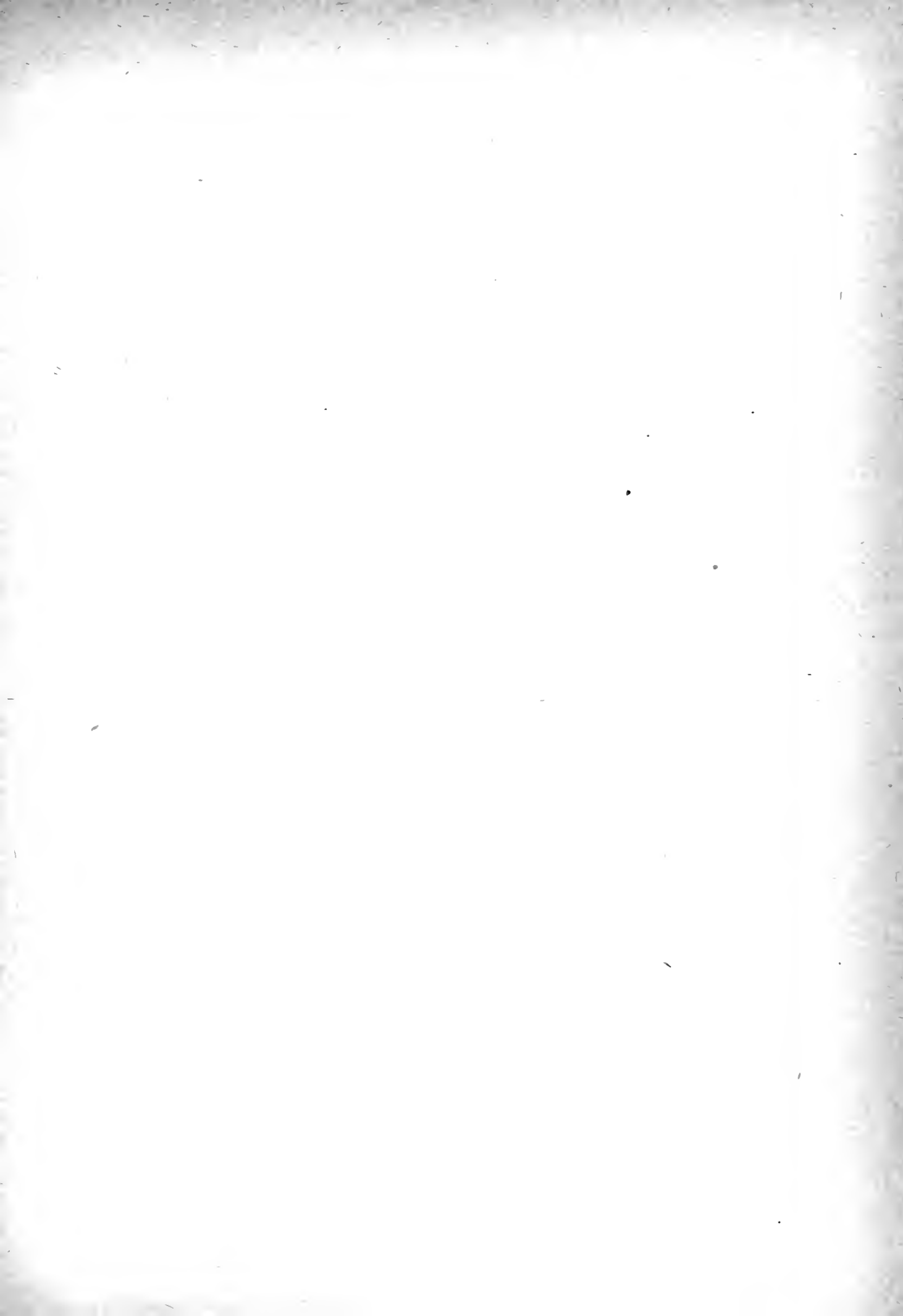
PLATE XI.

FIG. 25. Embryo nearly ready to hatch, released from the egg membranes. ×70. Some food
yolk is still unabsorbed; swimming hairs very rudimentary; compare Fig. 11.

FIG. 26. Right first antenna of older larva. ×70.

FIG. 27. Profile view of hinder end of abdomen of same larva. ×28.

FIG. 28. Second maxilla of same larva. ×276.

FIG. 29. Mandible of same larva. ×276.

FIG. 30. First maxilla of same larva. ×276.

FIG. 31. Portion of third maxilliped of same larva. ×70.

FIG. 32. Terminal segment of second pereiopod of same larva. ×70.

FIG. 33. First pereiopod of same larva. ×70.

FIG. 34. Portions of third, fourth, and rudimentary fifth pereiopods of same larva. ×70.

REFERENCE LETTERS.

A. I, first antenna.
A. II, second antenna.
Md., mandible.
Mxpd. I, III, first and third maxillipeds.
R., rostrum.
Th., Th. 1, first maxilliped.
Th. 3–Th. 5, third to fifth maxillipeds.
1, first maxilliped.

Plate XI

Fig.25.

R.

At.

Fig.27.

Fig.26.
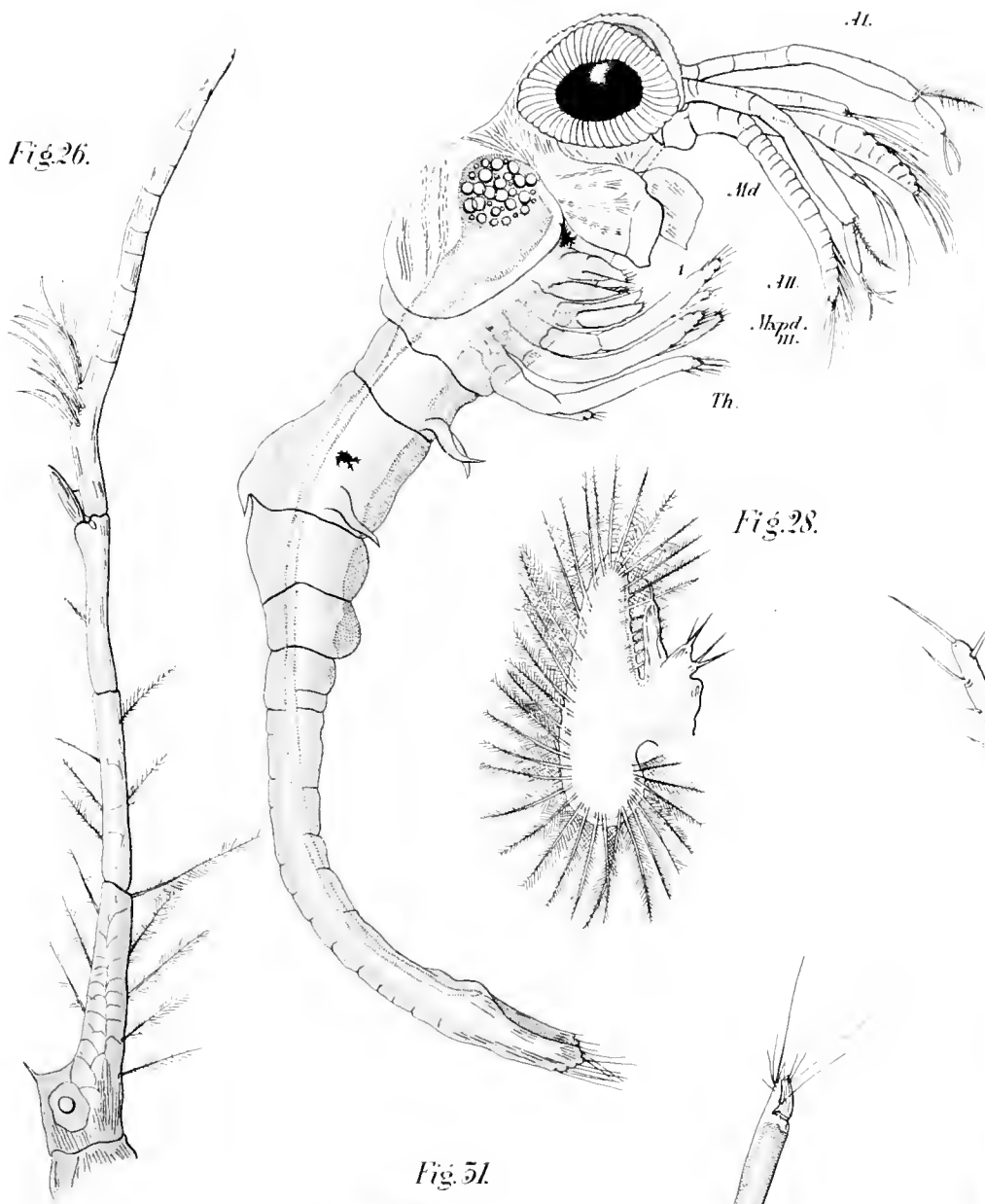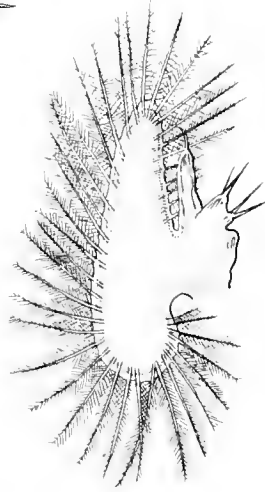
Md

Al.

Mxpd.
m.

Th.

Fig.28.

Fig.29.

Fig.34.

Th.3.

Fig.35.

Th.4.

Th.1.

Fig.51.

Fig.30.

Fig.32.

Mxpd.1.

Th.5.
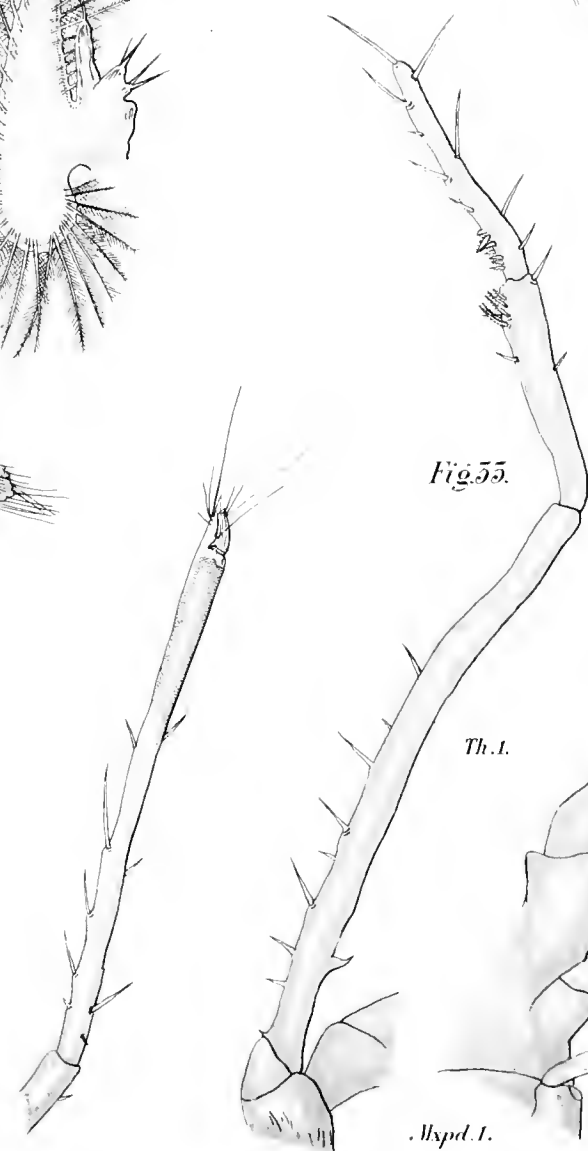
F.H.Herrick, del.

STENOPUS HISPIDUS.
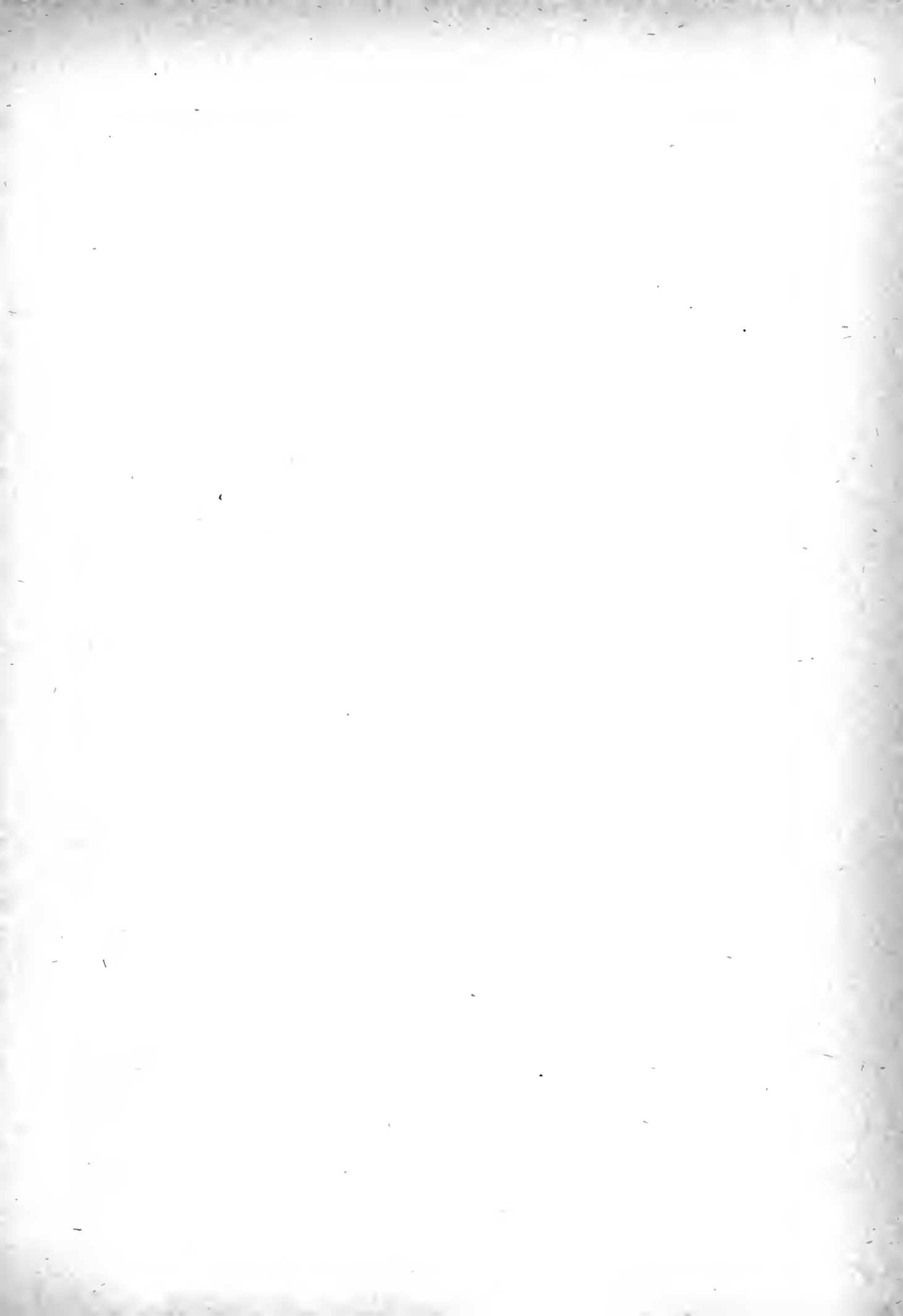
PLATE XII.

Fig. 35. Older larva, taken in the tow-net outside of Nassau Harbor May 7, 1887. L=9^{mm}. L. of eye-stalk=2^{mm}. L. between eyes=4.7^{mm}. ×15. The long flagella of the antennæ are conventionally represented to bring them into the plate. They trail above and behind the animal as it swims through the water.

Plate XII.

Figure 35.

STENOPUS HISPIDUS.

PLATE XIII.

Plate XIII

Fig.36.

Fig.37.

Fig.38.

Fig.41.

Fig.39.

Fig.42.

Fig.40.

Fig.43.
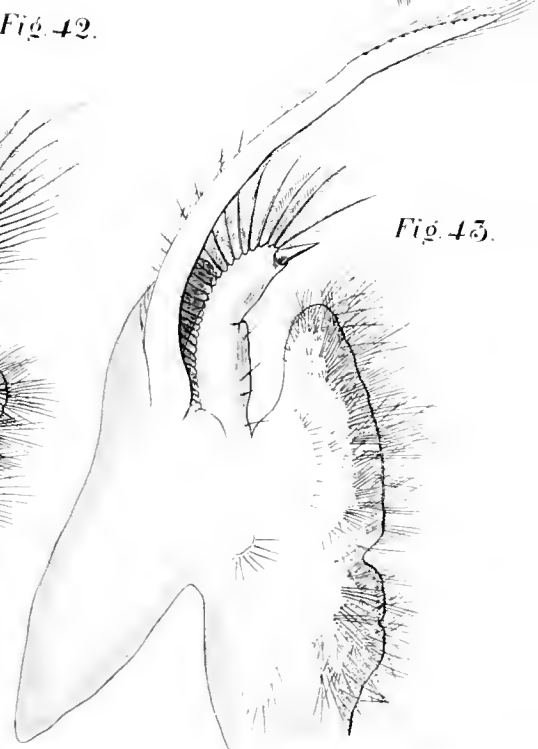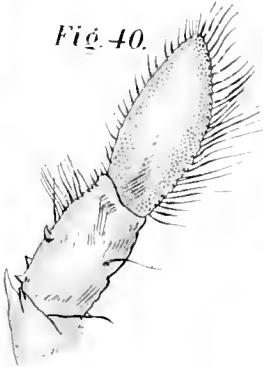
Fig.44.

Fig.45.

Fig.46.

Fig.47.

F.H.Herrick, del.

STENOPUS HISPIDUS.
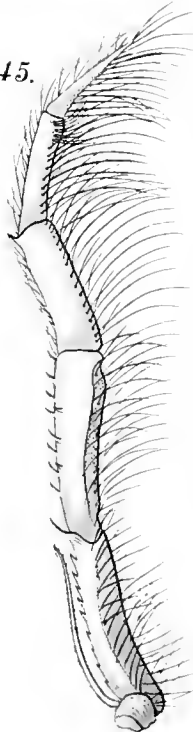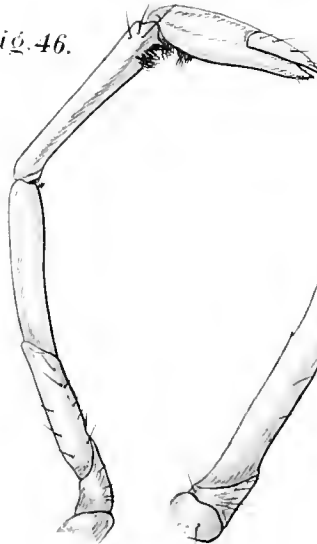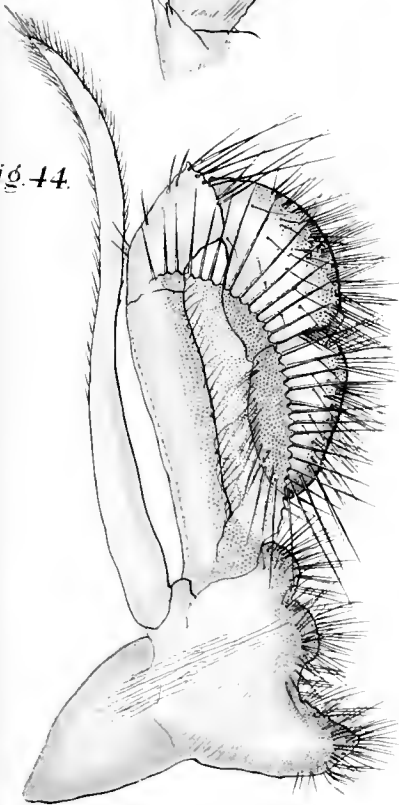
PLATE XIV.

Metamorphosis of Gonodactylus chiragra, drawn from life by W. K. Brooks.

FIG. 1. Dorsal view of egg just before hatching.
FIG. 2. Front view of the same egg.
FIG. 3. Side view of the larva immediately after hatching.
FIG. 4. Side view of the same larva after the first molt.
FIG. 5. Side view of the same larva after the second molt.
FIG. 6. Dorsal view of the larva at the beginning of its pelagic life.

Plate XIV.

GONODACTYLUS CHIRAGRA.
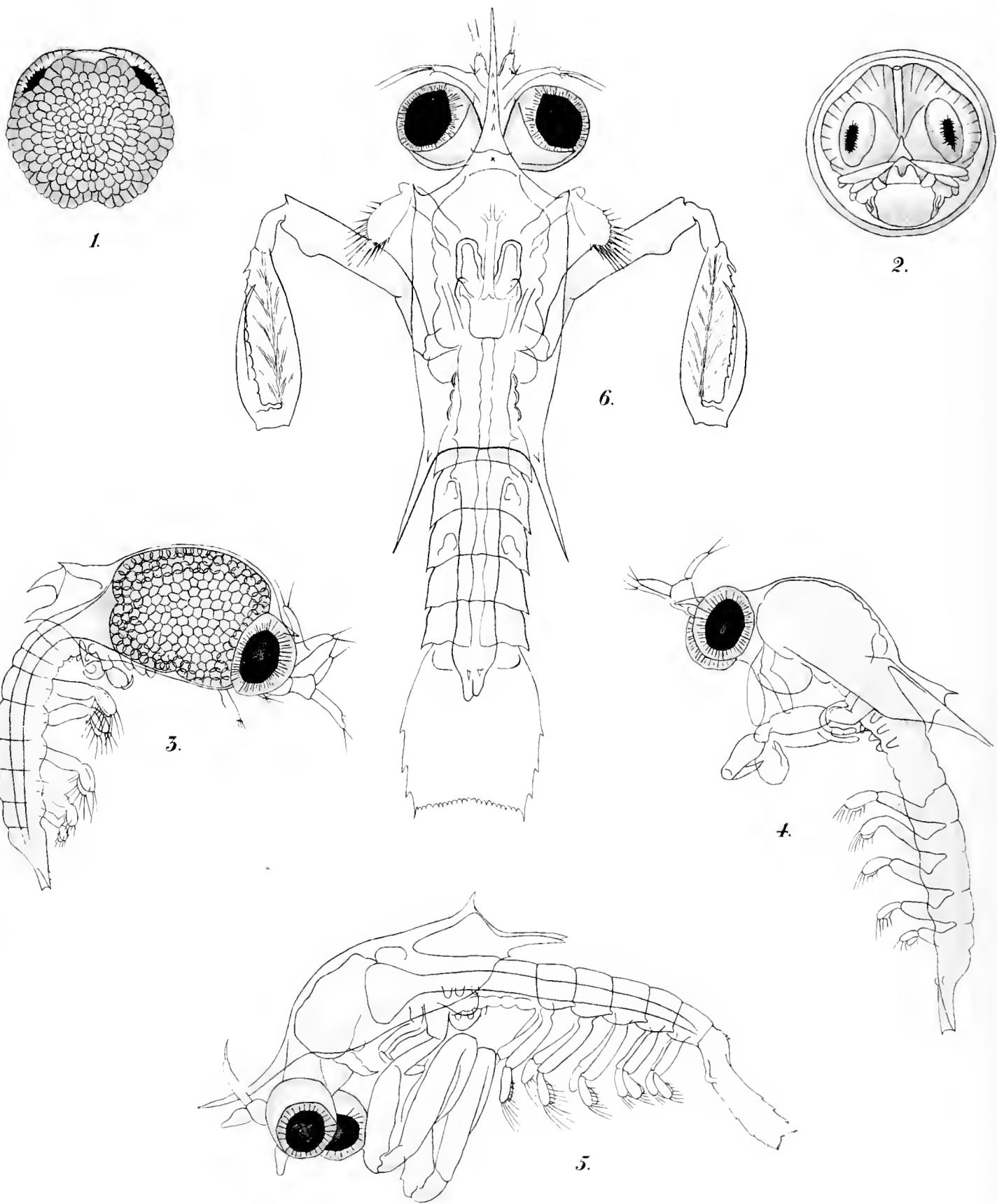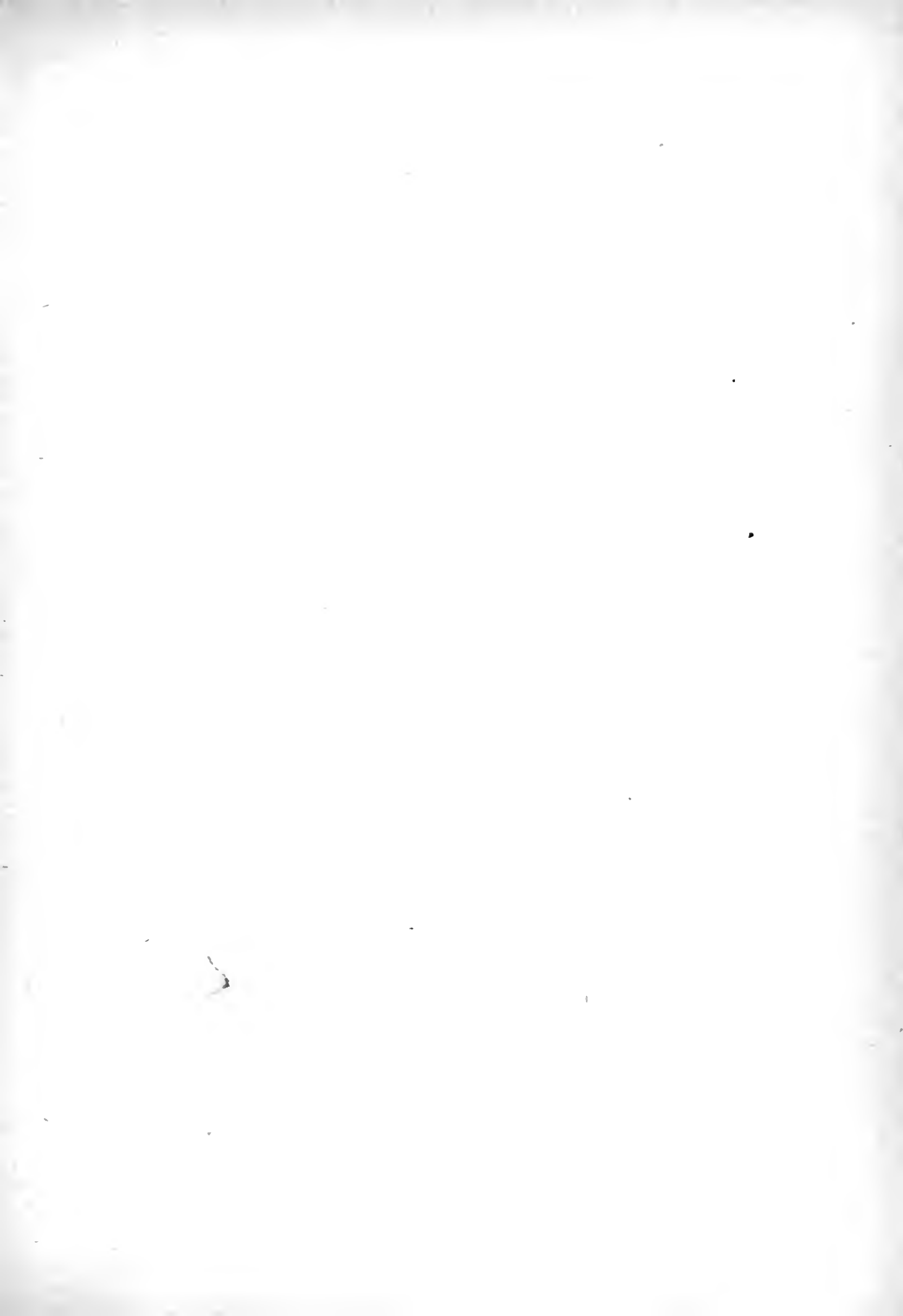
Plate XV.

Metamorphosis of Gonodactylus chiragra, drawn from life by W. K. Brooks.

Fig. 7. Dorsal view of the larva shown in Pl. xiv, Fig. 3.
Fig. 8. Ventral view of the same larva.
Fig. 9. Dorsal view of the larva shown in Pl. xiv, Fig. 4.
Fig. 10. Ventral view of the larva shown in Pl. xiv, Fig. 5.
Fig. 11. An older larva in dorsal view.
Fig. 12. Same in ventral view.
Fig. 13. Raptorial claw of a still older larva.
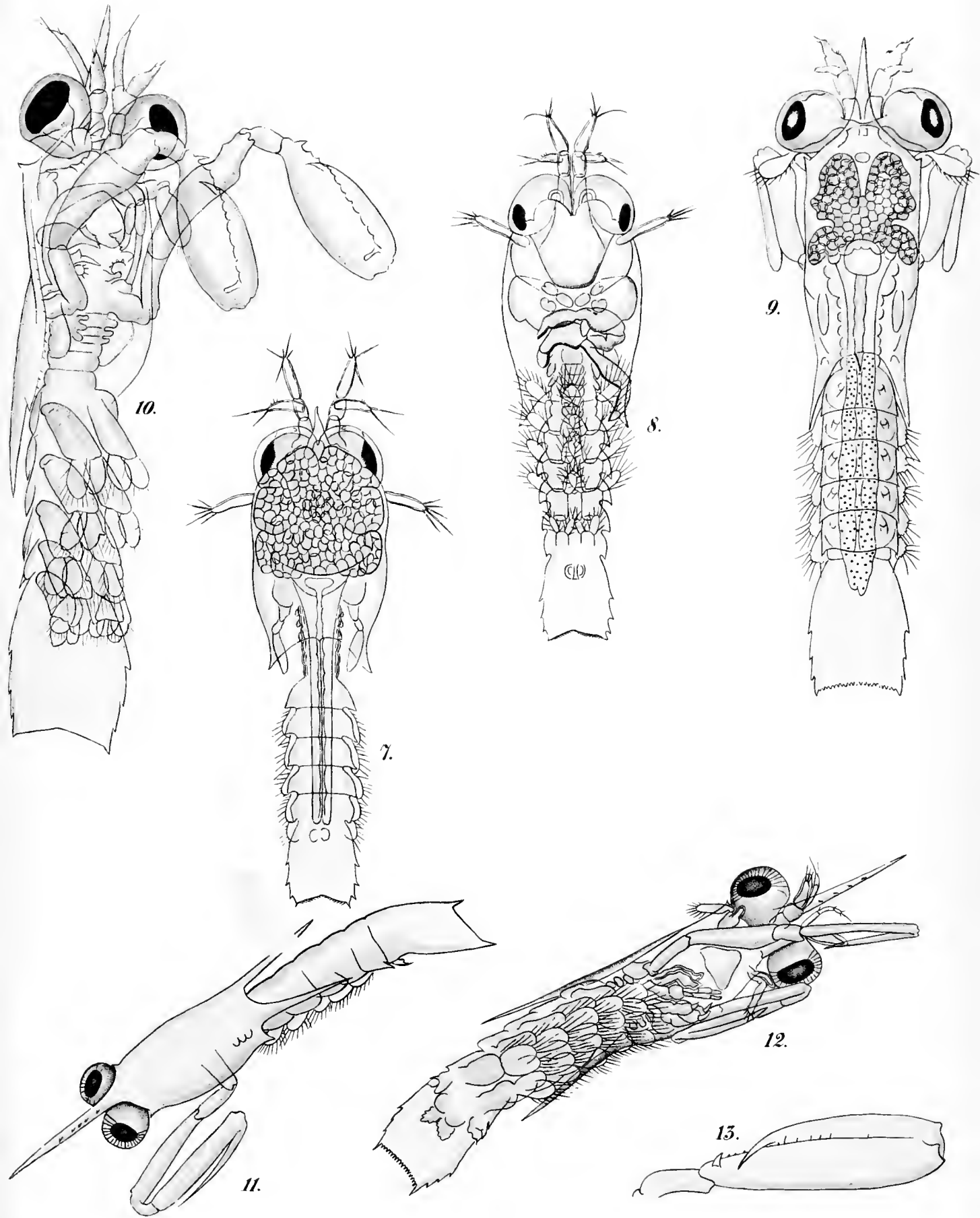
Plate XV.

GONODACTYLUS CHIRAGRA.
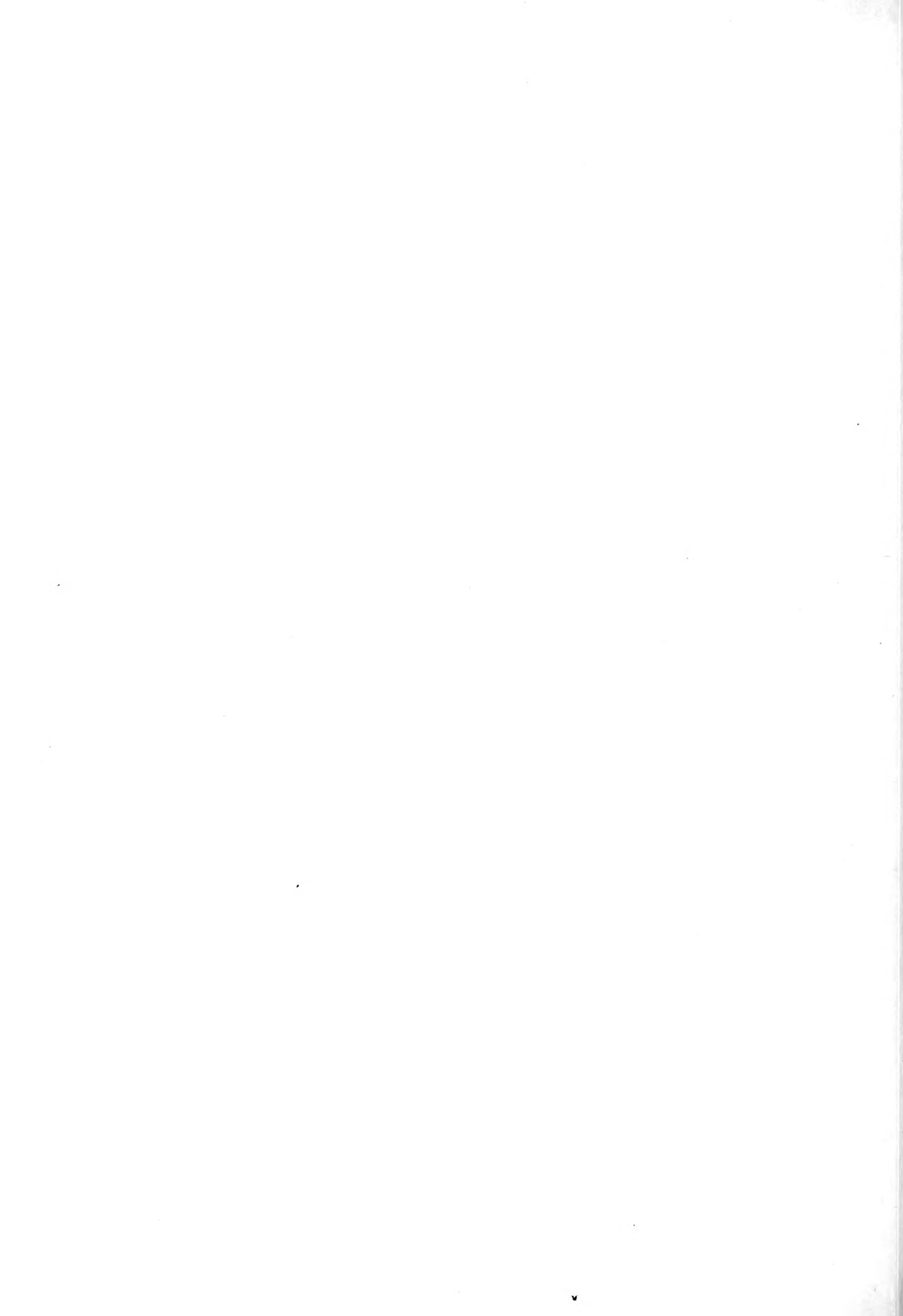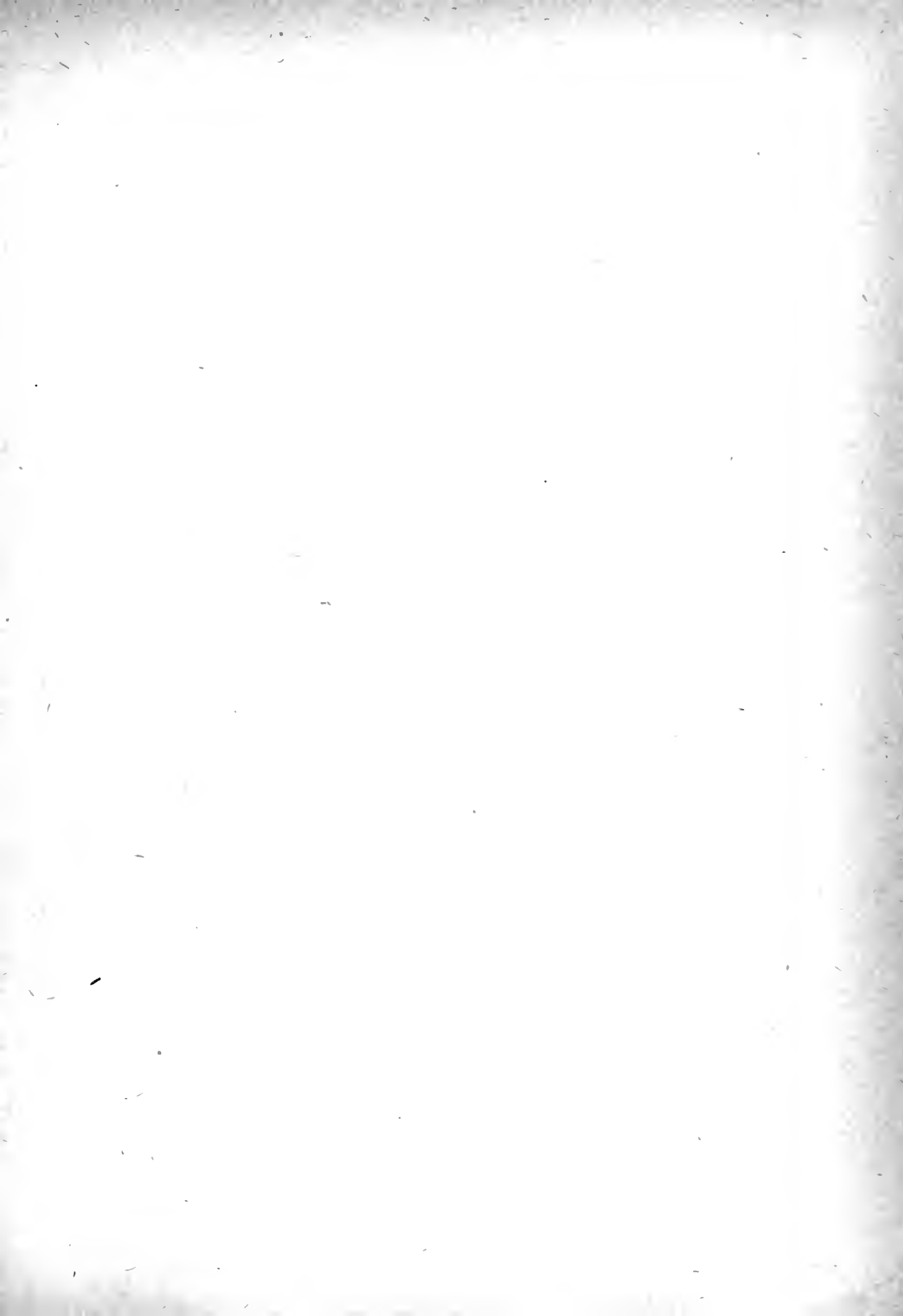
PLATE XVI.

Metamorphosis of Alpheus, drawn by W. K. Brooks and F. H. Herrick.

FIG. 1. Third larval stage of *Alpheus minor* from below, drawn by W. K. Brooks.

FIG. 2. Second larval stage of *Alpheus minor*, about one-tenth of an inch long, drawn from below by W. K. Brooks.

FIG. 3. Telson of the Nassau form of *Alpheus heterochelis* during the second larval stage, drawn at 10 a. m., April 17, 1887, by F. H. Herrick.

FIG. 4. Second antenna of *Alpheus minor* during the first larval stage, from the inside drawn by W. K. Brooks, May 13, 1881, D. 2. (Zeiss lenses.)

FIG. 5. First and second maxillæ of the Nassau form of *Alpheus heterochelis* during the fourth larval stage, drawn by W. K. Brooks from a sketch by F. H. Herrick. The larva at this stage is shown in Pl. XII, Fig. 3.

FIG. 6. First maxilla of *Alpheus minor* during the first larval stage, drawn at Beaufort, June 2, 1881, by W. K. Brooks, D. 2.

FIG. 7. Second maxilla of the same larva.

FIG. 8. Mandible of the same larva.
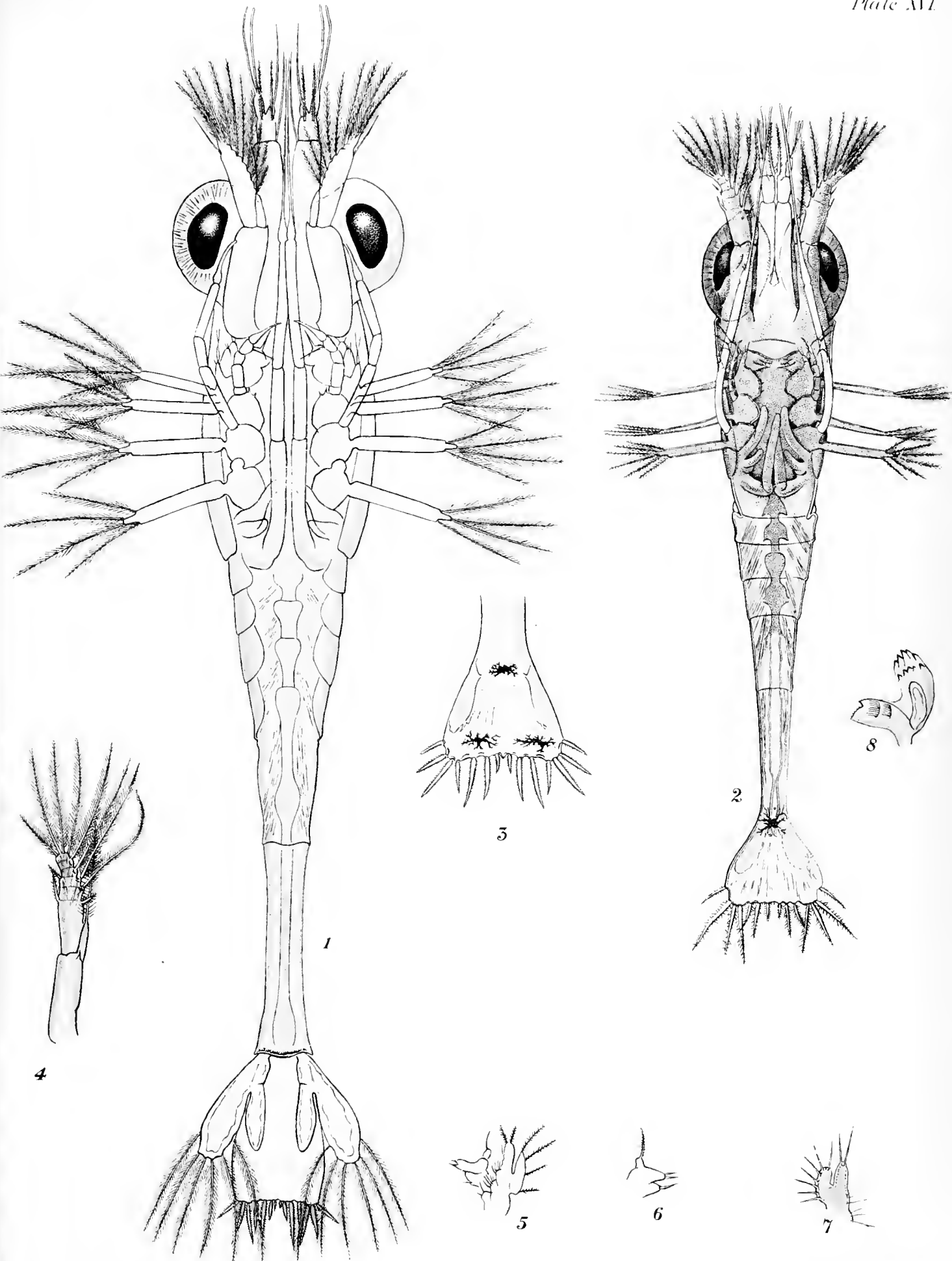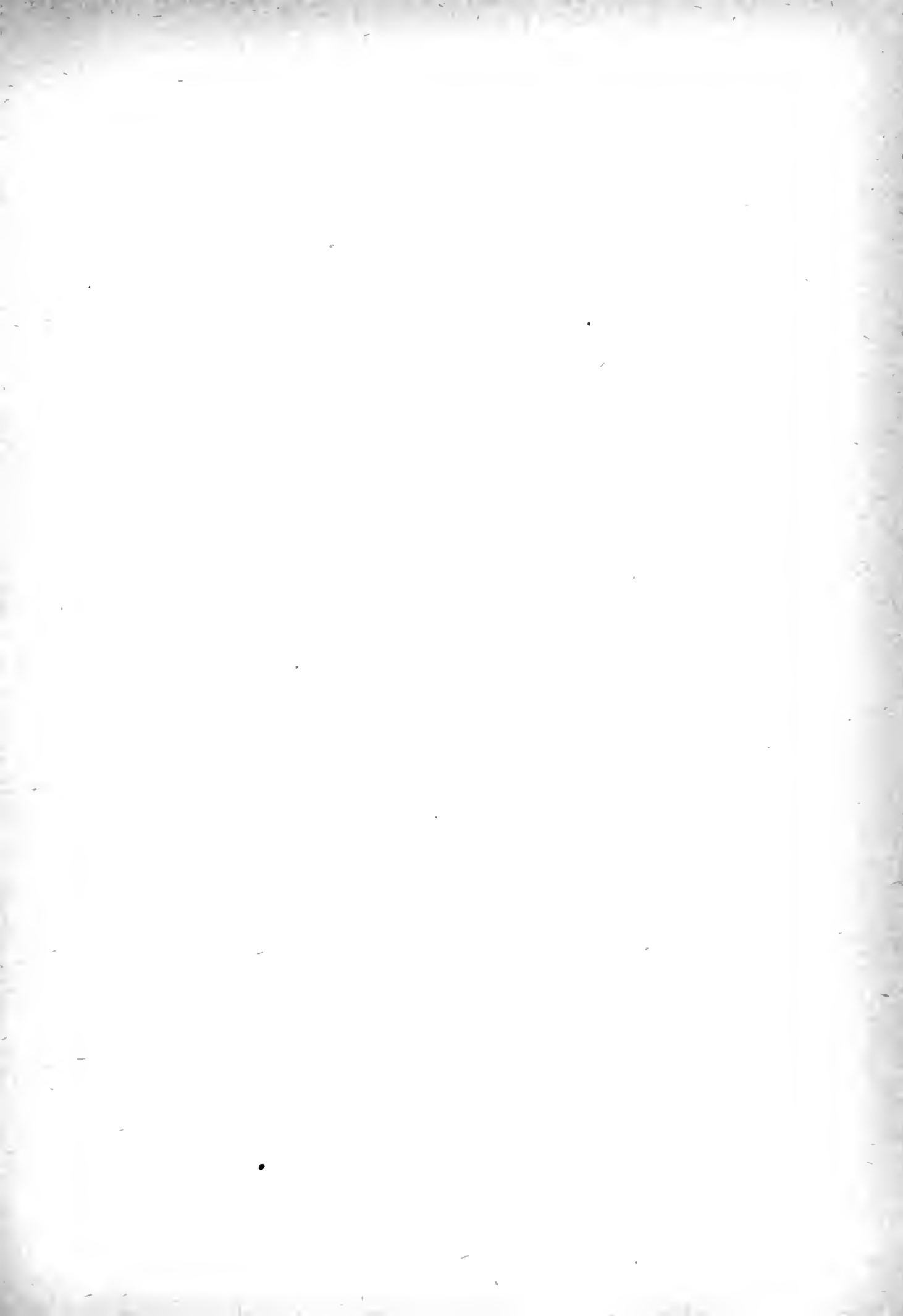
Plate XVI

ALPHEUS

PLATE XVII.

Metamorphosis of Alpheus, drawn from nature by W. K. Brooks.

FIG. 1. Side view of *Alpheus minor* after the second molt and in the third larval stage. Zeiss A. 2. This larva was about ninety-five one-thousandths of an inch long from the tip of the rostrum to the tip of the telson.

FIG. 2. Dorsal view of *Alpheus minor* after the first molt and in the second larval stage. This specimen was hatched at 9 p. m., May 30, 1881, and the drawing was made at 9 a. m. on May 31. The specimen was eight one-hundredths of an inch long.

FIG. 3. Dorsal view of a young specimen of *Alpheus heterochelis* from Beaufort. The specimen was one-fifth of an inch long. It was reared from the egg in an aquarium in the laboratory, and it was fifteen days old when the drawing was made. It is a little older than those which are shown in Pl. xx, Figs. 2 and 3.
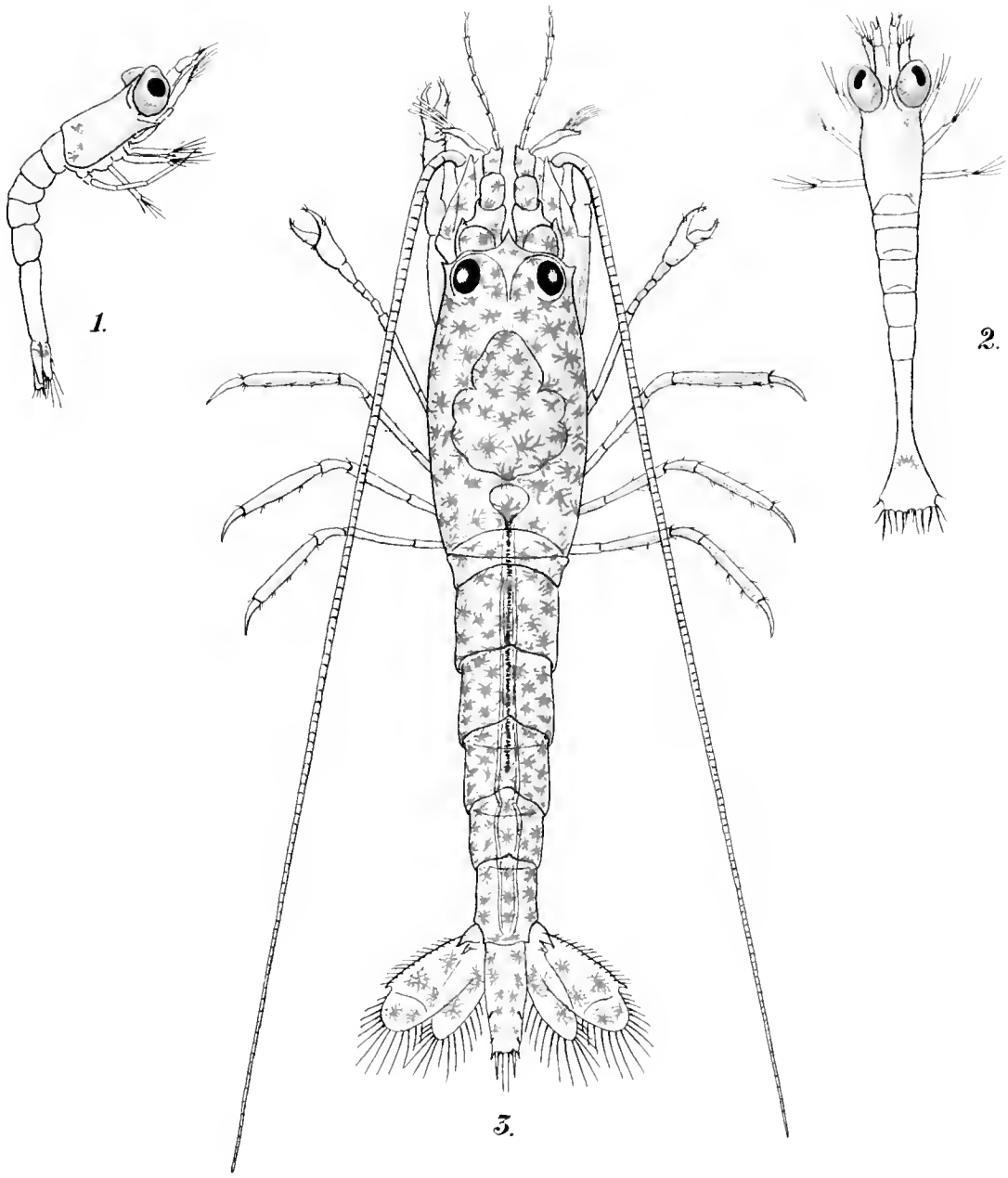
Plate XVII.

ALPHEUS

Plate XVIII.

Metamorphosis of Alpheus, drawn by W. K. Brooks from sketches by F. H. Herrick.

Fig. 1. Side view of first or second larval stage of *Alpheus heterochelis* from Nassau, drawn on
the night of April 15, 1887. Zeiss A. camera.

Fig. 2. Ventral view of the third larval stage of *Alpheus heterochelis* from Nassau, drawn April
18, 1887.

Fig. 3. Ventral view of fourth larval stage of *Alpheus heterochelis* from Nassau, drawn April
21, 1887.

Fig. 4. First maxilliped of the first larval stage of *Alpheus minor*.

Plate XVIII.
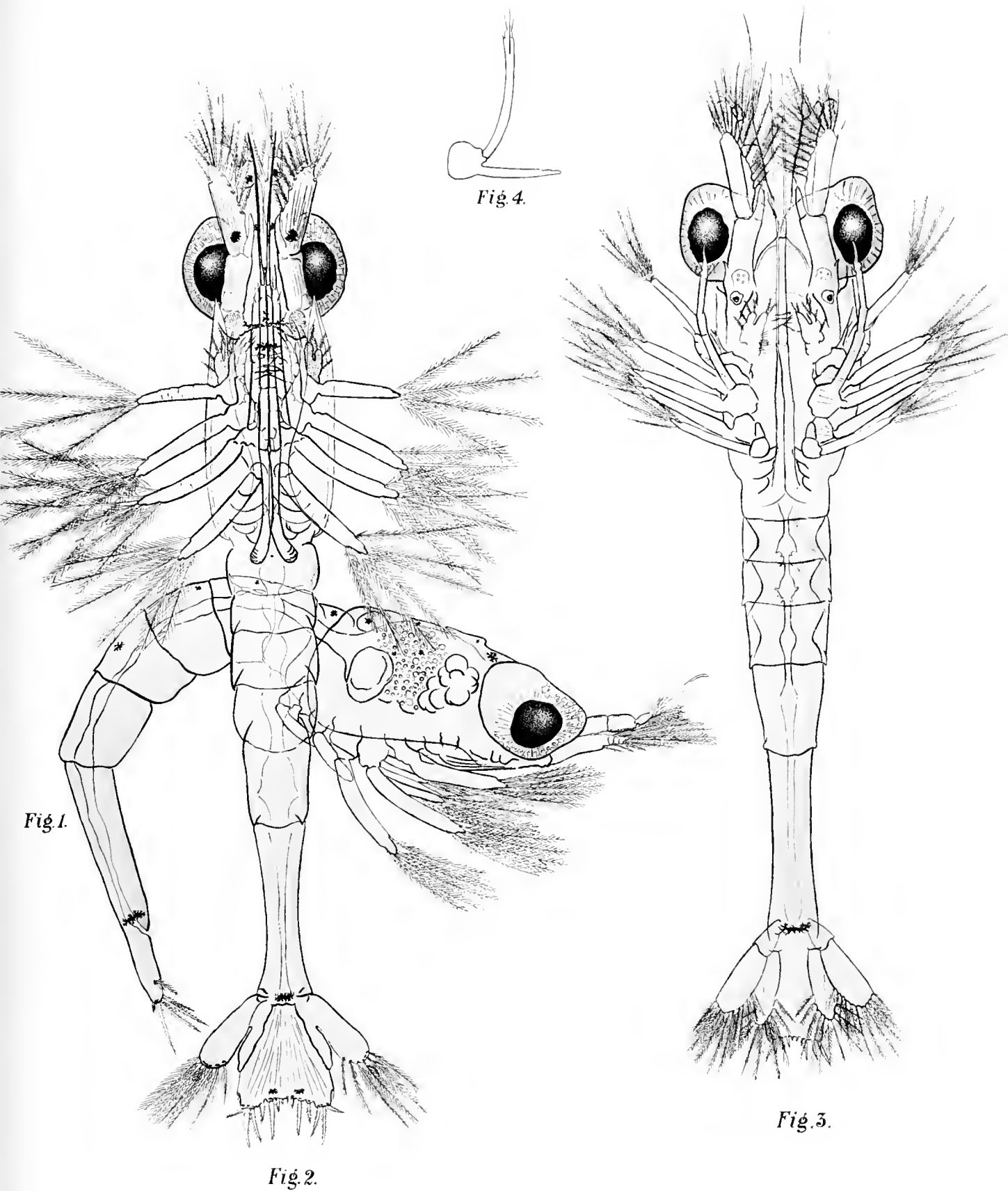
ALPHEUS

PLATE XIX.

Metamorphosis of Alpheus heterochelis at Beaufort, North Carolina, drawn from nature by W. K. Brooks.

FIG. 1. Ventral view of the larva immediately after hatching.
FIG. 2. Side view of the same larva.
FIG. 3. Dorsal view of the antennule of the same larva.
FIG. 4. Ventral view of the antenna of the same larva.
FIG. 5. Mandible of the same larva.
FIG. 6. First maxilla of the same larva.
FIG. 7. Second maxilla of the same larva.
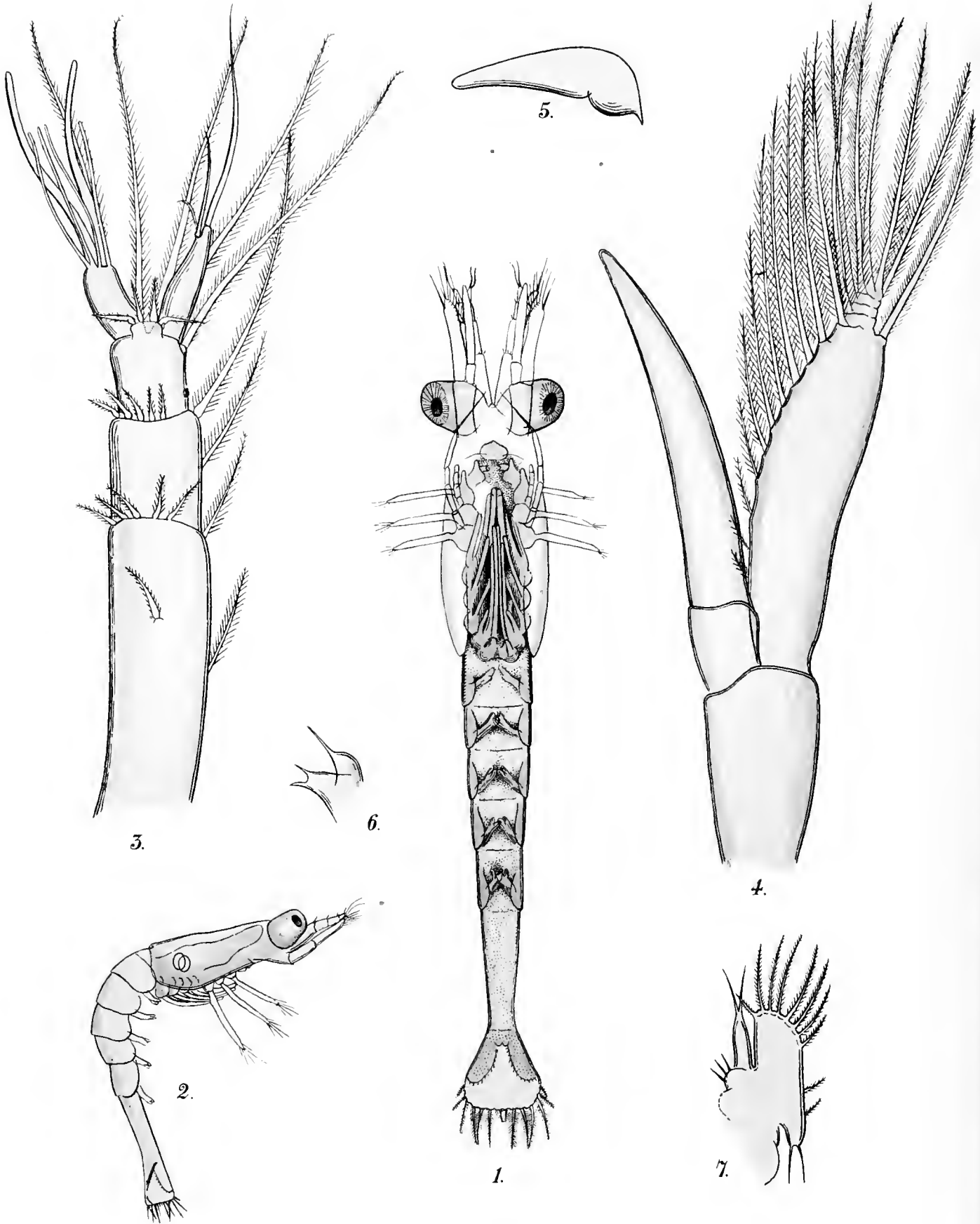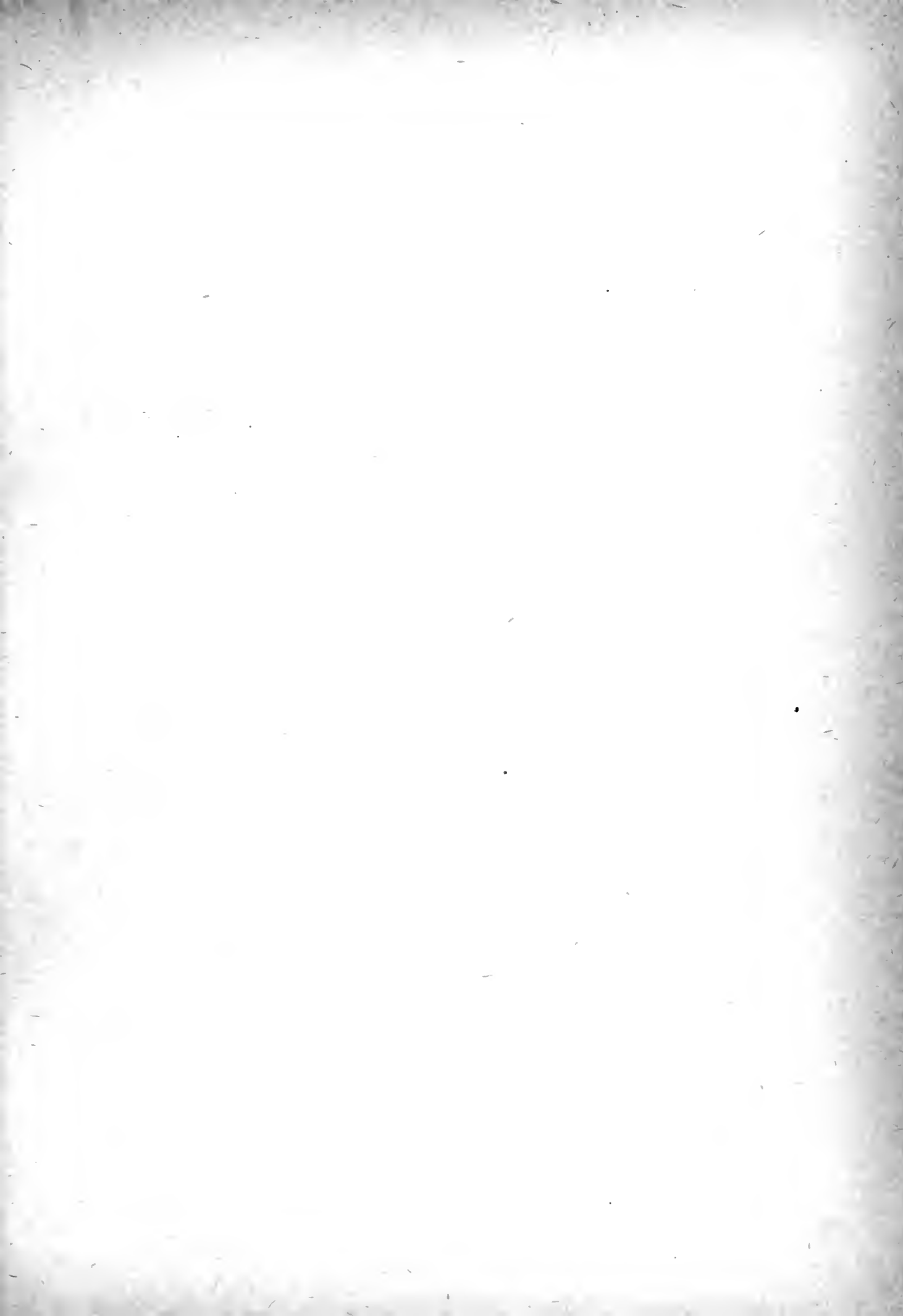
Plate XIX.

ALPHEUS

PLATE XX.

Metamorphosis of Alpheus heterochelis from Beaufort, North Carolina, drawn from nature by W. K. Brooks.

FIG. 1. Embryo just before hatching.

FIG. 2. View of a larva which was captured in the tow net at Old Topsail Inlet, North Carolina, June 25, 1883. It is about eighteen one-hundredths of an inch long, and is a little younger than the one shown in Pl. XVII, Fig. 3, and a little older than that shown in Fig. 3 of this plate.

FIG. 3. Ventral view of a larva little younger than Fig. 2.

FIG. 4. Telson and swimming appendages of the larva shown in Fig. 3.

FIG. 5 First maxilla of the same larva.

FIG. 6. Second maxilla of the same larva.

FIG. 7. First maxilliped of the same larva.

FIG. 8. Second maxilliped of the same larva.

FIG. 9. Third maxilliped of the same larva.

Plate XX.

2.

1.

7.

5.

6.

3.

4.

S.

9.
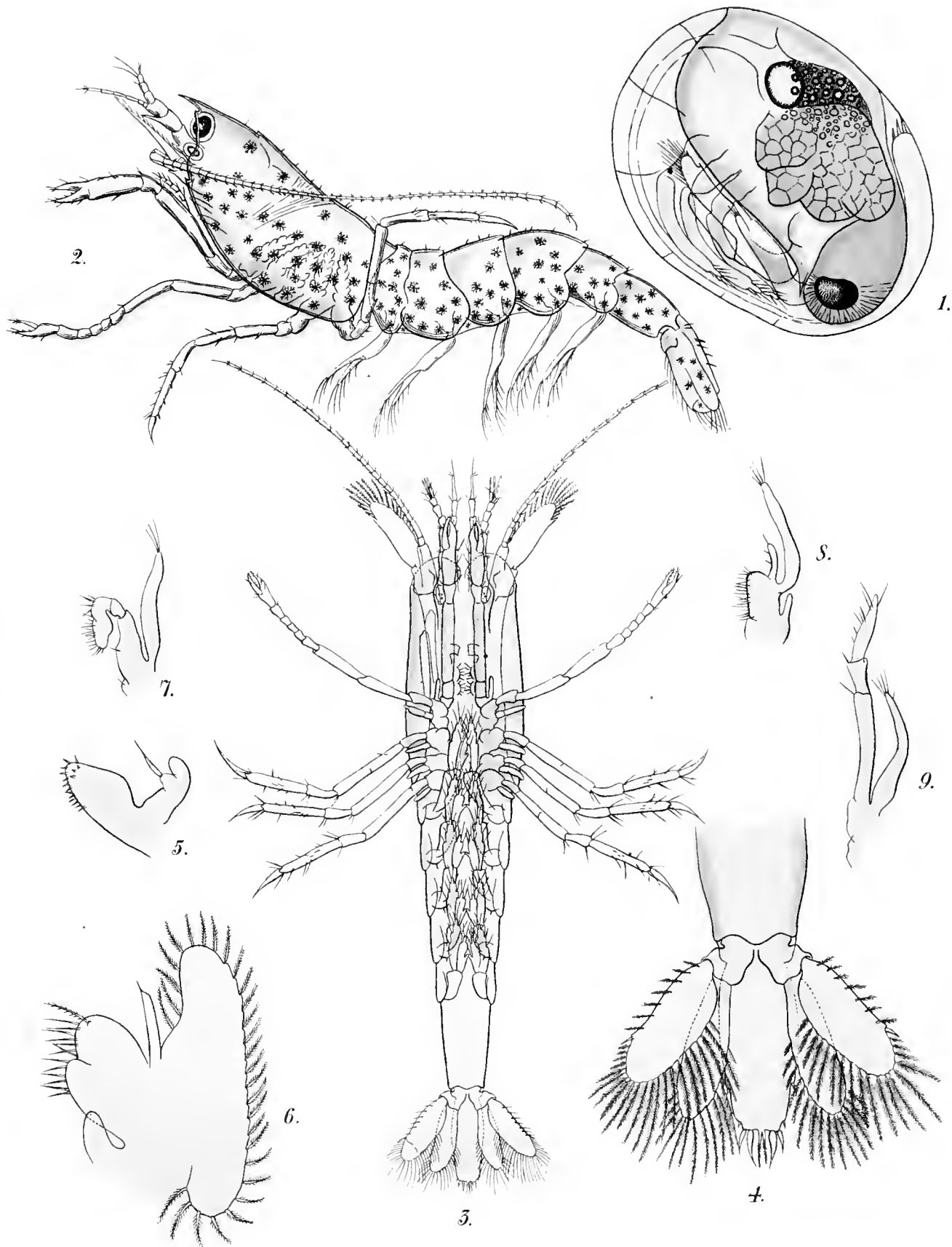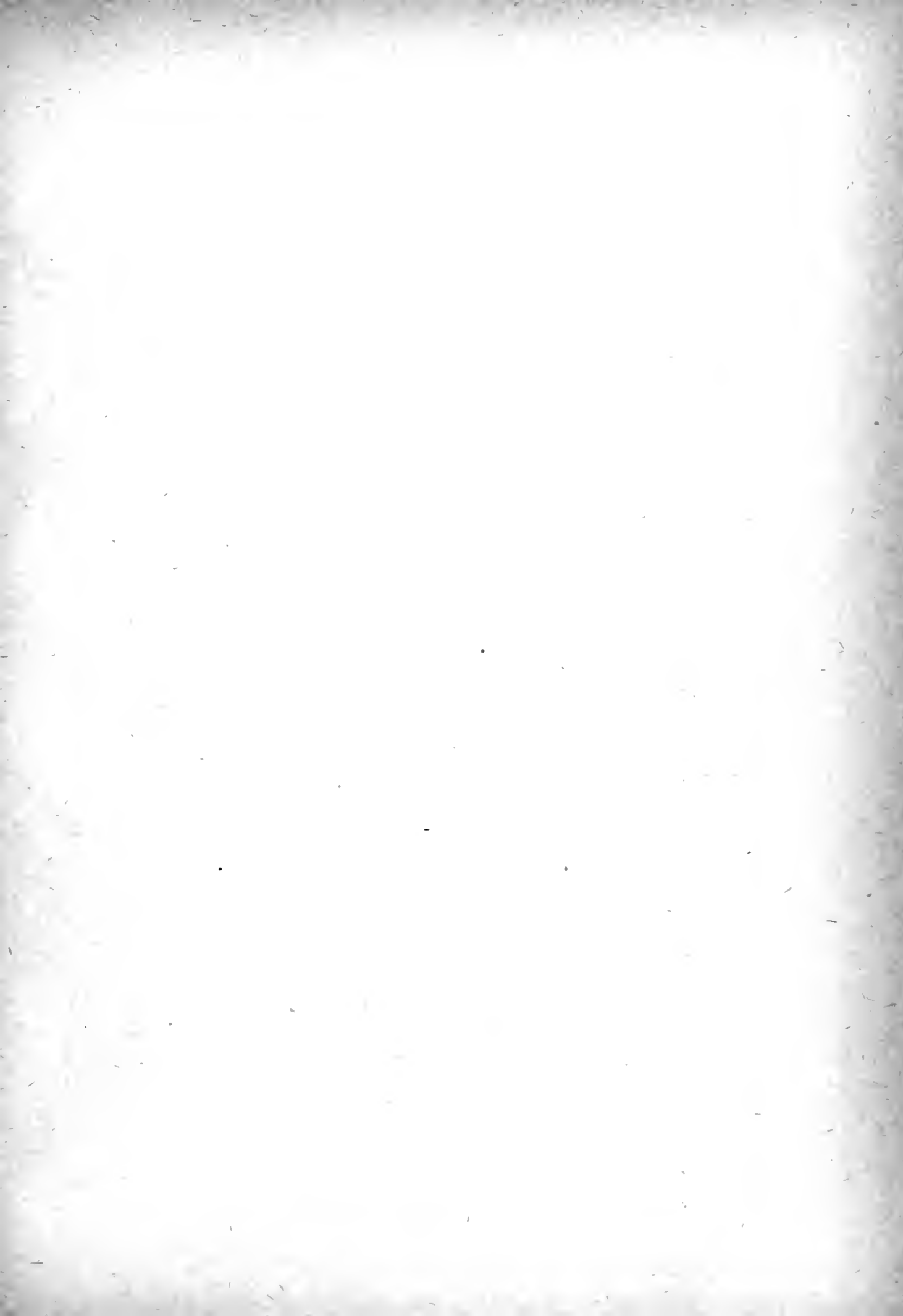
ALPHEUS

Plate XXI.

Fig. 1. First larva of *Alpheus sauleyi*, var. *brevicarpus*, from "loggerhead" spouge.   Hatched at 4 p. m., June 10, 1887.   A small amount of unabsorbed food yolk remains in the stomach.   ×26.

Fig. 1*a*. Line to indicate length of larva.   L.=3.5^{mm}.

Fig. 2. Second larva of same, from brood hatched on evening of June 8.   Food yolk nearly absorbed.   About twenty-four hours old.   ×26.

Fig. 2*a*. Line to show length of larva.   L.=4^{mm}.

Fig. 3. Head of young from same brood.   Four days old.   ×52.

Fig. 4. Right first pereiopod of larva of *A. sauleyi*, var. *brevicarpus*, before the molt preparatory to stage shown in Fig. 1.   Seen from inner side.   ×52.   Swimming hairs of exopodites rudimentary.

Fig. 5. Egg embryo of *A. sauleyi*, var. *longicarpus*, nearly ready to hatch.   The large chela of the left first pereiopod is conspicuous below the antennae.   ×46.

Fig. 5*a*. To show natural size of the same.   Slightly too large.   Dimensions: $\frac{4}{100} \times \frac{6}{100}$ inch.

Fig. 6. First and second maxilla of first larva (Fig. 1) before preparatory molt.   The parts are gloved with the embryonic skin, which is usually cast off at the time of hatching. ×227.

Fig. 7. Left first pereiopod of same, seen from inner side.   ×52.

Fig. 8. Third larva of *Alpheus sauleyi*, var. *brevicarpus*.   From same brood as second larva, Fig. 2.   Not over twenty-eight hours old.   Food yolk not wholly absorbed.   ×26.

Fig. 9. Telson and rudimentary uropods, seen from below.   ×52.

Plate XXI

1.

Fig. 1a.

2.

Fig. 2a.

3.

6.

4.

5.

Fig. 5a.

7.

8.

9.

F.H.Herrick, del.
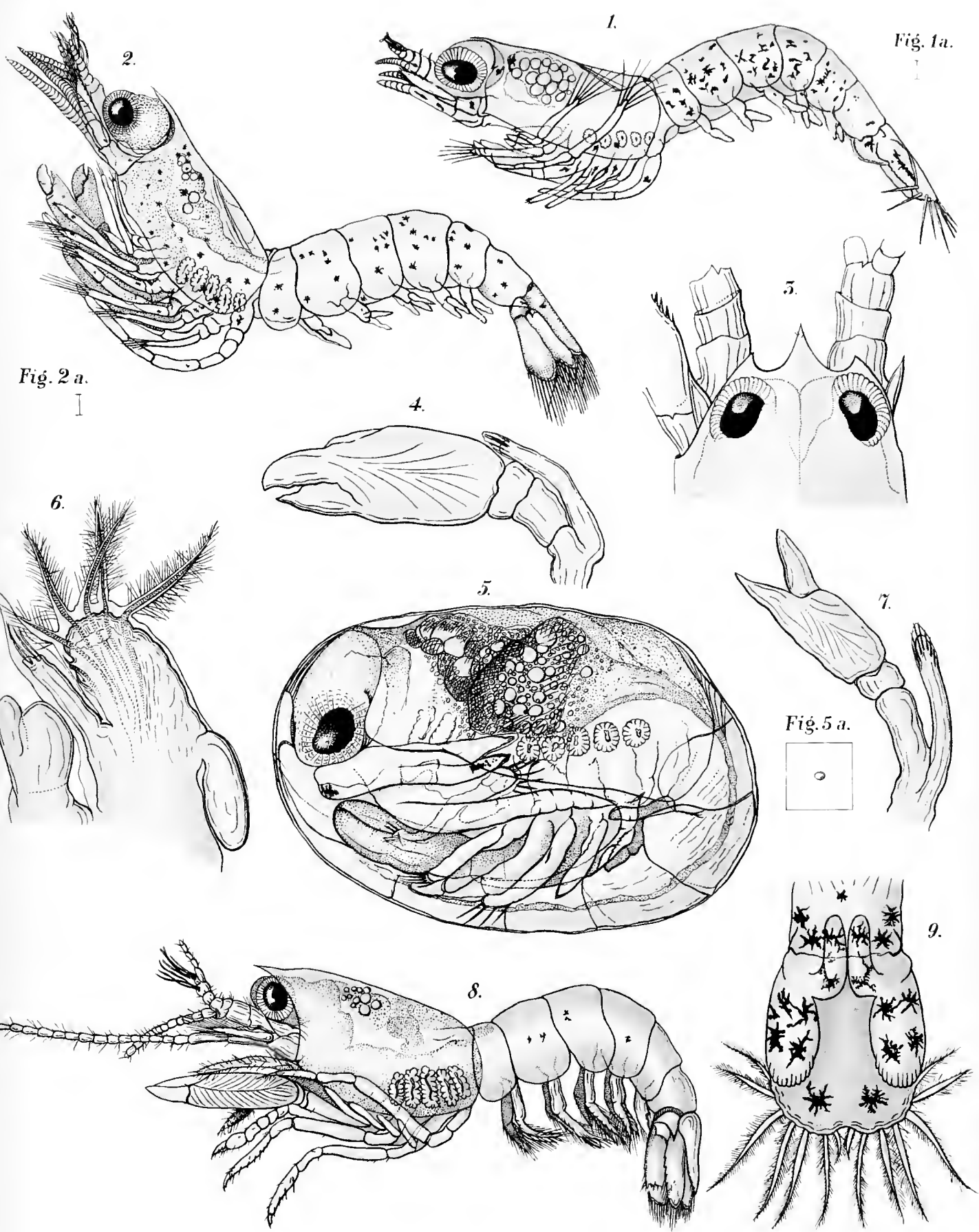
ALPHEUS SAULCYI

PLATE XXII.

FIG. 1. Left second pereiopod of first larva of *A. sauleyi*, var. *brevicarpus*, from inside. ×64.

FIG. 2. Left third pereiopod of same, from inside. ×64.

FIG. 3. First maxilla of first larva of *A. sauleyi* from brown sponge. ×255.

FIG. 4. Left second abdominal appendage of first larva of *Alpheus sauleyi*, var. *brevicarpus*. ×64.

FIG. 5. Left first abdominal appendage of the same. ×64.

FIG. 6. Rostrum of the same, seen from above. ×64.

FIG. 7. Right second antenna of the same, seen from below. ×64.

FIG. 8. Right first antenna of the same, seen from above. ×64.

FIG. 9. Second antenna of young of *Alpheus sauleyi*, var. *brevicarpus*, six and a half days old. ×64.

FIG. 10. First antenna of the same. ×64.

FIG. 11. Head of male of *Alpheus sauleyi*, var. *longicarpus*, from "loggerhead" sponge. Median spine of rostrum wanting. Drawn from life. L.=5.5^{mm}. ×31.

FIG. 12. Mandible of first larva of *A. sauleyi*, var. *brevicarpus*. ×255.

FIG. 13. Left second antenna of male of *A. sauleyi*, seen from below. No. 8 of Table I, p. 385. ×33.

FIG. 14. Left second antenna of female of *A. sauleyi*. From No. 9 of Table I. ×33.

FIG. 15. Small chela of larva of *A. sauleyi*, var. *brevicarpus*, shown in Fig. 17, at time of hatching. Compare this with the same appendage of the adult. ×64.

FIG. 16. First pereiopod (small chela) of young of *A. sauleyi*, var. *brevicarpus*. From green sponge. Compare this with Fig. 3, Pl. XXIV. ×64.

FIG. 17. Front of a larva of *A. sauleyi*, var. *longicarpus*, which was hatched April 25. Drawn under pressure; eyes slightly distorted. Equivalent to the ordinary third larva, Fig. 8, Pl. XXI. ×64.

FIG. 18. Part of stalk of right first antenna of male of *Alpheus sauleyi*, seen from below, showing the aural scale. The median eye is seen on the right, between the basal segments of the antennules. From No. 8 of Table I. ×26.

Plate XXII
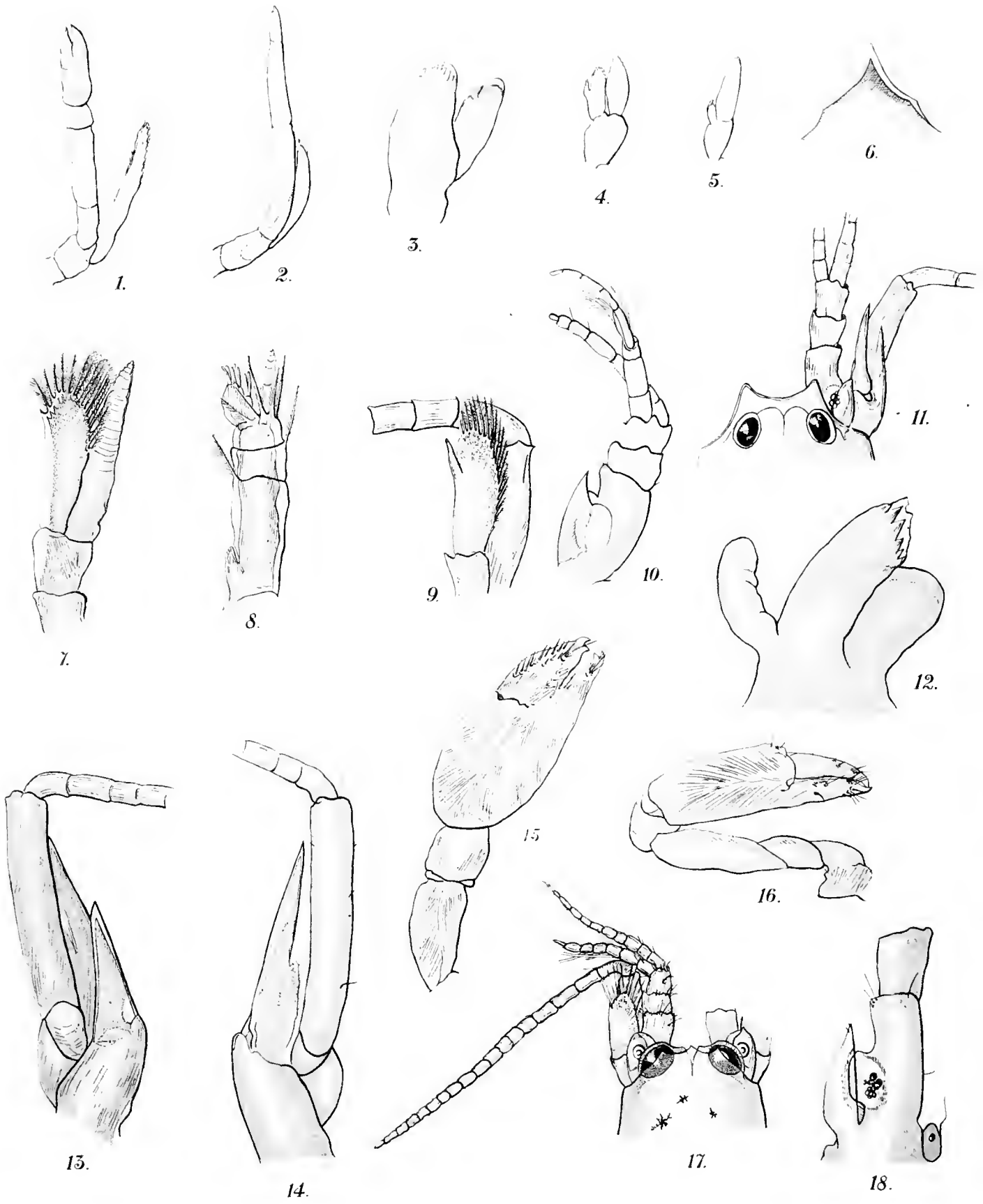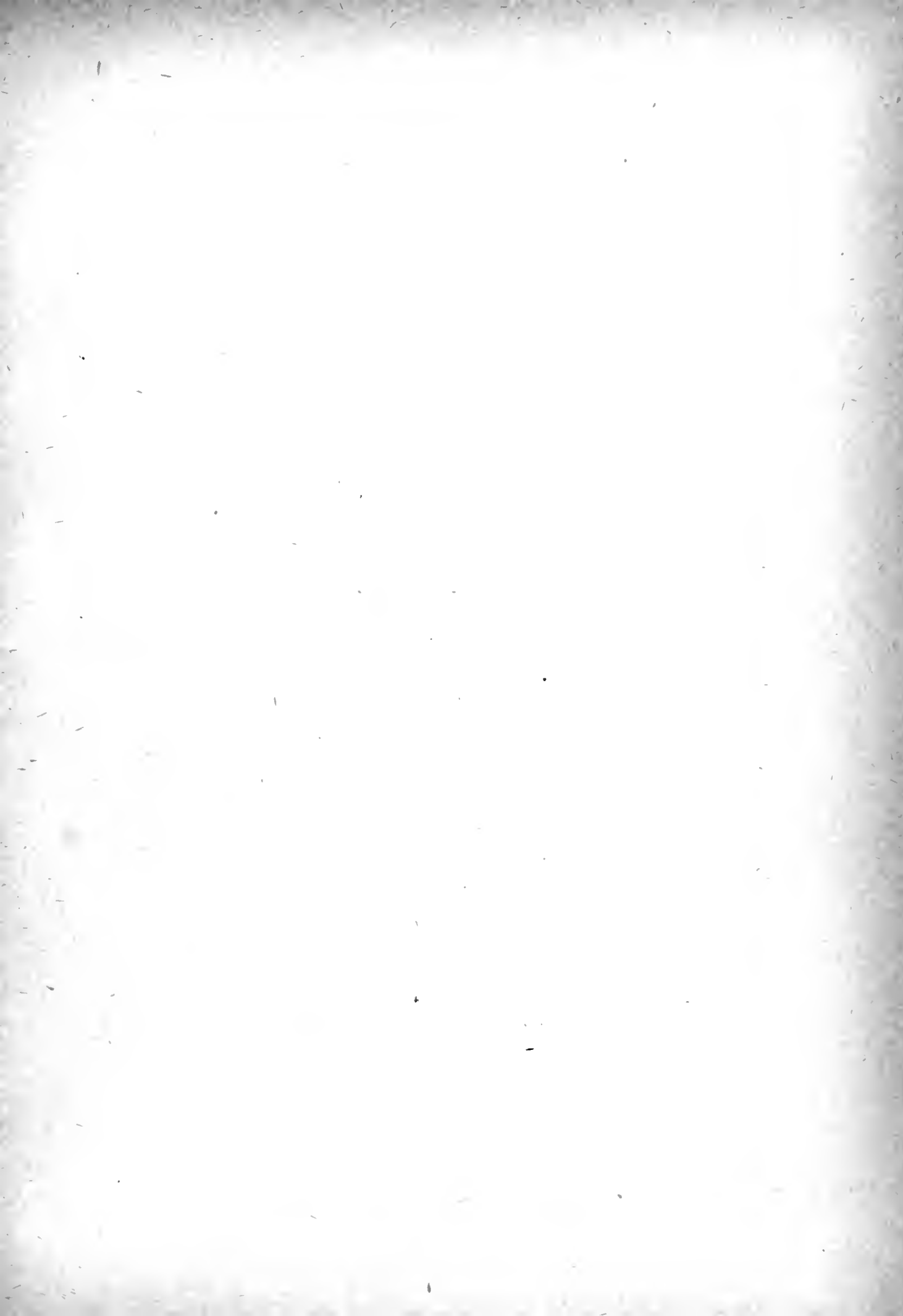
ALPHEUS SAULCYI.

PLATE XXIII.

Fig. 1. Right second pereiopod of male of *Alpheus saulcyi*, var. *brevicarpus*, seen from the outer side. ×33.
Fig. 2. Terminal segments of right fifth pereiopod of the same. ×33.
Fig. 3. Left mandible of the same, seen from the outer side. ×64.
Fig. 4. Left first antenna, and left compound eye of the same, seen from above. ×33.
Fig. 5. Left third maxilliped of the same, seen from outer side. ×33.
Fig. 6. Right second maxilliped of the same, seen from the outer side. ×64.
Fig. 7. Right first maxilliped, seen from the outer side. ×64.
Fig. 8. Right second antenna of the same, seen from above. ×33.

Plate XXIII

Fig 2.

Fig 1.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

F.H. Herrick, del.
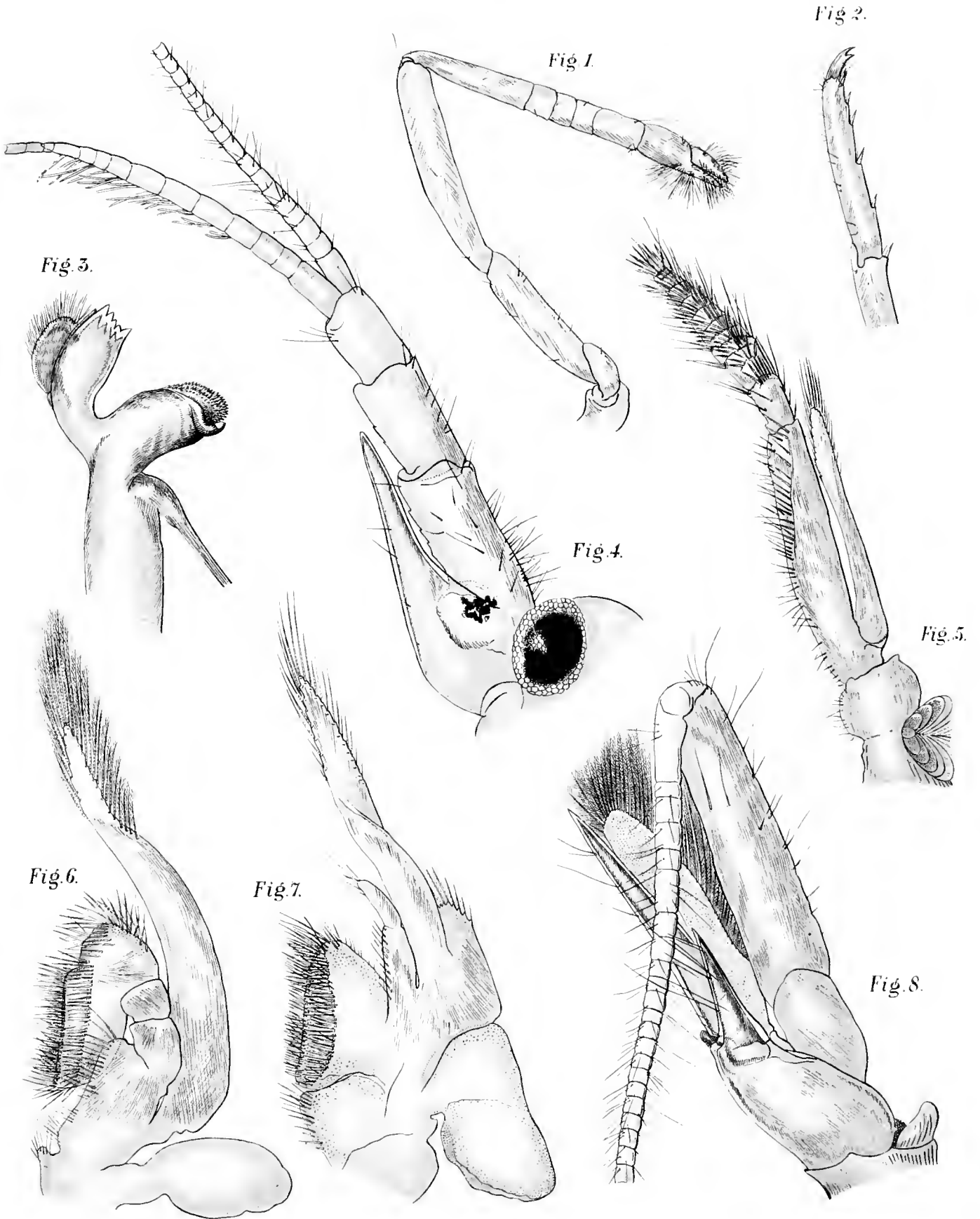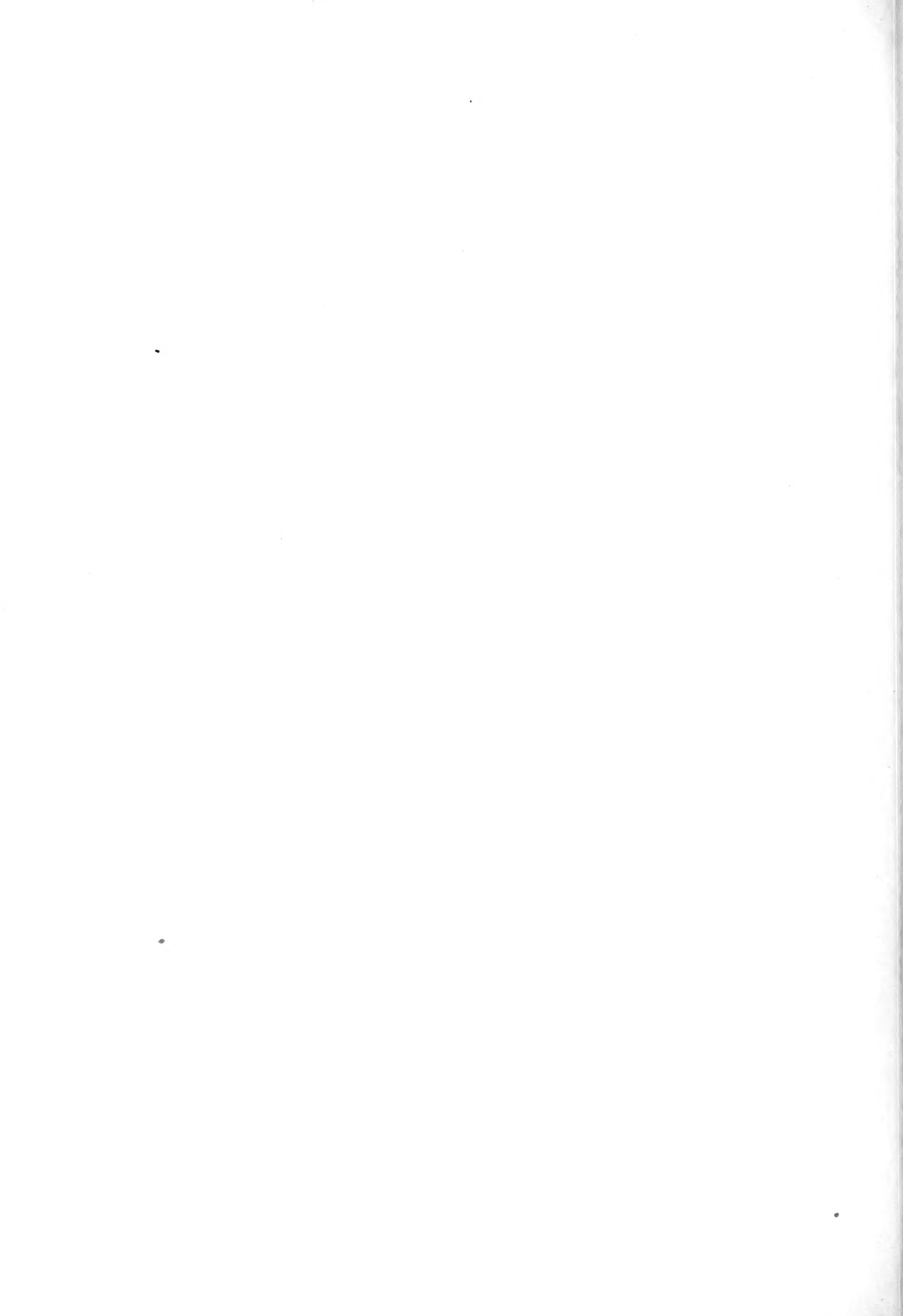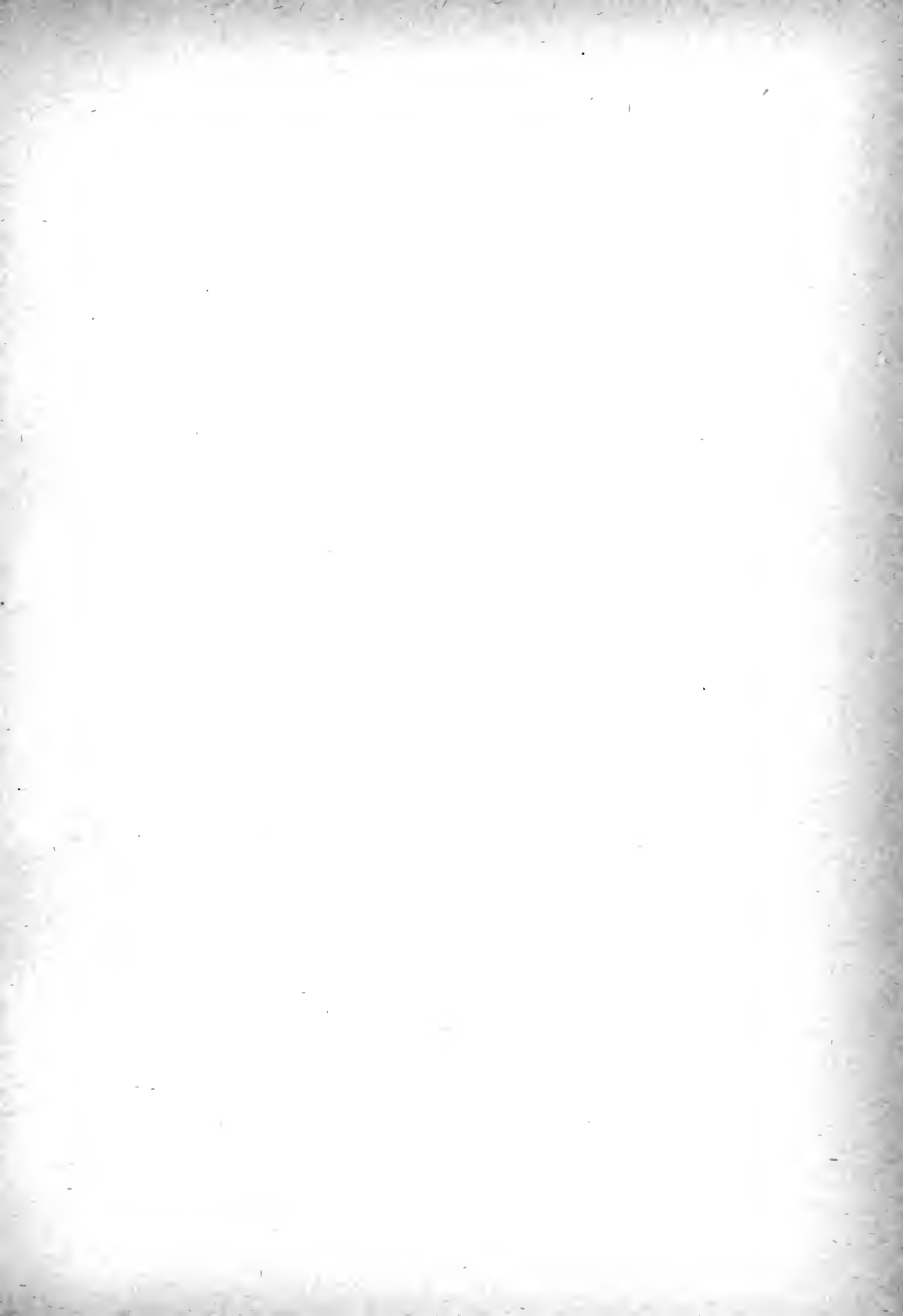
ALPHEUS SAULCYI.

Plate XXIV.

Fig. 1. Right fifth pereiopod of male of *Alpheus sauleyi*, var. *brevicarpus*, seen from outer side. ×33.

Fig. 2. Small chela of male of *A. sauleyi*, var. *longicarpus*. From No. 9, Table I. ×33.

Fig. 3. Small chela of male of *A. sauleyi*, var. *brevicarpus*. From No. 8, Table I. Compare with the typical form of the other variety, shown in Fig. 2. ×33.

Fig. 4. First pleopod of male of *A. sauleyi*, from "loggerhead" sponge. ×33.

Fig. 5. Left first pleopod of female of *A. sauleyi*, from "loggerhead" sponge. A single egg is seen, attached to three hairs of the protopodite. The hairs are coated with glue, and the gluey threads are twisted into a chord, which is continuous with a thin sheet of this substance (the membrane of attachment or secondary egg-membrane which envelopes the egg). Below is seen a single hair, from which an egg has broken loose. Drawn from an alcoholic specimen. ×33.

Fig. 6. Right second pleopod of larger female of *A. sauleyi*, showing a number of eggs attached, seen from behind. ×14.

Fig. 7. First maxilla of *A. sauleyi*. Endopodite bent out of position, to a point below the large coxopodite. ×64.

Fig. 8. Large chela of female of *A. sauleyi*, from "loggerhead" sponge. Compare with the *brevicarpus* shown in Pl. IV. ×33.

Fig. 9. Right second maxilla of *A. sauleyi*, seen from outer side. ×64.

Plate XXIV.
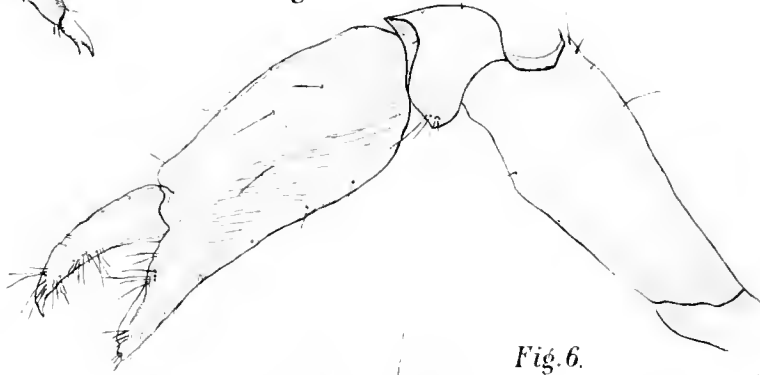
Fig.1.

Fig.2.

Fig.3.

Fig.4.

Fig.6.

Fig.5.

Fig.7.

Fig.8.

Fig.9.

C.H.Herrick, del.

ALPHEUS SAULCYI,
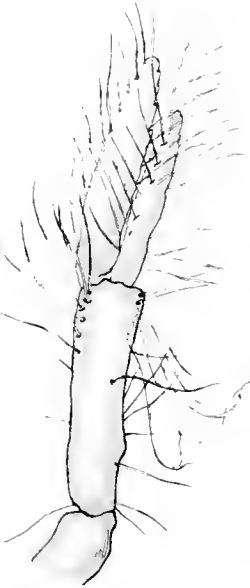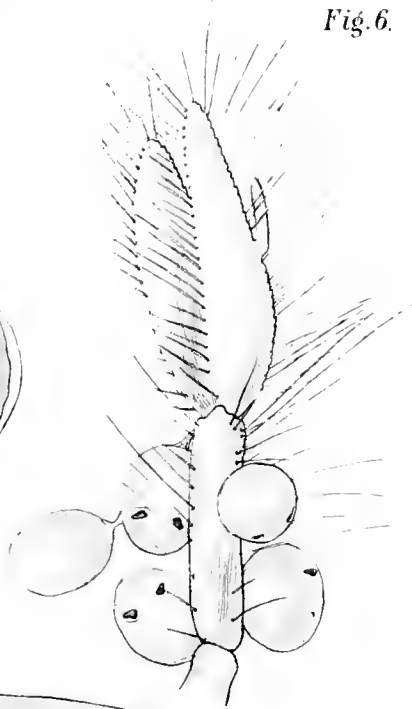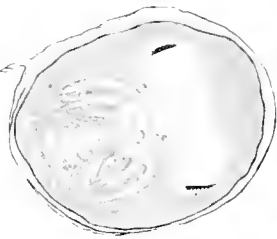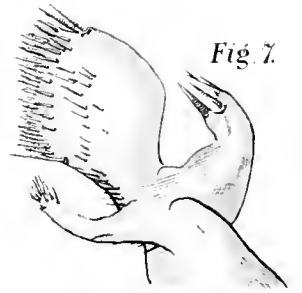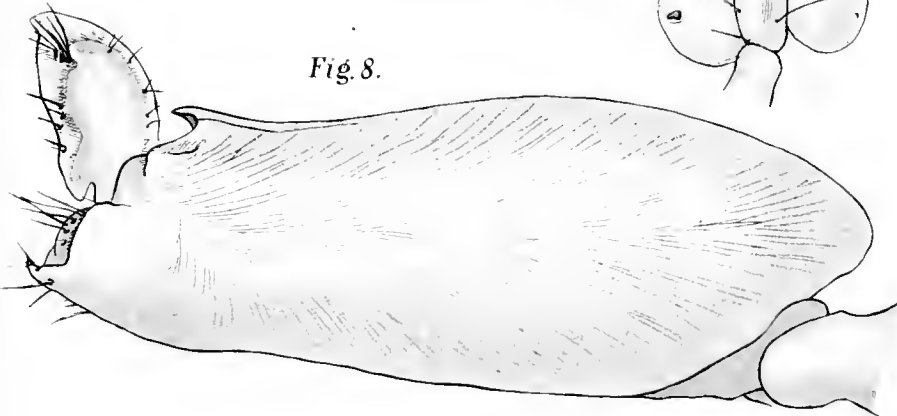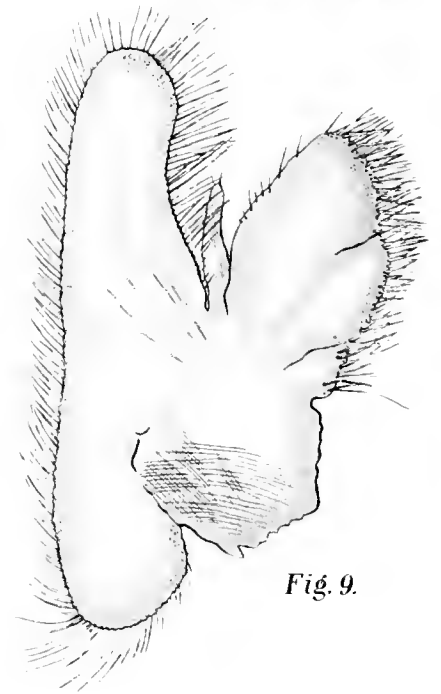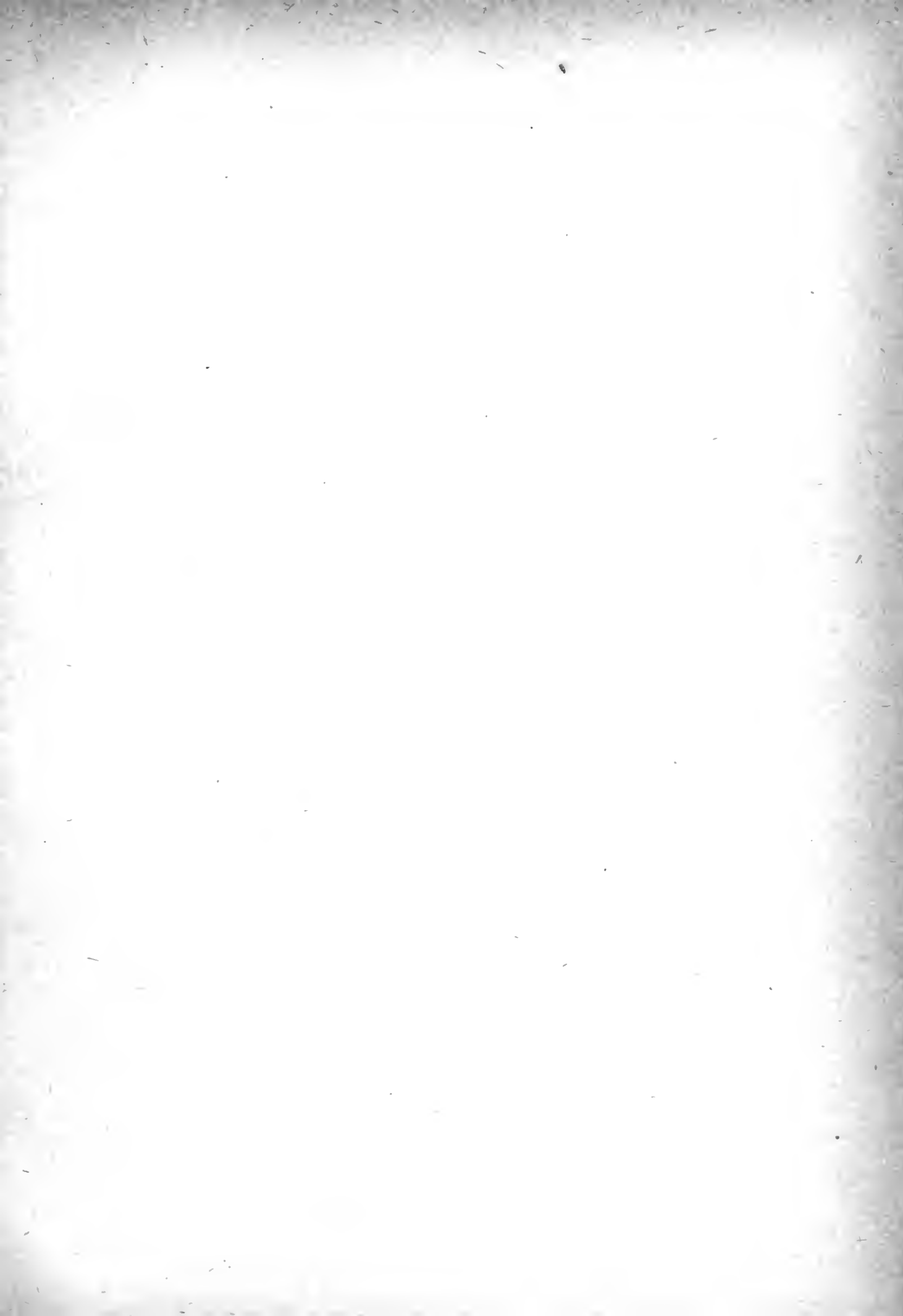
Plate XXV.

Fig. 1. Surface view of segmenting egg of *Hippa talpoides*. Thirty-two yolk pyramids present. ×38.

Fig. 2. Embryo of *Hippa talpoides*, showing optic disks and thoracic-abdominal plate. ×38.

Fig. 3. The central part of a transverse section of the ovary of the lobster, *Homarus americanus*, to show the progressive development of ova; from the same series as that represented, with less enlargement, in Fig. 6. Ovary taken in January. ×281.

Fig. 4. Section of egg of *Hippa talpoides* in yolk segmentation. Sixty-four yolk pyramids present. ×70.

Fig. 5. Part of segmenting egg of *Alpheus minor*, showing a single large nucleus and two smaller nuclei. Compare with Fig. 23. ×281.

Fig. 6. Central portion of transverse section of ovary of the lobster, corresponding nearly to that shown in Fig. 3, showing the germogenal areas and the irregularly radiating blood sinuses. The diameter of the entire ovary is about twice that of the part represented. The largest peripheral ova have an average diameter of about one thirty-third of an inch, and their contents is only about one-eighth that of the ripe egg. ×70.

Fig. 7. Egg-nauplius embryo of *Hippa talpoides*. Appendages appear as simple buds. ×38.

Fig. 8. Post-nauplius stage of *Hippa*. Abdomen bilobed at tip. Buds of at least three pairs of post-mandibular appendages. Figs. 1, 2, 7, and 8 are made from pen-and-ink sketches, and show only the general appearance of the embryo and its relation to the yolk.

REFERENCE LETTERS.

Ab. P., thoracic abdominal plate.
B. C., blood cell.
Bl. S., blood sinus.
Ch., chitinous eggshell.
Ch. M., limiting membrane of blood sinus.
Ct. S., ovarian stroma.
E. f., egg follicle.
F. C., egg follicle.
Ger., germogenal area.
I. E., ovarian stroma (undifferentiated).
o, o¹–o⁷, nuclei of ovarian stroma and developing eggs.
O. D., optic disk.
O. L., optic lobe.
Y. P., yolk pyramid.
Y. S., yolk spherule.
Vac., yolk vacuole.

Plate XXV.

HIPPA, HOMARUS AND ALPHEUS.
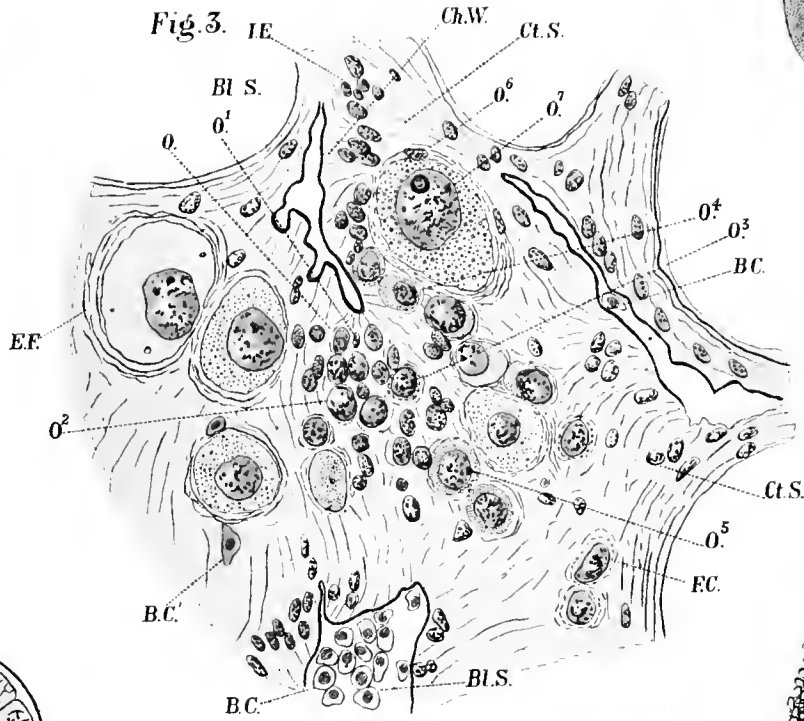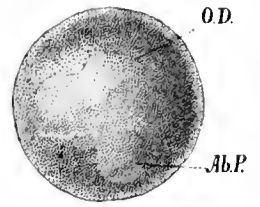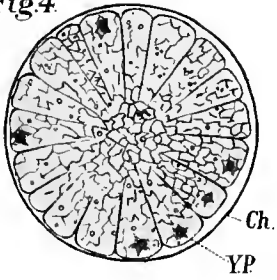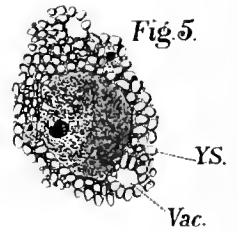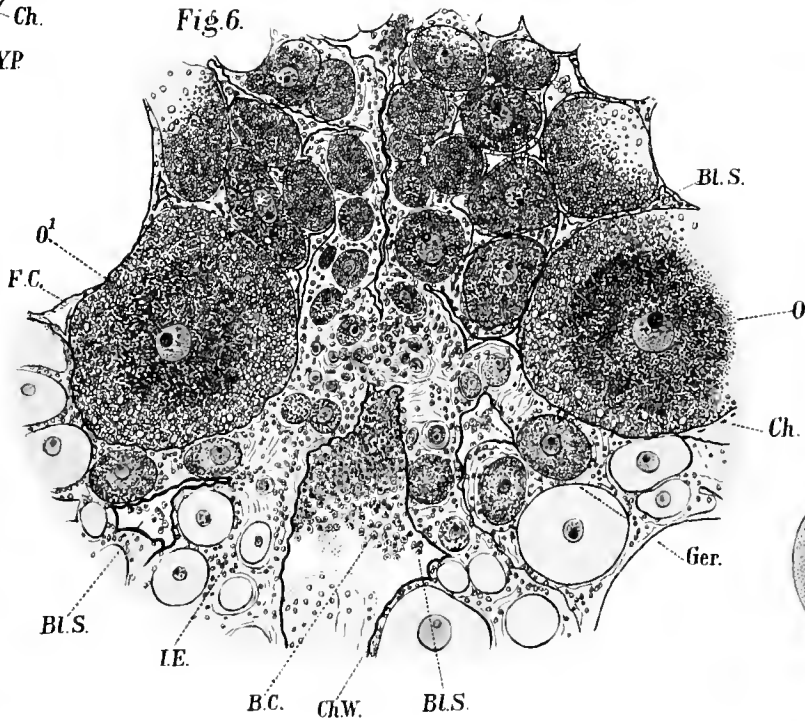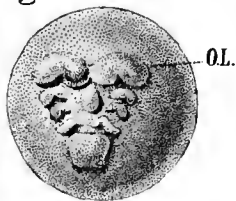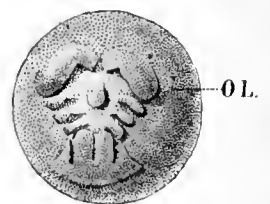
PLATE XXVI.

FIG. 9. Section through segmenting egg of *Alpheus sauleyi*. Eight cells present. Yolk unsegmented. Egg membranes diagramatically represented. ×70.

FIG. 10. Surface view of the same. Sixteen cells present. Yolk pyramids formed. The peripheral nuclei are seen through a thin layer of yolk. ×70.

FIG. 11. Transverse section through the immature ovaries of *Alpheus*. Ovary taken in June, from female "in berry." Diameter of largest ovarian egg, one one hundred and sixty-eighth of an inch. Diameter of extruded egg, one fiftieth of an inch. Contents of ovarian egg, one thirty-seventh of that of the extruded egg. ×281.

FIG. 12. Section through segmenting egg of *Alpheus minor*, from Beaufort, North Carolina, showing nests of nuclei. ×70.

FIG. 13. Swarm or nest of nuclei, like those of preceding figure. ×281.

FIG. 14. Section through egg of *Alpheus minor*, cutting segmentation nucleus. Nucleus elongated, with irregular, indefinite boundary. ×70.

REFERENCE LETTERS.

Al. C., alimentary canal.

B. C., blood cell.

B. S., blood space (possibly unnaturally distended).

Ch., chitinous egg envelopes.

D. A., dorsal aorta.

e, e¹, young ova.

F. E., ovarian stroma.

F. E.¹, follicular epithelium.

F. C., follicular epithelium.

Ger., germogen.

Ger.¹, position of germogen in ovary, with ova nearly ripe.

G. V., germinal vesicle.

O. W., ovarian wall.

SS, swarm of nuclear bodies.

Vac., yolk vacuole.

Vit., vitellogen.

x, cell shown in Fig. 30.

Y. P., yolk pyramid.

Plate XXVI.

Fig.9.

Fig.10.

Ch.

x.

Y.P.

Fig.11.

Vac. *Vit.* *Ch.* *Ger.* *B.C.* *D.A.*

F.E.¹

B.S. *e*

Y. *G.V.*

B.C. *F.C.*

F.E.

e¹ *E.C.* *e.¹*

O.W. *B.S.* *G.V.*

F.E. *Al.C.*

Fig.12. *Fig.13.* *Fig.14.*

Ch. *Ch.*

S.S. *Vac.*

Ch. *Vac.*

Y.S.

ALPHEUS SAULCYI AND A. MINUS.
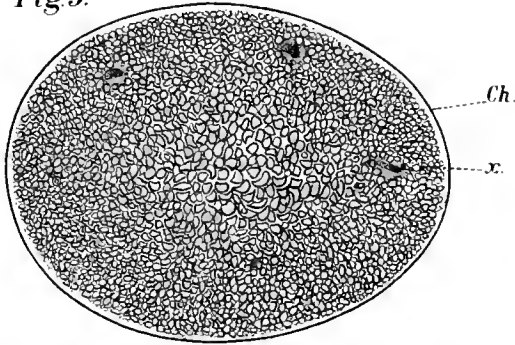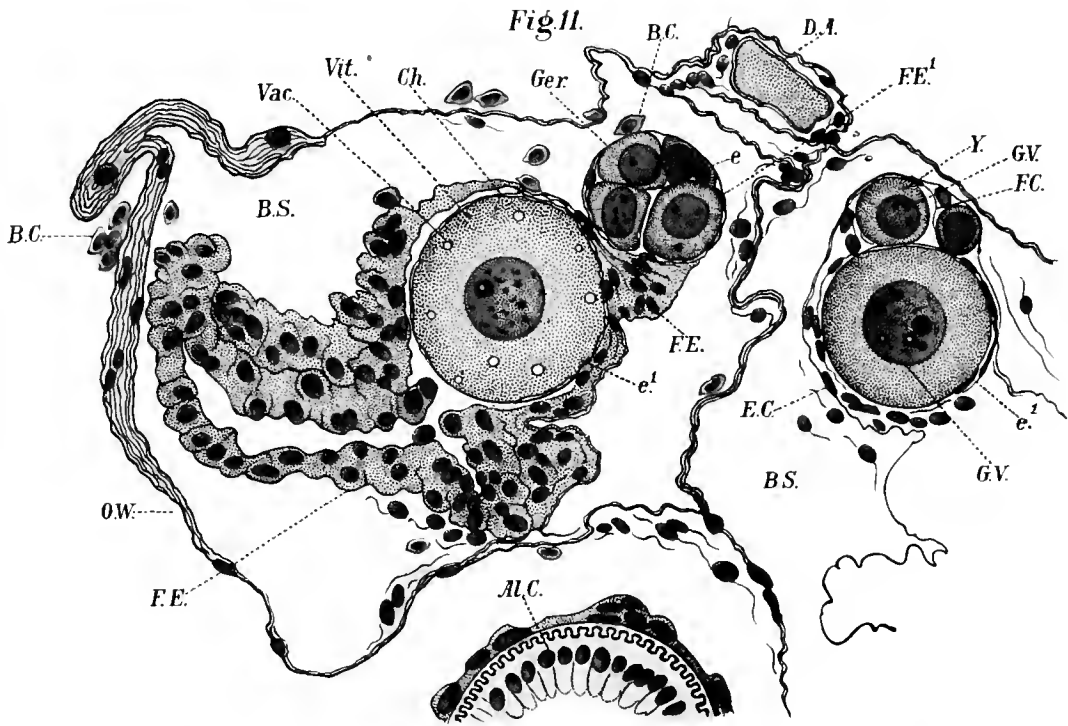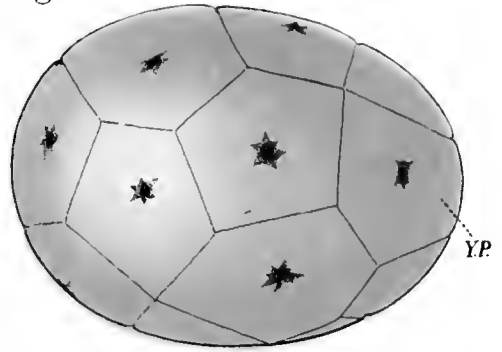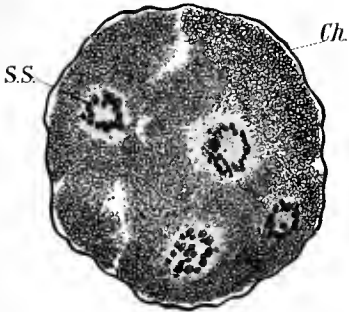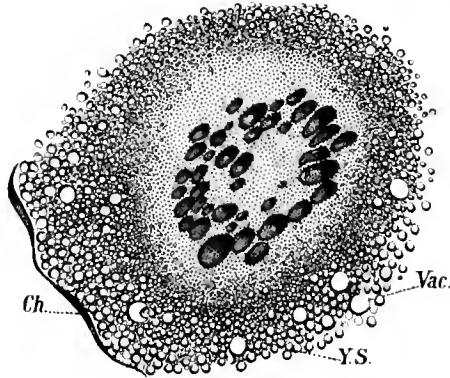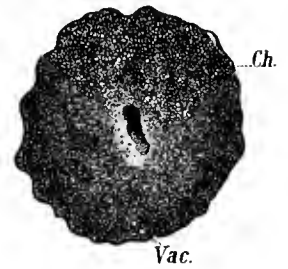
Plate XXVII.

Fig. 15. Section of egg of Bahaman variety of *Alpheus heterochelis* in typical yolk pyramid stage Sixty-four cells present.   ×70.

Fig. 16. Segmentation nucleus of egg of *A. sauleyi*, nearly central in position.   ×277.

Fig. 17. Section of an egg of *A. sauleyi*, which was normally laid but unfertilized, showing the female pronucleus.   ×70.

Fig. 18. Degenerating nuclei containing spore-like bodies, from the egg-nauplius embryo, the structure of which is shown in Pls. XLI–XLIII.   ×610.

Fig. 19. Blood cells of adult Alpheus.   ×610.

Fig. 20. Endodermal cells from the ventral wall of the primitive alimentary cavity of *Astacus fluviatilis*.   After Reichenbach (54) Taf. VIII, Fig. 67.   This is taken from the egg-nauplius stage to show the origin of "secondary mesoderm." The elements here marked m^1, k are described as cells which have originated from the endoderm, and completed their metamorphosis into ordinary mesoderm cells. These may be compared directly with *b*, Fig. 18, and *s*, s^2, Fig. 21, from the egg-nauplius of *Alpheus sauleyi*, and are rather to be regarded as nuclear bodies in the earlier stages of *retrogressive* metamorphosis.   ×256.

Fig. 21. Part of transverse section through the foregut of the egg-nauplius of *Alpheus sauleyi*, to show the degenerative cell products.   ×610.

REFERENCE LETTERS.

A. Y. S., altered food-yolk.
Ch., chitinous egg membranes.
ec., ectoblast.
i., nuclear body, with vesicular chromatin mass.
k, k^1, l, m, m^{1-3}, nuclear products in yolk.
Mes., mesoblast.
N., *N.¹*, nuclei of entoblastic cells.
n., nucleolus of entoblastic cell (not clearly shown).
Ol., oil drop.
Ret., protoplasmic reticulum.
S, *s*, s^2., degenerative products.
Sep., cleavage plane.
Std., foregut.
Vac., yolk vacuole.
Y., yolk.
Y. P., yolk pyramid.
Y. S., yolk sphere.

Plate XXVII

ALPHEUS AND ASTACUS.
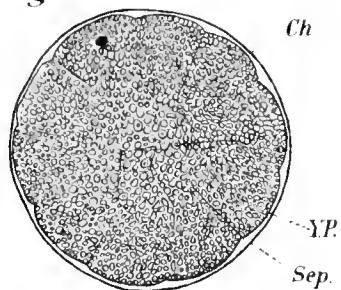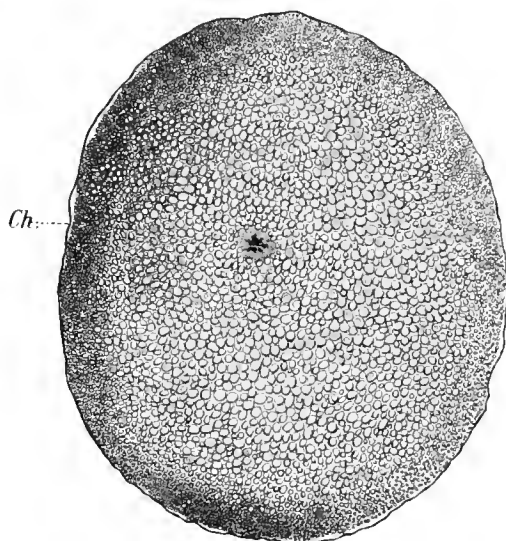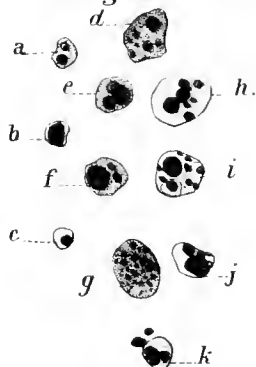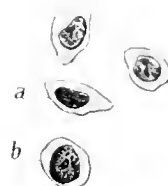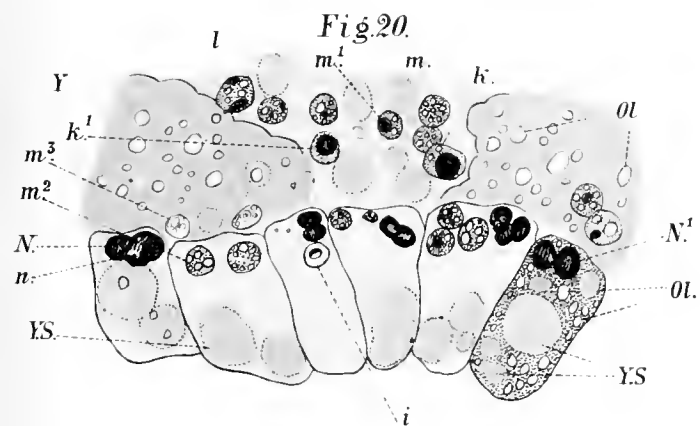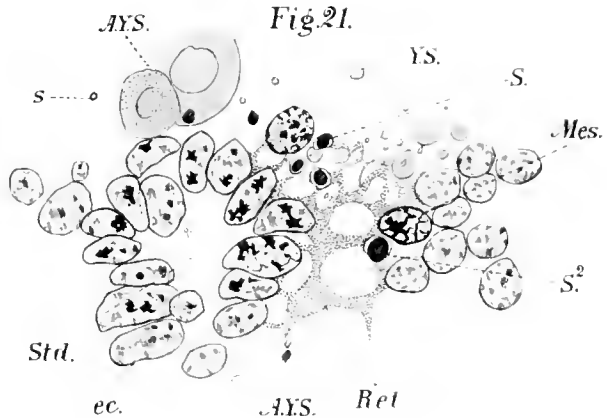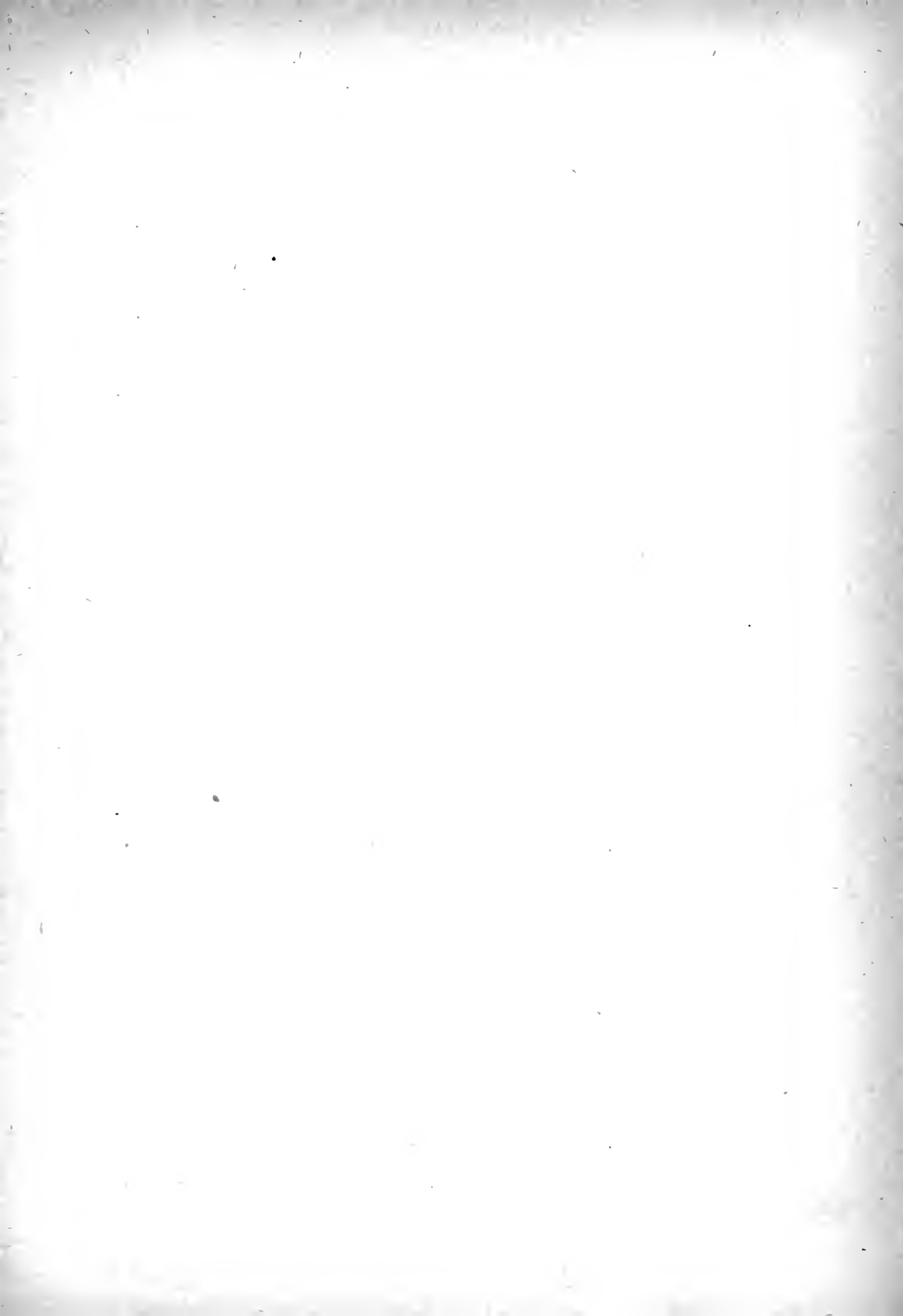
Plate XXVIII.

Fig. 22. Part of section of segmenting egg of *Alpheus minor* from Beaufort, North Carolina, showing nuclear body in clear area.   ×277.

Fig. 23. Swollen, probably degenerating, elements, from segmenting egg of *A. minor*.   ×277.

Fig. 24. Section through base of yolk pyramid of egg of *Palæmonetes vulgaris*.   About sixty-four cells present.   ×277.

Figs. 25, 26. Two successive sections through clear area in segmenting egg of *Alpheus minor*, showing degenerative products and nuclear bodies in process of breaking up.   ×277.

Fig. 27. Part of section through segmenting egg of *Pontonia domestica*, before cleavage of the yolk.   The egg contains three nuclei, one of which is seen to be in karyokinesis.   ×277.

Fig. 28. Part of section of an Alpheus egg in same stage as that shown in Fig. 9.   Cell dividing indirectly and in horizontal plane.   ×277.

Fig. 29. Section of egg of *Alpheus minor*, probably at close of segmentation.   ×277.

Fig. 30. Enlarged view of cell *x*, and part of section shown in **Fig.** 9.   ×277.

REFERENCE LETTERS.

Ch., egg membranes.
N., nucleus.
P. A., protoplasmic area.
P. N., perinuclear protoplasm.
SC, SC[1-5], degenerating cell products.
Y, yolk.
Y. B., yolk ball.
Y. S., yolk sphere.
Vac., vacuole.

Plate XXVIII.

Fig.22.
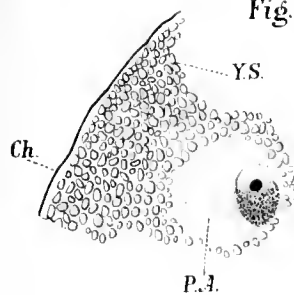
Fig.23.
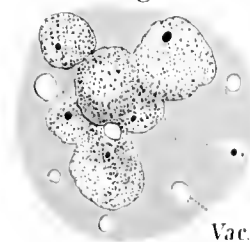
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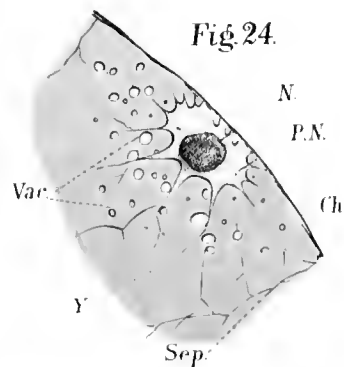
Fig.25.
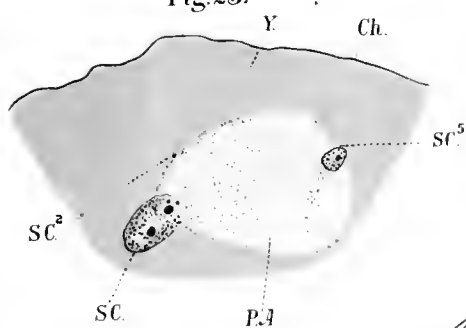
Fig.26.

Fig.27.

Fig.28.

Fig.29.

Fig.30.

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ALPHEUS AND PONTONIA.
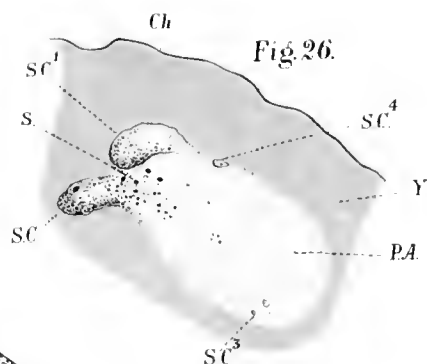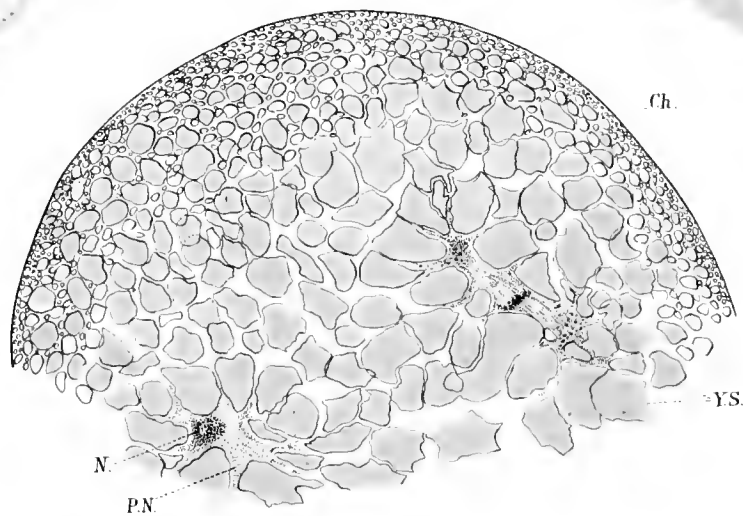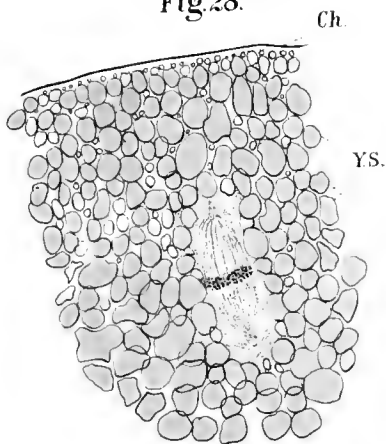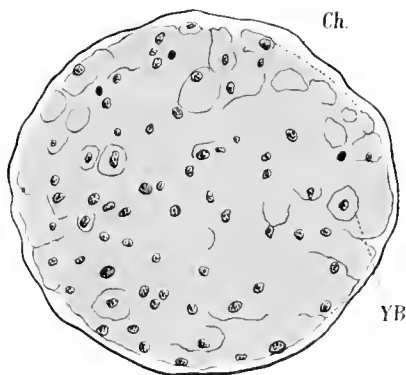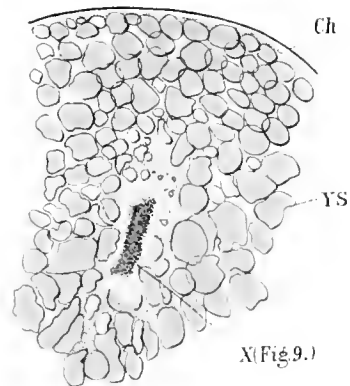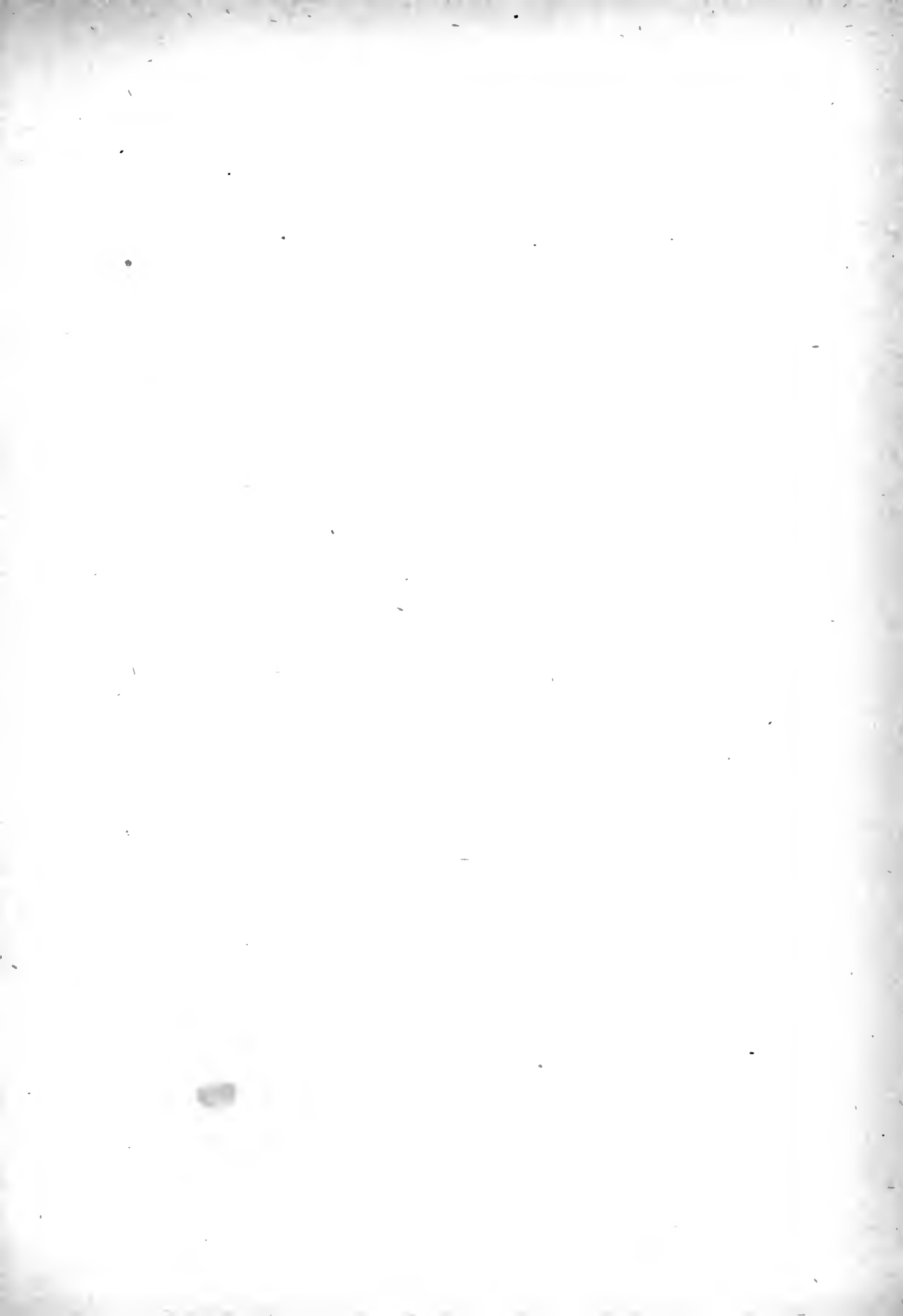
PLATE XXIX.

FIG. 31. Part of section of egg of Bahaman variety of *Alpheus heterochelis*, showing two yolk pyramids. Same stage as Fig. 15. Sixty-four cells present. ×277.

FIG. 32. Part of transverse section of egg-nauplius of *A. saulcyi*, showing the fold of one of the antennæ and the mesoblastic cells and degenerative products contained within it. ×610.

FIG. 33. Wandering cells in yolk above the same embryo, showing protoplasmic union. ×610.

FIG. 34. Part of section of egg of the Bahaman *heterochelis* in egg-nauplius stage, showing wandering cells, which have left the yolk and have attached themselves to the superficial ectoblast. The nuclei are flattened against the surface, but are clearly distinguished from the epiblast. ×610.

FIG. 35. Part of transverse section of older embryo, showing blood cells and wandering mesoblast cell (*Mes.*). Eye-pigment beginning to form. ×610.

FIG. 36. Part of longitudinal section of embryo shown in Fig. 153, to show the degenerative products of the dorsal plate. ×610.

REFERENCE LETTERS.

App., appendage.
A. Y. S., altered yolk.
B. C., blood corpuscle.
Ch., egg membranes.
C. P., united pseudopodia of two wandering cells.
Ect., ectoblast.
Ep., spindle-shaped nuclei of surface epiblast.
Mes., *Mes.*[1], mesoblast.
Mu., muscle cells.
Pn., cell protoplasm.
Pl., coagulated blood.
s, *s*[1], degenerative cell products.
Sep., inner wall of yolk pyramid.
S. W., outer wall of yolk pyramid.
Y. C., wandering cells.
Y. S., yolk sphere.
Vac., vacuole.

Plate XXIX

Fig. 31.

Y.S.

Sep.

PN.

S.W.

Ch.

Fig. 33.

C.P.

Y.S.

Fig. 32.

Vac.

Y.S.

S.

Mes.

Ect.

Ect.

Mes.[1]

App.

S.[1]

Fig. 34.

Ch.

Ep.

Y.C.

Y.S.

Fig. 35.

Mu.

B.C.

Y.S.

Mes.

Vac.

B.C.

Pl.

Ect.

App.

Fig. 36.

Ect.

S.

Y.S.

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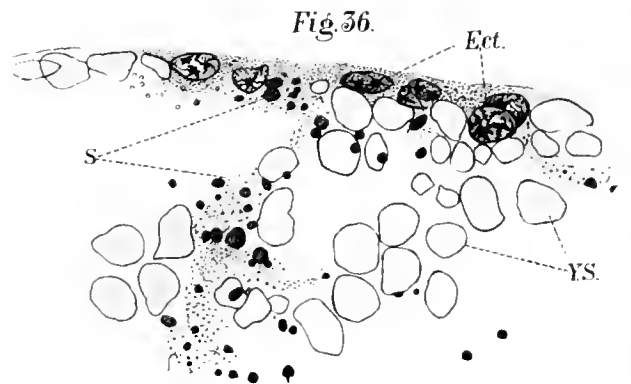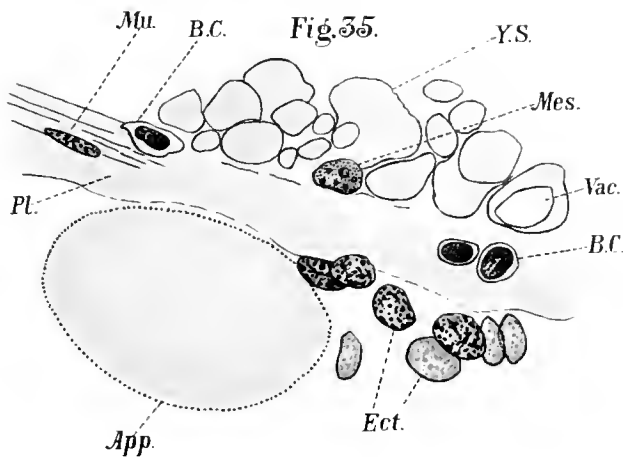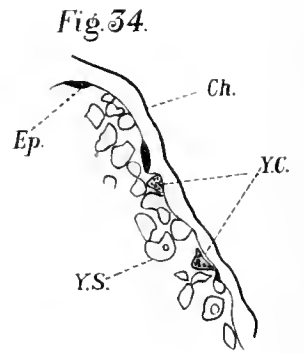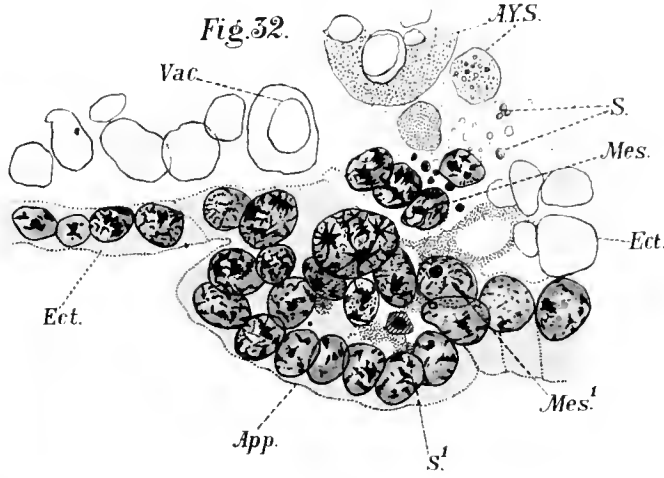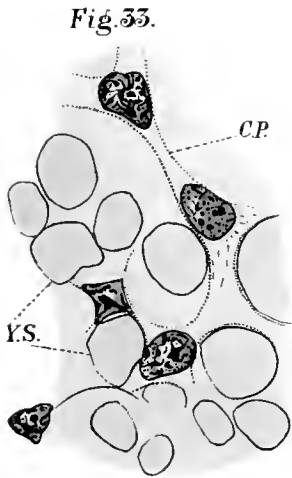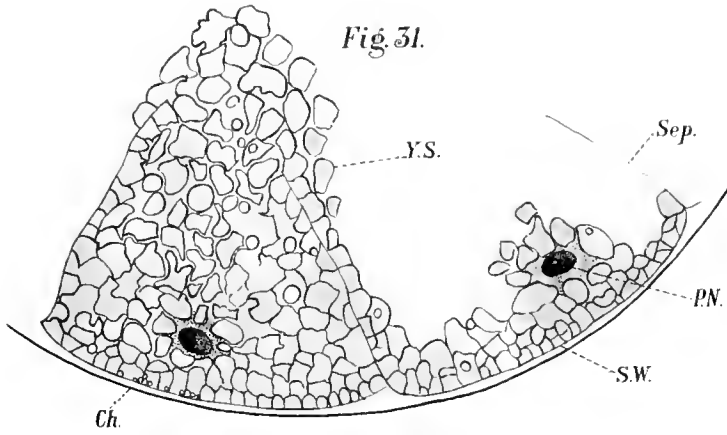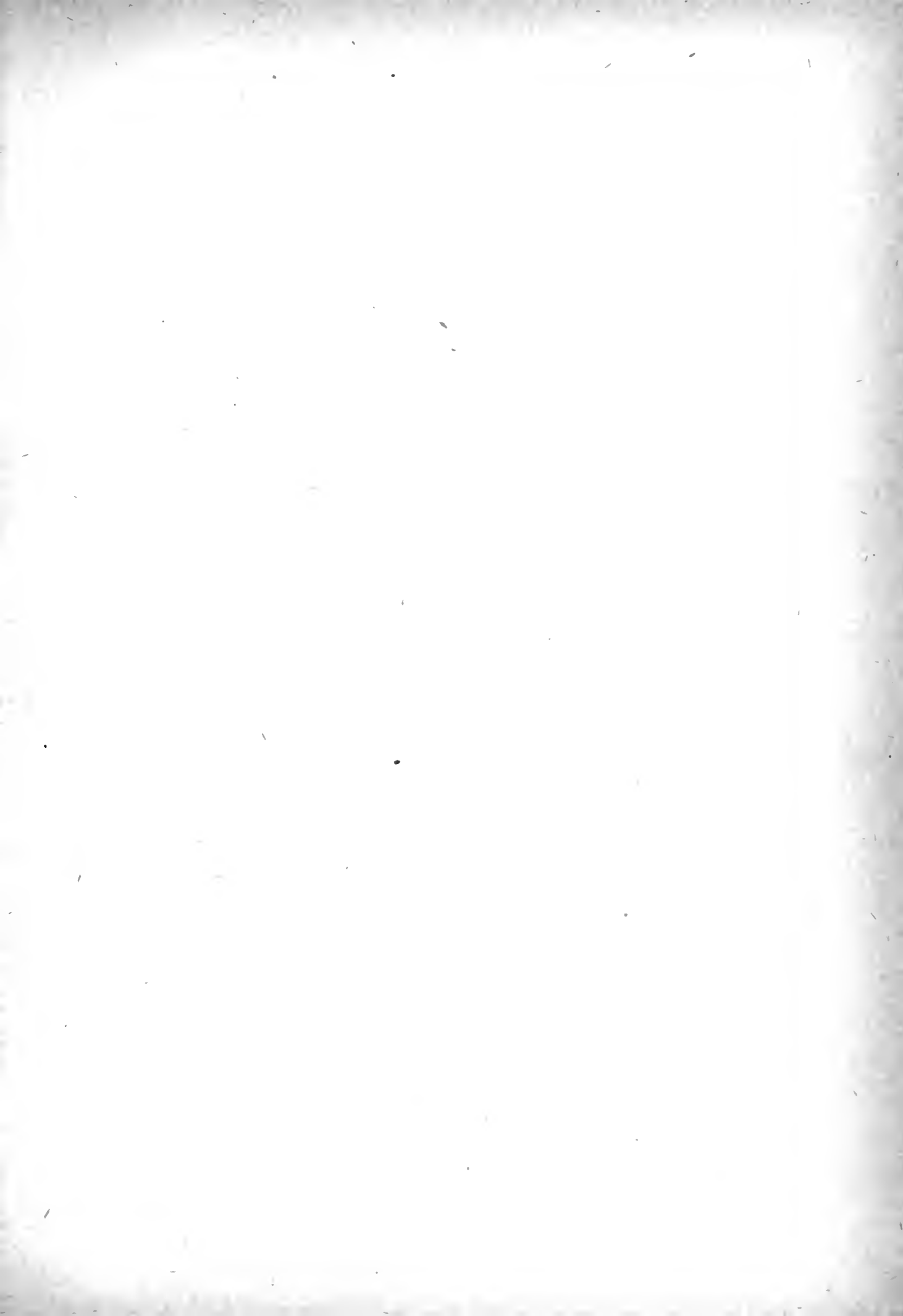
ALPHEUS

Plate XXX.

Fig. 37. Part of section of egg before invagination stage, showing primary yolk cells. All the figures on this plate, excepting Fig. 46, refer to the Bahaman form of *Alpheus hetero-chelis.* ×277.

Fig. 38–44. Consecutive sections of the same egg, showing the progress of the primary yolk cells in their migration from the blastoderm to the central parts of the egg. ×70.

Fig. 45. Section through the same egg, showing semidiagrammatically the structure of the yolk. ×70.

Fig. 46. Section through the egg of *A. saulcyi* at a slightly later stage, but before invagination. The blastodermic cells lie at the surface, the primary yolk cells toward the center of the egg. Traces of the primary yolk cleavage are still seen at the surface, and a secondary cleavage has occurred below the surface. ×70.

Fig. 47. Surface view of the side of egg, corresponding to the germinal area in nearly the same stage. ×70.

Fig. 48. Tangential section, showing blastodermic cells of same egg. ×277.

REFERENCE LETTERS.

a, a¹⁻⁵, cells migrating from blastoderm into the yolk.
Bd. C., blastodermic cell.
Ch., eggshell.
G. D., embryonic area.
Sep., yolk cleavage plane.
Y. B., yolk ball.

Plate XXX

Fig.37.

Ch.

Sep.

Fig.38.

Ch

Sep.

a^6
a^1

Fig.39.

Sep.

a^3

a^2 a

Fig.40.

a^3

a^2 a

Fig.41.

a^4 a^5

Fig.42.

a^7

a^4 a^5

Fig.43.

Fig.44.

Fig.45.

Sep.

Ch.

Fig.46.

Sep.

Y.B.

Fig.47.

G.D.

Fig.48.

Bd.C.

Y.

ALPHEUS
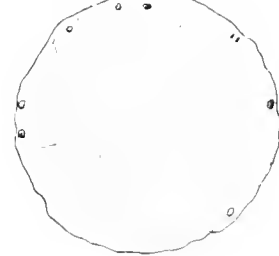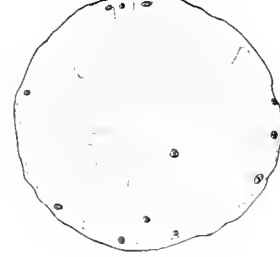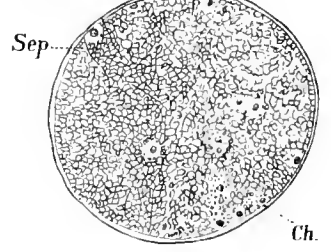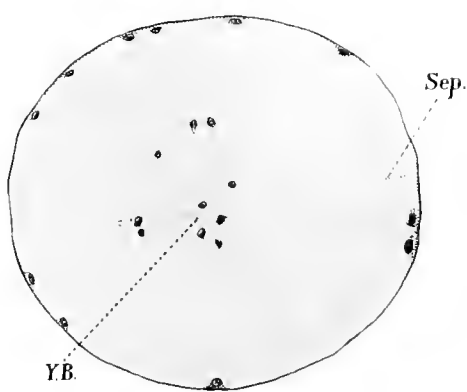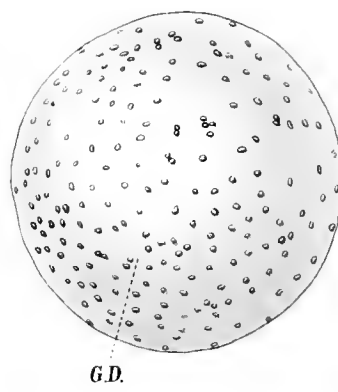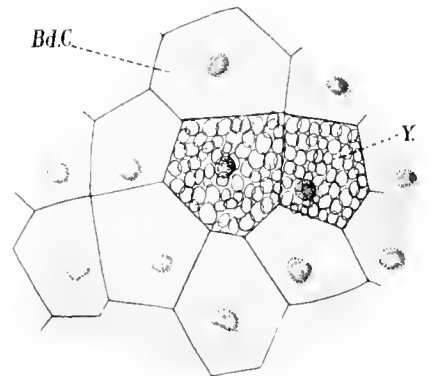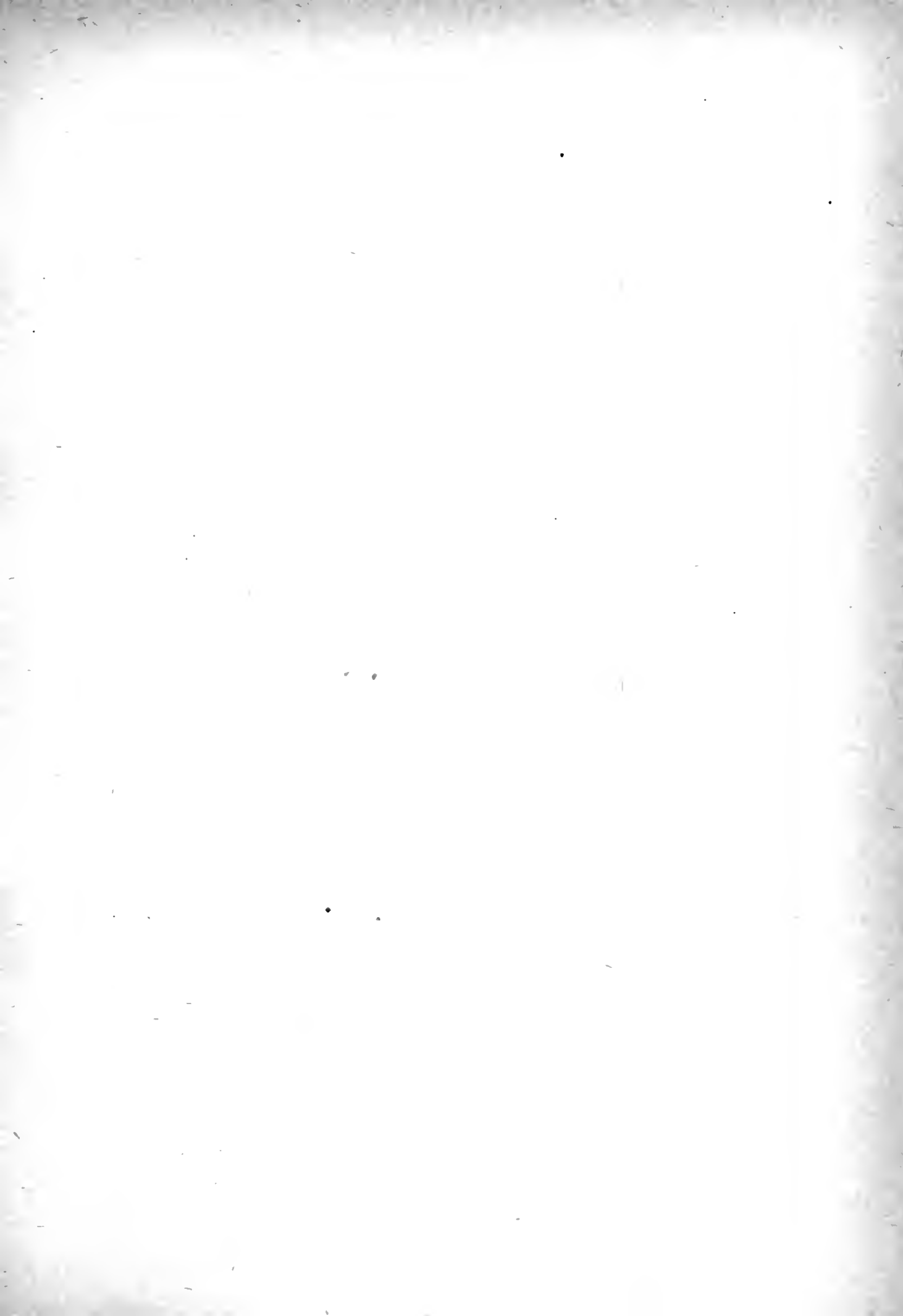
Plate XXXI.

Figs. 49–55. Serial transverse sections through the embryo in the invagination stage. In the most anterior section the germinal area (*G. D.*) is traversed, and in Fig. 53 the shallow depression in the middle of the invaginate area is cut through. In Fig. 54 (*G. D.*) we see the forward extension of the invaginate cells and the first trace of the thoracic-abdominal plate. The distinction between the primary yolk cells (Figs. 49, 52, 53–55) and the invaginate wandering cells (*b*, *b²⁻⁵*, Figs. 52–54) and their product, which now begin their migrations, is very plainly shown. In Fig. 50, which cuts the shallow pit at the surface of the invaginate area, we see the amœboid cells with large granular nuclei making their way from the bottom of the pit into the depths of the yolk. Figs. 49, 52–55, ×115. Figs. 50, 51, ×291.

REFERENCE LETTERS.

b, *b²-b⁵*, in-wandering cells derived from the invaginate cells and their products.
Ch., egg capsule or shell.
Ep., ectoblast.
G. D., embryonic area.
I. C., invaginate cell.
Ig., pit formed by the invagination.
Y. B., yolk ball.
P. Y. C., primary yolk cell.
Y. S., yolk sphere.

Plate XXXI.

Fig. 49.

Ep

Y.C.

Ch.

Fig. 50.

Y.S

b.⁴

b.³

Ep.

lg.

Ch

Fig. 51.

I.C.

Ch.

lg.

Ep.

Fig. 52.

Ep.

Ch.

b

lg.

Fig. 54.

b.⁵

G.D.

Fig. 53.

Ep.

Y.B.

d.¹

b.²

lg.

Fig. 55.

Y.C.

Ep.

G.D.

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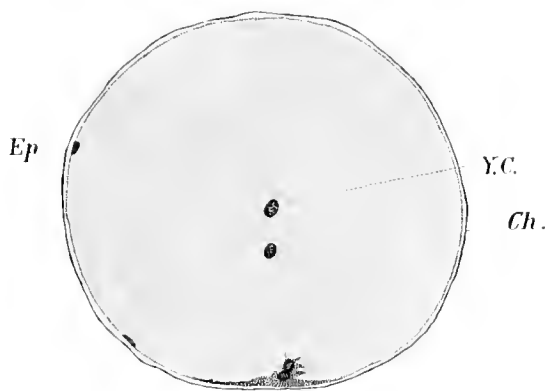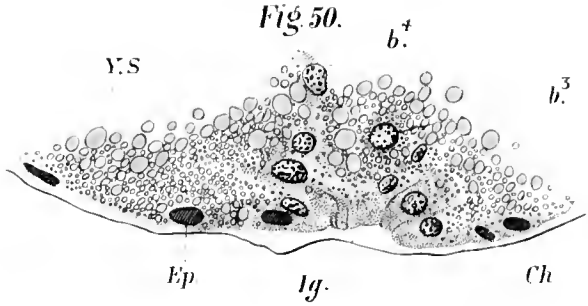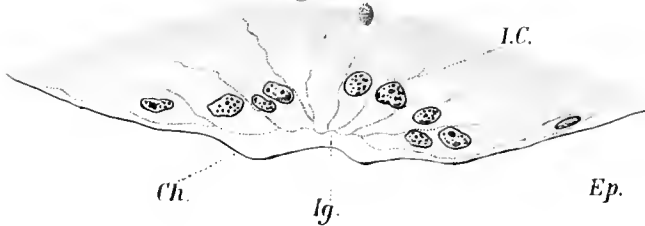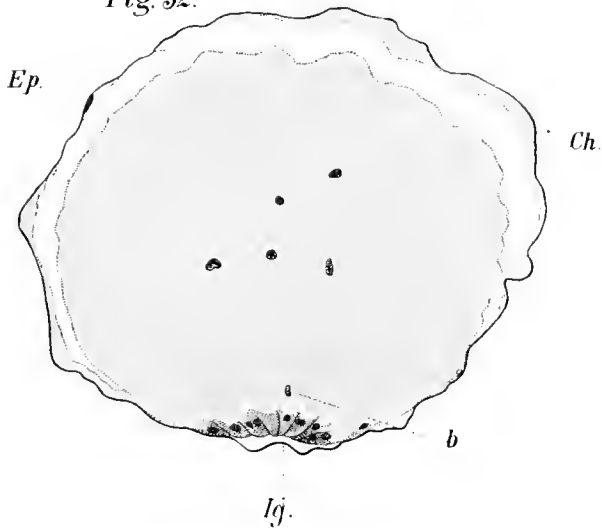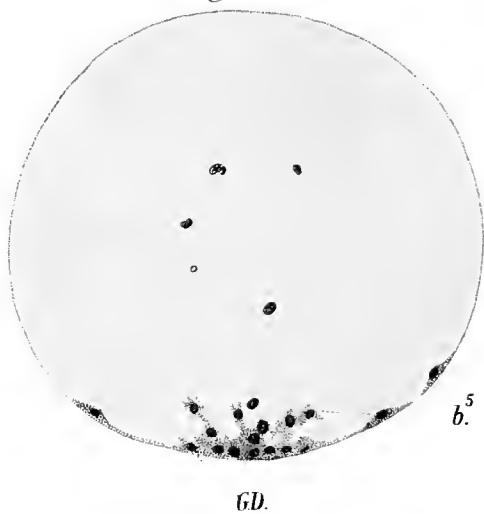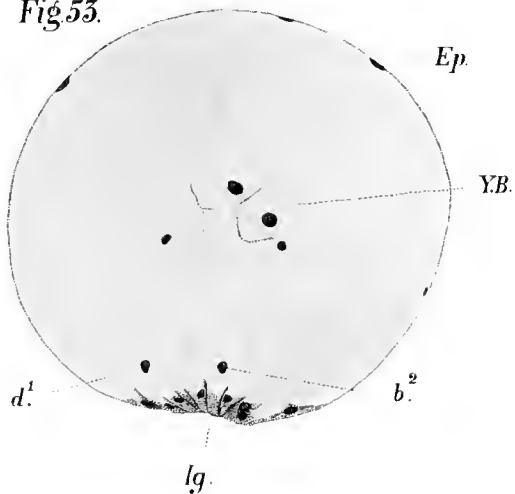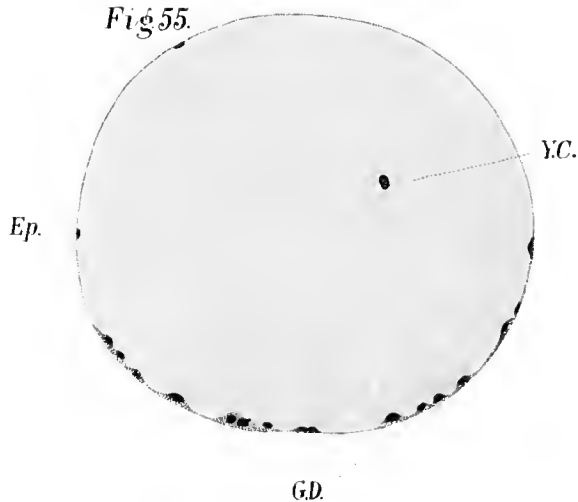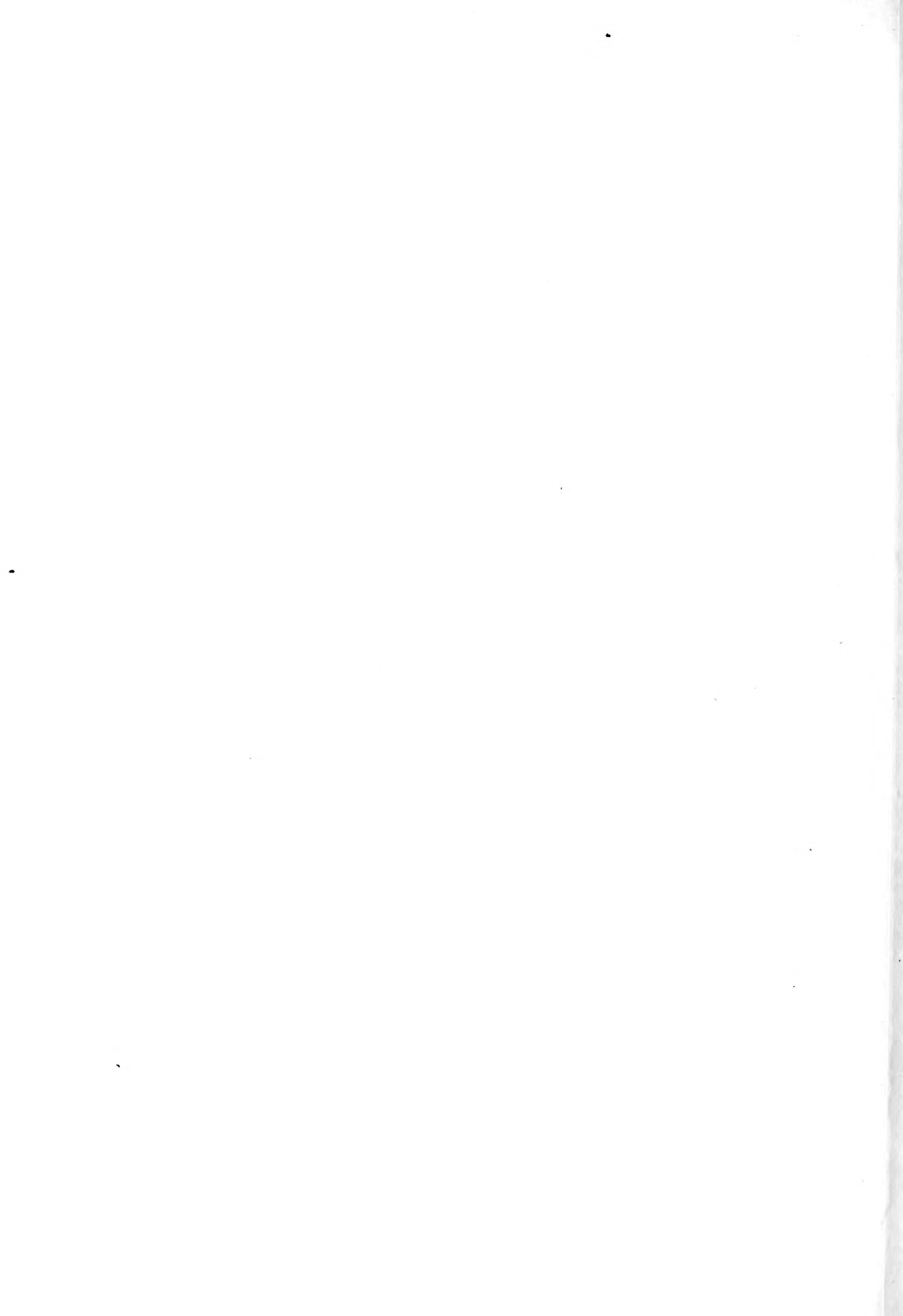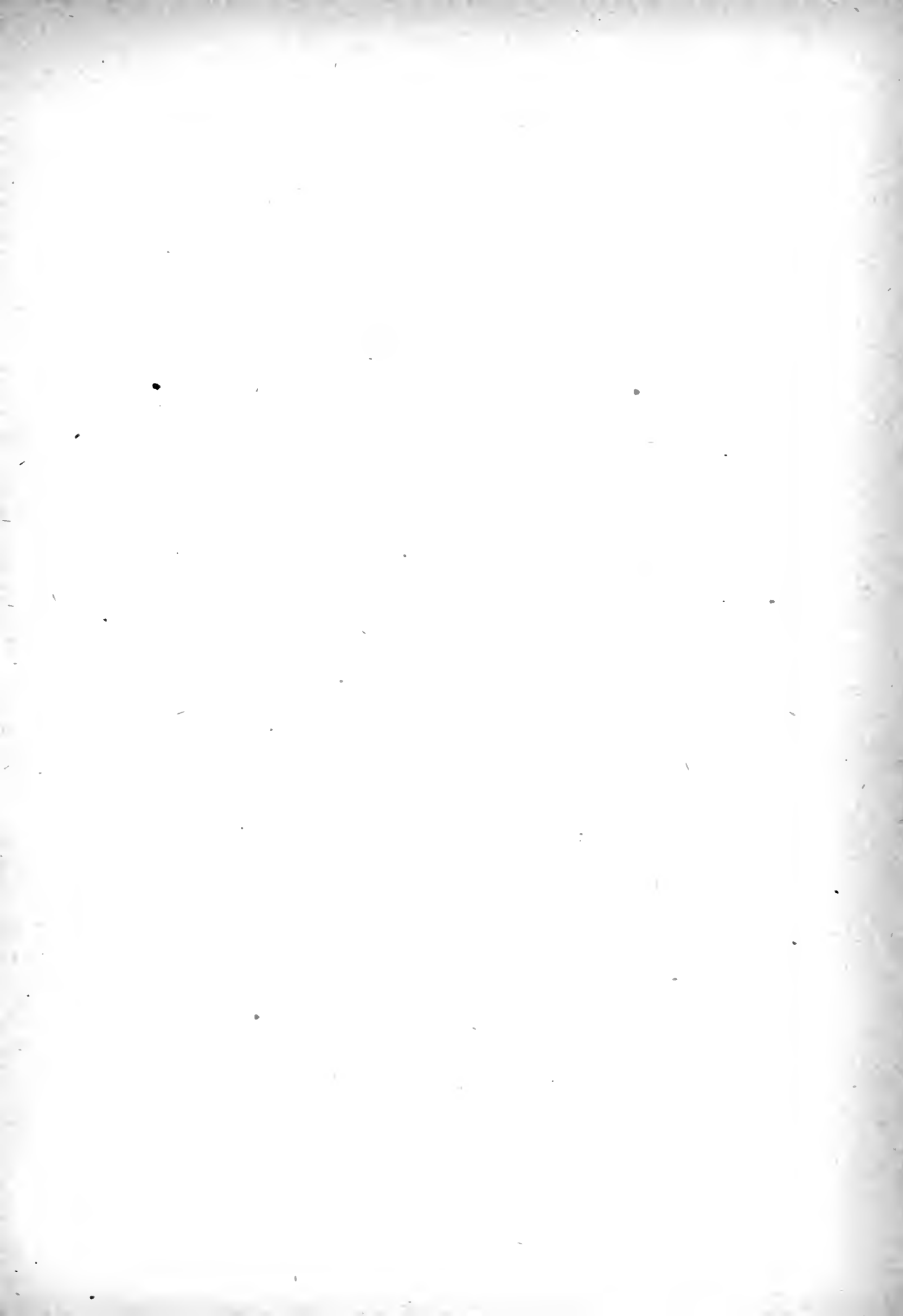
Plate XXXII.

Figs. 56, 59, 60. Longitudinal serial sections through the entire embryo in the stage shown in Fig. 58. Fig. 59 is median. The primary yolk cells ($P. Y. C.$, Fig. 60) can still be distinguished from the wandering cells derived from the invagination ($S. Y. C.$, Fig. 60). In Fig. 59 a primary yolk cell ($P. Y. C.^1$) is in the metakinetic stage of division. Traces of the primary segmentation of the yolk are still present, and the secondary yolk segmentation is very marked in the neighborhood of the wandering cells. Where the shell ($Ch.$) is not removed it is seen to be considerably distended and to have epiblastic cells sticking to it, showing the close adherence which normally exists between the egg membranes and the egg. ×115.

Fig. 57. Section through egg, cutting germinal disk just before invagination. Twenty and one-half hours older than yolk-pyramid stage seen in Fig. 15. ×73.

Fig. 58. Surface view of embryo after the appearance of the thoracic-abdominal plate and the optic disks. The shallow depression which marked the invaginate area has disappeared. Its approximate position is indicated by $Ig.$ Compare $Ig.$, Fig. 59. ×291.

REFERENCE LETTERS.

$Ab. P.$, ventral plate.
$Ch.$, eggshell.
$Ep., Ep.^1$, ectoderm.
$G. D.$, germinal disk.
$Ig.$, pit of invagination.
$L. Cd.$, lateral ventral bands.
$O. D.$, optic disk.
$P. M.$, wandering cells, seen below surface, coming off from ventral plate.
$P. Y. C., P. Y. C.^1$, primary yolk cells.
$Sep.$, yolk cleavage plane.
$S. Y. C., S. Y. C.^1$, wandering cells derived from the invaginate cells and their products.
$T. Cd.$, cell area uniting optic disks.
$Y. B.$, yolk ball.
$Y. C.$, primary yolk cell.

Plate XXXII

Fig.56.
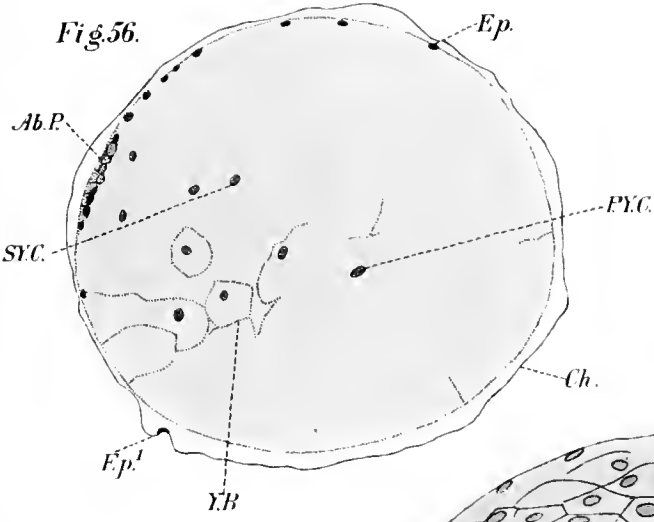
Fig.57.

Fig.58.

Fig.59.

Fig. 60.

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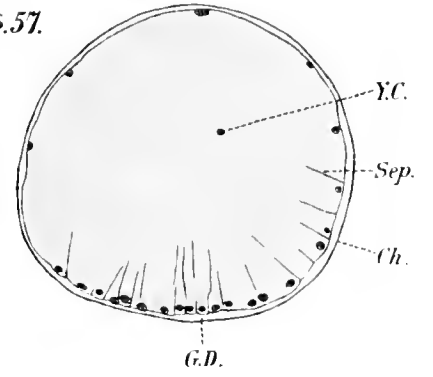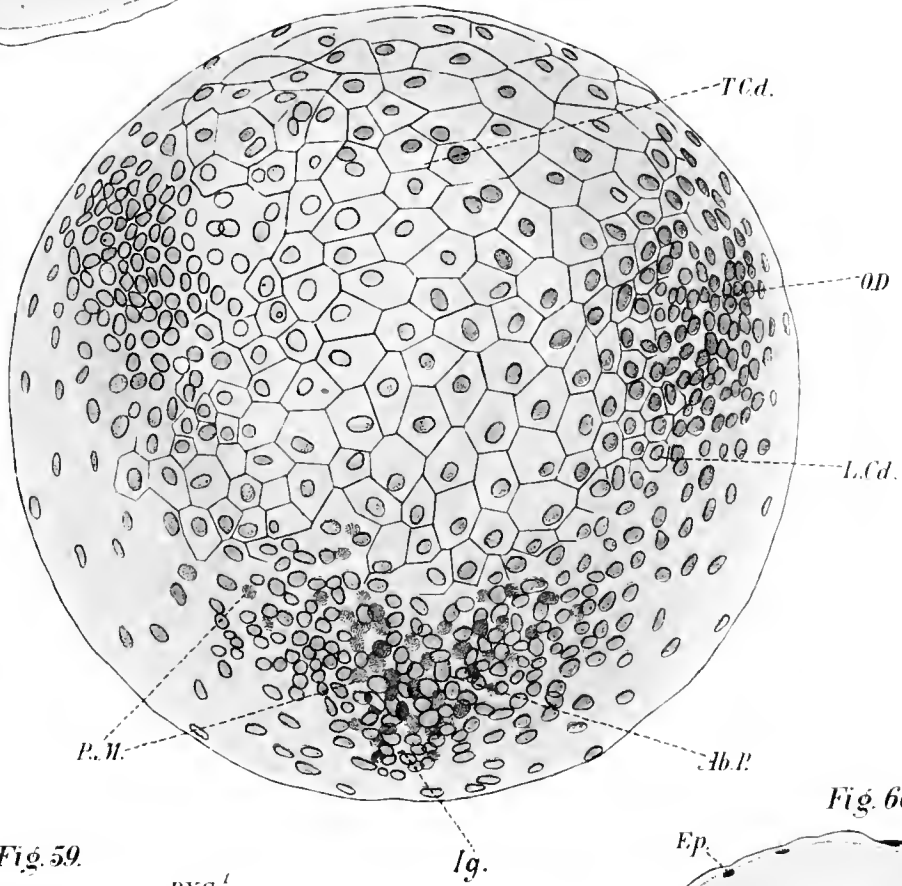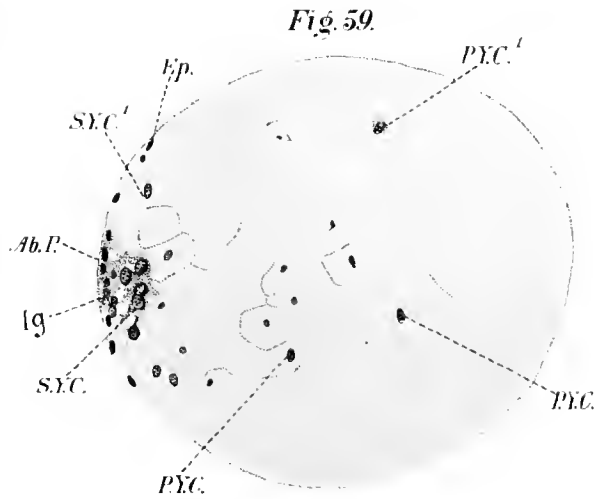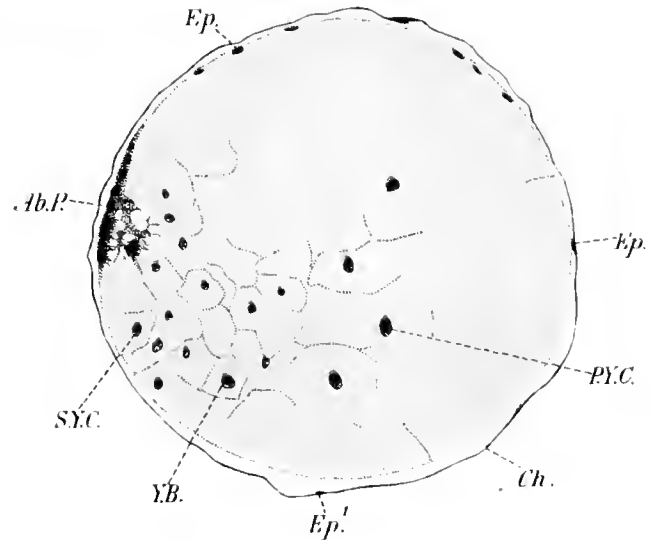
PLATE XXXIII.

FIGS. 61, 62, 68, 69. Transverse sections of embryo in stage shown in Fig. 58, Pl. XXXII. Fig. 61 cuts the thoracic-abdominal plate, and Figs. 68 and 69 involve the optic disks. Primary yolk cells (*P. Y. C.*, Fig. 69) are still plainly distinguishable. ×115.

FIG. 63. Portion of median longitudinal section of the same stage. The larger and clearer nuclei in the invaginate area represent the mother cells of both mesoderm and endoderm. The yolk ball or secondary yolk segment is characteristic of this stage. ×291.

FIGS. 64–67. Consecutive transverse sections of left optic disk of same stage before any thickening has occurred. The most anterior section is represented in Fig. 64. ×291.

REFERENCE LETTERS.

Ab. P., ventral plate.
Ch., eggshell.
Ep., ectoderm.
Ig., invaginate cavity.
L. Cd., lateral ventral cord.
O. D., optic disk.
P. Y. C., primary yolk cells.
Sep., yolk cleavage plane.
S. Y. C., in-wandering cells derived from ventral plate.
Y. B., yolk ball.

Plate XXXIII

Fig. 61.

Ab.P.

Ch.

P.Y.C.

P.Y.C.

Ep.

Fig. 62.

L.Cd.

P.Y.C.

Ch.

Ep.

Fig. 63.

S.Y.C.

S.Y.C.

lg.

Y.B.

Ep.

Y.S.

Ch.

Fig. 64.

O.D.

Ch.

Y.S

Fig. 65.

Fig. 66.

Fig. 67.

Ep.

Fig. 69.

T.C.d.

O.D.

O.D.

P.Y.C.

Sep.

Fig. 68.

O.D.

Y.B.

P.Y.C.

Ep.

Sep.

Ep.

ALPHEUS
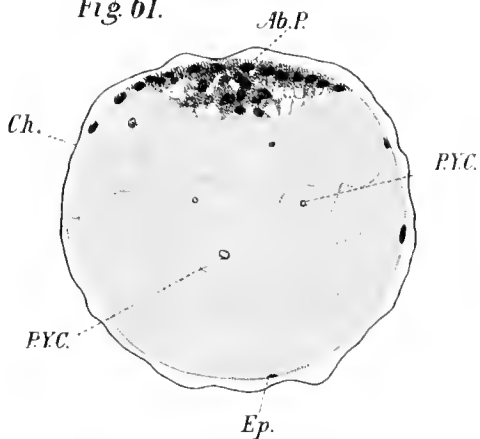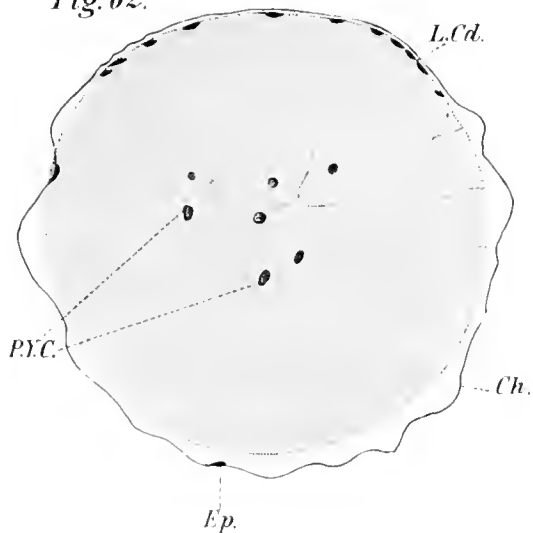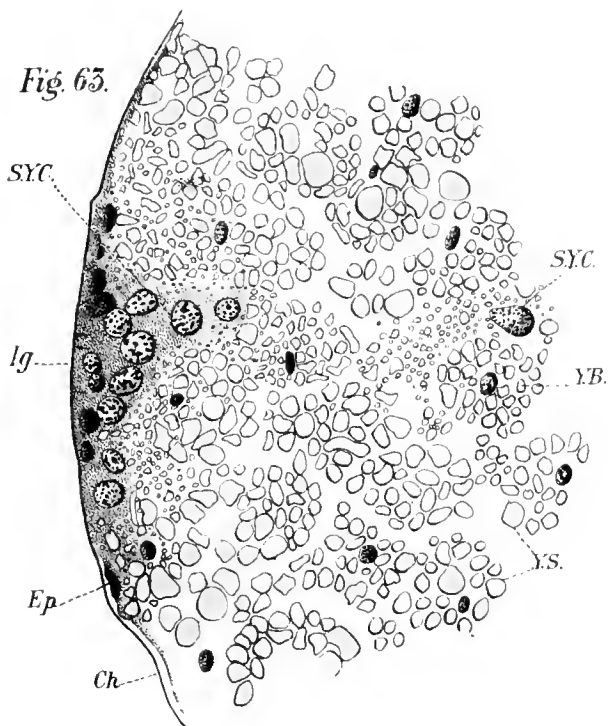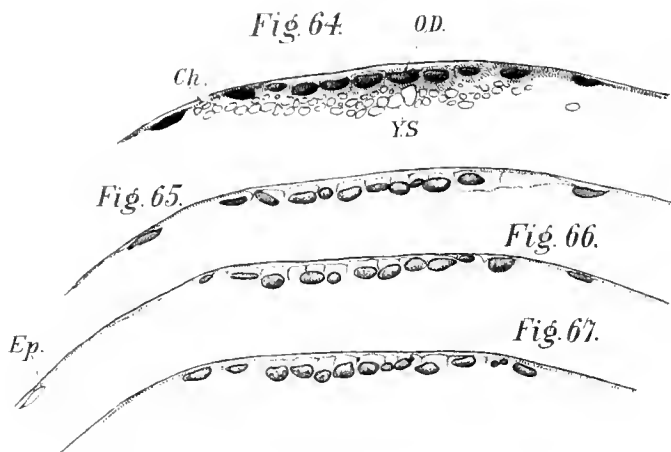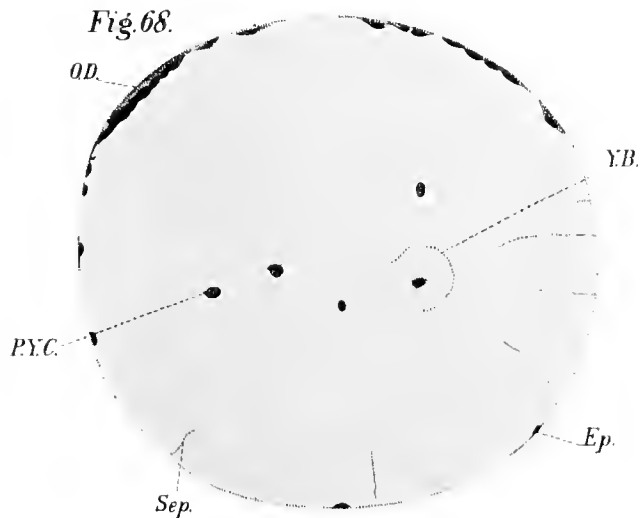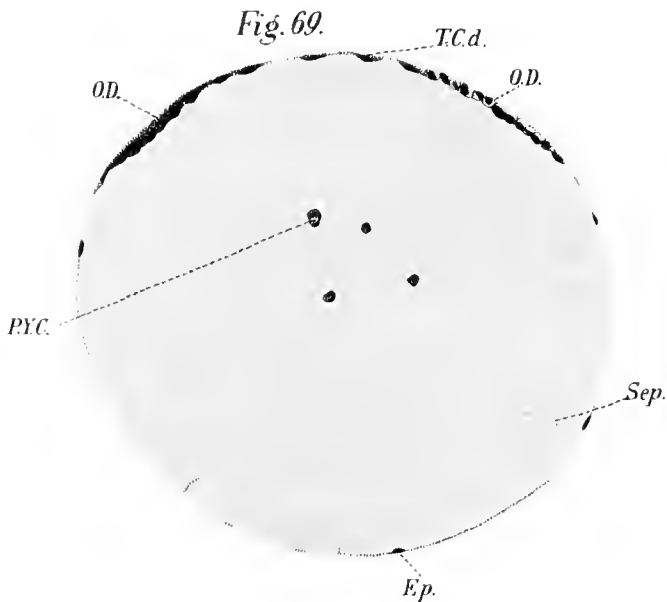
Plate XXXIV.

(Stage IV.)

Figs. 70, 71, 73, 74. Longitudinal serial sections of the entire embryo in the stage shown in Fig. 72. In Fig. 73 the plane of section is nearly median. The primary yolk cells are now generally indistinguishable from the other wandering cells. Compare cut, Fig. 11, which shows the distribution of the wandering cells at this stage. ×115.

Fig. 72. Surface view of embryo in Stage IV. Rudiments of the mandibles and first pair of antennæ are present. An area of cell ingrowth in the optic disks (*C. M.*) is characterized by the large size of the nuclei. From them and their products the optic ganglion takes its origin. Some of the surface cells on either side of the middle line were accidentally cut away. ×291.

REFERENCE LETTERS.

A. (I.), proliferating center of first antenna.
Ab. P., ventral plate.
C. M., proliferating area of optic disk.
Ep., ectoderm.
L. Cd., lateral ventral cord.
Md., proliferating center of mandible.
O. D., optic disk.
T. Cd., transverse cord uniting optic disks.
Y. B., yolk ball.
Y. C., *Y. C.¹*, wandering cells.

Plate XXXIV.

Fig.70.

O.D.

Y.C.

Ep.

Fig.71.

L.Cd.

O.D.

Y.C.¹

Ep.

Fig.72.

T.Cd.

C.M.

O.D.

A(1).

L.Cd.

Md.

Ab.P.

Fig.73.

Ab.P.

Y.C.

Y.C.

Ch.

Ep.

L.Cd.

Fig.74.

Ab.P.

Y.C.

Ep.

Y.C.

Y.B.

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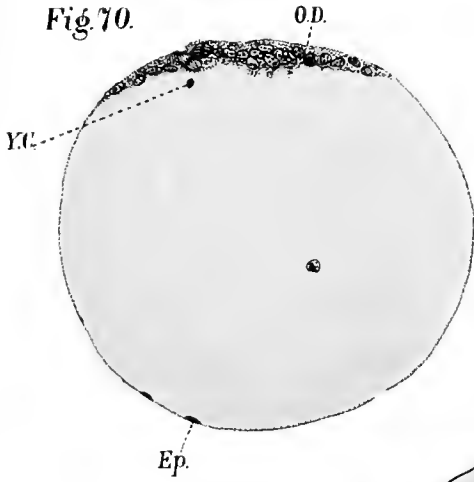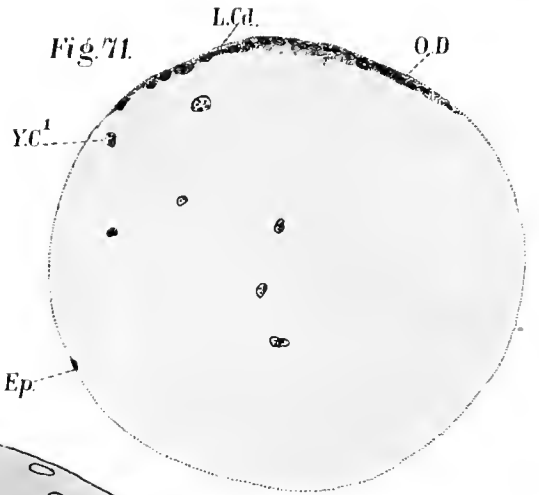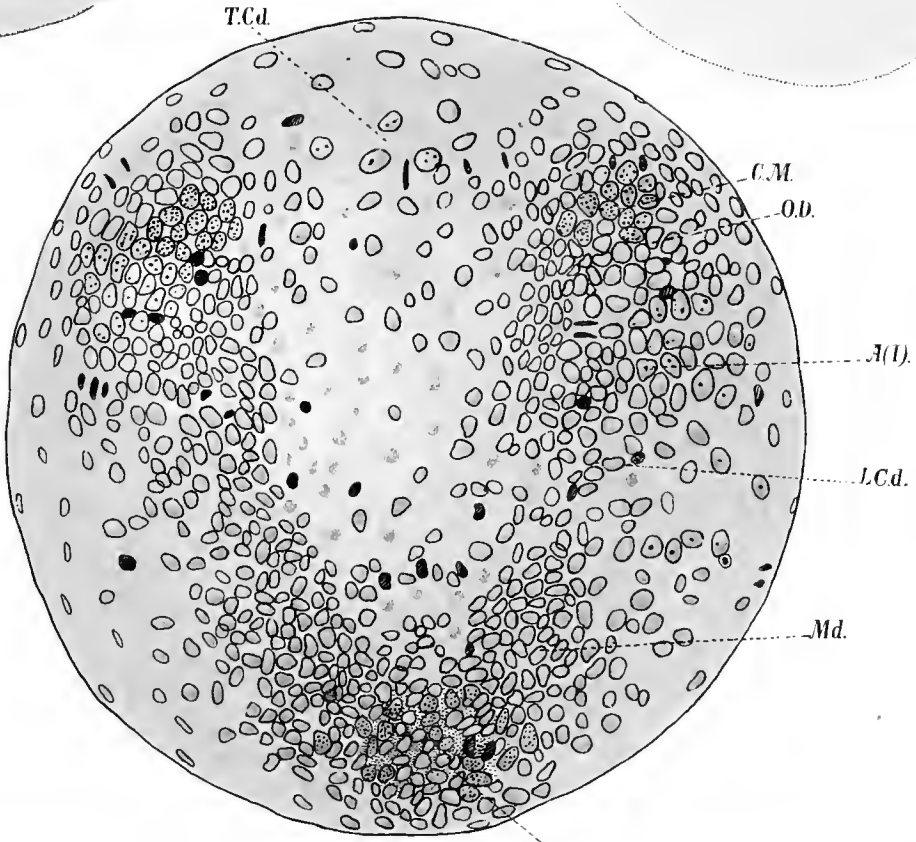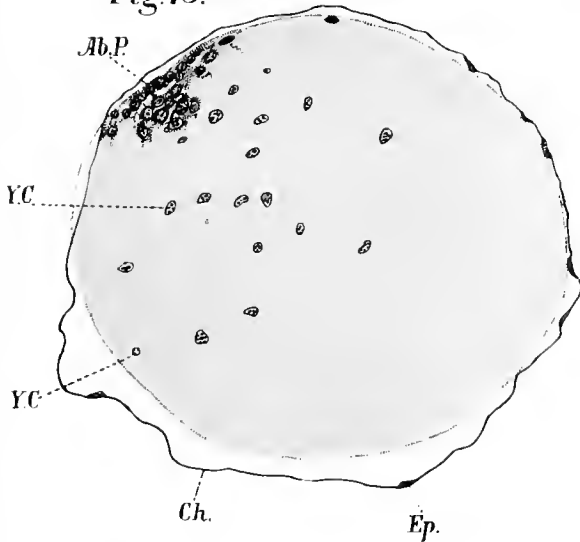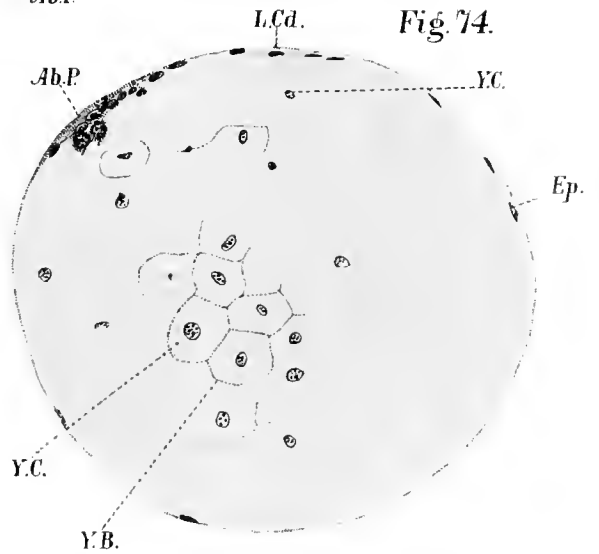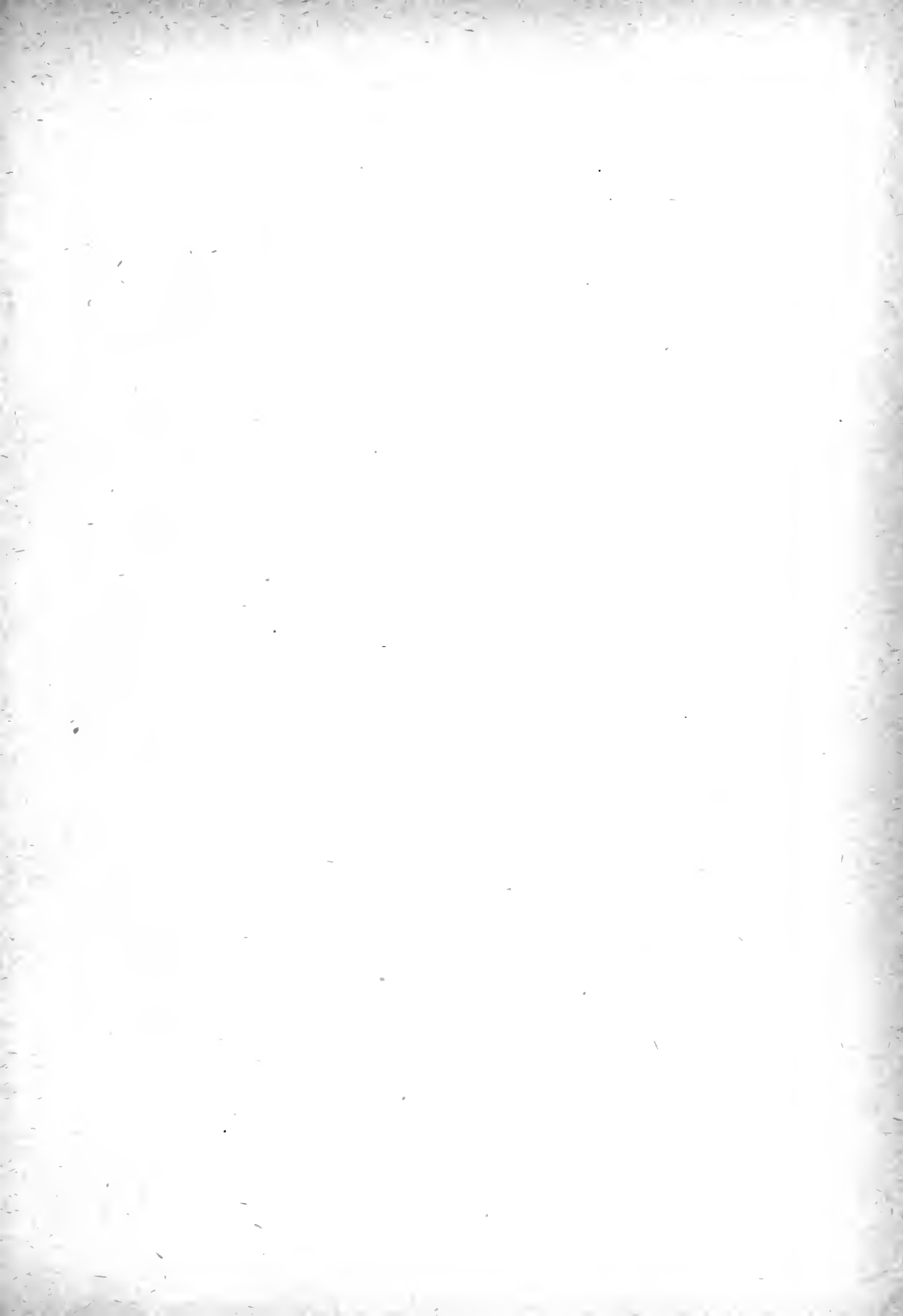
Plate XXXV.

(Stage IV.)

Fig. 75. Median longitudinal section ot the entire embryo. One of the wandering cells, which is approaching the surface of the egg opposite the thoracic abdominal plate, is in the process of division.   ×115.

Figs. 76–83. Consecutive serial transverse sections through the left optic disk of same, to illustrate the earliest stages in the thickening of the disks. The most posterior section (Fig. 83) cuts the first pair of antennæ.   ×291.

Fig. 84. Transverse section through the middle of optic disks.   ×115.

Fig. 85. Transverse section through thoracic abdominal plate, showing the multiplication of surface cells, by which the plate is increased, and cells below the surface (Y. C.) which pass into the yolk.   ×291.

REFERENCE LETTERS.

A. (1), first antenna.
Ab. P., ventral plate.
Ch., eggshell.
C. M., proliferating area of optic disk.
ec., ec.$^{1-3}$, ectodermic cells of ventral plate (Fig. 85).   ec., (Fig. 80) ectodermic cell of optic disk.
Ep., ectoderm.
O. D., O. D^{1}., optic disks.
Ret., protoplasmic reticulum.
T. Cd., transverse cord.
Y. B., yolk ball.
Y. C., Y. C.$^{1-2}$, wandering cells.
Y. S., yolk sphere.

Plate XXXV

Fig.75.

Ab.P.   Y.C.'   T.Cd.

Y.C.

Y.C.²

Fig.76.

Fig.77.   Ch.

O.D.

Fig.78.   Y.S.   Ep.

Fig.79.

C.M.

Fig.80.
(O.D.' Fig.84)   ec.

Fig.84.

O.D.'   O.D.

Y.B.   Ch.

Y.C.

Fig.81.

Ep.

Fig.82.   A.D.

Fig.83.

Fig.85.   ec' ec²   ec³
            ec.
Ch.

Ep.

Ret.

Y.S.

Y.C.

ALPHEUS

Plate XXXVI.

(Stage V.)

Figs. 86, 87. Parts of longitudinal sections of embryo seven or eight hours older than that shown in Fig. 72. The optic disk (*O. D.*) is cut in Fig. 86, and in Fig. 87 its inner part is involved, with the outer border of the thoracic abdominal plate. There is no sharp demarcation between the protoplasm and the yolk, as is indicated by the dotted lines under the embryonic layers. ×291.

Figs. 88–89. Longitudinal serial sections through the entire embryo, somewhat younger than the last, and six hours older than that represented in Fig. 72. The optic disk is sectioned in Fig. 90 through its central proliferating area (*C. M.*), and the rudiments of the three naupliar appendages appear in Fig. 89. ×115.

Fig. 91. Transverse section cutting optic disks of embryo about nineteen hours older than that of Fig. 72 and twelve hours older than that represented by Figs. 86, 87. Wandering cells (*Y. C.¹*) have traveled to remote parts of the surface, and karyokinetic figures (*Y. C.²*, Fig. 89) prove that they are in active division. ×115.

REFERENCE LETTERS.

A. (*I*), rudiment of first antenna.
A. (*II*), rudiment of second antenna.
Ab. P., ventral plate.
App., area of appendages.
Ch., eggshell.
C. M., proliferating area of optic disk.
ec., migrating ectoblast cell.
Ep., ectoderm.
Md., rudiment of mandible.
O. D., optic disk.
S., product of degenerating chromatin.
St. A., sternal area.
T. Cd., transverse cord.
Y. C., *Y. C.¹⁻³*, wandering cells.
Y. S., yolk sphere.

Plate XXXVI

Fig.86.
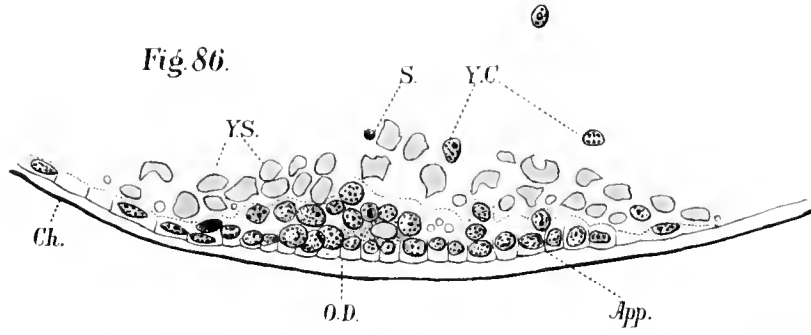
Fig.87.
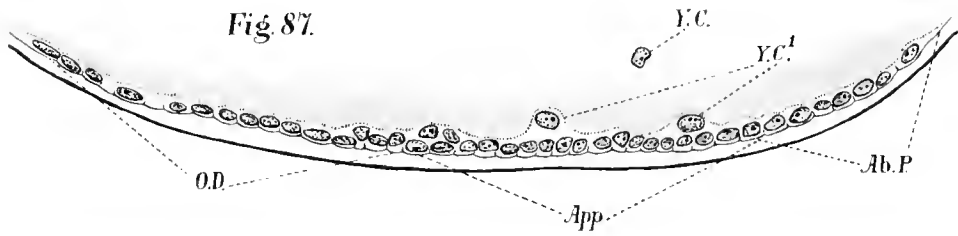
Fig.88.

Fig.90.

Fig.89.

Fig.91.

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ALPHEUS
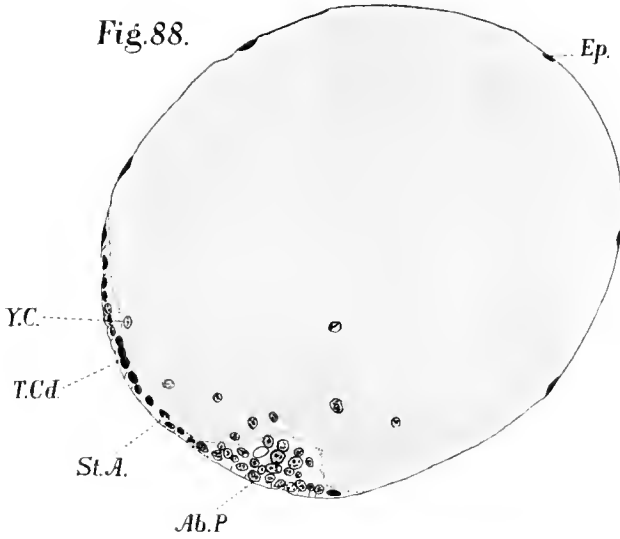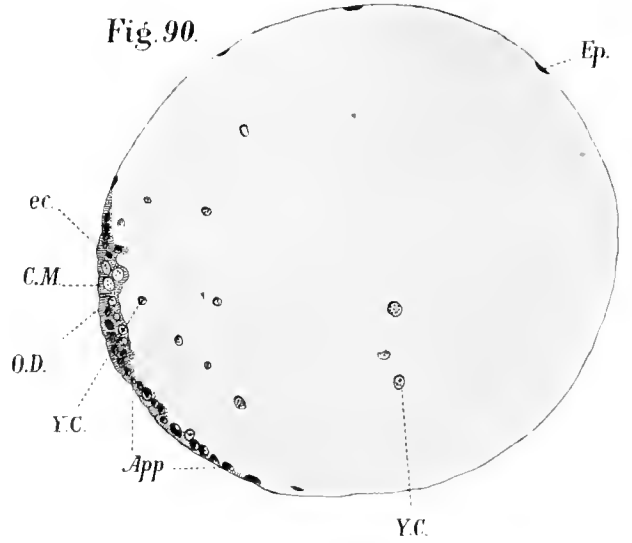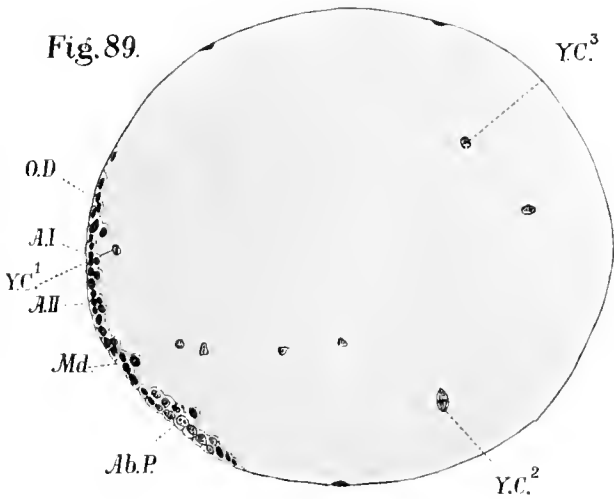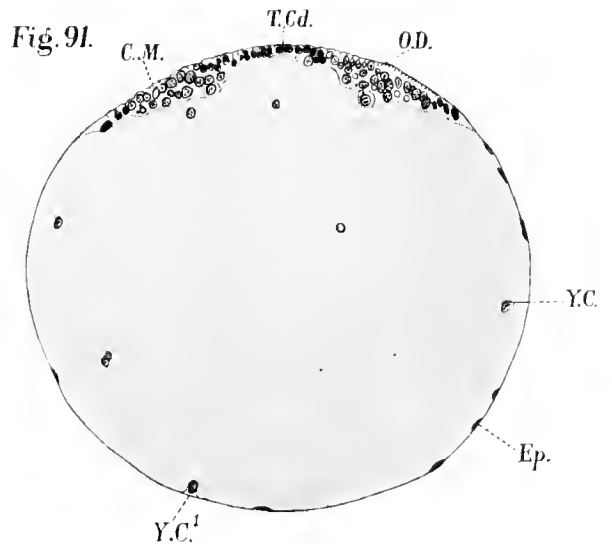
PLATE XXXVII.

(Stages V–VI.)

FIG. 92. Part of transverse section, showing the structure of the keel-shaped ventral plate, and indicating the origin of mesoblast from the surface of the latter. ×291.

FIG. 93. Surface view of embryo with buds of naupliar appendages. The intermediate area (*St. A.*) is covered by a single layer of ectoderm. The invagination of the mouth has not yet appeared. Some nuclei of cells which lie immediately below the surface, especially in the thoracic abdominal plate region, are represented. ×291.

FIGS. 94–95. Transverse sections of embryo, belonging to the same series as Fig. 92, to illustrate the structure of the thickening optic disks. Degenerating nuclear products ($s.^1$, $s.^2$, Fig. 95) are present, and two cells are seen delaminating side by side in Fig. 95.

REFERENCE LETTERS.

A. (*I*), rudiment of first antenna.
A. (*II*), rudiment of second antenna.
Ab. P., ventral plate.
C. M., proliferating area of optic ganglion.
Ect., ectoderm.
Md., rudiment of mandible.
Mes., wandering cells (mesoblast) attached to ectoderm.
O. G., rudiment of optic ganglion.
O. D., optic disk.
$s.^1$, $s.^2$, products of degenerating chromatin.
St. A., sternal area.
T. Cd., transverse cord uniting optic disks.
Y. C., wandering cell; *Y. C.*^{1}, wandering cell degenerating.

Plate XXXVII.

Fig. 92.

AbP.

s.¹

Ect.

Fig. 93.

TCd.

O.D.

C.M.

O.G.

A(I).

A(II).

St.A.

Md.

AbP.

Fig. 94.

Y.C.

Y.C.¹

Mes.

C.M.

Fig. 95.

s.²

s.¹

O.G.

Mes.

Ect.

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ALPHEUS
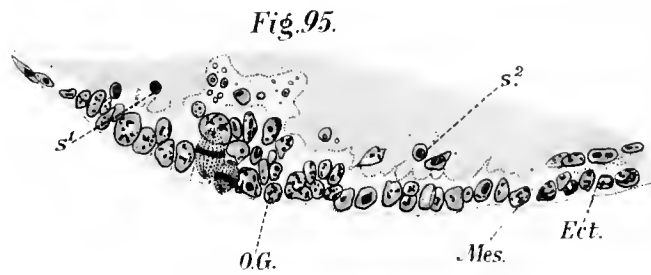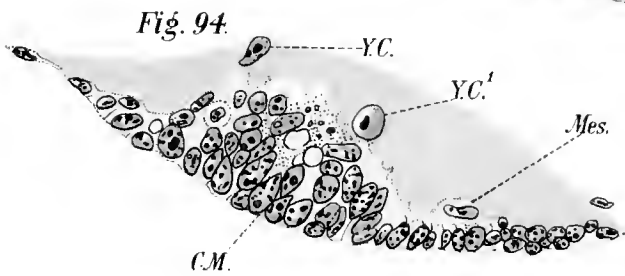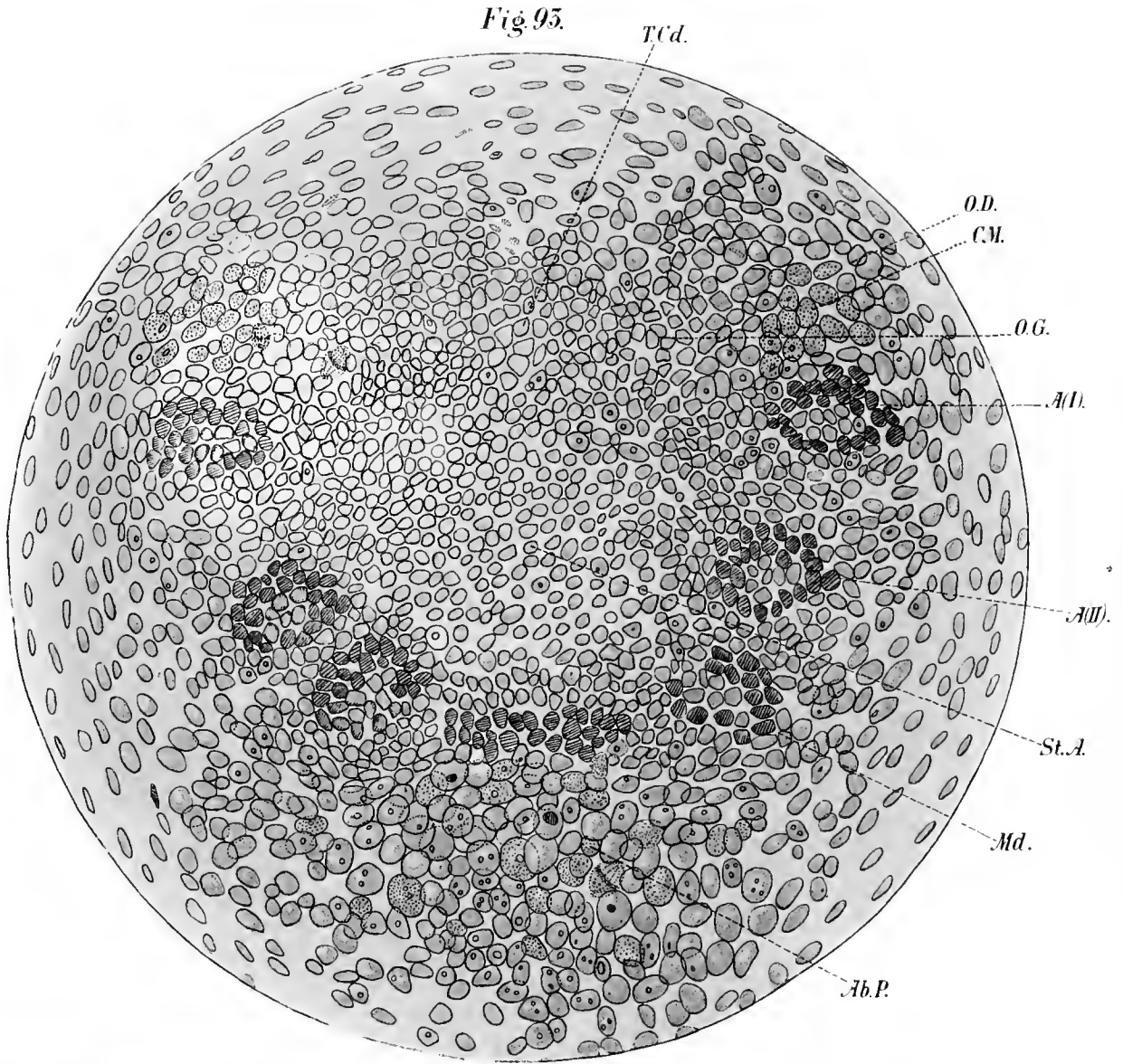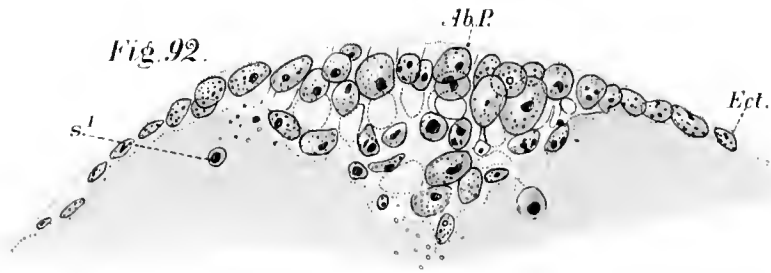
Plate XXXVIII.

(Stage VI.)

Figs. 96–97. Longitudinal sections through the embryo shown in Fig. 93. The more lateral of the two, Fig. 96, cuts the middle of the optic disk, and shows the large cells of the proliferating area, one of which is caught in the act of dividing. Fig. 97 cuts the inner portion of the optic disk and the ventral plate on a level with the budding mandible (Md.). ×295.

Figs. 98–100. Longitudinal serial sections through an embryo six hours older, from the same batch of eggs. The mouth (Fig. 98, Std.) has already appeared. The mesoblast, formed chiefly from wandering cells, is well established on either side of the middle line of the body, and is well seen under the folds of the appendages (Fig. 100, Mes.) into which it extends. The mesoblast represented by the lower layers of the ventral plate is still being increased by the migration of cells from the surface of this plate, as is indicated by cell ec., which is interpreted as a superficial cell about to migrate (in Fig. 98). In Fig. 100 a cell at the surface of the optic disk is in the act of delaminating. Large numbers of degenerating cells and their products are now encountered (S. C., s.). ×295.

REFERENCE LETTERS.

A. (I), bud of first antenna.
A. (II), bud of second antenna.
Ab., Ab. P., Ad. P., ventral plate.
App., area of appendages.
C. M., proliferating area of optic disk.
ec., ec.¹, migrating and dividing cells at *surface* of ventral plate.
Ect., Ep., ectoderm.
Md., rudiment of mandible.
Mes., mesoderm.
O. C., optic ganglion.
O. D., optic disk.
s., s.¹⁻², products of degenerating chromatin.
S. C., S. C.¹⁻², cells in various stages of degeneration.
St. A., sternal area.
Std., stomodæum.
T. Cd., Transverse sheet of ectoderm uniting optic disks.
Y., Y. S., yolk spheres.

Plate XXXVIII.

Fig. 96.

Fig. 97.

Fig. 98.

Fig. 99.

Fig. 100.

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ALPHEUS
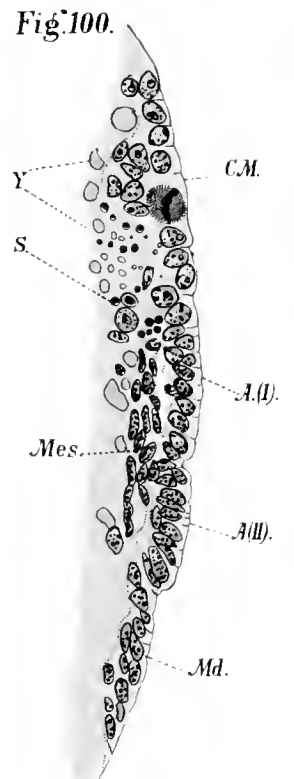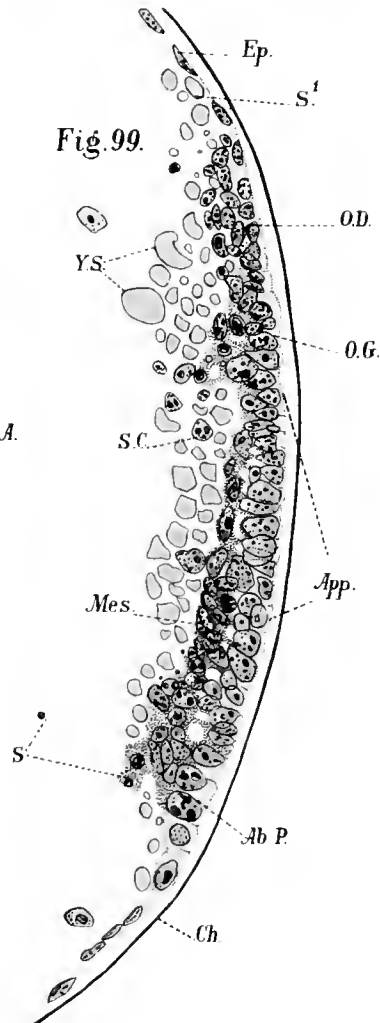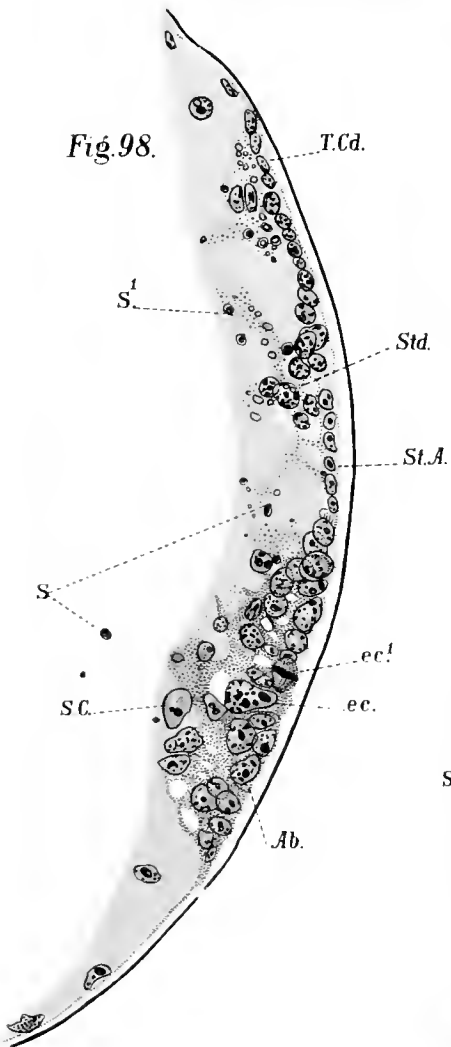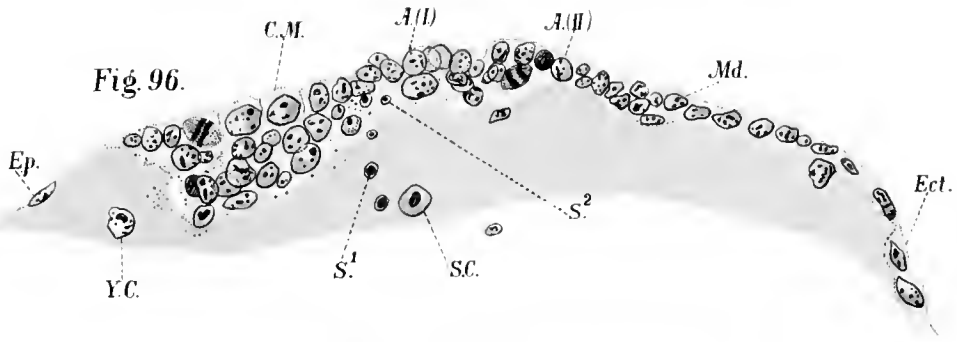
PLATE XXXIX.

(Stage VI.)

FIGS. 101–105. Serial longitudinal sections of early nauplius embryo, twelve and one-half hours older than that represented by Figs. 98–100, Pl. XXXVIII, and eighteen and one-half hours older than the stage represented in Fig. 93, Pl. XXXVII. The thoracico-abdominal fold or papilla is now forming, apparently by the ingrowth of the surface ectoblast (Fig. 104, *Ab. C.*). Fig. 102 is exceptionally favorable in showing the undoubted delamination of two cells standing side by side at the surface of the optic disk (*ec.*). The common radial division of the ectoderm of the thoracico-abdominal region and other parts is illustrated by the cell *ec.*[1] of the same section. Fig. 105 cuts the straight tubular stomodæum. ×295.

FIG. 106. Longitudinal median section of embryo several hours older than the last. A deep, narrow, transverse furrow (*Ab. C.*) now abruptly separates the thoracico-abdominal papilla from the sternal area lying between it and the stomodæum. ×291.

FIG. 107. Transverse section through the optic disks, from same stage. Cell delamination in this region is again met with. ×291.

FIG. 108. Longitudinal lateral section through entire egg, showing the distribution of wandering cells, and the relations of the embryo to the ovum. The eggshell is unnaturally distended. An inner molted membrane is present, as is better shown in Fig. 106 and Fig. 104, *M b.*

In Fig. 108 a large cell is seen at the surface, and below this a large cell followed by a row of similar cells. The first two cells possibly represent a budding ectoblast and mesoblast, and the rows of cells at the surface and below it are possibly derived from them. ×115.

REFERENCE LETTERS.

A. (*I*), bud of first antenna.
A. (*II*), bud of second antenna.
Ab., thoracico-abdominal papilla.
Ab. C., transverse superficial furrow by which fold of the thoracico-abdominal process is formed.
A. Y. S., products of degenerating chromatin.
B. Z., budding zone.
Ch., eggshell.
C. M., proliferating area of optic disk.
Cl. S., cells on ventral side of yolk next to optic disks, probably representing mesoblast derived from wandering cells.
ec., *ec.*[1], dividing ectoblastic cells.
Ect., *Ep.*, ectoderm.
M., wandering cell at surface behind thoracico-abdominal fold (Fig. 108).
Mb., embryonic molt.
Md., rudiment of mandible.
Mes., mesoblast.
O. D., optic disk.
O. G., optic ganglion.
O. S. G., brain.
Pd., proctodæum.
S., *S. S.*, products of degenerating chromatin.
S. C., degenerating cells.
St. A., sternal area.
Std., stomodæum.
Y., *Y. S.*, yolk.

Plate XXXIX
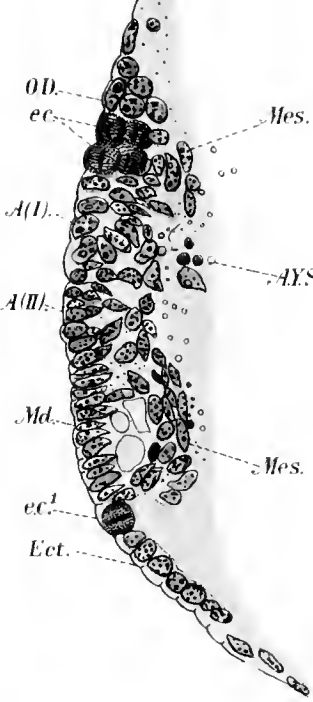
Fig. 101.   Fig. 102.   Fig. 103.   Fig. 104.
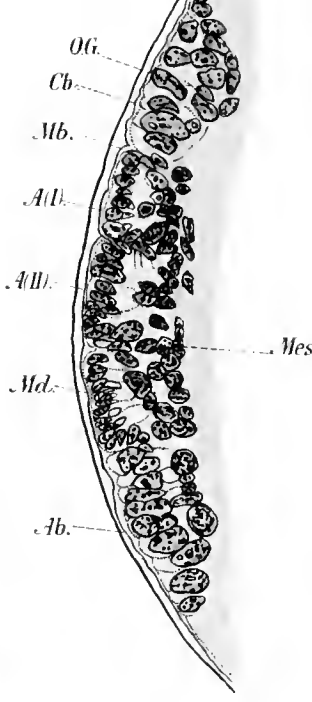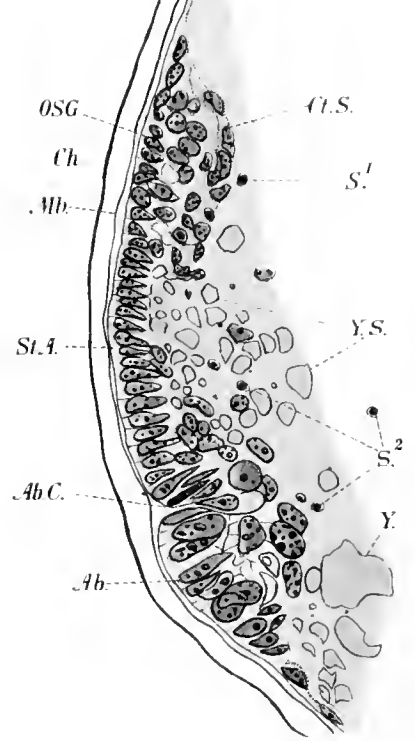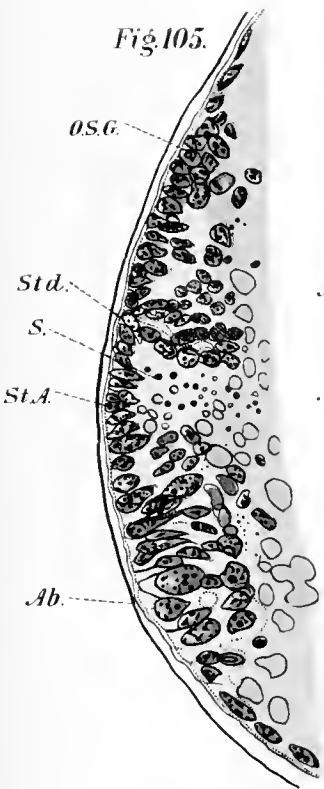
Fig. 105.   Fig. 106.   Fig. 107.   Fig. 108.

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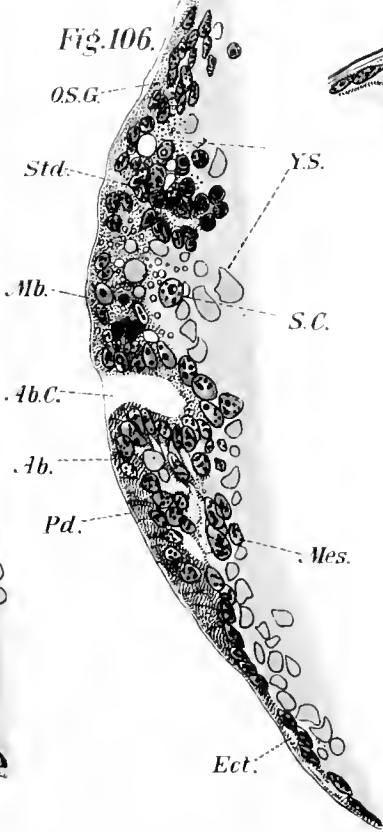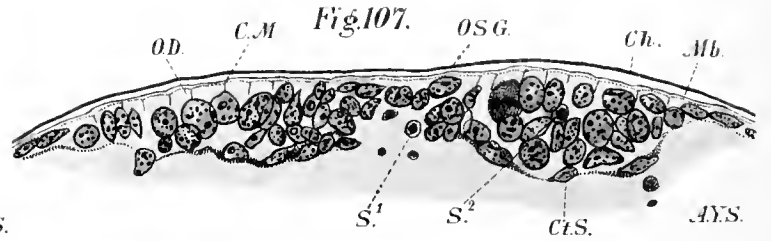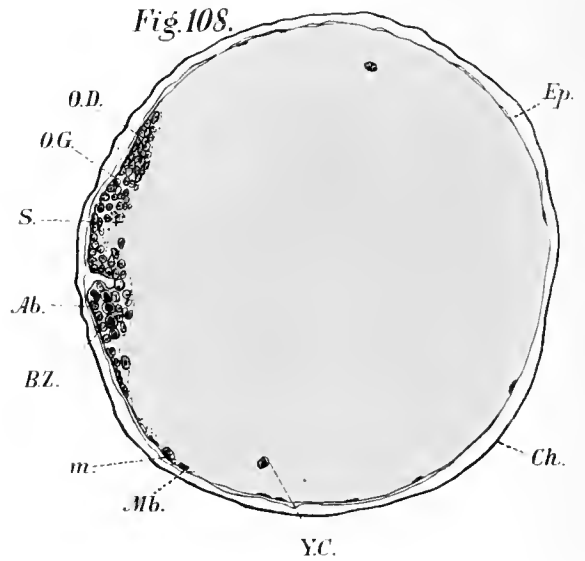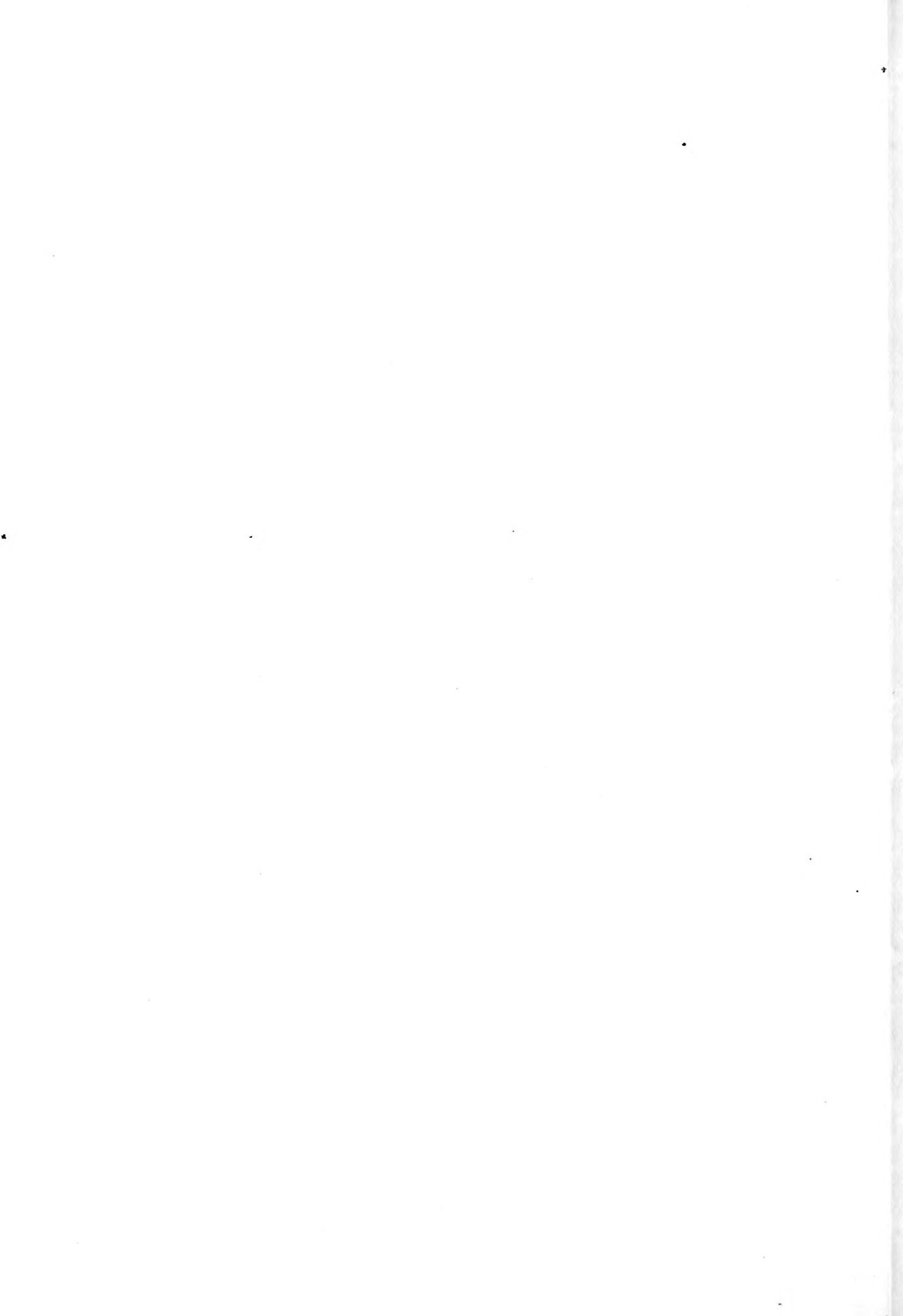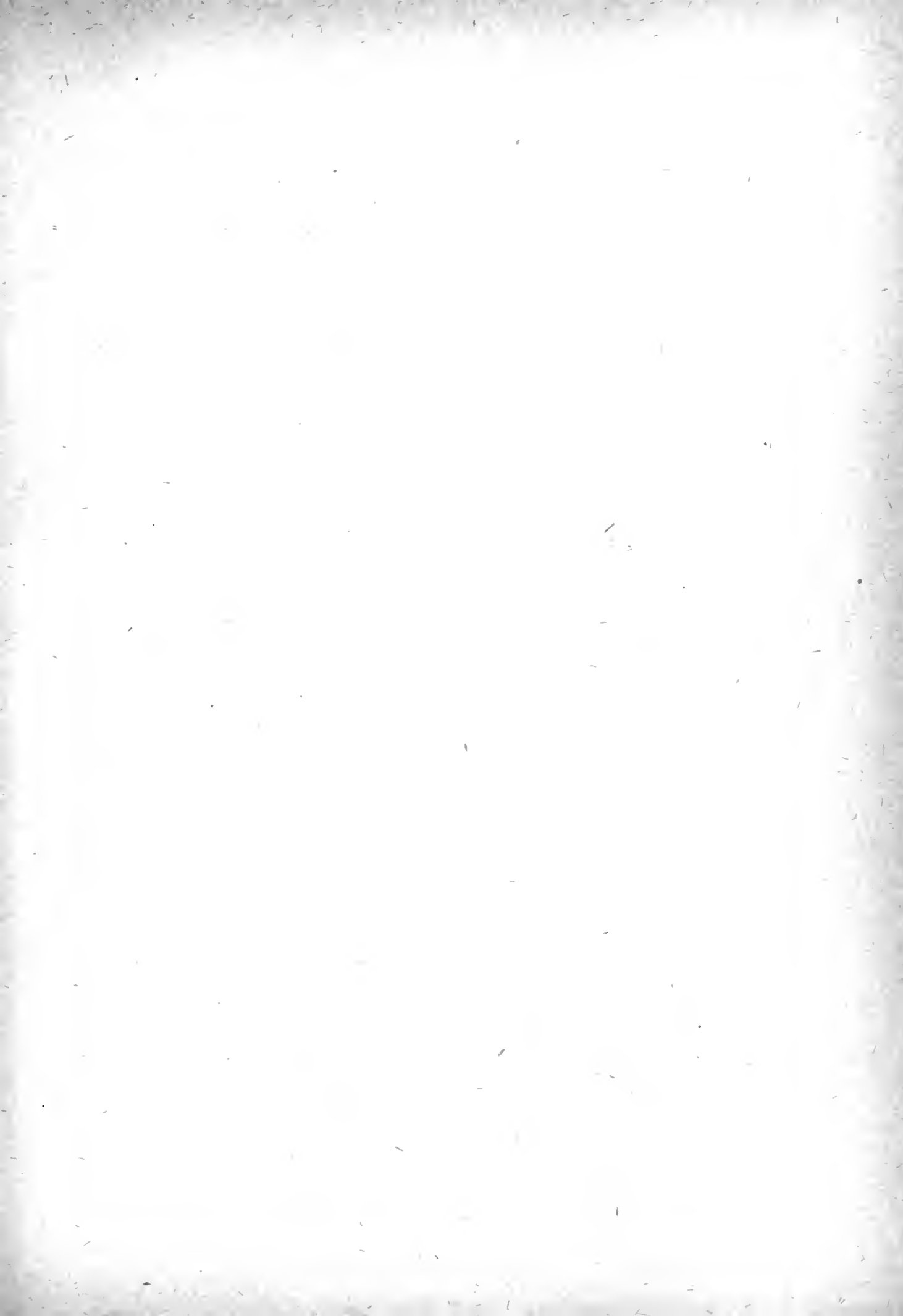
Plate XL.

(Stage VI.)

Fig. 109. Sketch of egg-nauplius. Anus not so clearly seen in surface view, as represented in this and the following figure. Mouth on a level with antennules. ×72.

Fig. 110. Sketch of older embryo. Appendages all bending backwards and inwards toward middle line. ×72.

Fig. 111. Egg-nauplius less developed than shown in Fig. 109, but from same batch of eggs. The position of the mouth, which is post-antennal from the first, is now on the middle line between the antennæ and the antennules. The probable position of the anus is indicated, but it could not be clearly seen. The bud which represents the endopodite of the antenna is just appearing on the right side. ×157.

Fig. 112. Oblique transverse section, through egg-nauplius of a common shore crab of Beaufort, North Carolina, probably *Sesarma*. ×286.

Fig. 113. Median longitudinal section, through a similar embryo. The egg membranes are not naturally shown. The yolk is diagramatically represented. Wandering cells occur in it (*Y. C.*), and in Fig. 113 degenerative products (*Deg.*) are met with. ×286.

REFERENCE LETTERS.

A., anus.
A. (I), antennal bud.
A. (I), antennular bud.
Ab., thoracico-abdominal fold.
Ch., eggshell.
Deg., degenerative cell products.
Ep., ectoderm.
Gl., ectoblast of neural plate.
H., mesoblast cells, forming rudimentary heart.
Hg., hind gut.
Lb., labrum.
Md., mandibular bud.
Mes., mesoblast below surface.
O. G., optic ganglion.
O. L., optic lobe.
O. S. G., S. O. G., rudimentary brain.
Std., stomodæum.
Vac., vacuole.
Y. C., wandering cells.
Numbers 114–125 mark the planes of the transverse and longitudinal sections represented on Pls. XLI–XLIII.

Plate XL

Fig. 109.

O.L.
SOG.
A.(I).
Std.
Lb.
A.(II).
Md.
Ab.
A.

Fig. 110.

O.L.
O.S.G.
A.(I).
Std.
Lb.
A.(II).
Md.
Ab.
A.

Fig. 111.

Ep.
O.G.
O.L.
SOG.
Lb.
Std.
A.(I).
A.(II).
Mes.
Md.
Mx.(1).
Ab.
A.

114
115
116
117
118
119
120
121
127
122
123
124

H.

125.

Fig. 112.

Ab.
H.G.
Gl.
Y.
Vac.
Ep.
Y.C.
Ch.

Fig. 113.

SOG
Std.
Lb.
Deg.
Ab.
Hg.
Ch.
Ep.

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ALPHEUS AND SESARMA[2]
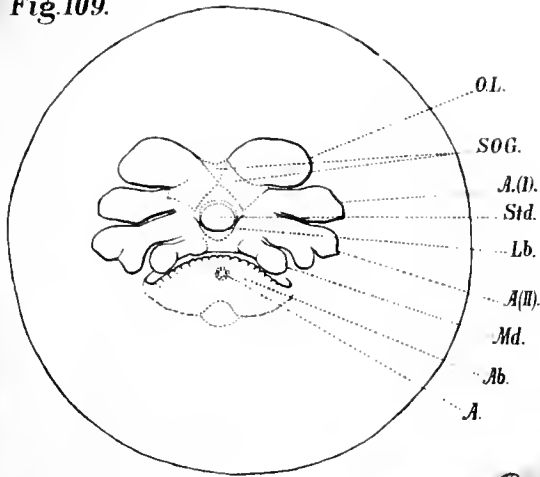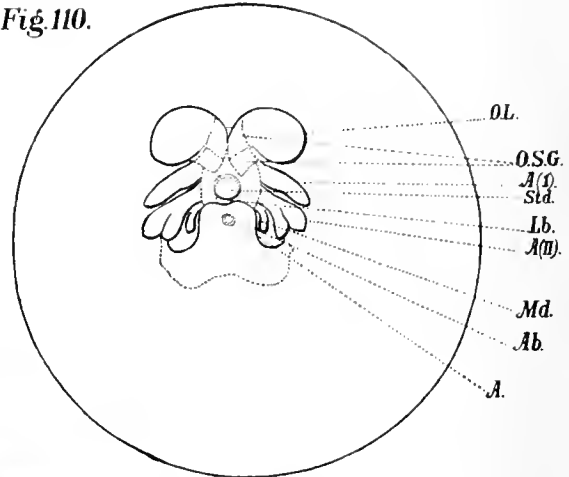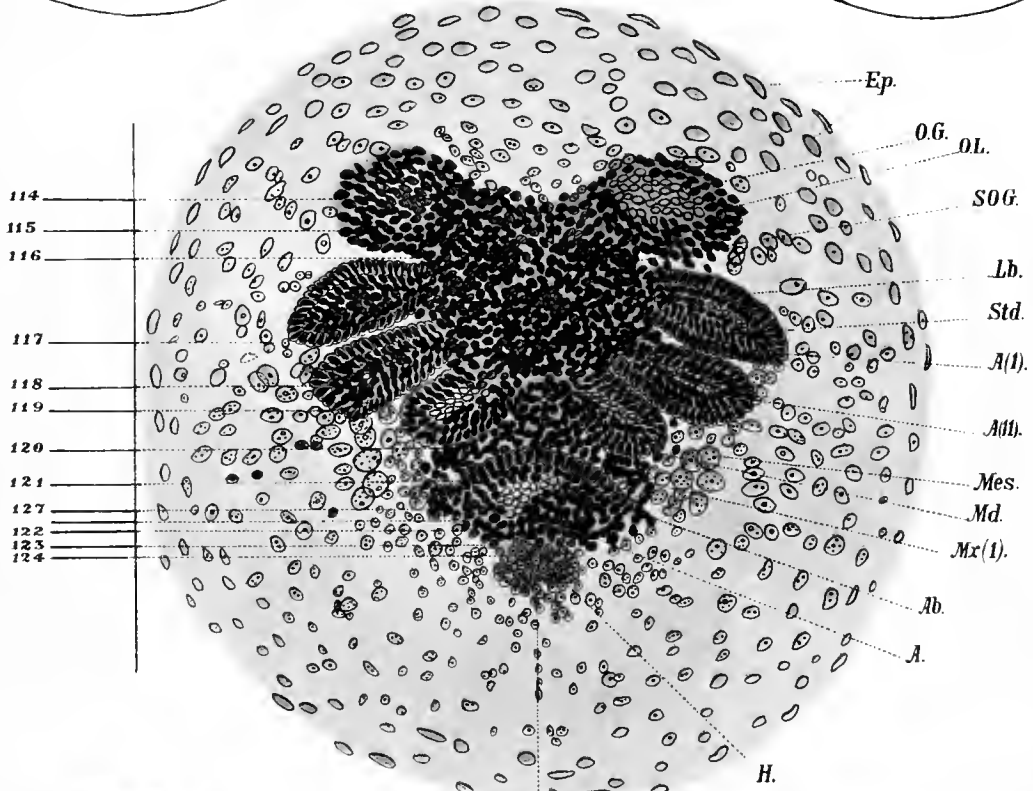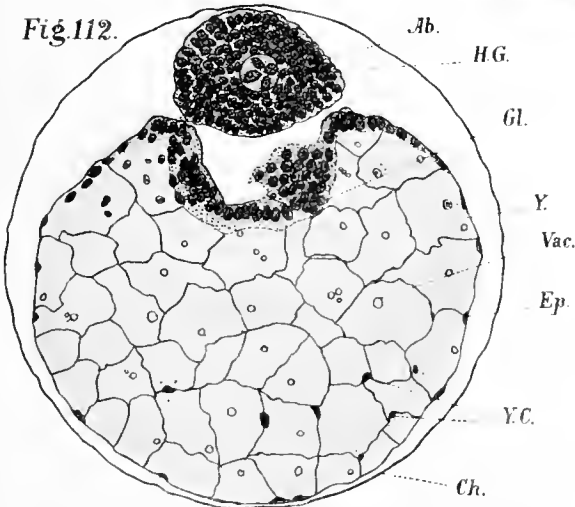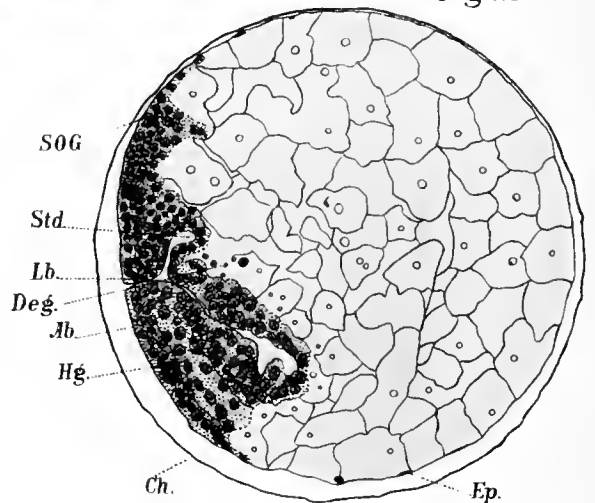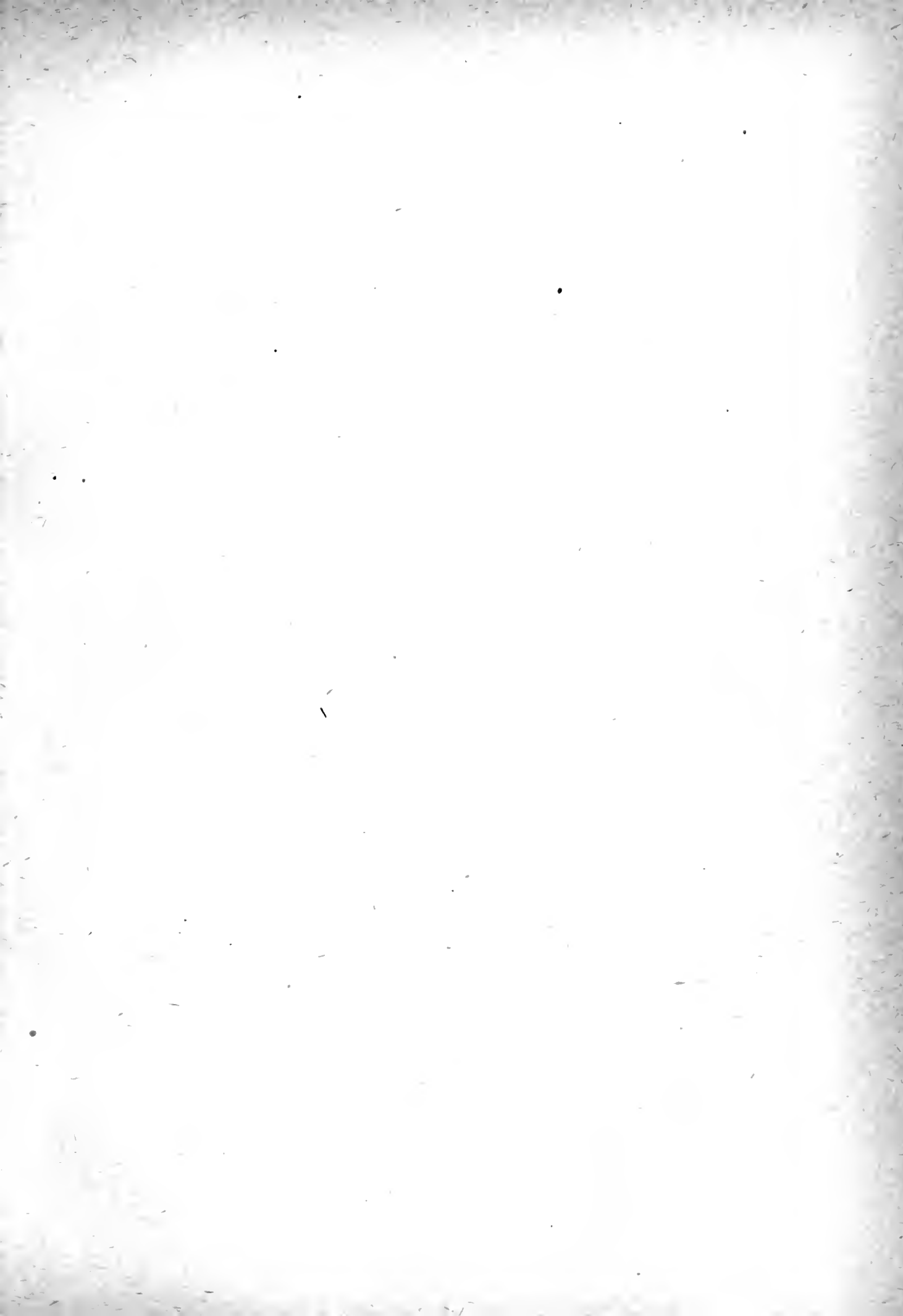
Plate XLI.

(Stage VI.)

Figs. 114-118. Transverse serial sections of egg-nauplius in stage shown in Fig. 109. Plane of section indicated in Fig. 111, which is from an embryo a trifle less advanced. The lobular condition of the enlarged optic disks is well shown in Figs. 114, 115. In Fig. 114 a delaminating cell (*cc.*) at the surface of the optic lobe is cut, and in Fig. 115 a superficial ectodermic cell next the brain is dividing perpendicularly. The intimate fusion of the brain and the optic ganglion is seen in Figs. 115, 116. Fig. 117 cuts the stomodæum passing through the mouth and the antennæ. Mesoblast is already well established in the pockets of all the appendages, as indicated at an earlier period. Degenerating cell products (*S., A. Y. S.,* Fig. 18) are very abundant in the region of the stomodæum, and occur also in the appendages (*S.-S.¹, S. C.,* Fig. 118). ×291.

REFERENCE LETTERS.

A. (I), antennal bud.
A. (II), antennular bud.
A. Y. S., alteration products of yolk.
Ct. S., cells partially covering brain, derivatives from yolk-wandering cells.
cc., surface cell of ectoderm dividing horizontally.
Ect., Ep., ectoderm.
Md., mandibular bud.
Md. G., mandibular ganglion.
M. F., median furrow.
O. G., optic ganglion.
O. L., optic lobe.
Ret., protoplasmic reticulum.
S. S.¹, products of cell degeneration.
S. O. G., brain.
Std., stomodæum.
Vac., vacuole.
Y., Y. C., yolk.

Plate XLI.

Fig. 114.

Y.S.

Ep

cc.   O.G.   S.¹   O.L.

Fig. 115.

Y.S.

O.L.   S.O.G.   O.G.

Fig. 116.

Vac.   A.Y.S   ct.S.   Y.C.

Ect.

O.G.   M.F.   S.O.G.

Fig. 117

A.Y.S.   Y.C.   S.

Ect.

A.(II).   A.(II)

Mes.

Ret.   Std.   S.C.

A.Y.S.

Vac   Y.

Fig. 118.

Ect.

A.(II).   A.(II).

S.¹   M.d.   M.d.G.   M.F   S.C.   S.

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ALPHEUS SAULCYI.
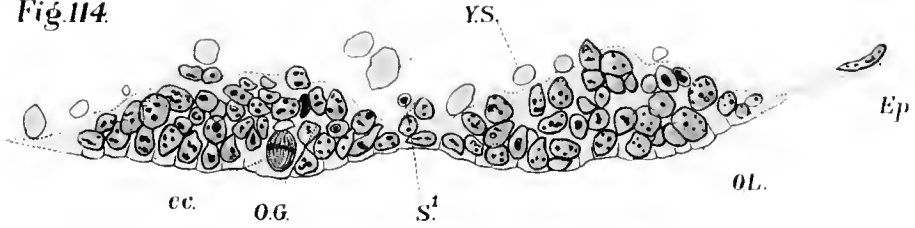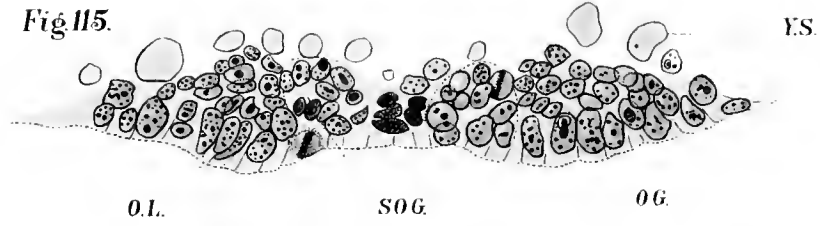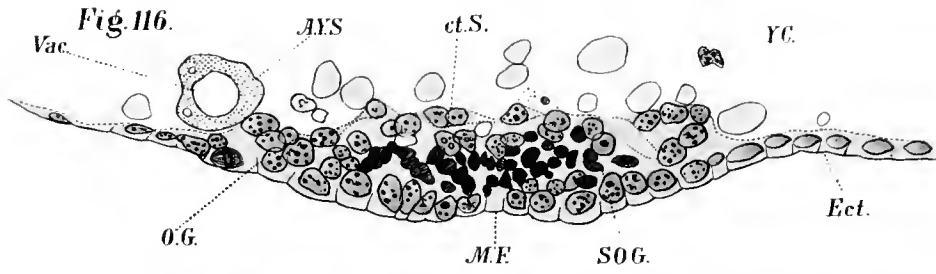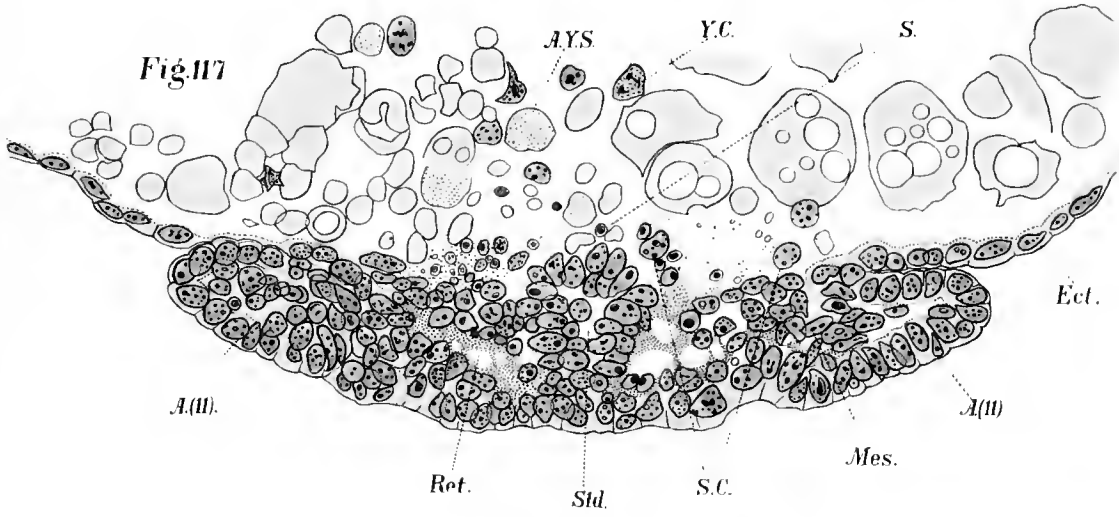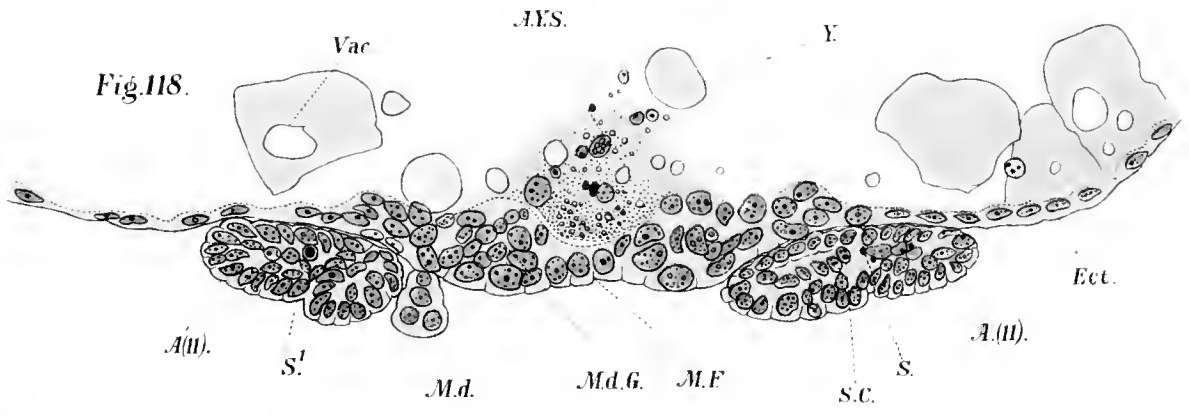
Plate XLII.

(Stage VI.)

Figs. 119–122. Serial transverse sections of the egg-nauplius, continued from Pl. XLI. In Fig. 120 a transverse row of cells with large clear nuclei is seen. This is probably a series of budding ectoblasts and mesoblasts, already referred to. Wandering cells appear to be settling down upon all parts of the embryo. In the thoracico-abdominal fold (Fig. 122, *mu.*) the abdominal muscles are already undergoing differentiation out of the mesoblast of the ventral plate. ×295.

REFERENCE LETTERS.

A., anal invagination.
A. (II), antennal bud.
Ab., abdomen.
A. Y. S., yolk undergoing change.
B. Z., budding zone.
Ect., ectoderm.
Hg., intestine.
Md., mandible.
Md. G., mandibular ganglion.
Mes., mesoderm.
M. F., median groove.
Mu., muscle cells.
Mx. (I), first maxillary bud.
s.', products of cell degeneration.
S. C., degenerating cells.
Y., yolk.
Y. C., Y. C.', wandering cells.
Vac., vacuole.

Plate XLII

Fig. 119.

Fig. 120.

Fig. 121.

Fig. 122.

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ALPHEUS SAULCYI.
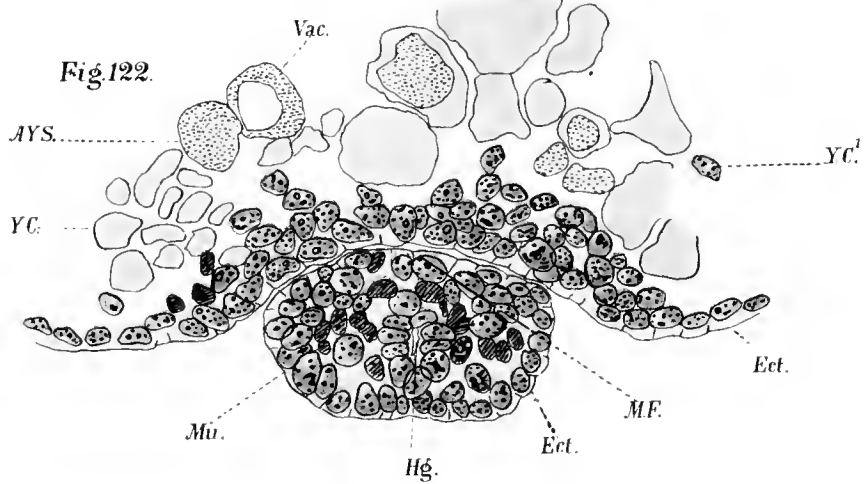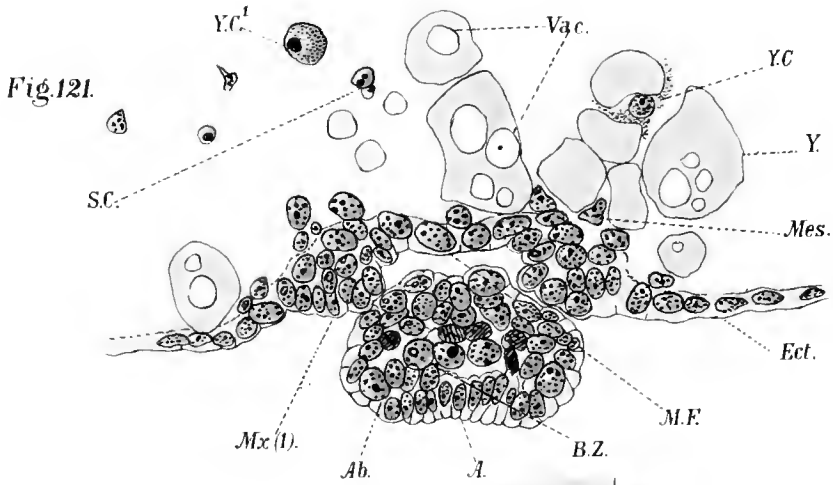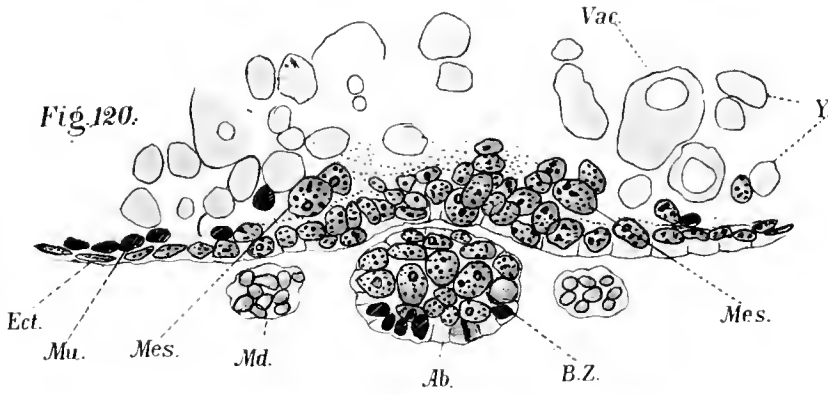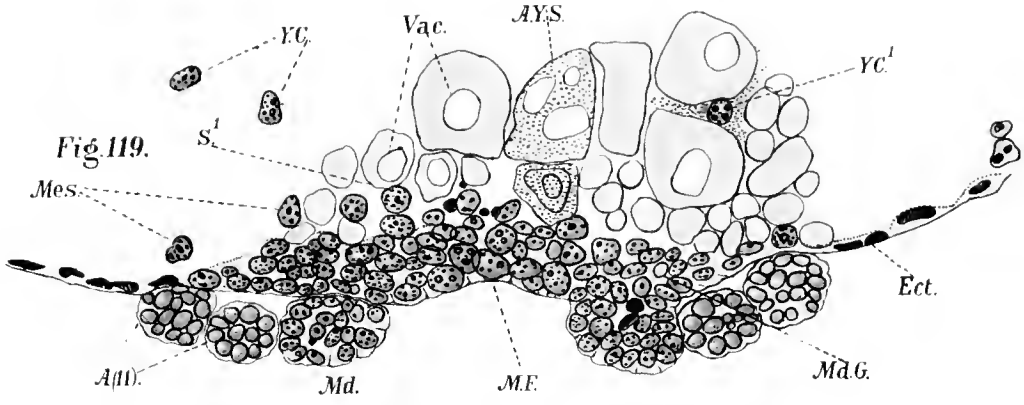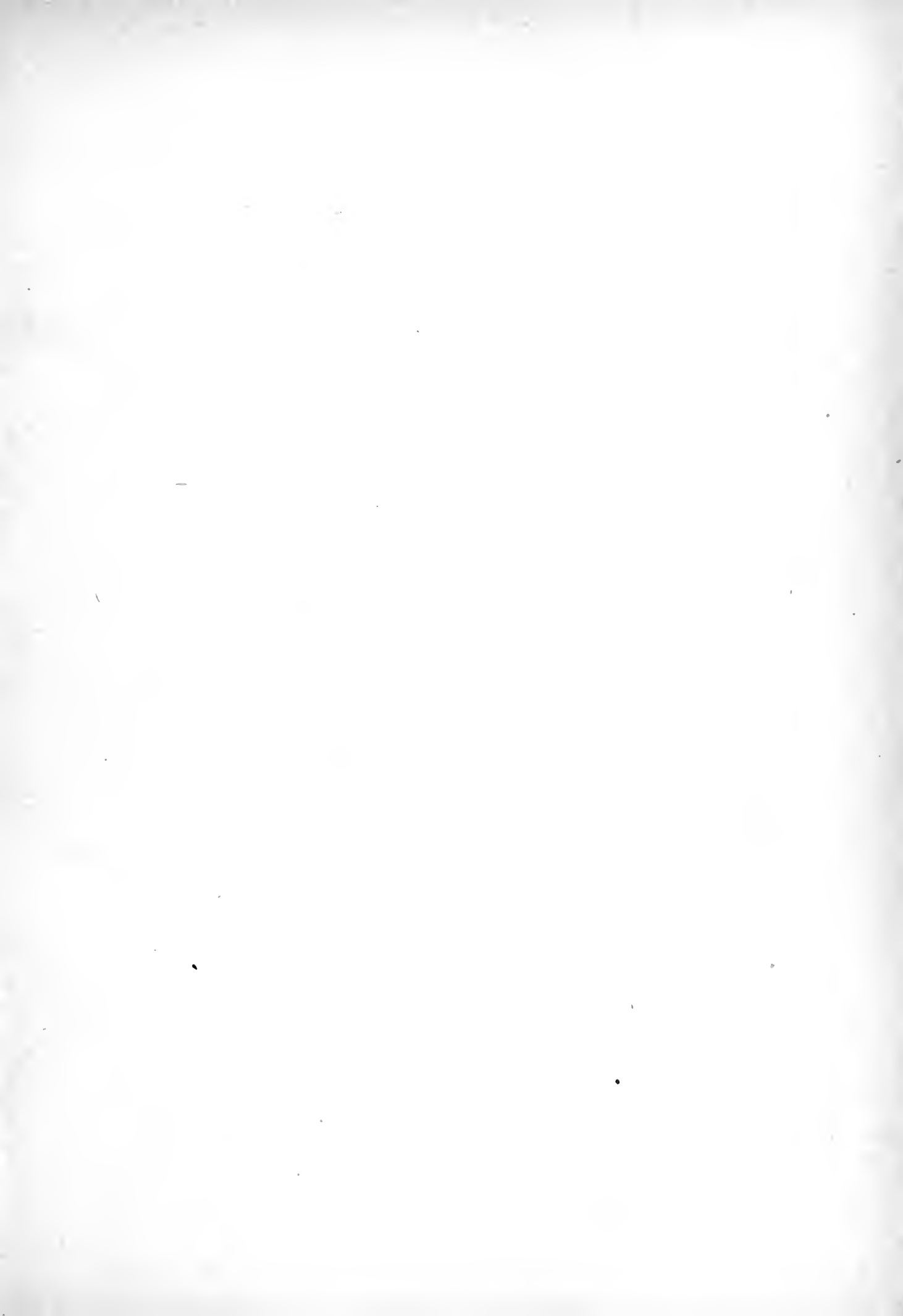
PLATE XLIII.

(Stage VI.)

FIGS. 123, 124. Completion of series of transverse sections of egg-nauplius. Cells marked *Mes.* probably represent endoderm in Fig. 124. The heart is being formed at about this time out of mesoblast cells at *H*, Fig. XLIII, and the endoderm forms a plate between it and the central yolk (v, Fig. 133). ×295.

FIG. 125. Median longitudinal section of same stage. Compare with Fig. 106. The thoracico-abdominal fold is now distinctly directed forward, and is overgrowing the sternal area between it and the mouth. The stomodæum is a bent tube. ×295.

FIG. 126. Transverse section, cutting proctodæum. From an embryo of about the same age as that represented in Fig. 106. ×295.

FIG. 127. Transverse section of embryo and entire egg on level with anus, showing wandering cells (*Y. C., Y. C.*$^{1-2}$). ×74.

REFERENCE LETTERS.

A., anal invagination.
Ab., abdomen.
A. Y. S., altered food yolk.
Ch., eggshell.
Ect., Ep., ectoderm.
Gl., ganglionic rudiment.
H., rudiment of heart.
Hg., intestine.
Lb., labrum.
Mb., embryonic molt.
Mes., mesoderm.
Mo., mouth.
Pd., region of proctodæal invagination.
s., s^1*.*, products of cell degeneration.
S. C., wandering cells, probably in early stages of degeneration.
S. O. G., rudiment of brain.
St. A., sternal area.
Std., stomodæum.
Y., yolk.
Y. C., Y. C.$^{1-2}$, wandering cells.
Y. S., yolk spherules.
Vac., vacuole.
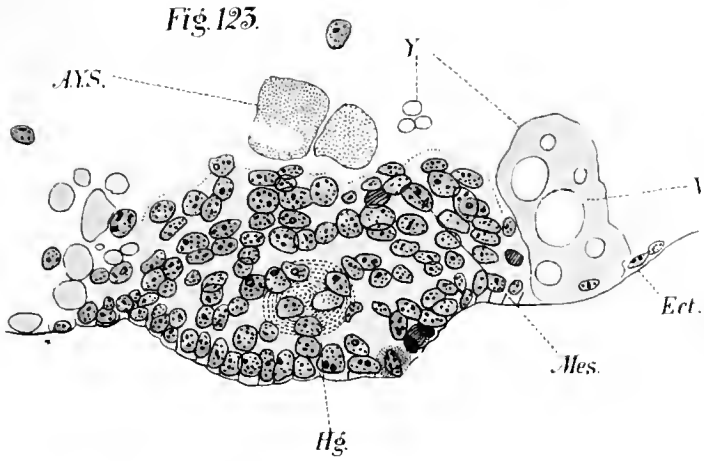
Plate XLIII

Fig. 123.

Fig. 124.

Fig. 125.

Fig. 126.

Fig. 127.

F. H. Herrick, del

ALPHEUS SAULCYI
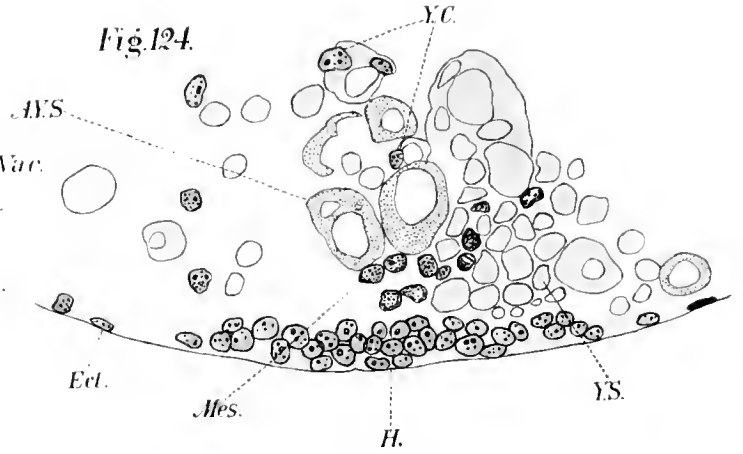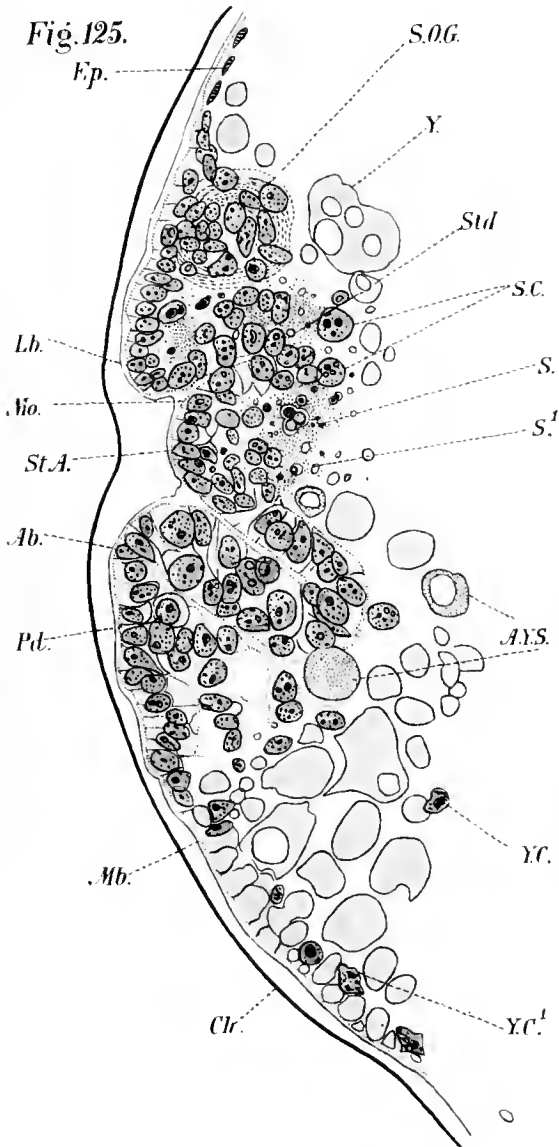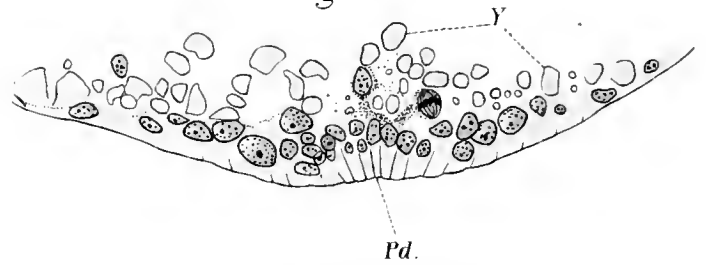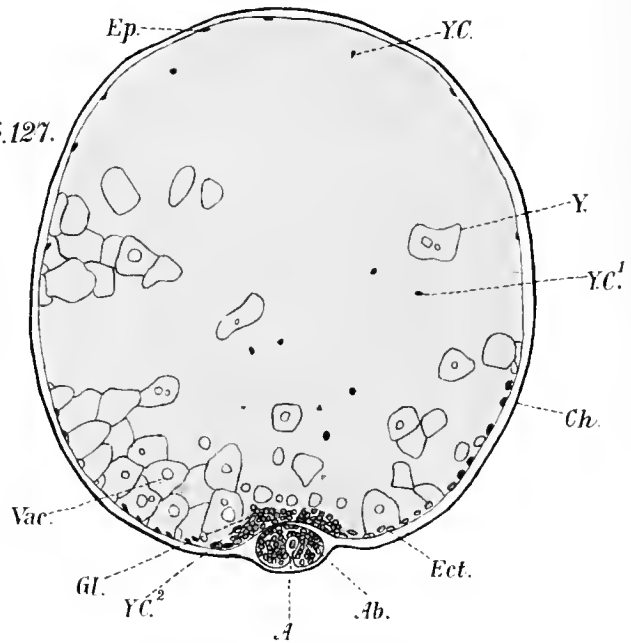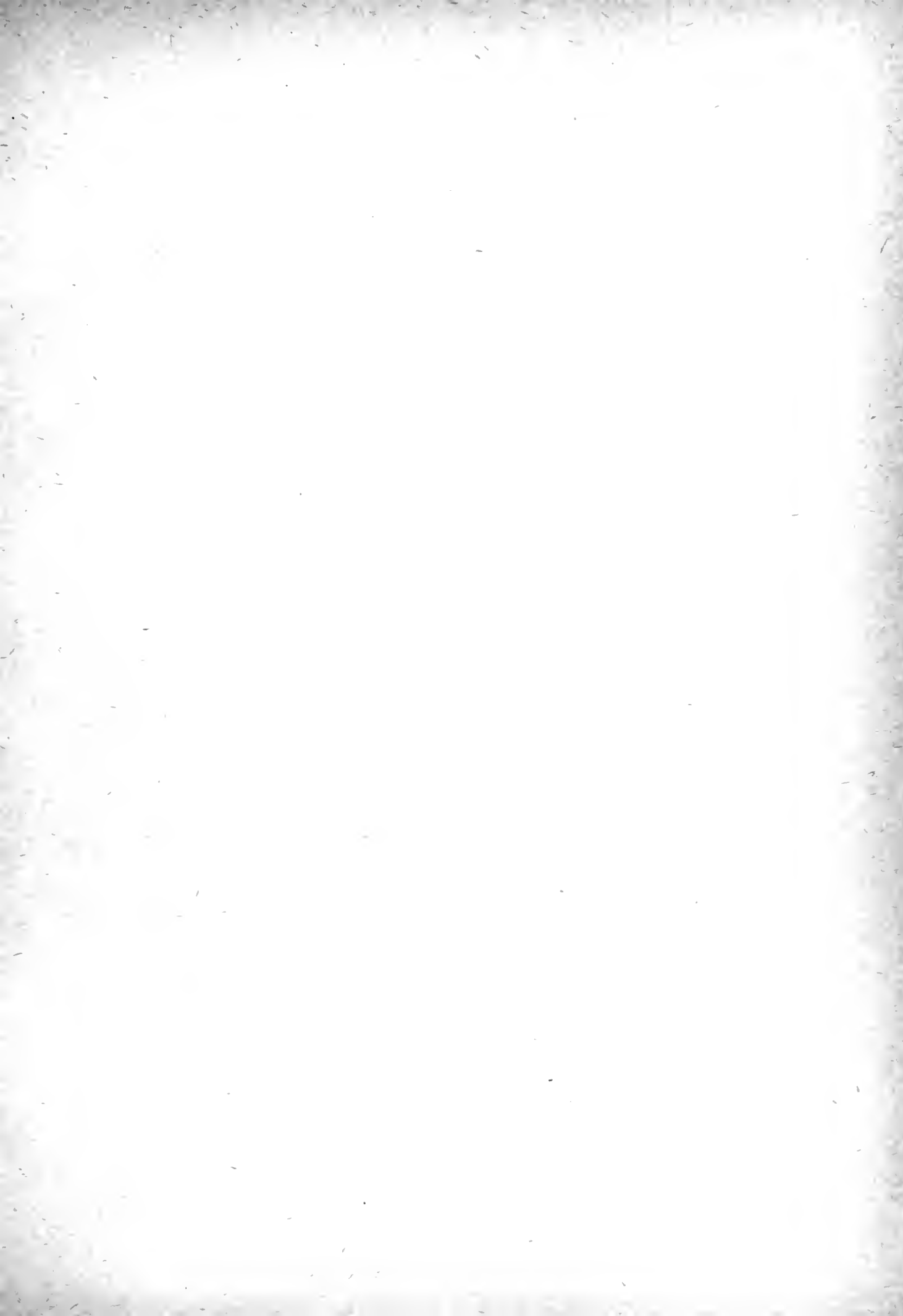
PLATE XLIV.

(Stage VII.)

Fig. 128. Transverse section through embryo, in the region of the first maxilla. Nervous system not yet differentiated from the skin. ×234.

Fig. 129. Lateral longitudinal section through optic lobe and extremities of antennæ. The differentiation between the retinal and ganglionic parts of the eye is very clear. Mesoblastic cells, representing rudimentary muscles, are seen attached to the body wall. ×234.

Fig. 130. Surface view of embryo of this stage, with buds of four post-mandibular appendages present. The antennæ are covered with a hairy exuvium, which was probably stripped off from the antennules in this preparation. The mouth is concealed by the labrum, which nearly meets the thoracico-abdominal fold. The anus is situated nearly at the extremity of the latter, which is slightly emarginated. ×137.

Fig. 131. Median longitudinal section in the series from which Fig. 129 was taken. ×234.

Figs. 132-135. Serial transverse sections through embryo in similar stage. The germinal layers, definitely established in the egg-nauplius stage, are clearly differentiated at this period. An incomplete layer of elongated cells (probably mesoblastic in origin, coming from wandering yolk cells), Mes., Figs. 131, 132, is seen between the yolk and the neural thickening, from which the nervous system is in process of development. In Fig. 134 rudimentary muscles suspend the stomodæum to the body wall, and in Figs. 133 and 135 the three germinal layers can be clearly seen. The heart is represented by the space filled with mesoblast and serum, between the entoblastic lamella and the ectoblast. ×234.

REFERENCE LETTERS.

A. I, first antenna.
A. II, second antenna.
Ab., thoracico-abdominal fold.
A. Y. S., alteration products of the yolk.
Ect., ectoderm.
End., endoderm.
G. L., rudiment of optic ganglion.
Gl. A. II, antennular ganglion.
Lb., labrum.
Mes., mesoderm.
Mo., mouth.
Mu., rudimentary muscles.
Mx. I, first maxillary bud.
O. E., retinal portion of optic lobe.
S. O. G., brain.
Std., stomodæum.

Plate XLIV
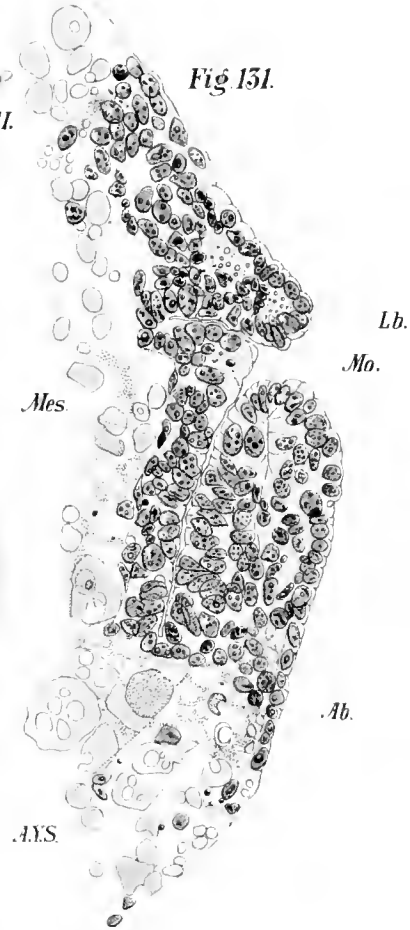
Fig. 128.

Fig. 131.

Fig. 129.
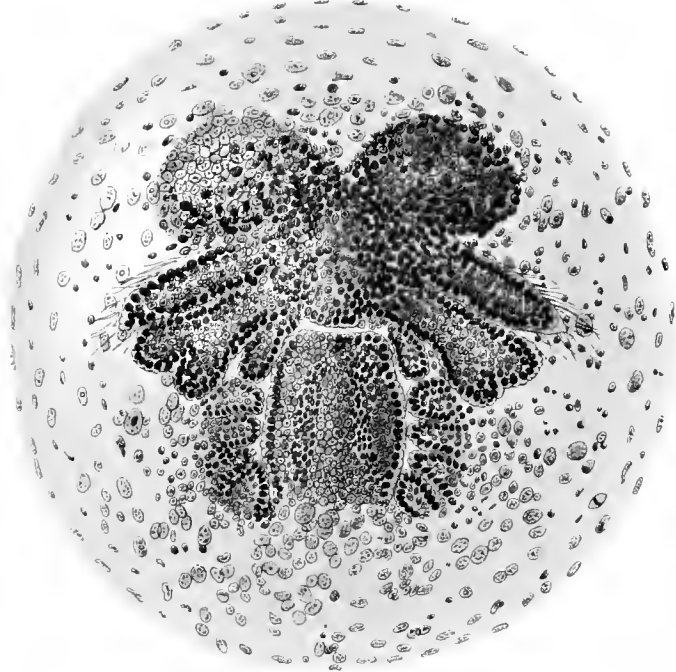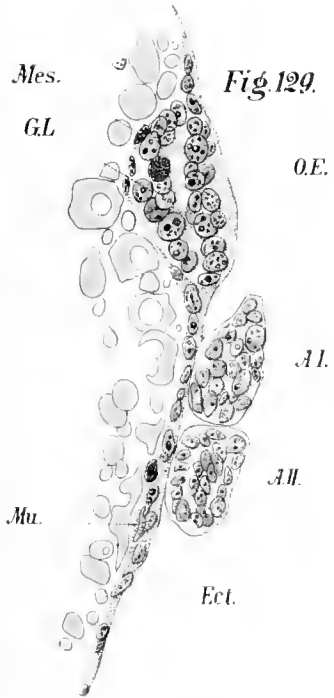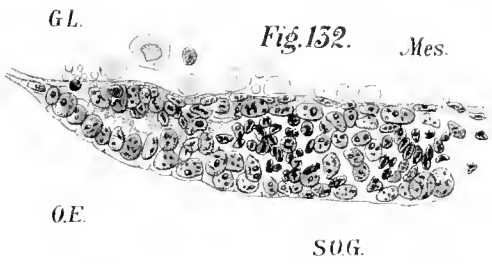
Fig. 130.

Fig. 132.

Fig. 133.

Fig. 134.

Fig. 135.

ALPHEUS
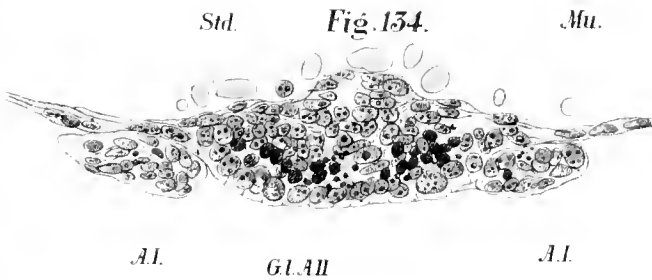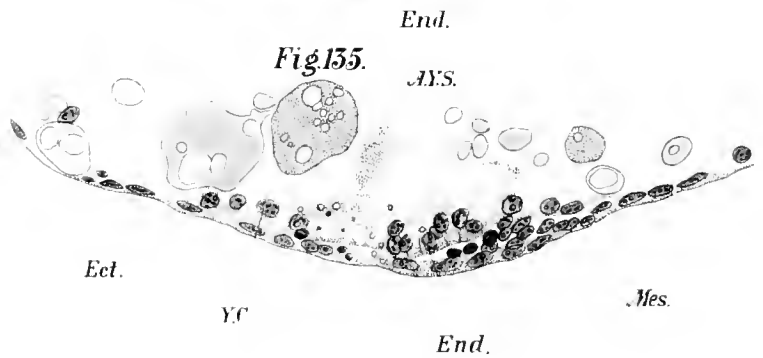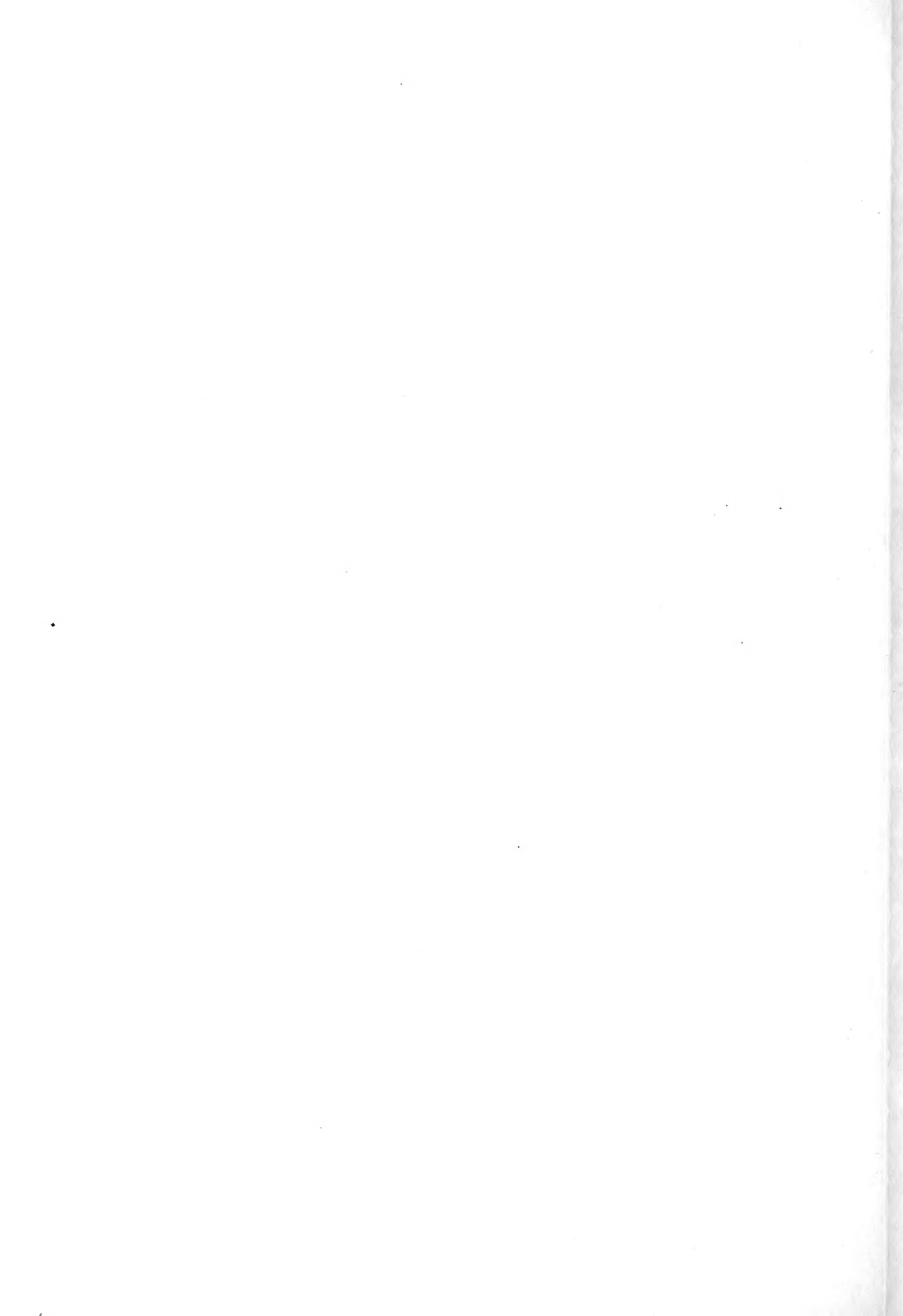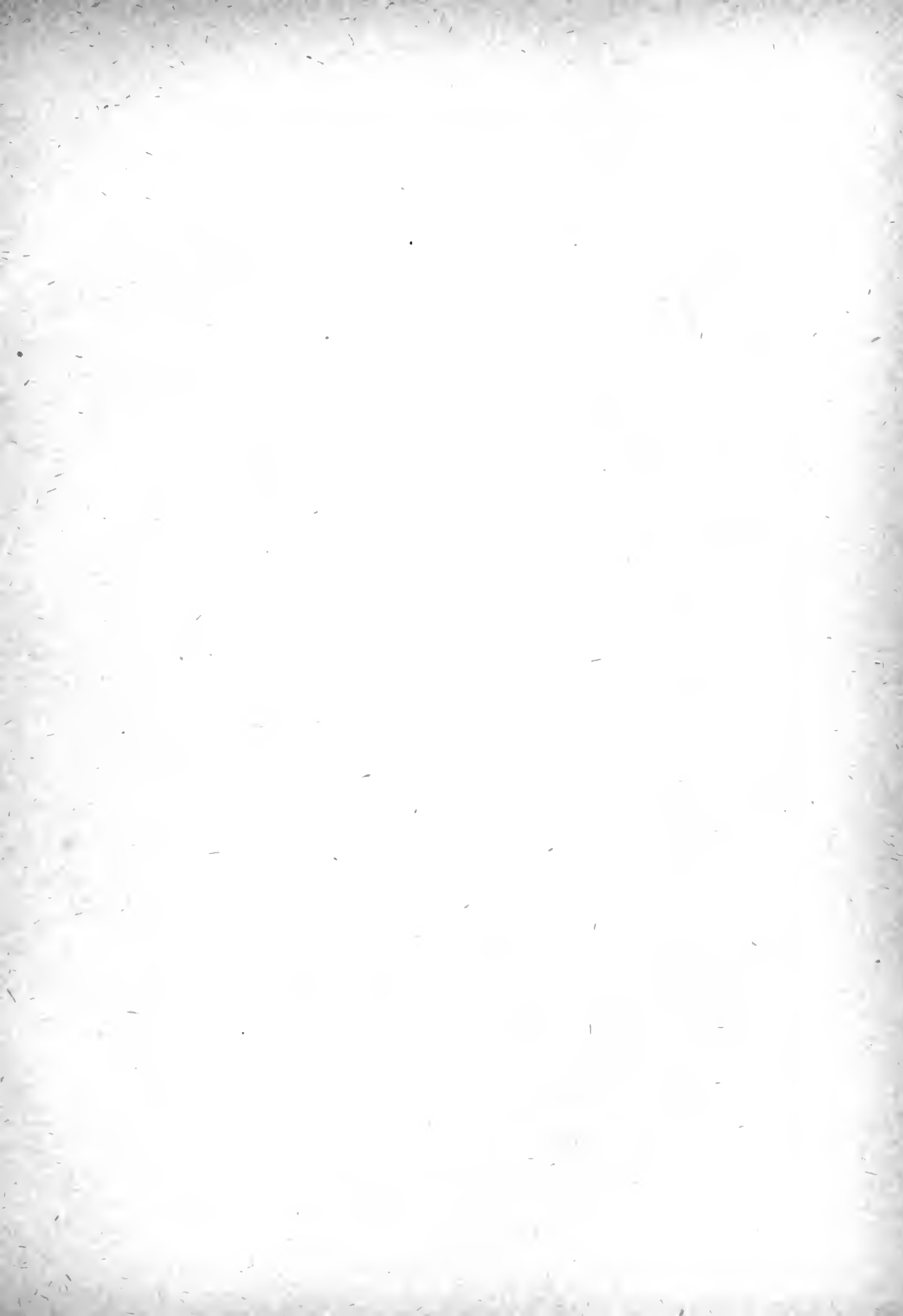
PLATE XLV.

(Stage VIII.)

FIG. 136. Lateral longitudinal section of embryo in stage intermediate between VII and VIII, represented in surface view in Fig. 110. To this phase also belong Figs. 137, 144, and 145. Fig. 136 is to be compared with the slightly older embryo in Fig. 129. Blood cells (*B. C.*) and other wandering cells are here seen settling down upon the body wall. A wandering cell is also seen nearly in contact with the optic ganglion. ×241.

FIG. 137. Transverse section of embryo in same phase, just behind the level of the first antennæ, showing the relations of the wandering cells at this period to the embryo and egg. ×61.

FIGS. 138, 139. Serial longitudinal sections through embryo in Stage VIII. Fig. 138 should be compared with Figs. 136 and 129. All the ganglia of the nervous system, at least as far back as the eighteenth segment, are marked at the surface by deep constrictions. The ganglia of the nineteenth and twentieth segments are less distinct. The ganglia of the eleventh segment lie in the angle made by the thoracico-abdominal flexure. Wandering cells occur in the yolk, but are less abundant, and the products of cell degeneration, which enter into the general nutrition, have mostly disappeared. ×241.

FIGS. 140–143. Parts of sections taken at various points on the surface of the egg (series to which Figs. 136, 137, 144, 145, belong), remote from the embryo, to show the rôle of certain wandering cells which reach the surface and represent mesoblast. In Fig. 140 two cells (*ms., ms.¹*) are partially flattened against the surface, but here, as in Fig. 142, the wandering cell *ms.* is clearly distinguishable from the spindle-shaped ectoderm cell on the left. Compare Fig. 34. ×241.

FIGS 144–145. Serial longitudinal sections through the embryo and entire egg to show the distribution of the wandering cells. Certain wandering cells not yet flush with the surface, enter into an organ—the dorsal plate (*Dp.*)—which is characteristic of a later stage (Fig. 153, *Dp.*). The strictly superficial cells of the dorsal plate are probably in all cases ectoblast, and some of the wandering cells degenerate before they reach the surface ectoblast.

There seems to be a general dispersal of wandering cells from the vicinity of the thoracico-abdominal fold. The wandering cells which appear in this part were taken from four consecutive sections, including that represented in the drawing. ×61.

REFERENCE LETTERS.

A. I, first antenna.
A. II, second antenna.
au., lower margin of optic lobe.
A. s. a., superior abdominal artery.
B. C., blood corpuscle.
b. m., basement membrane.
ch., eggshell.
Dp., dorsal plate.
End., endoderm.
G. IV–XVIII, segmental ganglia.
Gl., gangliogen.
H., heart.
hd., hypodermis.
Hg., hindgut.
mes., mesoblast.
mo., mouth.
ms., ms.¹, wandering cells at surface.
O. L., optic lobe.
Rt., retinogen.
Std., stomodæum.
Th. ab., thoracic-abdominal fold.
y. c., wandering cells.

Plate XLV.

136. 137. 138.

139.

140. 141. 142. 143.

144. 145.

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Sackett & Wilhelms Lithographing Co. New York

ALPHEUS
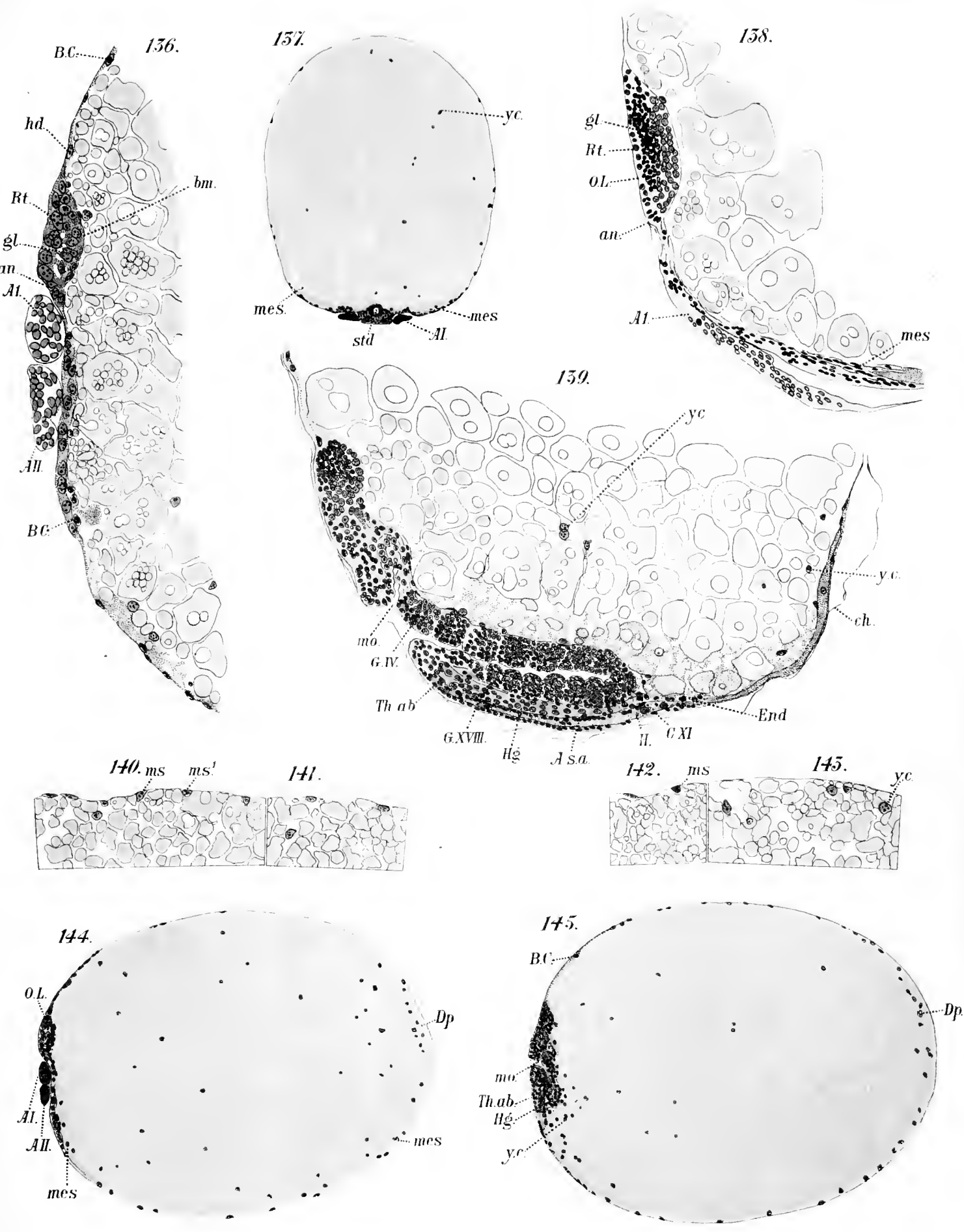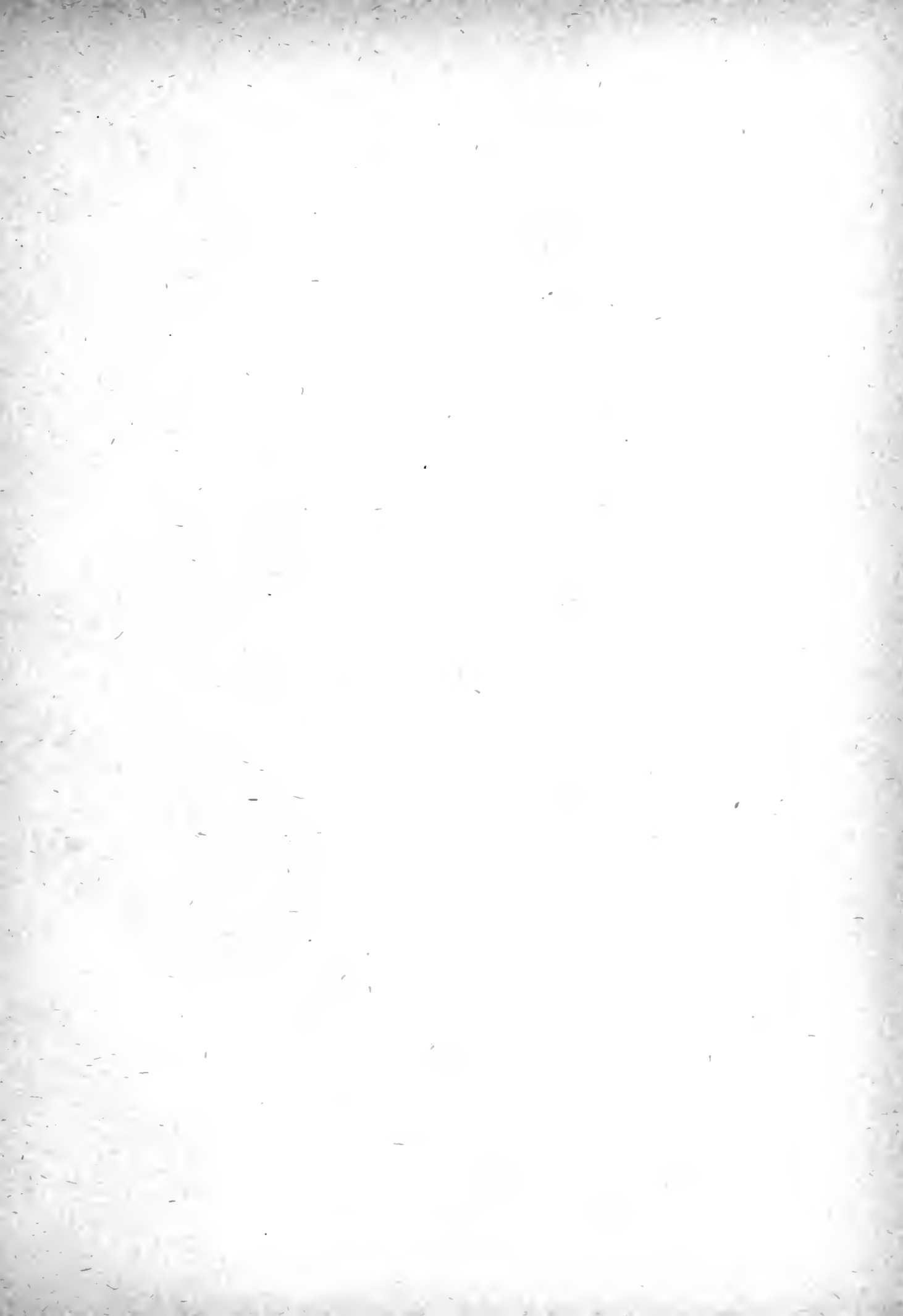
Plate XLVI.

(Stage IX.)

Figs. 146–151. Serial transverse sections, through the embryo or *A. saulcyi*, at the time when pigment is first deposited in the eye. In Fig. 146 the developmental history of the retinal layer is well shown. ×230.

Fig. 152. Nearly median longitudinal section of embryo in similar stage. ×58.

Fig. 153. Sagittal section of similar embryo, showing degenerating elements in yolk below dorsal plate. ×58.

REFERENCE LETTERS.

A. I, first antenna.
A. II, second antenna.
Ab., abdomen.
B. C., blood corpuscle.
B. S., blood space.
cp., carapace.
Deg., degenerating cells.
Dp., dorsal plate.
End., endoderm.
fg., foregut.
fs., fiber mass of nervous system.
g. II–III, brain.
g. c., ganglion cell.
g. m. a., anterior gastric muscle.
H., heart.
hd., hypodermis.
Hg., hindgut.
Lb., labrum.
Md., mandible.
Mes., mesoblast.
Mu. f., flexor muscle.
ocm., œsophageal commissure.
o. g., optic ganglion.
O. L., optic lobe.
pk., punct substanz.
pr., perineurium.
Rt., retinogen.
S. O. G., supra-œsophageal ganglion.
T., telson.
Tc., transverse commissure.
Th., thorax.
Vac., vacuole.
y., yolk.
Y. C., wandering cells.

Plate XLVI.

146.

og.   gc.   SOG.

Rt.

B.S.

149.

B.C.   B.S.   mes.   fg.
cp.   fs.   Lb.

Al.
All.   Md.   Ab.   Hg.

147.

B.S.
Al.   gII.   T.   gc.   T.   Tc.

150.

B.S.   pk.   vac.   y.

cp.

hd.

Ab.   Hg.   mu.f.

148.

vac.   y.   YC.   mes.   fg.
Cp.   fs.
B.S.
Al.
All.   Ab.   Lb.   ocm.

151.

cp.

Ab.

152.   B.S.   y.c.   BC.

H
End.
Th.   Ab.   pr.   fg.   gIII.   gII.   OG   gma   B.S.

153.   OL.   Deg.

Dp.
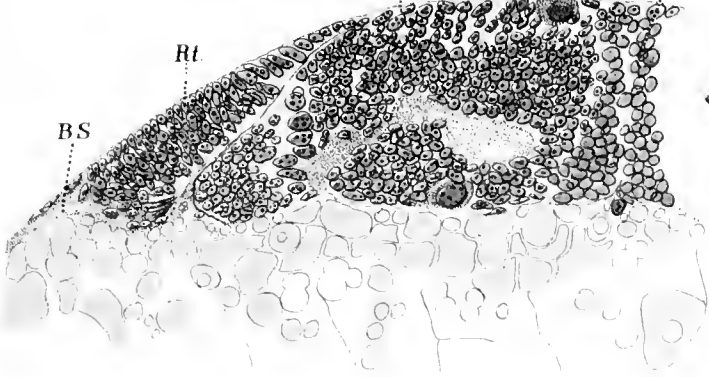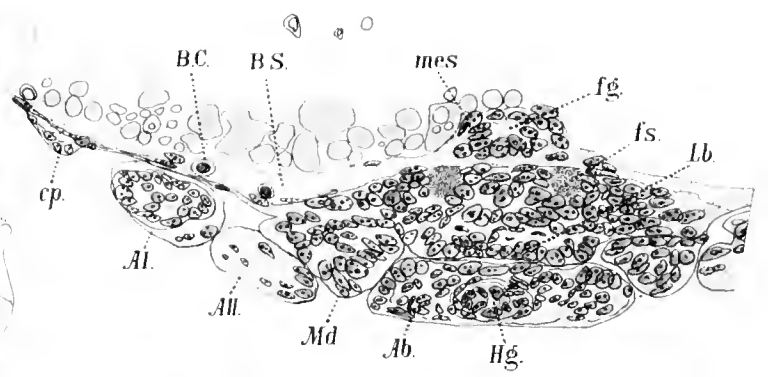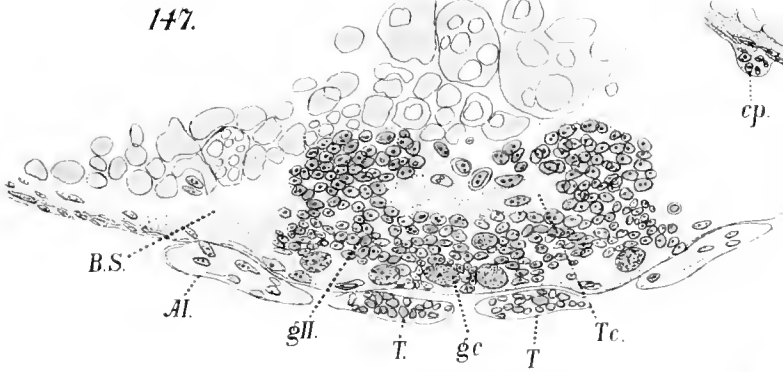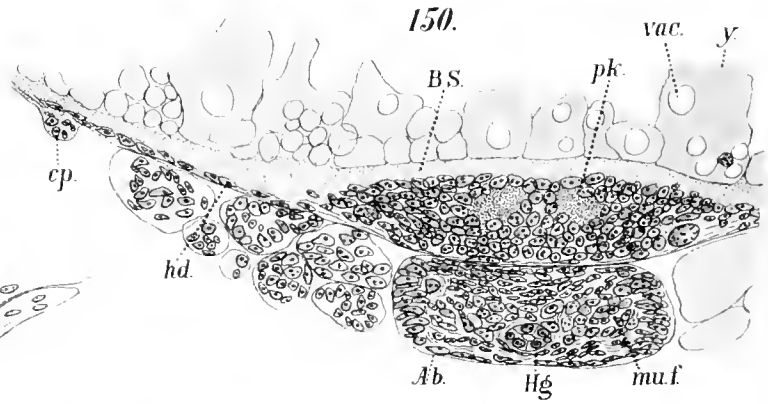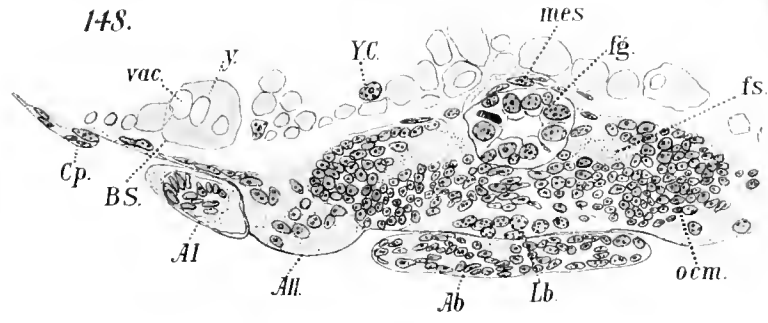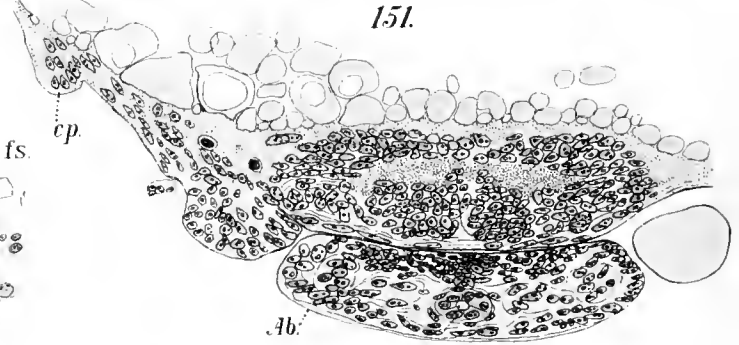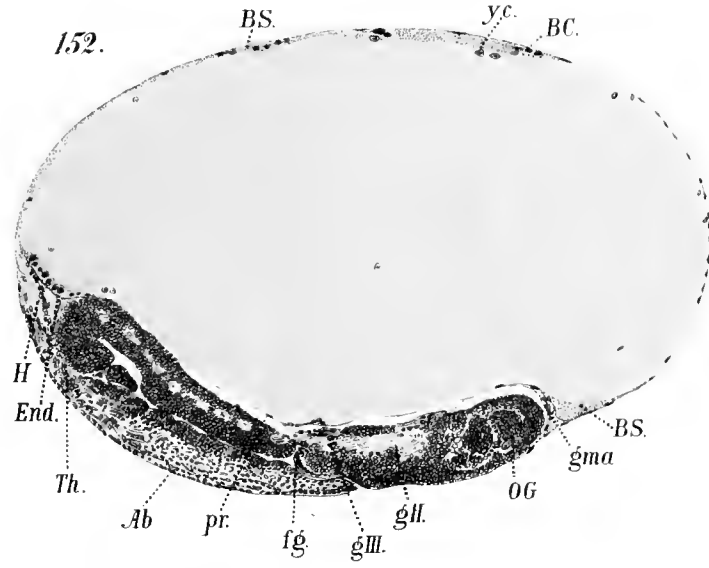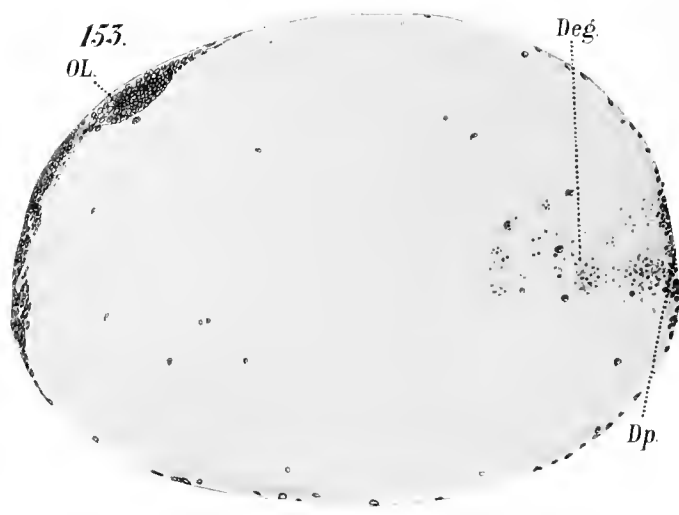
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ALPHEUS

PLATE XLVII.

(Stage IX.)

FIGS. 154, 155. Transverse sections through entire embryo of *Alpheus saulcyi*. In Fig. 154 a yolk nest is cut. Blood spaces occur near the surface of the egg.   ×61.

FIG. 156. Cell nest, containing degeneration products. Its position in the yolk is shown in Fig. 154.   ×245.

FIG. 157. Part of median longitudinal section through the thoracic-abdominal flexure. The growing endodermal epithelium and its fusion with the lining of the intestine are particularly well shown. Wandering cells appear to be uniting with the endoderm.   ×245.

FIG. 158. Sketch of egg embryo, *Alpheus saulcyi*, of same phase as that represented by Fig. 157.   ×61.

FIG. 159. Horizontal section through brain and eyestalks of a slightly older embryo.   ×61.

FIG. 160. Part of transverse section of similar embryo on level with the mandibles.   ×245.

FIG. 161. Superficial part of section of egg, showing surface cells, blood corpuscles, and a wandering cell on the edge of the blood space.   ×245.

REFERENCE LETTERS.

A. I, first antenna.
A. II, second antenna.
Ab., abdomen.
aor., aorta.
a. y. S., granulated yolk products.
B. C., blood cell.
B. S., blood space.
Ch., eggshell.
cp., carapace.
Deg., products of cell degeneration.
Ect., ectoderm.
End., endoderm.
fs., fiber-substance of nerve cord.
G. IV, ganglion of mandible.
gc., ganglion cell.
gf., fiber ball of second antenna.
H., heart.
hd., hypodermis.
hg., hindgut.
lf., lateral fiber-mass of brain.
Md., mandible.
Mes., mesoblast.
Mu., muscle cells.
Mu. f., flexor muscle.
Mts., metastoma.
n. c., neural cord.
O. G., optic ganglia.
of., optic enlargement.
p. c., pillars of carapace.
p. r., perineurium.
p. s., pericardial sinus.
Rt., retinogen.
Std., stomodæum.
vac., vacuole.
y. c., wandering cell.
y. n., yolk nest.

Plate XLVII

ALPHEUS
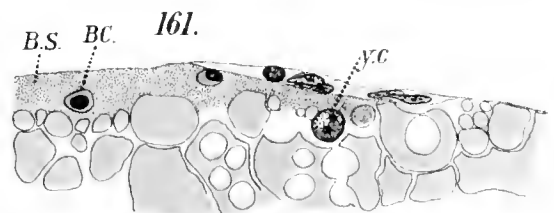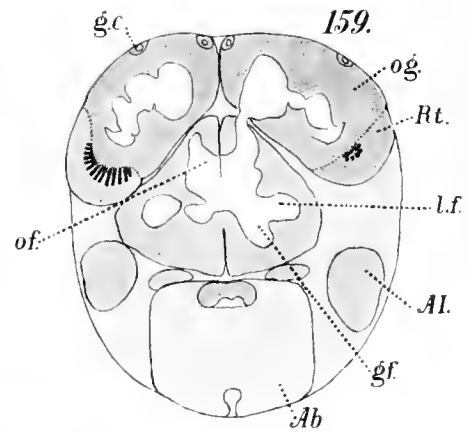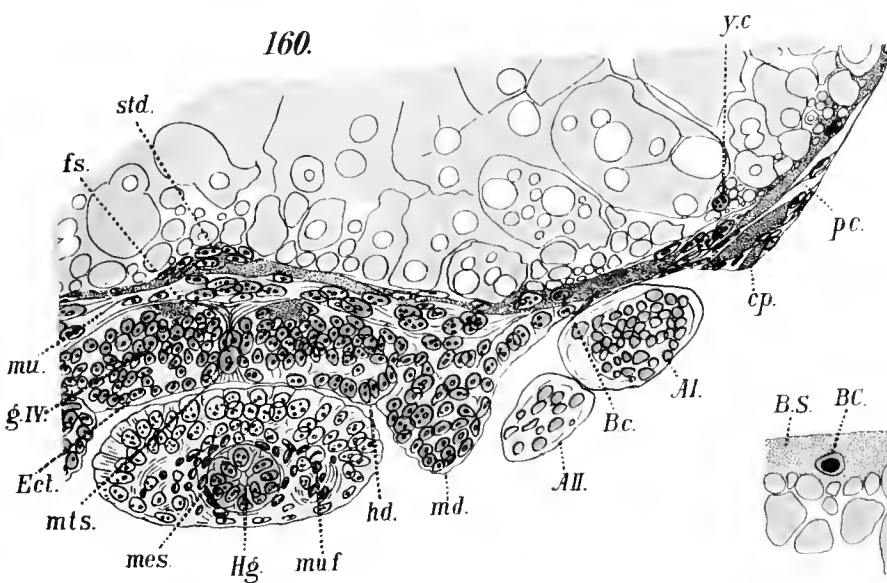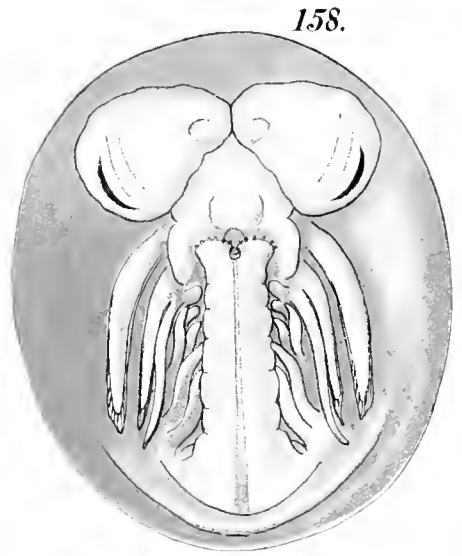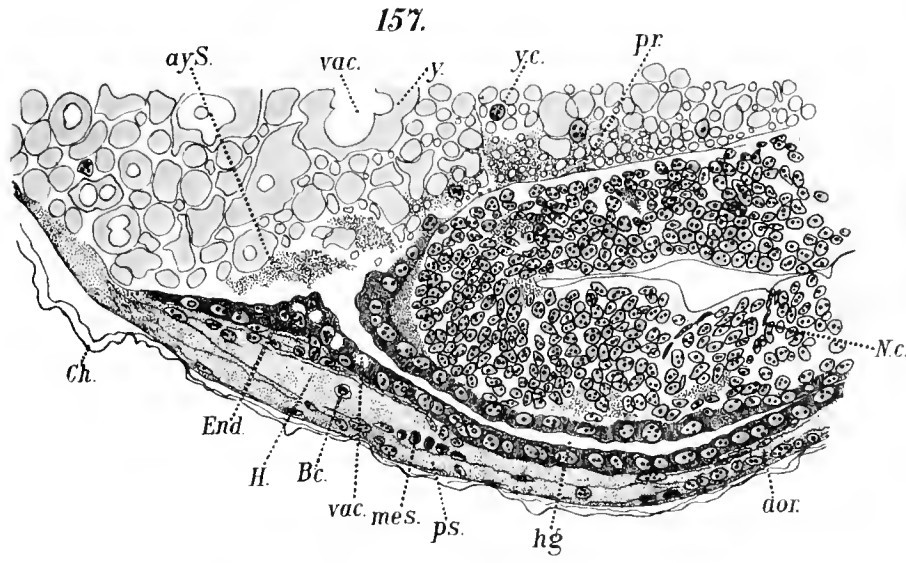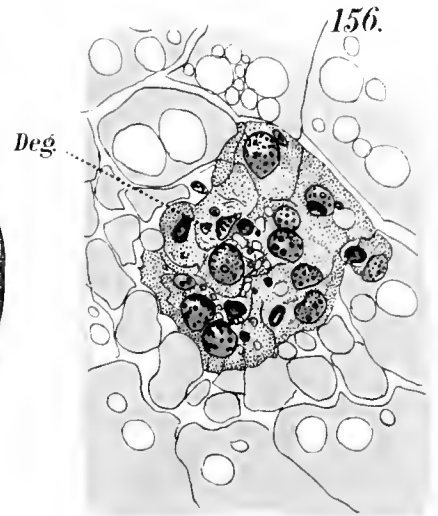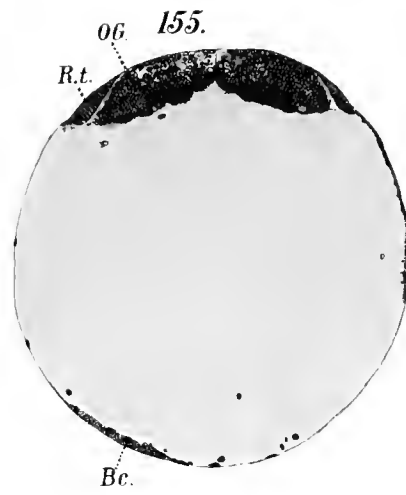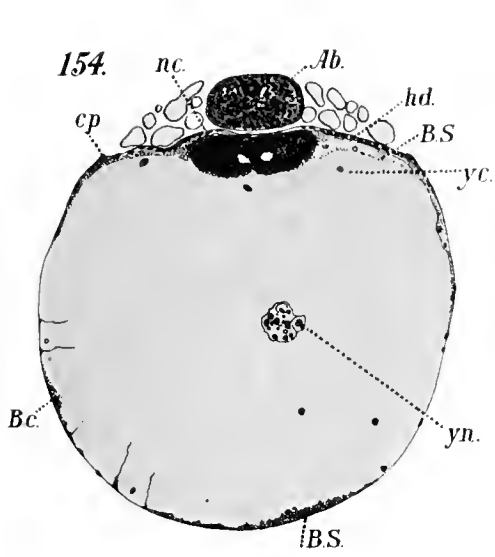
PLATE XLVIII.

(Stage X.)

FIGS. 162–165. Parts of serial sections through the region of the heart and thoracic-abdominal
fold to show the extension and relations of the endoderm.   ×57.

FIGS. 166—167.   Parts of serial transverse sections of the embryo of *Alpheus saulcyi*.   ×125.

FIG. 168. Median longitudinal section through a slightly older embryo, showing the ventral
endodermic fold (*f*), the foregut still screened from the yolk, and the nervous
system separated from the skin.   ×227.

REFERENCE LETTERS.

Ab., abdomen.
Ab. g. I, first abdominal ganglion.
aor., aorta.
B. C., blood cell.
B. S., blood space.
cc., crystalline cone cells.
Deg., products of degeneration.
Ecp., proximal retinular cells.
End., endoderm.
f., ventral endodermic fold.
g. m. a., anterior gastric muscle.
H., heart.
Hg., hindgut.
imb., intercepting membrane.
mg., mesenteron.
mo., mouth.
mpgI, first maxillipedal ganglion.
Mu. E., extensor muscles.
Mu. f., flexor muscles.
O. G., optic ganglia.
p. s., pericardial sinus.
Rt., retinogen.
S. O. G., supra-œsophageal ganglion.
T., telson.
Th., thorax.
Th. g. I, ganglion of first ambulatory limb.
y. c., wandering cells.

Plate XLVIII

162.

163.

164.

166.

165.

167.

168.
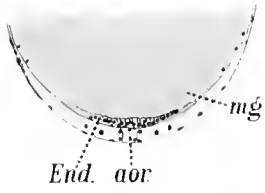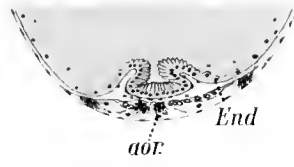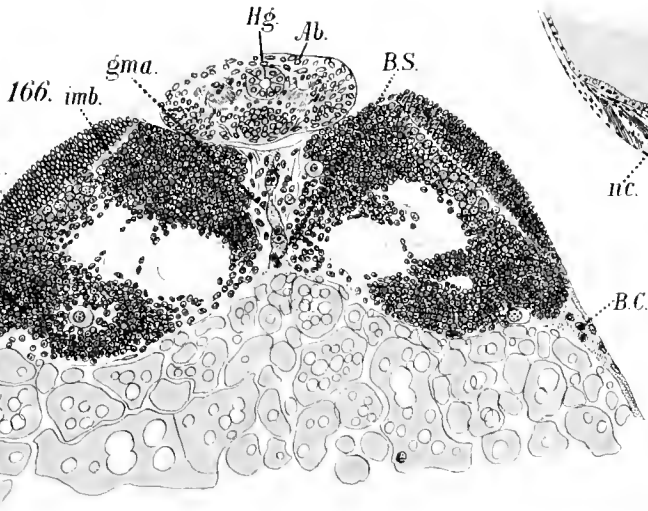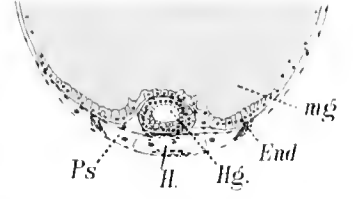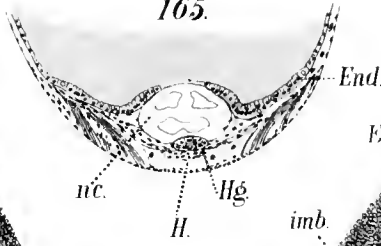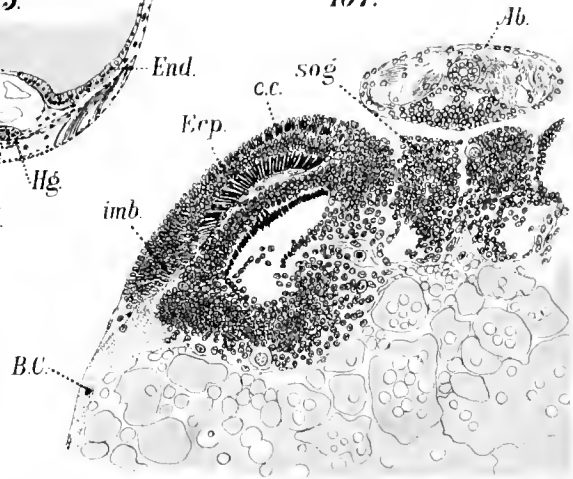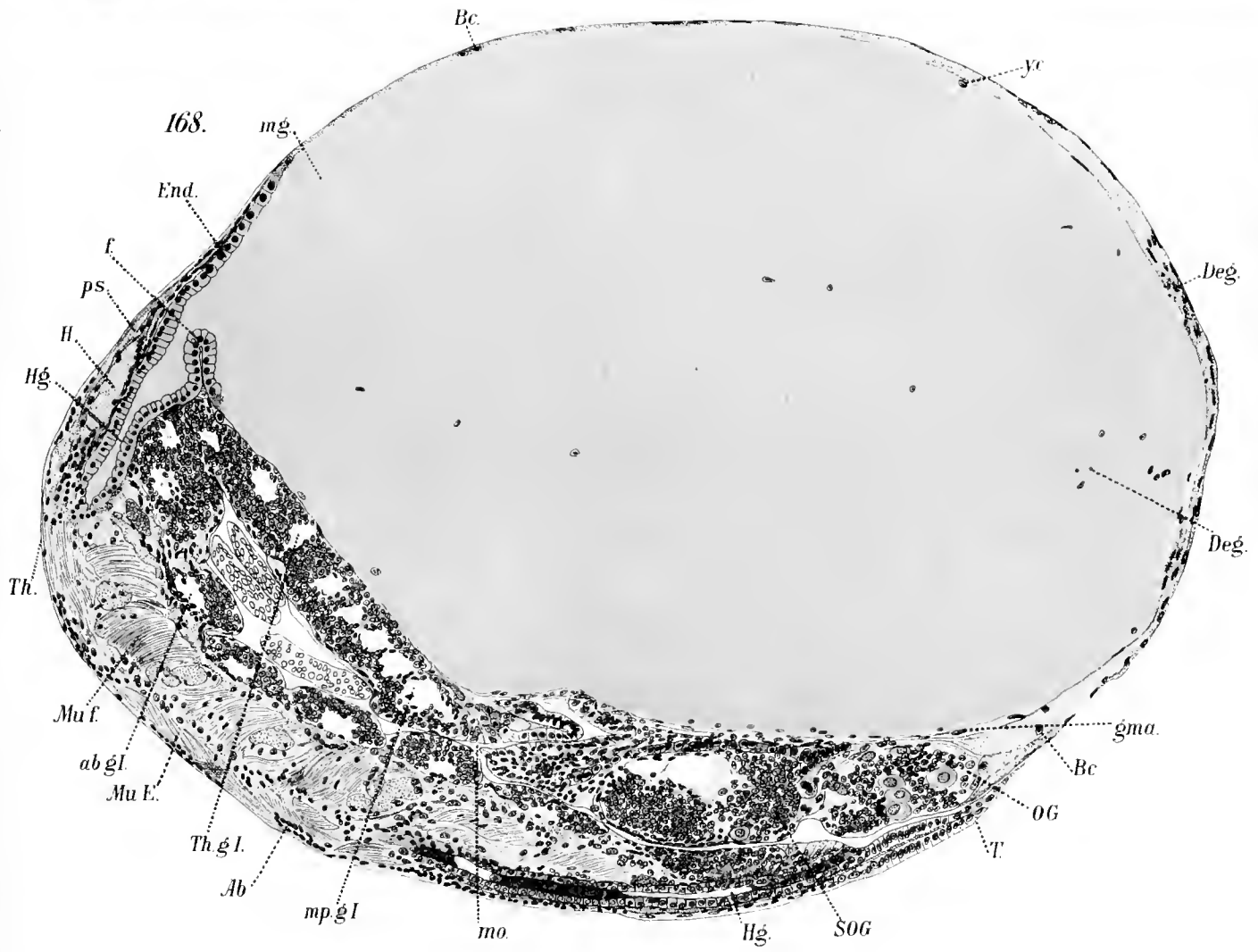
ALPHEUS

PLATE XLIX.

(Stages X and XII.)

FIGS. 169–173. Parts of serial transverse sections through the embryo of *Alpheus saulcyi* in Stage X. In Fig. 173 the reproductive organ *R. O.* is cut.   ×129, (Fig. 173, ×234.)

FIG. 174. Horizontal section through nervous system of the first larva, on a level with the œsophageal commissures.   ×234.

FIGS. 175, 176. Transverse sections through the neural cord of the first larva. In Fig. 176 the transverse commissure of the ganglia of the tenth segment is cut and in Fig. 175 the short longitudinal commissures between the tenth and eleventh segments are sectioned.   ×129.

REFERENCE LETTERS.

A. I, first antenna.
A. II, second antenna.
Ab., abdomen.
ag., antennal gland.
B. c., blood corpuscles.
B. S., blood sinus.
Br., branchia.
cp., carapace.
End., endoderm.
fg., foregut.
g. c., ganglion cell.
Hd., hypodermis.
Hg., hindgut.
l. f., lateral fiber-mass of brain.
Md., base of mandible.
Mes., mesoderm.
Mg., mesenteron.
Mu., muscle.
Mu. e., extensor muscles of abdomen.
Mu. f., flexor muscles of abdomen.
Mx., base of maxillæ.
Mxpd., base of maxillipeds.
n. c., neural cord.
of., optic fiber-mass of brain.
o. g., optic ganglion.
Pr., perineurium.
R. O., reproductive organ.
sog., brain.
t. c., transverse commissure.
g. c., wandering cells.

Plate XLIX.

ALPHEUS

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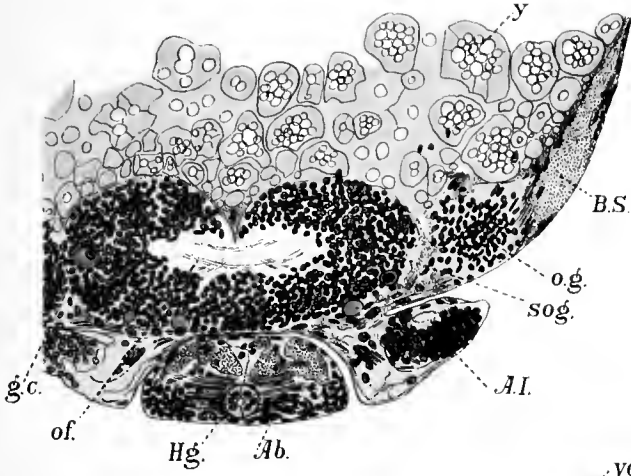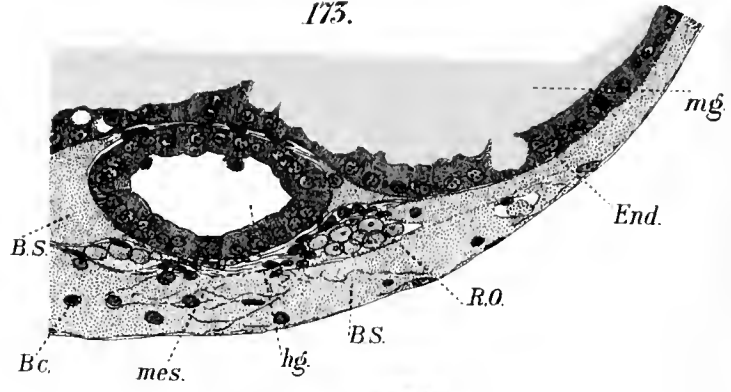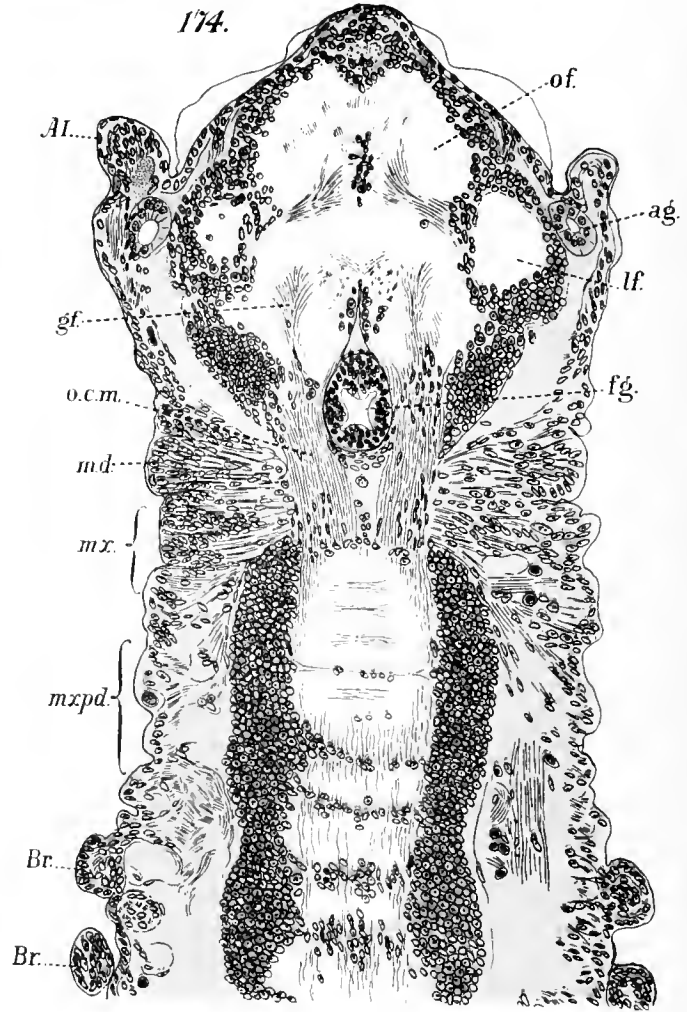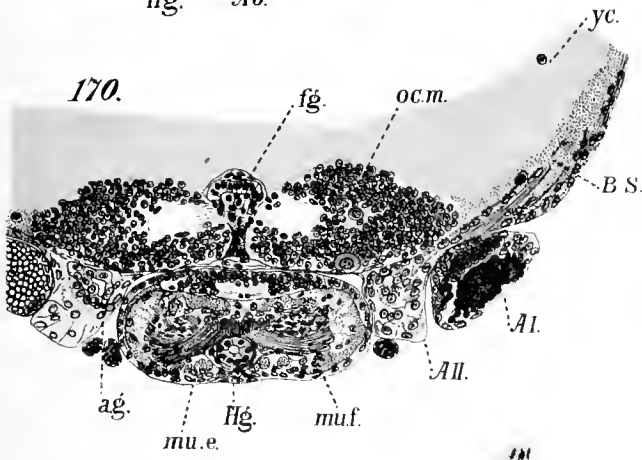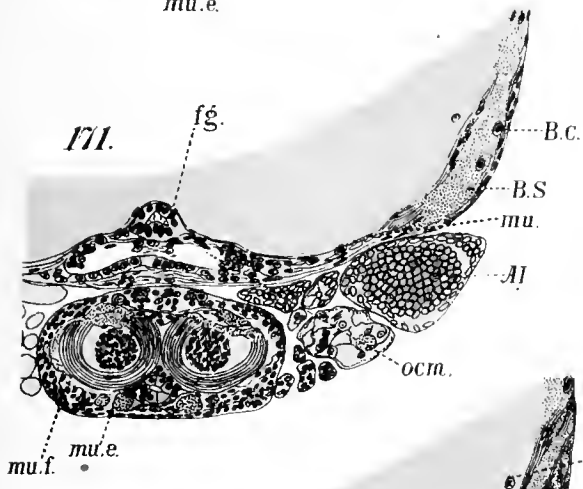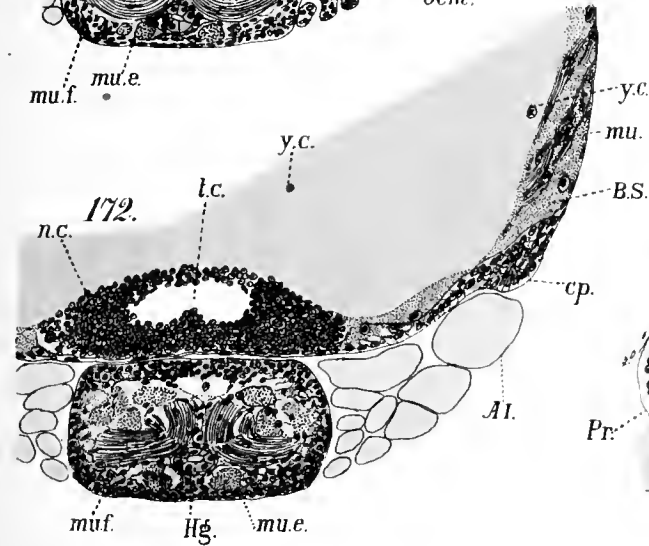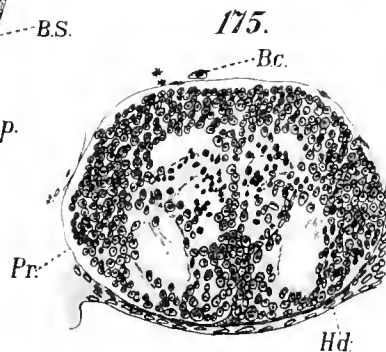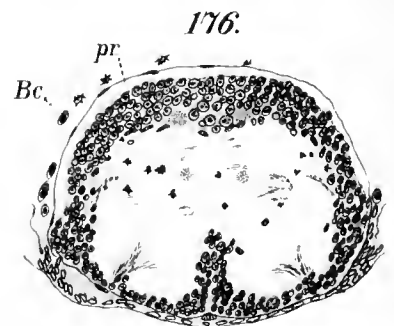
PLATE L.

(Stage XI.)

FIGS. 177–179, 181, 182. Serial transverse sections of the embryo of *Alpheus heterochelis*, which is nearly ready to hatch. The shell is somewhat diagramatically represented and appears thickened in Fig. 182, owing to a coagulable substance beneath it. The cells represented in the yolk in Fig. 182 appear to be endoderm cells, which have become mechanically detached from the walls of the mesenteron. ×74.

FIG. 180. Nearly median longitudinal section through a similar embryo. The endodermal lining of the mesenteron is not yet nearly completed. ×74.

REFERENCE LETTERS.

Ab, *VI*, ganglion of sixth abdominal appendage.
ag., antennal ganglion.
ans., anus.
ch. ex., external chiasma.
ect., ectoderm.
end., endoderm.
fg., foregut.
gma., anterior gastric muscle.
H., heart.
hg., hindgut.
hy., hypodermis.
lf., lateral fiber-mass of brain.
mg., mesenteron.
mg.[1] *mg.*[3] of other figures, posterior lobe of midgut.
mu. f., flexor muscles of midgut.
mu. e., extensor muscles of midgut.
oem., oesophageal commissure.
o. pd., optic peduncle.
Ret., retina.
sog., brain.
T., telson.
1–4, ganglia of eye-stalk.
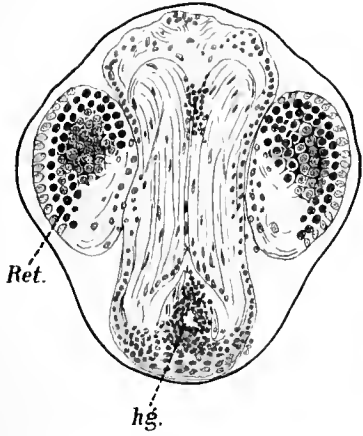
Plate L.
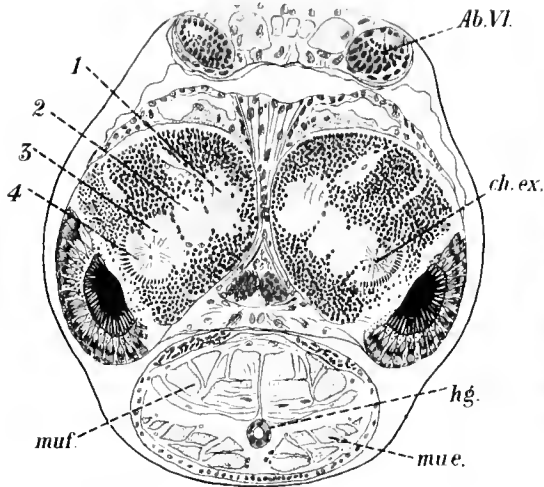
Fig.178

Fig.177.

Fig.179.

Fig.180.

Fig.181.

Fig.182.

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ALPHEUS HETEROCHELIS.
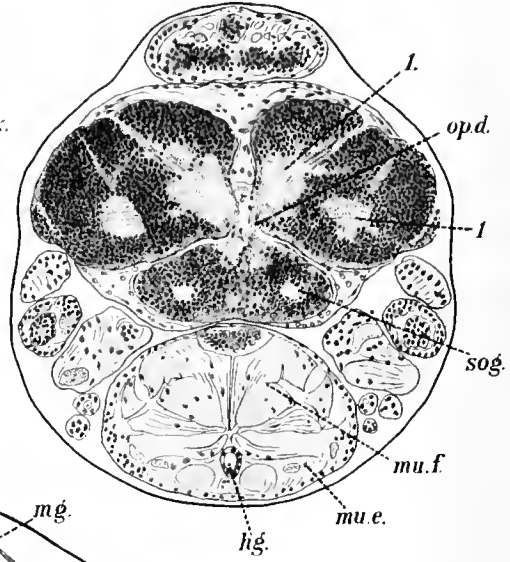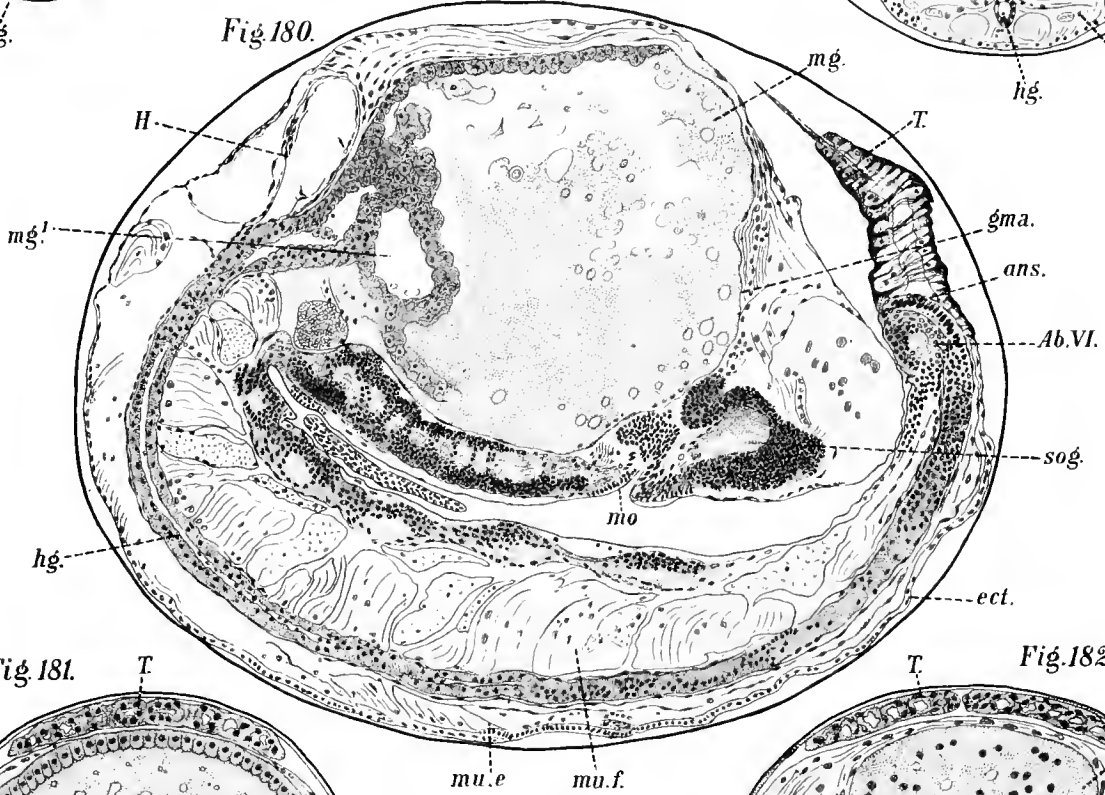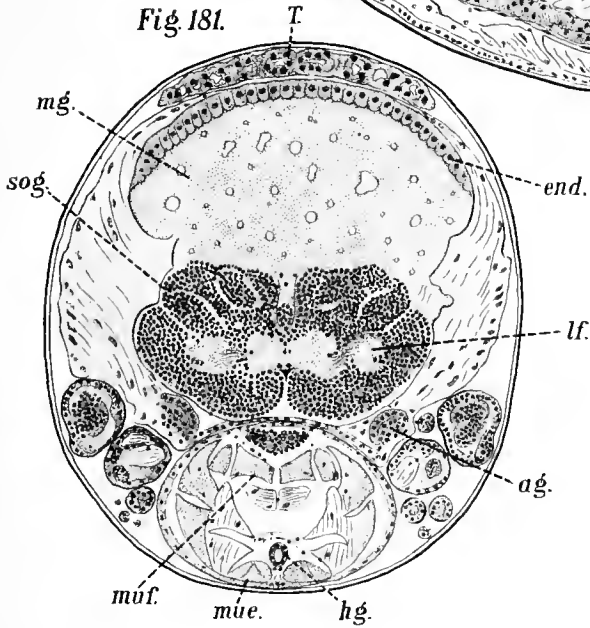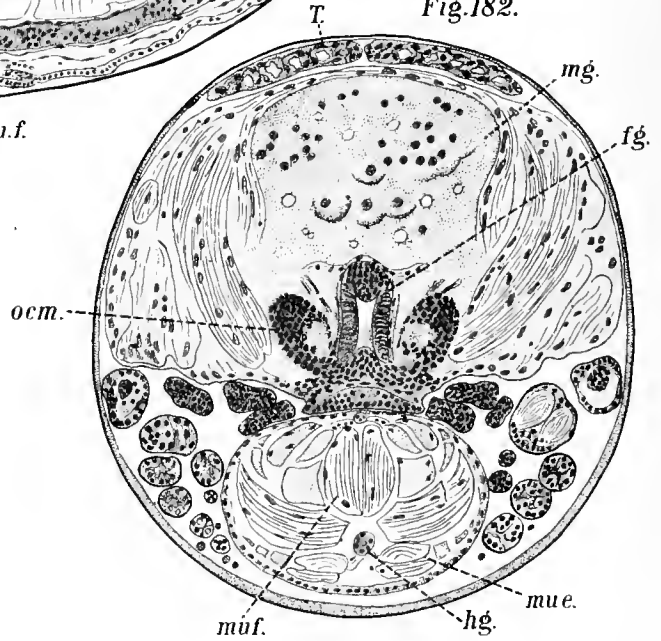
Plate LI.

(Stage XI.)

Figs. 183–186. Continuation of series of transverse sections of embryo begun on Plate L.   ×74.

Fig. 187. Part of sagittal section of similar embryo, cutting eyestalk somewhat obliquely.   The specimen was depigmented in nitric acid.   The distal retinular cells, occupying the spaces (*Pg. c.*) between the peripheral ends of the cones, are not represented.   ×305.

REFERENCE LETTERS.

ac. P., accessory pigment cells.
ad. m., adductor of mandible.
a. sa., superior abdominal artery.
bg., branchiostegite.
b. v., blood vessel.
c . crystalline cone.
cg., corneagen.
ect., ectoderm.
end., endoderm.
fg., foregut.
H., heart.
hy., hypodermis.
imb., intercepting membrane.
mg., midgut.
mg.³, posterior lobe of midgut.
Mu., muscle of eyestalk.
Mu. e., extensor muscles of abdomen.
Mu. f., flexor muscles of abdomen.
o. c. m., œsophageal commissure.
Pg. C., position of distal retinular cells.
Ps., pericardial sinus.
Rtu., proximal retinular cells.
Rtu.¹, nuclei of proximal retinular cells.
3, 4, ganglia of eyestalk.
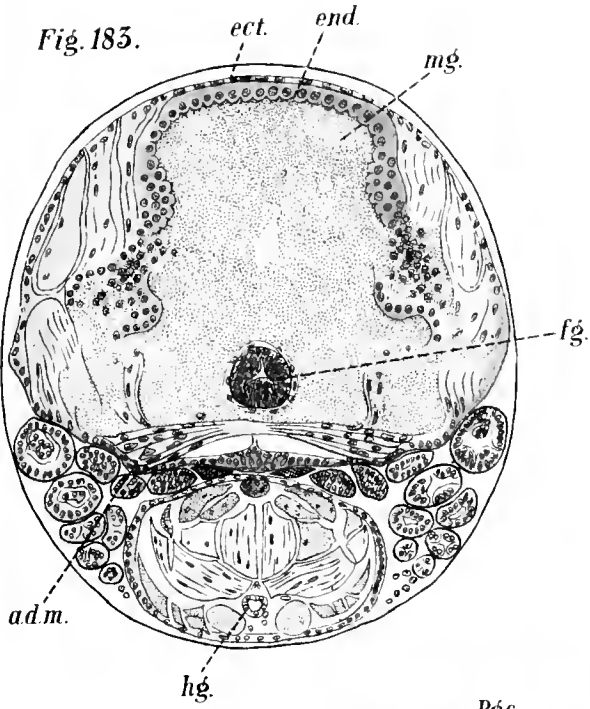
Plate LI.

Fig. 183.

Fig. 184.

Fig. 185.

Fig. 186.

Fig. 187.

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ALPHEUS
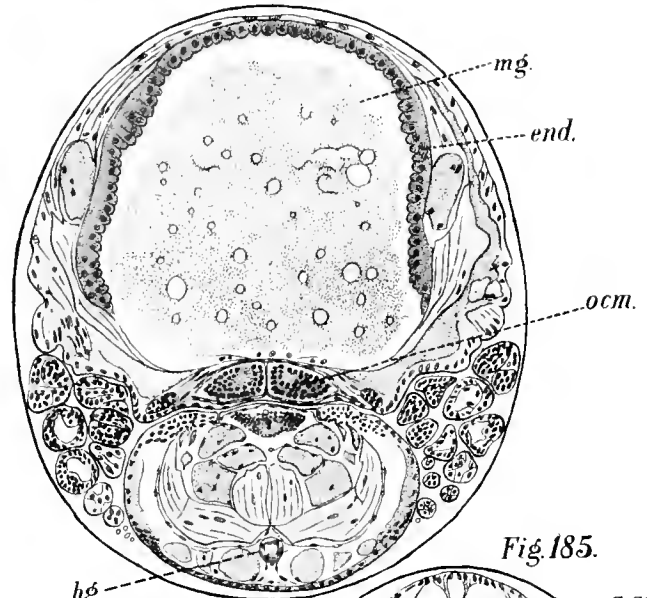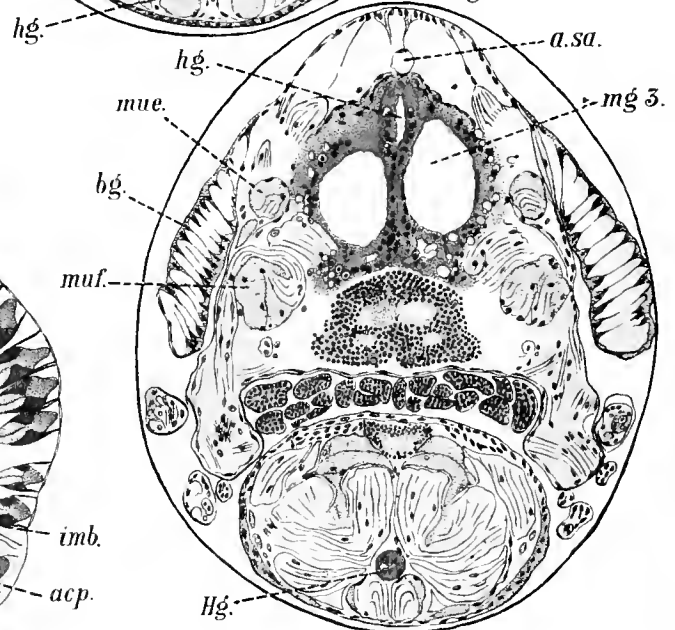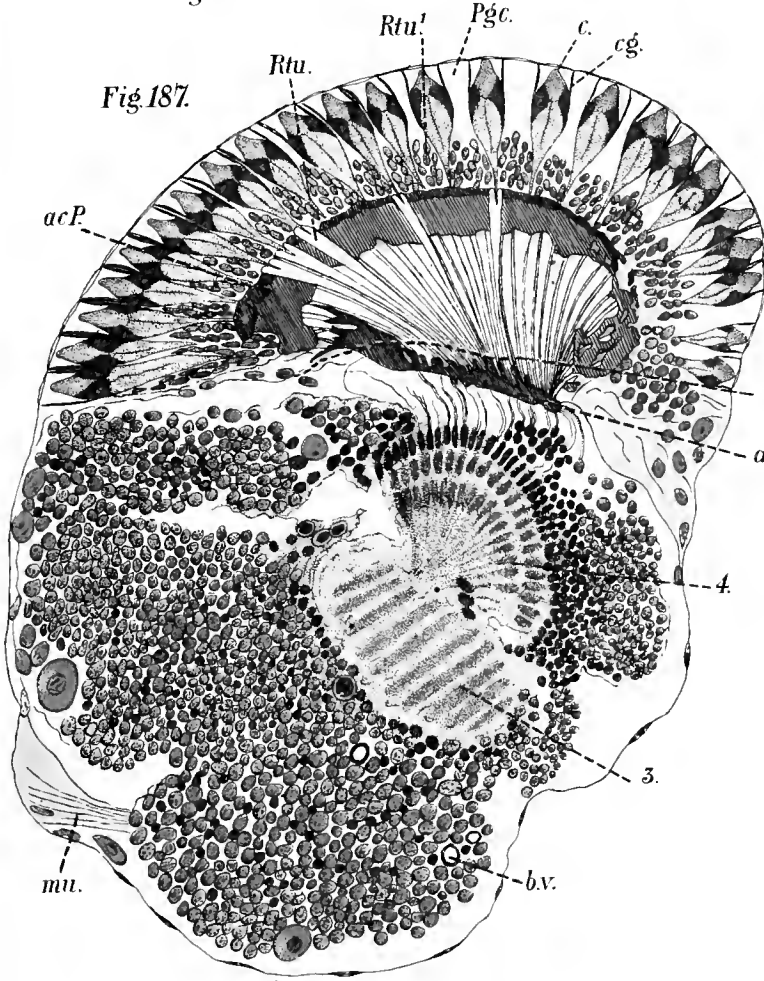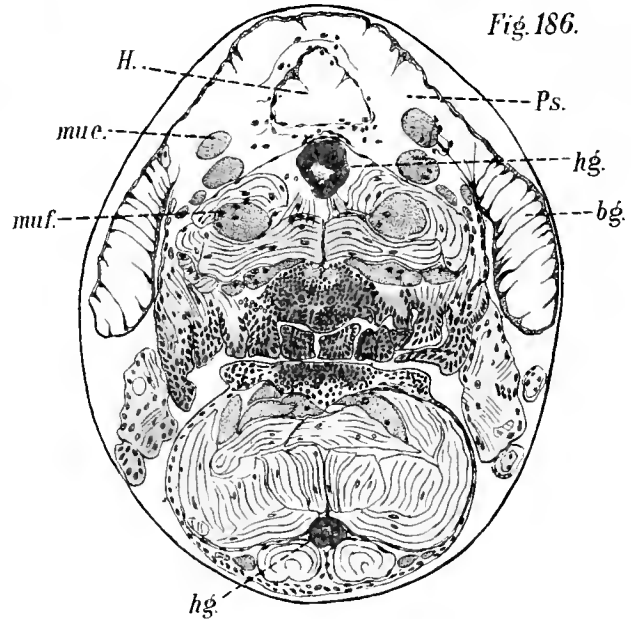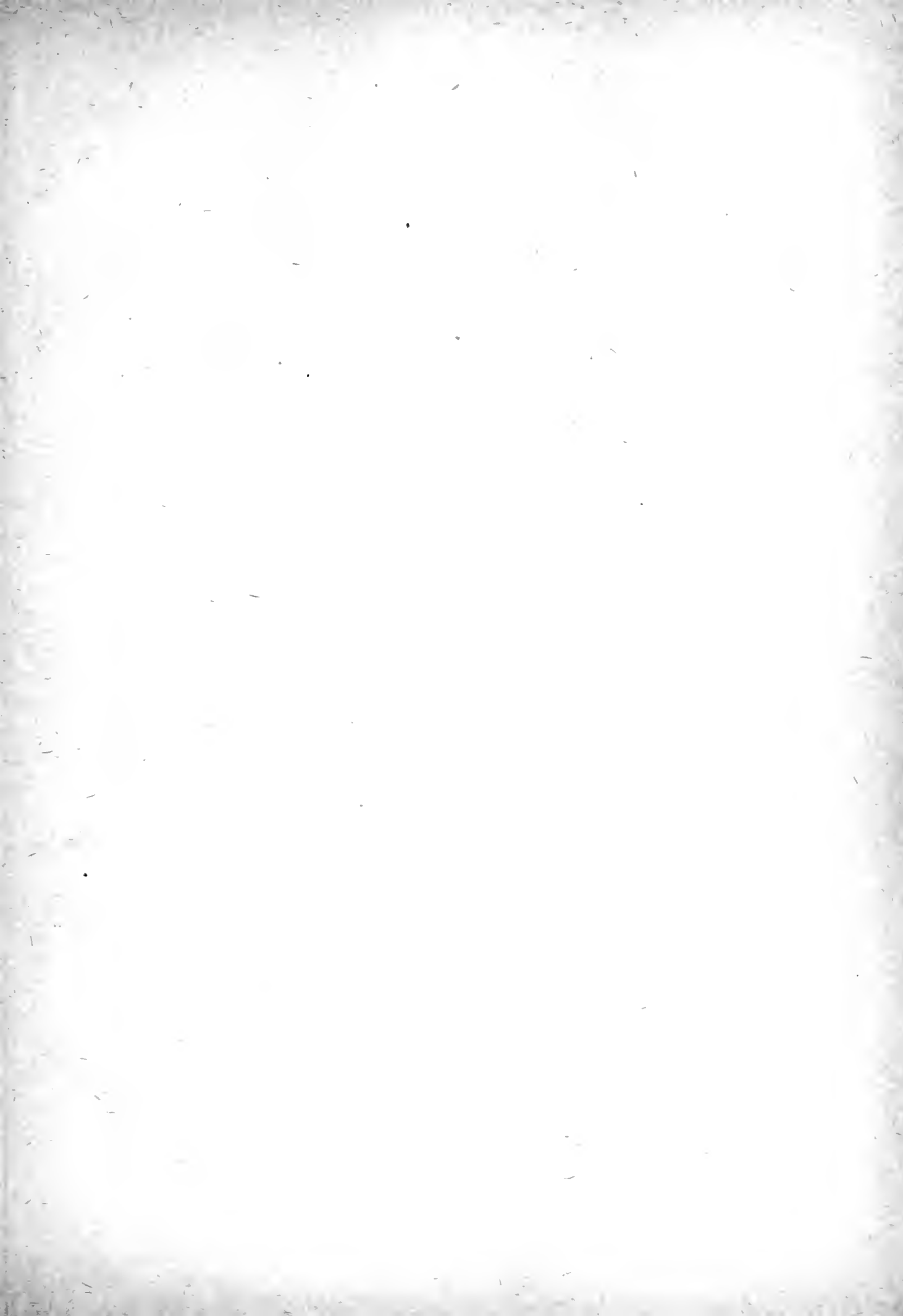
PLATE LII.

FIGS. 188, 189. Parts of transverse serial sections through the embryo of *Palæmonetes vulgaris*, at the stage when pigment is just appearing in the eyes. In the anterior section (Fig. 188) the retinogen is a unicellular layer. ×305.

FIGS. 190–191. Parts of serial transverse sections through the brain, the optic ganglia, and eye of an embryo of *Alpheus heterochelis*. In the anterior section (Fig. 190) the clusters of cells which represent the ommatidia are well shown. Numerous ganglion cells are dividing. ×305.

FIG. 192. Part of transverse section through eye, optic ganglion, and brain at a later stage. ×305.

REFERENCE LETTERS.

A. I, first antenna.
Ab., abdomen.
cc., crystalline cone cells.
imb., intercepting membrane.
mes., mesoderm.
Ret., retina.
rtl.⁸, rudimentary eighth proximal retinular cell.
sog., brain.
T., telson.
X., stratum of large ganglion cells.
1, 3, 4, proximal, external middle, and distal segments of optic ganglion.
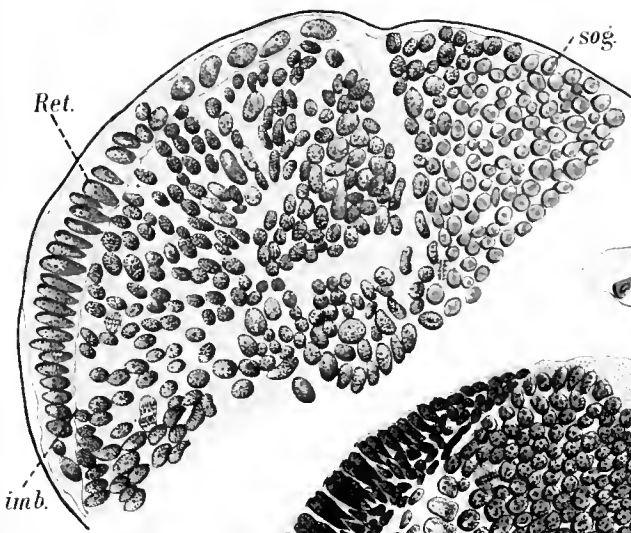
Plate LII.

Fig. 188.

Fig. 189.

Fig. 190.

Fig. 191.

Fig. 192.

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ALPHEUS AND PALAEMONETES.
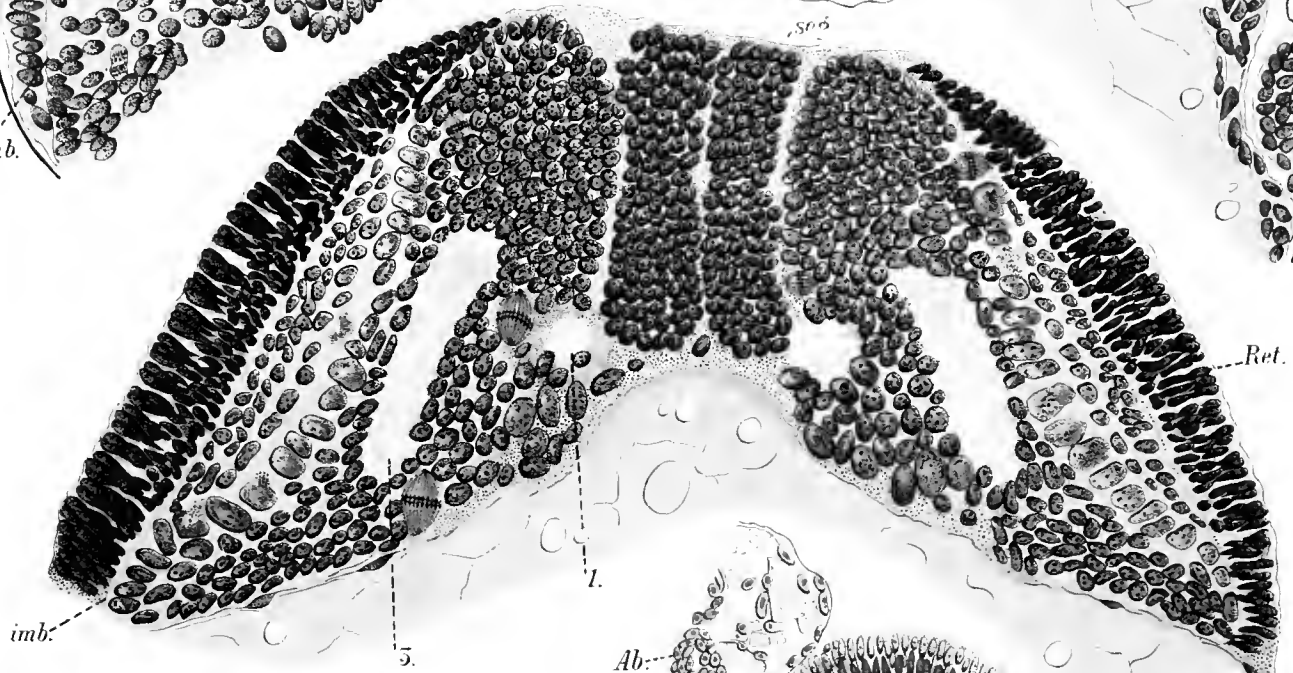
Plate LIII.

Fig. 193. Part of transverse section through an embryo of *Alpheus saulcyi*, which is nearly ready
to hatch, showing the third left branchia covered by the branchiostegite.   ×289.

Fig. 194. Part of sagittal section of eyestalk of a slightly younger embryo.   ×289.

Fig. 195. Part of transverse section, showing branchia, of the third larva of *Alpheus saulcyi* (twenty-
four hours old).   ×289.

Fig. 196. Nearly median longitudinal section of first larva of same.   The anterior lobes of the
midgut (mg^1) still contain unabsorbed yolk.   Compare Pl. XXI, Fig. 1.   ×58.

Fig. 197. Part of transverse section, showing the papilla, which bears the median eye in the first
larva of same.   ×289.

Fig. 198. Transverse section of first larva, cutting the lateral fiber balls of the brain, the anterior
lobes of the midgut, and the green gland.   ×289.

Fig. 199. Part of transverse section through an advanced embryo of *Alpheus saulcyi*, parasitized
by a fungus, most of the cells of which are encysted.   From brown sponge, Abaco,
Bahama Islands.   v, Appendix II.   ×186.

REFERENCE LETTERS.

ab., abdomen.
Ab. VI, sixth abdominal appendage.
acp., accessory pigment cells.
ag., green gland.
ag. s., end sac (?) of gland.
as. a., superior abdominal aorta.
bg., branchiostegite.
b. s., B. S., blood space.
br.³, branchia of third left ambulatory limb.
cc., crystalline cone cells.
cg., corneagen.
cl., lens.
co., crystalline cone.
cs., cs.¹⁻², cysts of parasite.
cs.³, smaller, naked cells of parasite.
g.¹ ²⁰, segmental ganglia.
gf., fiber-mass of second antenna.
gma., anterior gastric muscle.
H., heart.
Hd., hypodermis.
Hg., hindgut.
Lb., labrum.
l. c., longitudinal commissure.
mg., midgut.

mg.¹, anterior lobes of midgut.
mg.², lateral lobes of midgut.
mg.³, posterior lobes of midgut.
mo., mouth.
ms., masticatory stomach.
mu. e., extensor muscles of abdomen.
mu. f., flexor muscles of abdomen.
n. c., neural cord.
oc., ocellus.
oe., œsophagus.
O. G., o. g., optic ganglion.
of., optic enlargement of brain.
op., ophthalmic artery.
ps., pericardial sinus.
pr., perineurium.
R., rostrum.
Ret., retina.
rtl., nucleus of proximal retinular cell.
sog., brain.
Sp., parasitic growth.
St. s., sternal blood sinus.
T., telson.
y., yolk.

Plate LIII

ALPHEUS

Plate LIV.

Fig. 200. Ommatidium of eye of small adult *Alpheus sauleyi* (from brown sponge); pigment removed by nitric acid. ×294.

Figs. 201–204. Transverse sections through four adjacent ommatidia of first larva of same. In Fig. 201 the corneagen is cut, and in Fig. 202 the nuclei of the cone mother cells. In Fig. 204 the rhabdom is sectioned and the seven proximal retinular cells. ×294.

Figs. 205–208. Transverse sections through adjacent ommatidia of the adult eye, taken at various levels. Fig. 205, the deepest section, shows the peculiar seven-pronged figure of the rhabdom. The proximal retinular cells appear in sections, as if fused together. ×294.

Figs. 209–211. Transverse serial sections through the first larva of *Alpheus sauleyi*. ×74.

REFERENCE LETTERS.

A. I, first antenna.
A. II, second antenna.
a. cp., accessory pigment cell.
ac. pn., nucleus of accessory pigment cell.
ao., ear.
Bm., intercepting or basement membrane.
cc., crystalline cone cells.
cg., corneagen.
cl., lens.
Co., co., crystalline cone.
cmb., cone membrane.
hd., hypodermis.
me., membrane of distal retinular cells.
nf., nerve fibers.
oc., ocellus.
og., optic ganglion.
of., optic enlargement of brain.
pap., papilla of ocellus.
p. g. c., distal retinular cells.
R., rostrum.
Rb., rb., rhabdom.
Ret., retina.
rtl., proximal retinular cells.
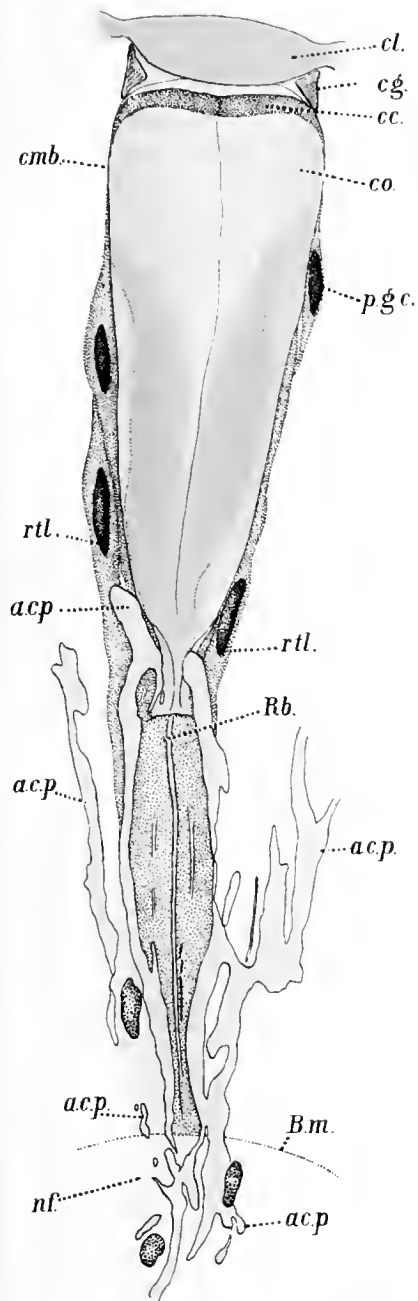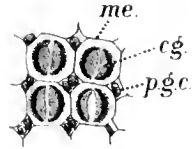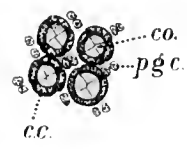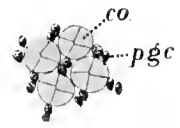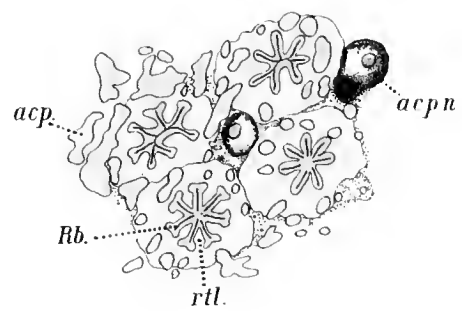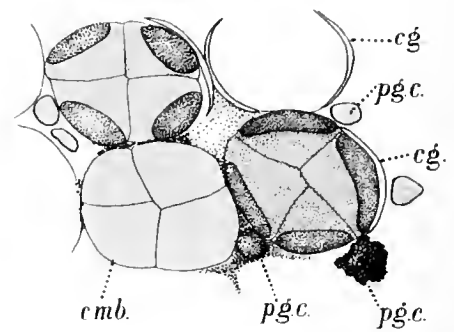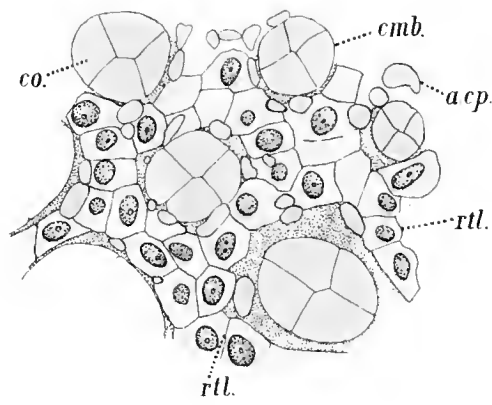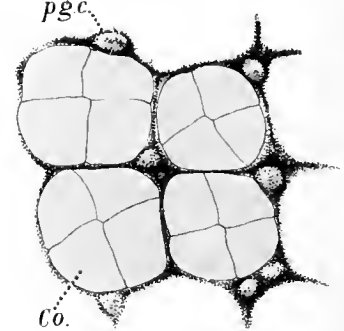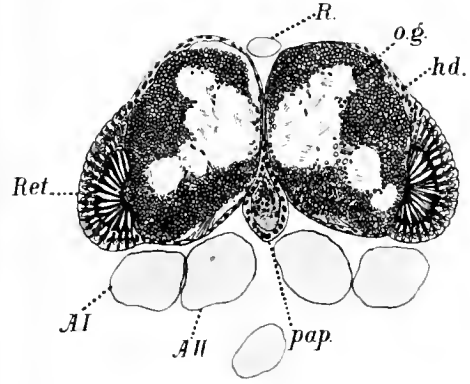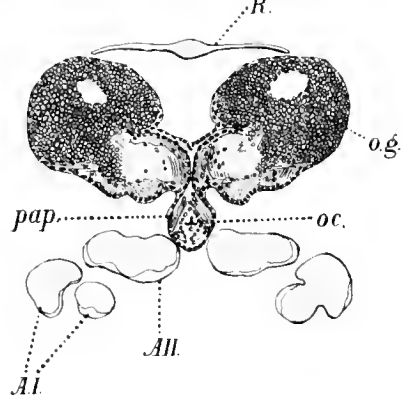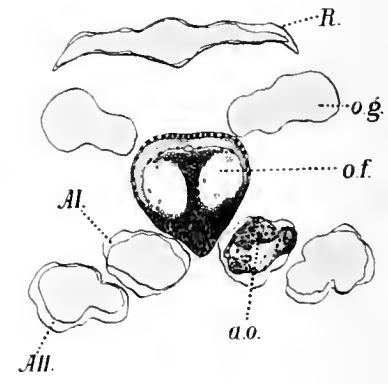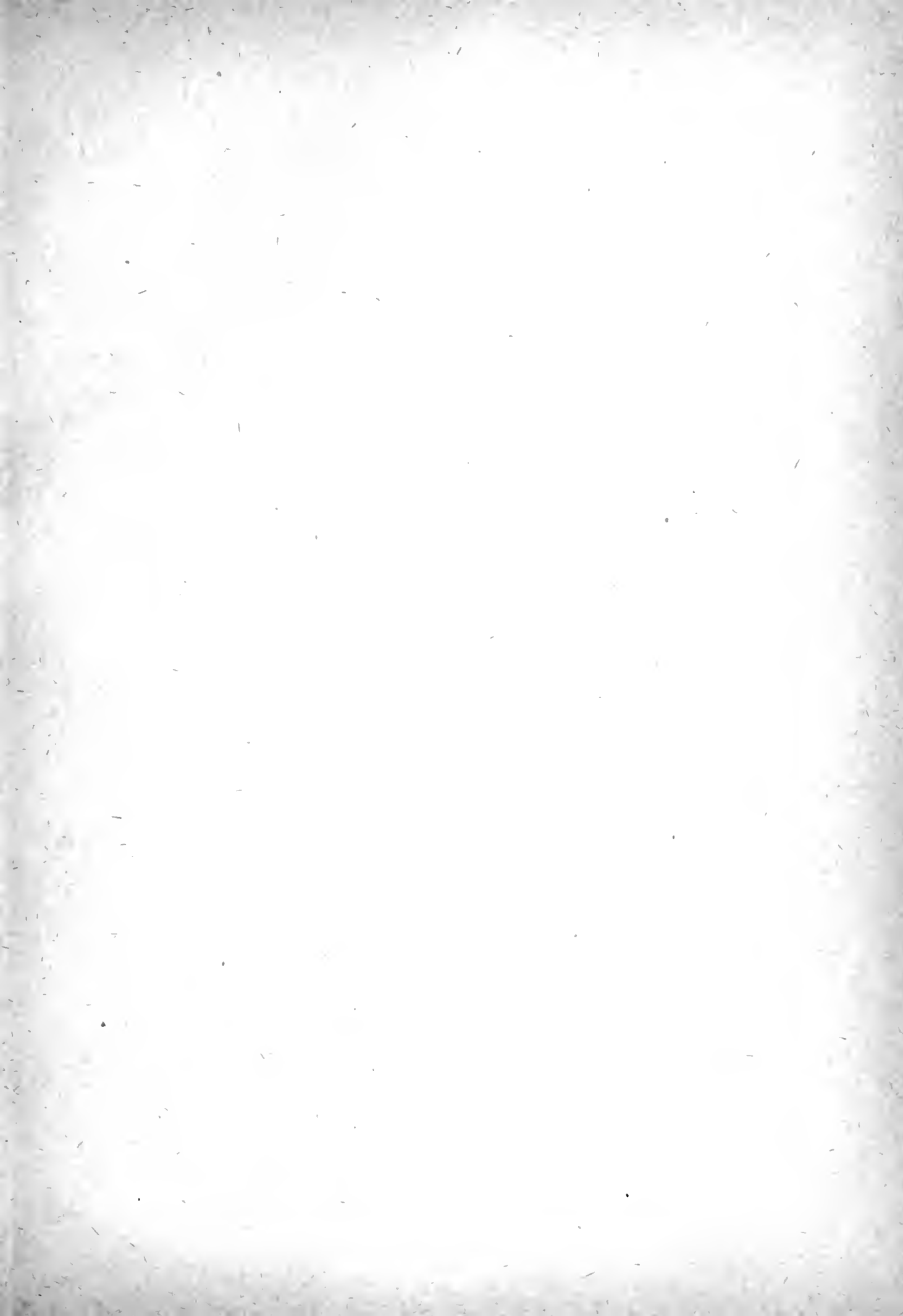
Plate LIV.

ALPHEUS

PLATE LV.

(Stage XII.)

FIGS. 212–223. Transverse serial sections of the first larva of *Alpheus sauleyi* from the same individual as Figs. 209–211, excepting Figs. 222, 223. ×73.

REFERENCE LETTERS.

A. II, second antenna.
ad. m., adductor of mandible.
ag., green gland.
af., antennular fiber-mass of brain.
ao., ear.
a. op., ophthalmic artery.
Bg., branchiostegite.
B. gl., gland-like body.
B. S., blood sinus.
fg., foregut.
fo., fiber-mass continued into œsophageal commissure.
gf., antennal fiber-mass.
gs., lateral pouch of masticatory stomach.
Lb., labrum.
lf., lateral fiber-mass of brain.
Md., mandible.
Mg., midgut.
Mg¹., anterior lobe of midgut.
Mg²., lateral lobe of midgut.
Mp., septum between anterior lobes of midgut.
M. S., masticatory stomach.
Mts., metastoma.
Mx. 1, first maxilla.
Mxpd. I, first maxilliped.
n. ag., antennal nerve.
n. an., antennular nerve.
oc., ocm., œsophageal commissure.
of., anterior fiber-mass and transverse commissure of brain.
p. V., pyloric valve of masticatory stomach.
st. s., sternal sinus.

Plate LX

FIRST LARVA OF ALPHEUS SAULCYI.
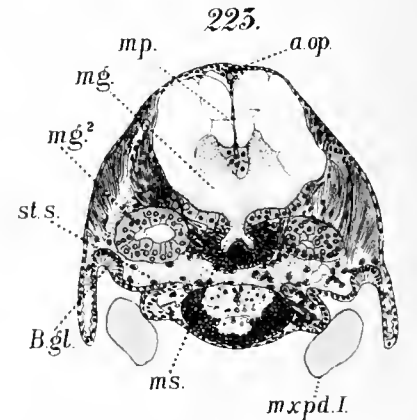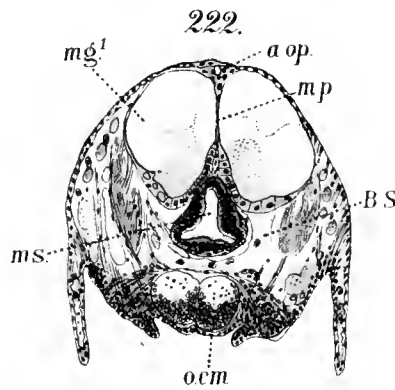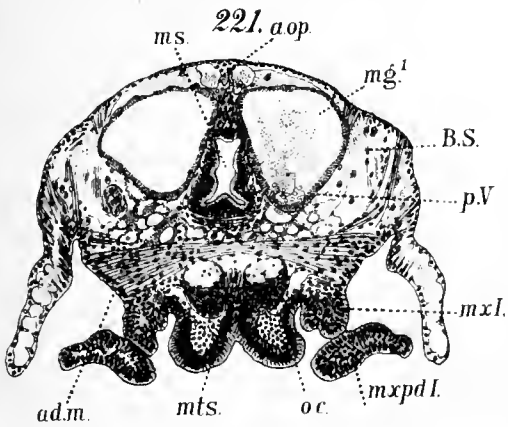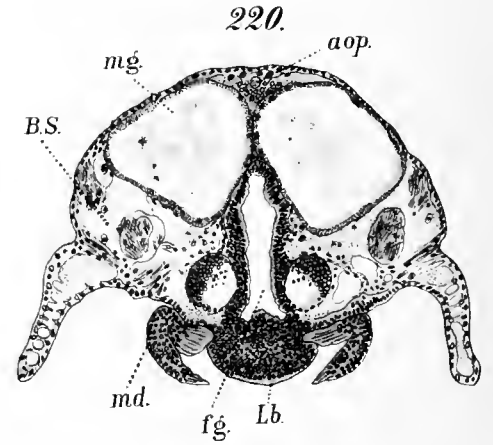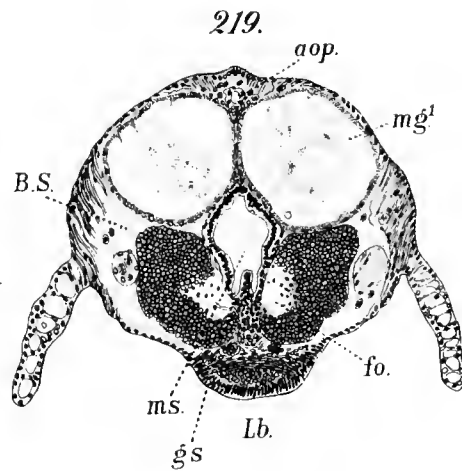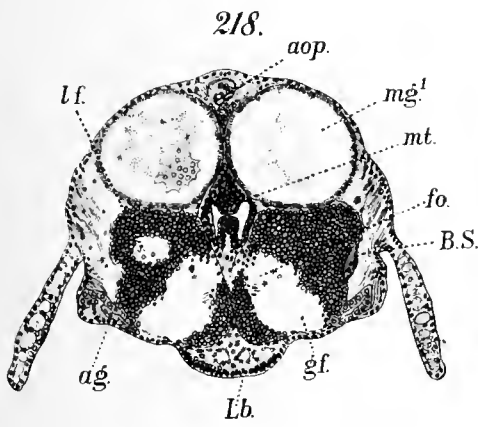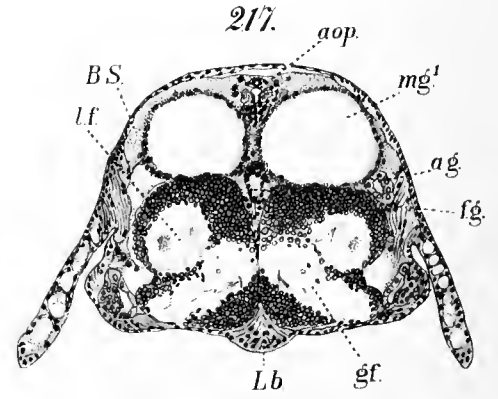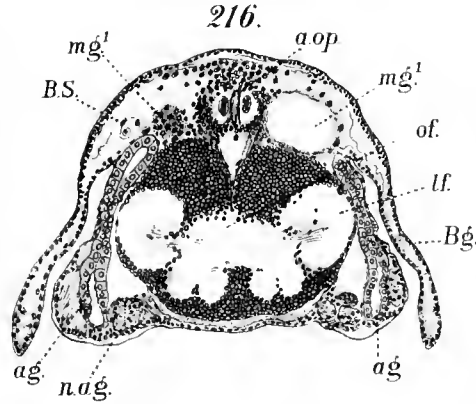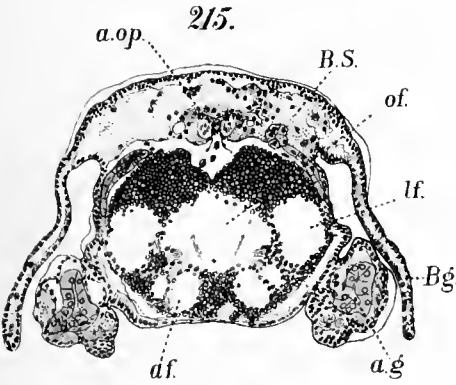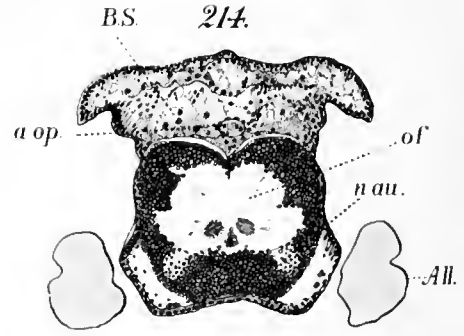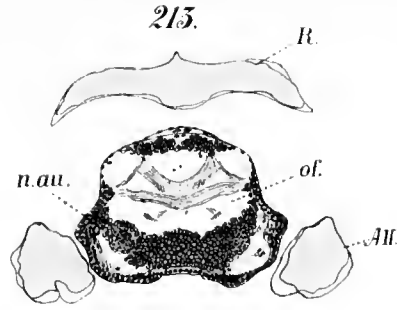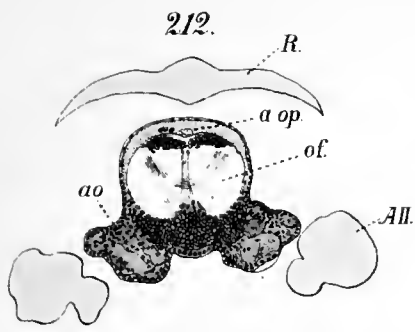
F.H. Herrick, del.

PLATE LVI.

(Stage XII.)

FIGS. 224-235. Serial transverse sections through the first larva, continued from Plate LV.   ×73.

REFERENCE LETTERS.

Ab. V, fifth abdominal appendage.
a. i. a., inferior abdominal aorta.
a. op., ophthalmic artery.
a. s. a., superior abdominal artery.
bg., branchiostegite.
br., branchia of ambulatory appendage.
B. S., blood sinus.
gg. $^{1-3}$, middle, ventral, and dorsal lobules of posterior lobe of midgut.
H., heart.
hg., hindgut.
hy., hypodermis.
lc. th.-ab., longitudinal commissures uniting last thoracic with first abdominal ganglia.
Mg., midgut.
Mg. ^{2}, lateral lobe of midgut.
Mg. ^{3}, posterior lobe of midgut.
Ms., masticatory stomach.
Mu. e., extensor muscles of abdomen.
Mu. f., flexor muscles of abdomen.
Mxpd. I-III, first to third maxillipeds.
pleu., pleuron.
ps., pericardial sinus.
Th. I-V, first to fifth ambulatory limb.
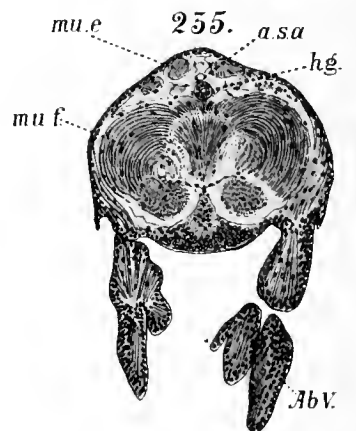
Plate LXI

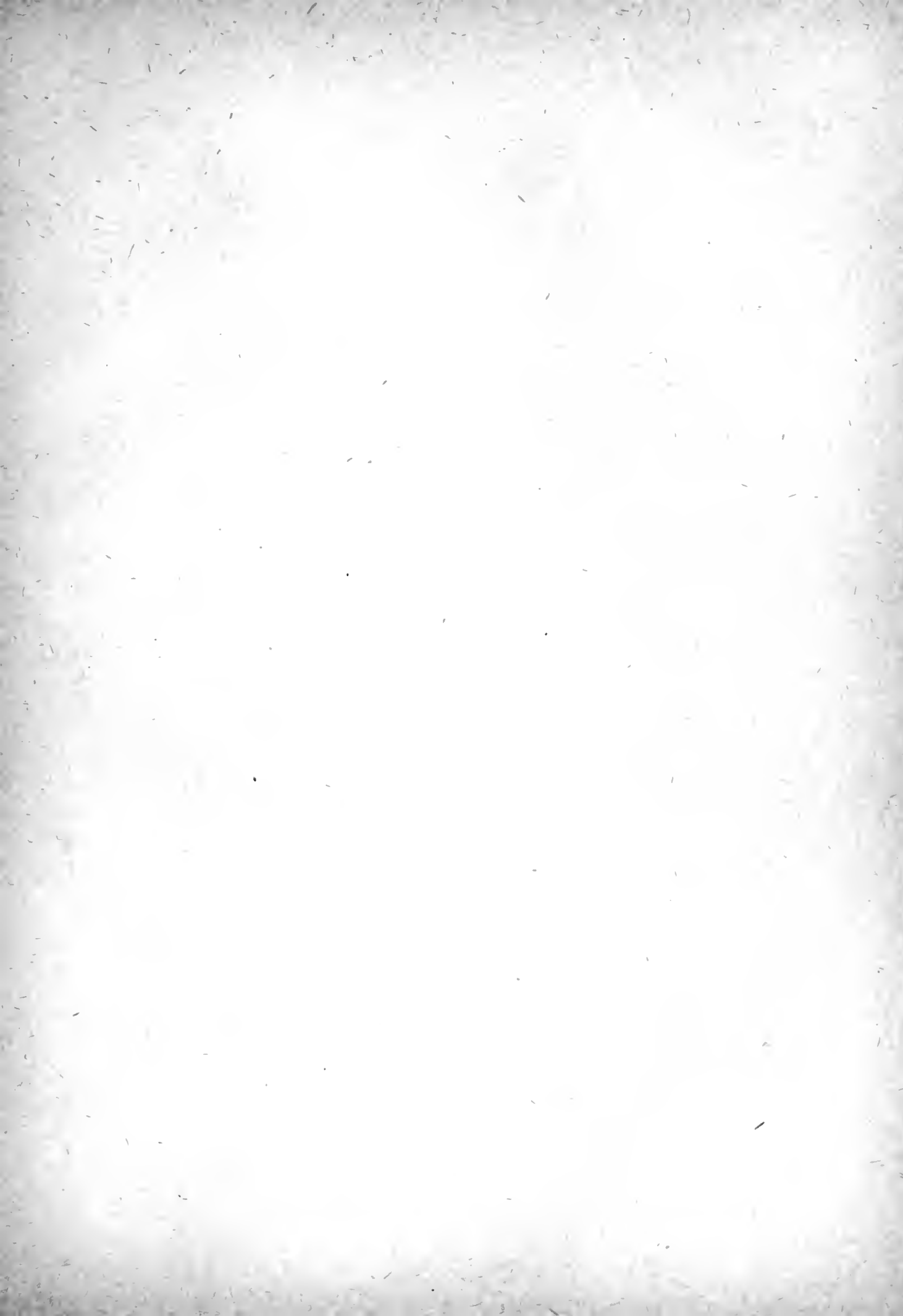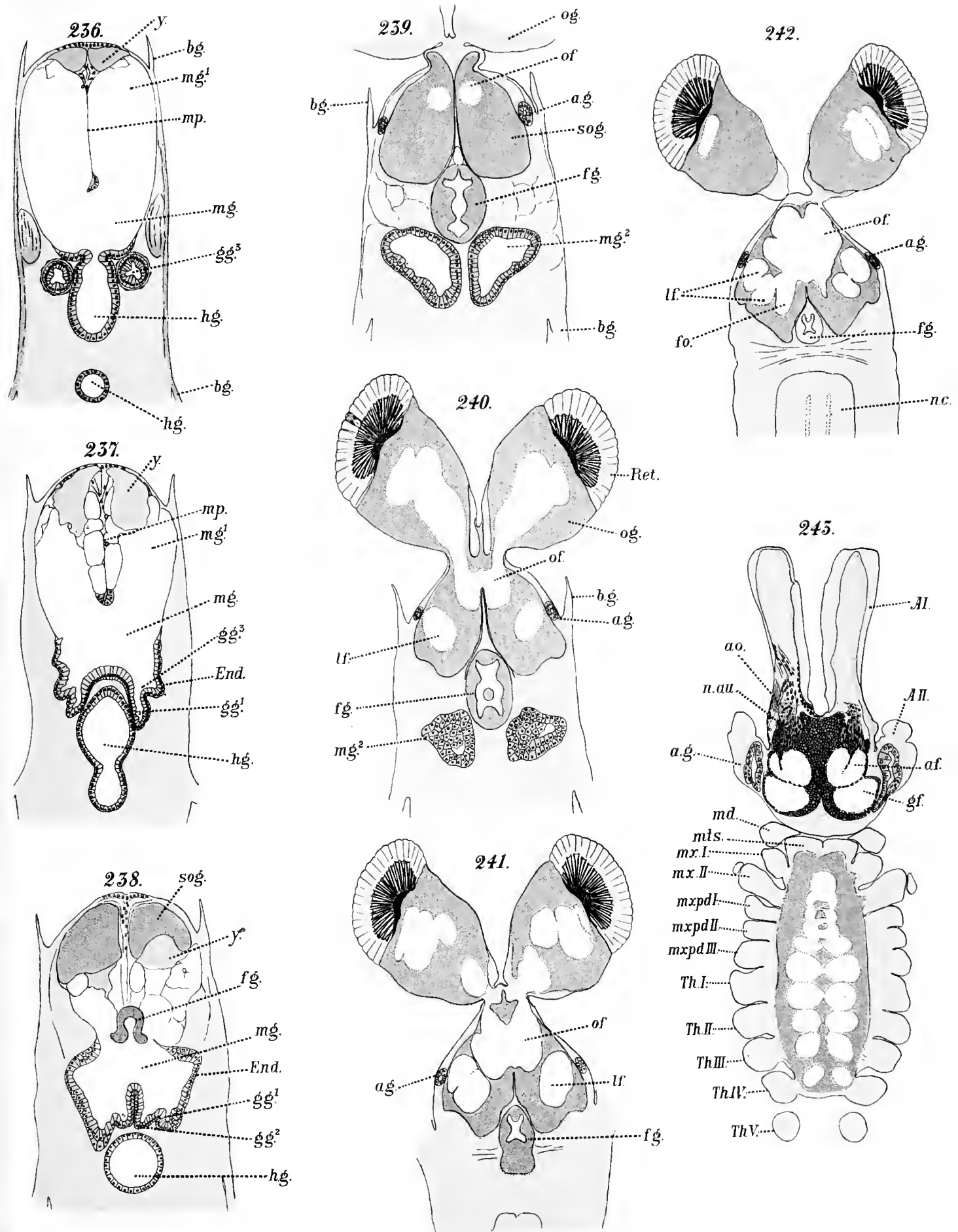F.H.Herrick, del

FIRST LARVA OF ALPHEUS SAULCYI.
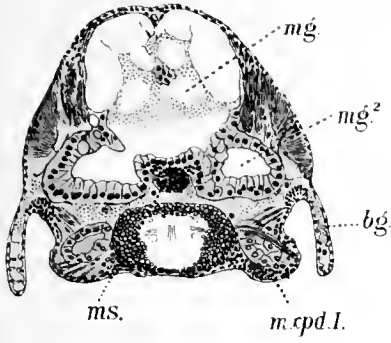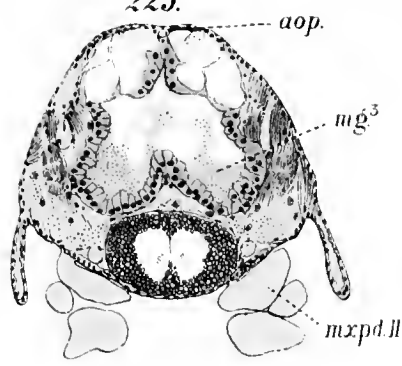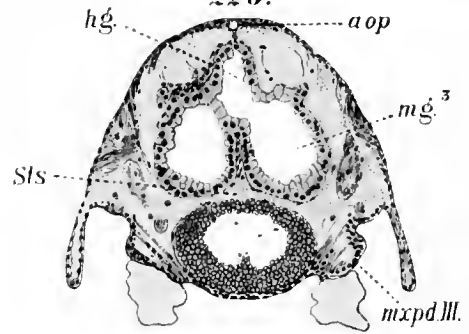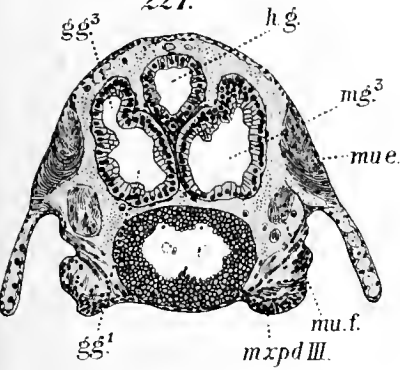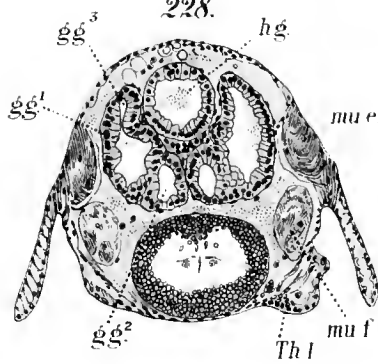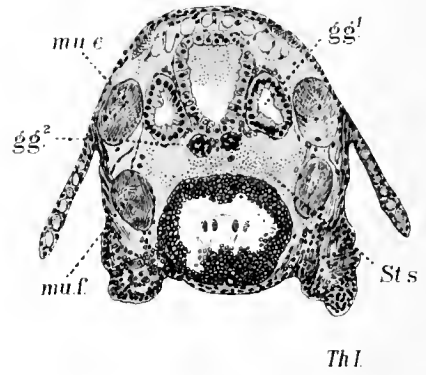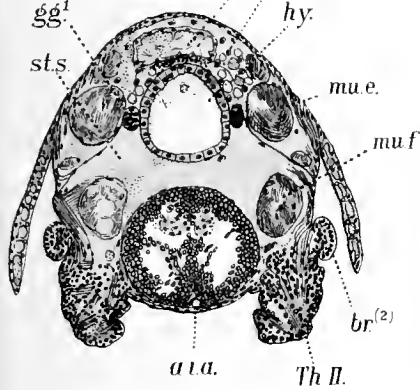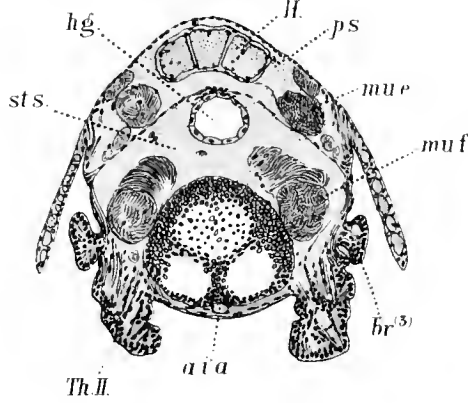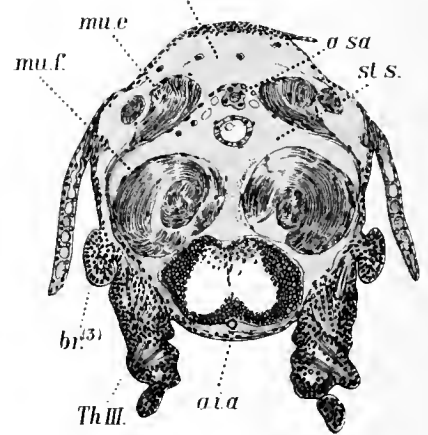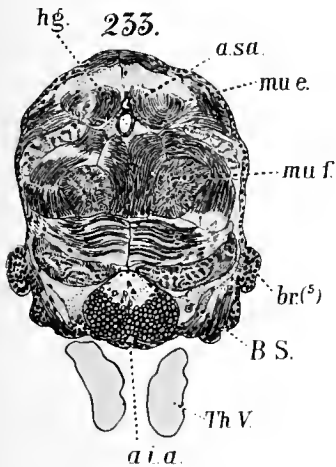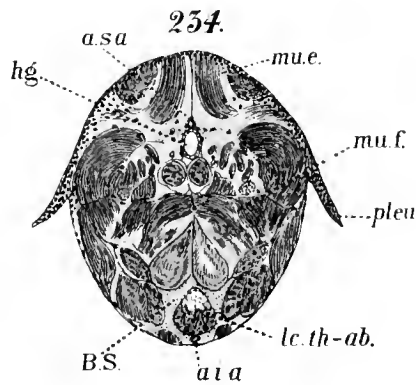
PLATE LVII.

(Stage XII.)

FIGS. 236–245. Horizontal sections of first larva, illustrating further the anatomy of the alimentary tract and the nervous system.   ×57.

REFERENCE LETTERS.

A. I, II, first and second antenna.
ag., green gland.
af., antennular fiber-mass.
ao., ear.
bg., branchiostegite.
End., endoderm.
fg., foregut.
fo., fiber-substance of œsophageal commissure.
gf., fiber-mass of second antennæ.
gg. $^{1-3}$, middle, ventral, and dorsal divisions of posterior lobe of midgut.
hg., hindgut.
lf., lateral fiber-mass of brain.
Md., mandible.
Mg., midgut.
Mg.[1], lateral lobe of midgut.
Mp., partition between anterior lobes of midgut.
Mts., metastoma.
Mr. I, II, first and second maxillæ.
Mxpd. I–III, first to third maxillipeds.
n. an., antennular nerve.
n. c., ventral nerve-cord.
of., anterior fiber-mass of brain.
og., optic ganglion.
Ret., retina.
Th. I–V, first to fifth ambulatory limbs.
y., yolk.

Plate LVII.

F.H.Herrick, del.

FIRST LARVA OF ALPHEUS SAULCYI.