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ON THE CARAPAX AND STERNUM OF DECAPOD CRUSTACEA.*

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The determination of the homology of the carapax and sternum among the Crustacea is rendered difficult by the endless variety of forms assumed by their constituent parts, and the consequent perplexing differences in the relation of these parts to each other. Before stating the conclusions and arguments in favor of the solution at which I have arrived after a study of several forms chiefly of the Decapod type, it may conduce to clearness to give in a few words, the main facts and conclusions of the previous writers on this subject.

Although Huxley (1) is the latest writer who expresses views on the homologies of the Crustacean carapax, he offers no new explanation but adheres to the old conception of a fusion of the terga of the fourteen anterior somites into a carapax. He writes (in describing *Astacus fluviatilis*) "The carapace, therefore, corresponds in position with the terga and tergal halves of the pleura of all the somites which are thus reflected into it, and these somites

* This paper was prepared in the Mus. Comp. Zoöl., under the direction of Prof. W. Faxon, in the college year 1882–83.

include all, without exception, from the last thoracic to the ophthalmic. * * * " At the sides of the antennulary and antennary somites the rostral prolongation of the carapace is the direct continuation outward of the epimera of these somites, and there is nothing to be compared to an apodeme, but the sternum of the ophthalmic somite after giving off the lamella which forms the inferomedian rostrum, is prolonged on each side of the middle line backwards and outwards into a free, expanded, thin, calcified process which applies itself against the carapace by its upper surface, and by its under surface gives attachment to the anterior gastric muscles. * * * On the dorsal surface there is no indication of any division of the carapace into terga corresponding with the sterna of the somites, but it is marked by a well-defined curved groove. * * * " The accompanying diagram explains his views of the somite in *Astacus*.

Milne-Edwards(2) considers the carapax in the majority of the Decapods to consist of a single piece, part of

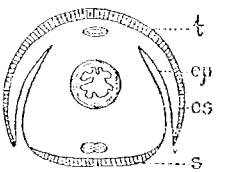

Diagram of crustacean segment; *ep*, epimerum; *es*, episternum; *s*, sternum; *t*, tergum.

which is furnished by the antennary and mandibulary somites respectively. This author states, that while in Squilla the carapax belongs almost entirely to the antennary segment, in Limnetis on the other hand, it pertains chiefly to the mandibulary somite. Furthermore, the tergum of the antennulary segment is entirely wanting in the Deca-

pods. He continues (*loc. cit.*, p. 233), "J'ai fait voir, dans un autre écrit que le carapace, lors même qu'elle recouvre la totalité du thorax aussi bien que toute la portion céphalique du corps doit être considérée comme une portion de la tête dont une portion du squelette s'est développée d'une manière excessif, et a chevauché en avant et en arrière sur les parties voisines ; j'ai établi aussi qu'elle appartenait au système des pièces tergales, et qui celles-ci n'étaient fournies ni par les anneaux ophthalmique ou antennulaire, ni par les zoonites céphaliques postérieures. Il me paraissoit probable qu'elle dépendait de l'anneau antennaire ou de l'anneau mandibulaire, c'est-à-dire du troisième ou du quatrième anneau de la tête, mais qu'elle ne procédait que d'un seul ces zoonites. Les faits dont il vient d'être question permettent de rectifier une partie de ces conclusions, et d'arriver à une approximation plus grande de la vérité. Effectivement l'arceau céphalique de la carapace des Décapodes me semble ne pouvoir être qu'une dépendence de l'anneau antennaire, tant à raison connexions avec les autres pièces du squelette tégumentaire, qu'en conséquence de l'origine des nerfs dont ses parties molles sont pourvues, puisque ces nerfs proviennent des ganglions cérébroides ou sous-œsophagiens, tandis que les nerfs appartenant au appendices du zoonite suivant, ou anneau mandibulaire, naissent des ganglions post-œsophagiens. Mais l'arceau scapulaire ou postérieur de la carapace de ces Crustacés doit pour des raisons analogues, être considéré comme étant étranger au troisième zoonite céphalique, et comme appartenant à l'anneau mandibulaire. La carapace serait donc un organ plus complexe que je ne le supposait d'abord, et serait formée par deux anneaux tergaux, dépendant du troisième et du quatrième anneaux de la tête, arceaux qui fournaient d'une indépendance presque complete chez les Paguriens et les Thalassines, mais ne seraient

représentés chez les Décapodes ordinaires que par un seul segment dorsal dû à l'ossification diffuse ou fusion des élémentes sclerodermique de toute la portion du squelette tégumentaire correspondant à ces deux arceaux. Mais chez les Crustacés inférieures, la carapace ne paraît avoir d'ordinaire une composition plus simple, et être formée tantôt par les analogues de l'arceau céphalique seulement, tantôt par les représentants de l'arceau scapulaire. Ainsi, chez les Squilles, la portion céphalique de la carapace est très-dévellopée ; mais toute la portion postérieure au scapulaire paraît manquer complétement, et chez les Limnadies, au contraire, l'espèce de coquille bivalve, qui tient lieu d'une carapace ordinaire, me paraît être due au développement excessif de la portion scapulaire seulement, et dépendre de l'anneau mandibulaire, ont peut-être même de l'un des zoonites suivant." Owen (3) reflects Milne-Edwards' views throughout as quoted above. Dana (4) differs from Milne-Edwards in that he considers the lateral (ventral) plates of the carapax of crabs to be true *terga* instead of epimera (*loc. cit.*, p. 27). He infers "that the epistome (or its anterior part) belongs to the second, or to the second and first normal segments, that is, to the antennulary or to the antennulary and ophthalmic segments. For convenience of reference I have compiled the following table from the author's statements of his views regarding the number of segments and what parts of each enter into the composition of the crab carapax.

1. Ophthalmic somite. Parts entirely wanting; appendages, however, *present*.

2. Antennulary somite. Sternum present (probably fused with the ophthalmic sternum into one piece); the other parts wanting; appendages present.

3. Antennary somite. The parts (sternum, tergum, episternal plate) present.

4. Mandibulary somite. The sternum, episternal plates, epimeral plates and tergum present.

After stating in a very clear manner the facts he had established, the author draws the following conclusions. The carapax of the Brachyura includes:

I. The first and second normal segments represented by the epistome, or its anterior position, and the inter-antennary septum.

II. The third normal segment, represented by the main body of the carapax, and the anterior portion of the prelabial plate or palate.

III. The fourth normal or mandibular segment represented by the posterior and outer part of the prelabial plate and the ventral pieces of the carapax.

Concerning the carapax of the Macroura the author again differs from Milne-Edwards in designating the lateral and posterior plates of the carapax of *Astacus mandibular terga* instead of epimera. After a careful comparative description of numerous forms both among the Macroura and the lower Crustacea (*loc. cit.*, pp. 32–37) in which he mentions several seemingly adverse cases, the author concludes that the origin of the carapax and the disposition of its parts are essentially the same throughout the class.

From the foregoing extracts it will be seen that Dana's views are in advance of those of the other investigators, but there yet remain several points of interest on which it is desirable to collect further evidence. Both Milne-Edwards and Dana have established with a high degree of probability the origin of the carapax from the terga of the mandibulary and antennary somites, but neither of them succeeded in finding a conclusive demonstration of the fact. In the very young *Squilla* the thoracic and abdominal segments of the body may, by careful dissection, be removed from their connection with the carapax, without disturbing the relation of the parts in intimate connex with the latter. In such a preparation the point of attachment will be seen to lie immediately behind the *mandibulary sternum*, fig. 15, z. Since both the *ophthalmic* and the *antennulary* segments are *entire and have no connection*

with the carapax it follows that the carapax in the young *Squilla* pertains to the antennary and mandibulary somite —to these and these only. The same is true of the zoea of *Porcellana*. The relations of the carapax in the young stages of *Cancer* and *Carcinus* could not be made out accurately, owing to the poor state of preservation of the specimens at my disposal. Among the Brachyura the tergum of the ophthalmic somite is *present as a distinct plate beneath the carapax* and may be exposed by cutting away the rostral region of the carapax, or it may sometimes be seen from behind (*e. g.*, *Platyonychus*, *Actæodes*, *Scylla*). The antennulary tergum, on the other hand, seems to have disappeared entirely.

The sternum of the ophthalmic somite, considered by Dana to be wanting among the Brachyura, is present, as it appears to me, in what has hitherto been considered as a portion of the antennary somite and designated the antennary septum (compare Huxley, *loc. cit.*, p. 296, fig. 76, *c.*). In *Actæodes*, figs. 4, 6 and 7, the sternum of this somite is a distinct cuneiform body, wedged in between the rostrum and the antennary sternum, but separated from both by sutures.

Its connection is more intimate with the antennary sternum than with the rostrum. The basal joints of the antennæ lie in contact with it, since it helps to form the inner angle of both antennary orbits. This wedge-shaped body extends backward *into* the facial region and furnishes the calcareous sockets for the bases of the eye-stalks; but has *nothing to do* with the orbital region. This latter has arisen by the overgrowth of the rostral region (*i. e.*, forwards) which at the same time has been forced downward into the facial area. This growth is well illustrated in the series from *Homarus*, through *Lithodes*, *Platyonychus*, *Scylla* and *Cancer*, to *Actæodes*.

In *Cancer*, fig. 3, the connection of the ophthalmic with the antennulary sternum is still closer and the former is a much thinner plate. In *Scylla*, fig. 9, the rostrum is hardly in contact with the ophthalmic sternum, although it is bent down close over it. The suture between the ophthalmic and antennary sterna is obliterated. In *Platyonychus*, fig. 1, the fusion between the two sterna is complete. In *Palinurus*, figs. 14 and 16, *Lithodes*, fig. 11, and *Homarus*, fig. 5, the rostrum has not encroached upon the ophthalmic somite and the sternum sustains its normal relations to the appendages.

Antennulary sternum. The antennulary sternum in *Actæodes* is an elongated, bar-shaped plate extending across the facial area immediately below the antennæ. The antennules abut upon its ends, while the ophthalmic sternum is fused to its upper part dividing it into halves. The figure formed by these two plates is that of a short-stemmed T inverted. This plate forms the floor of the antennary sockets. The suture between the antennulary and the antennary sterna is lenticular in form and occupied by a semicalcified membrane.

In *Cancer*, fig. 3 and *Platyonychus*, fig. 1, the parts included in the facial area are much less distinct. In *Scylla*, fig. 9, this sternal plate lies opposed to the upper margin (surface) of the antennary sternum, in the form of a thin calcareous plate. Its relations to the surrounding parts are, however, the same as in *Actæodes*. In *Lithodes*, fig. 11, the antennulary sternum resembles in all respects the ophthalmic, and consists of a smooth, scarcely calcified membrane stretched between the antennules. In *Palinurus*, figs. 14 and 16, the antennulary sternum is enormously enlarged and projects forward in the form of a truncated pyramid, equivalent to the "nasal region" of Milne-Edwards. Owing to the unusually large size

of the antennæ, the antennules have their insertion at the anterior end of this plate instead of at the sides as would normally be the case. A narrow extension of the main (fold) plate separates the basal joint of the appendages. In *Homarus* this sternum is moderately developed and occupies its normal position. There is no indication among the Macroura or the Brachyura, of the existence of any other parts of the typical somite in either of these two segments.

Antennary and mandibulary somites. As regards the sterna of the third and fourth somites in *Chlorodius* and *Scylla*, I cannot do better than refer to Dana's admirable description (*loc. cit.*, pp. 24–28). This description of *Chlorodius* will apply in every particular to *Actæodes*, figs. 4, 6 and 7. In *Cancer* and *Platyonichus* the facial region is too much fused to admit of any accurate distinction of the parts. In *Palinurus* the antennary sternum is greatly enlarged and forms the lower part of the nasal projection. At its upper termination it furnishes the basal portion of the antennulary sockets: from this point it spreads out rapidly and extends entirely across the ventral surface of the body forming the anterior, lower one-third of the boundary of each antennary socket. The openings of the green glands are near to its outer angle, on the suture separating it from the mandibulary sternum. Its connections with the anterior half or cephalic portion of the carapax are very distinct and in the form of a beaded suture. The mandibular sternum is separated from the episternal pieces by a short suture, these latter in turn are separated from the epimerals by a suture passing backward and inward toward the median ventral line. In *Lithodes*, figs. 11 and 13, and *Homarus*, figs. 5 and 17, the episternals and epimerals of both antennary and mandibulary somites are present and consequently one is able to

trace the connection of the two portions of the carapax with comparative ease. The episternals and epimerals of the antennary segment are calcified. The former appear on either side of the epistome or sternum as an oblong plate extending backward, downward and outward and also furnish the upper plate of the entrance to the gill-chamber. The epimeral plate is folded inward close upon the episternum of either side and is only to be seen when the edges of the carapax are spread apart. The episterna and epimera of the mandibular segment are represented by slightly calcified membranes more or less folded upon themselves. These plates are related to the mandibular sternum in a manner similar to that stated for that of the corresponding plates of the preceding segment. In *Squilla* the antennary sternum is especially prominent and reaches backward and downward in the form of a half cylinder, the sides of which are formed by the large episternal plates. The carapax is almost entirely made up by the antennary tergum, and the antennary somite furnishes further, fully one-half of the length of the cephalo-thoracic region of the body of this crustacean. The statement that the terga of the thoracic somites are covered by the cephalo-thoracic shield is not strictly true. The first two terga (counting from behind forwards) are entire and free, the third is united by a membrane to the posterior edge of the cephalothorax. The remaining terga are incomplete and unite with the carapax in a line curving from the point of attachment of the third, outwards and forwards on either side of the median dorsal line of the body (fig. 21).

Sternal plates, etc. Milne-Edwards considers the small calcareous plates found at the base of the thoracic appendages, which in the adult state are more or less fused with the sterna of the respective segments, to be the homologues of the episternal pieces of the typical arthropod

somite. From embryological evidence it appears very probable that these pieces originate as simple projections of the outer posterior angle of each sternal plate and that they are apparently cut off by the appearance of false sutures at a later period of development. The figures illustrating this point (figs. 18, 19, 22) hardly need any explanation beyond that given in the description of the plates. A comparison of figs. 18 and 22 is conclusive.

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EXPLANATION OF PLATES II AND III.

REFERENCE LETTERS.

a	antennule	*n*	membranous space
a'	antenna	*o*	eye or orbit
as	antennular sternum	*os*	ophthalmic sternum
a's	antennal sternum	*pg*	processes for attachment of gastric muscles
a't	antennal tergum	*r*	rostrum
a'tp	plates of antennal tergum	*s*	sternum
ap	appendage	*sp*	sternal piece
e	epimeral plate	*t*	tergum
e'	epimeral groove	*tht*	thoracic tergum
f	labrum	*y*	suture between mandibular and antennal sternum
g	plate covering green gland	*x*	suture between epimeral and tergal plates of mandibular segment
g'	plate between antennule and carapax	*z*	point of attachment of carapax to body
m	mandibular skeleton		
mem	membrane		
ms	mandibular sternum		
mt	mandibular tergum		
mp	anterior mandibular epimeral plate.		

Fig. 1. Ventral view of carapax of an immature *Platyonichus ocellatus*, caustic soda, acetic acid preparation; natural size.

Fig. 2. Ventral view of the carapax of *Etisus dentatus;* natural size.

Fig. 3. Carapax of *Cancer borealis* prepared in caustic soda, ventral view with the front slightly inclined forwards; natural size.

Figs. 4, 6 and 7. Carapax of *Actæodes* species? prepared in caustic soda and acetic acid; viewed from above, below and in front, respectively.

Fig. 5. Front view of the carapax of *Homarus americanus* with the appendages removed, fresh specimen, natural size.

Fig. 8. Ventral view of the connection of the mandibular episternum with the mandibular epimeron in *Scylla tranquebarica;* natural size.

Fig. 9. Carapax of *Scylla tranquebarica* from an alcoholic specimen; natural size.

Fig. 10. Carapax of *Chlorodius floridanus*, alcoholic specimen; enlarged.

Figs. 11 and 13. Front and ventro-lateral views of the carapax of *Lithodes maia* alcoholic specimen; natural size.

Fig. 12. Basal joints of right antenna of *Homarus americanus* showing the position of the green gland; natural size.

Figs. 14, 16 and 20. Lateral, frontal and ventral views of the carapax of *Palinurus* prepared in caustic soda; natural size.

Fig. 15. Ventral view of young *Squilla*, the thorax and abdomen of which have been removed by careful dissection; *z* shows the point of attachment of the thorax; enlarged ten diameters.

Fig. 17. Lateral view of carapax of *Homarus americanus*, caustic soda preparation; natural size.

Fig. 18. Sternum of megalops of *Cancer borealis*, showing the episternal pieces as projecting angles of the sternal plates; enlarged ten diameters.

Fig. 19. Sternum of zoea of *Cancer;* enlarged fifteen diameters.

Fig. 21. Lateral view of a sagittal section of cephalo-thoracic region of *Squilla*, caustic soda preparation; natural size.

Fig. 22 Ventral view of sternum of *Cancer borealis* (prepared in caustic soda) showing the "episternal pieces" of Milne-Edwards; natural size.

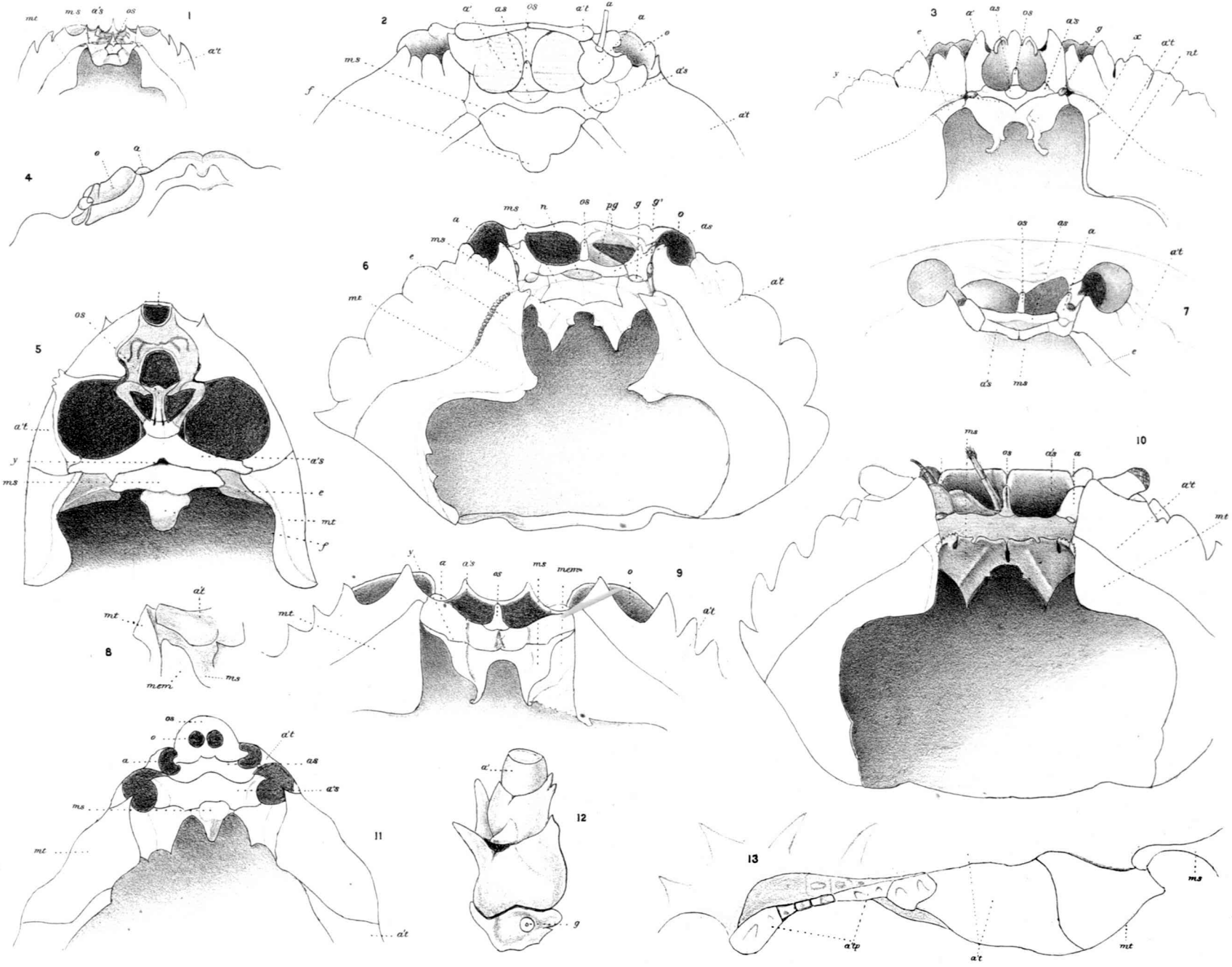
Fig. 23. Ventral view of a young *Pinnixa*; enlarged ten diameters.

Annual Meeting, Monday, May 18, 1885.

The annual meeting this evening at 7.30 o'clock. The President in the chair. Records of the last annual meeting read and approved.

The reports of the Secretary, Treasurer, Auditor, Librarian, Curators and Committees were read and duly accepted and ordered to be placed upon file.

Mr. T. F. Hunt, chairman of the committee on nominations, reported the following list of officers, which was duly elected; Messrs. Israel and Upham having been appointed to collect, assort and count the votes.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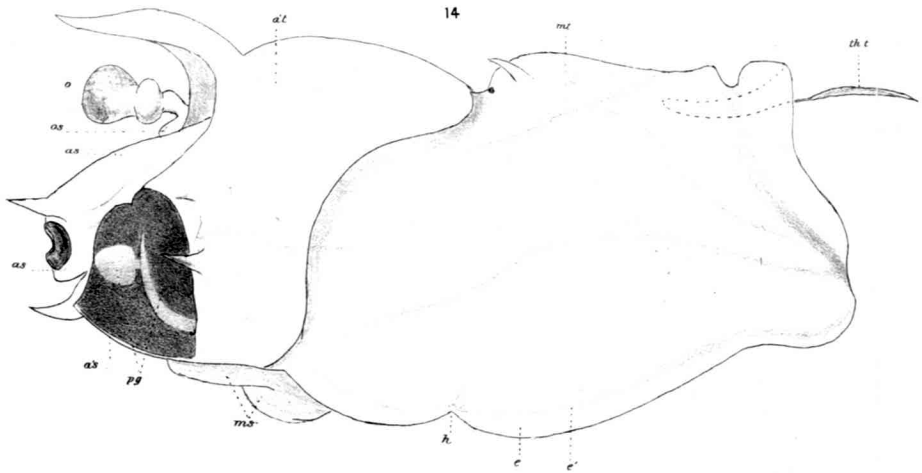

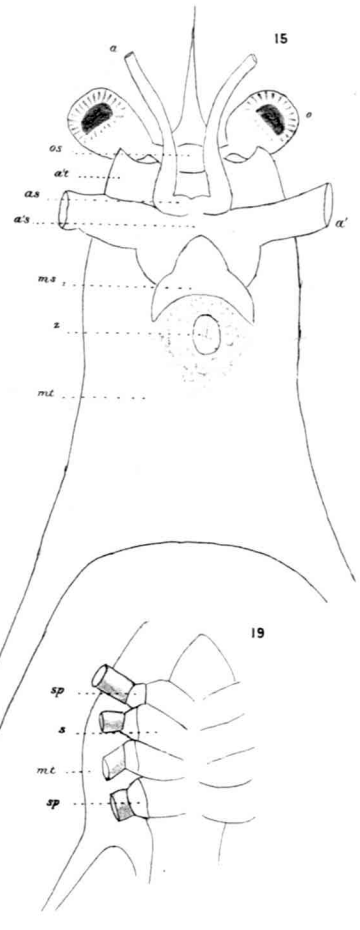

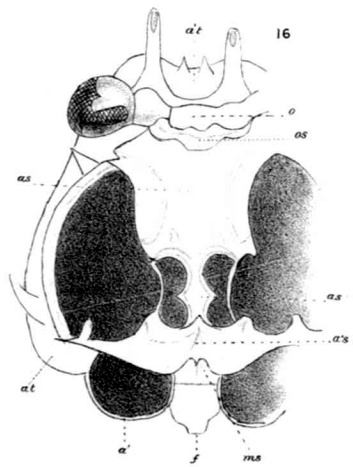

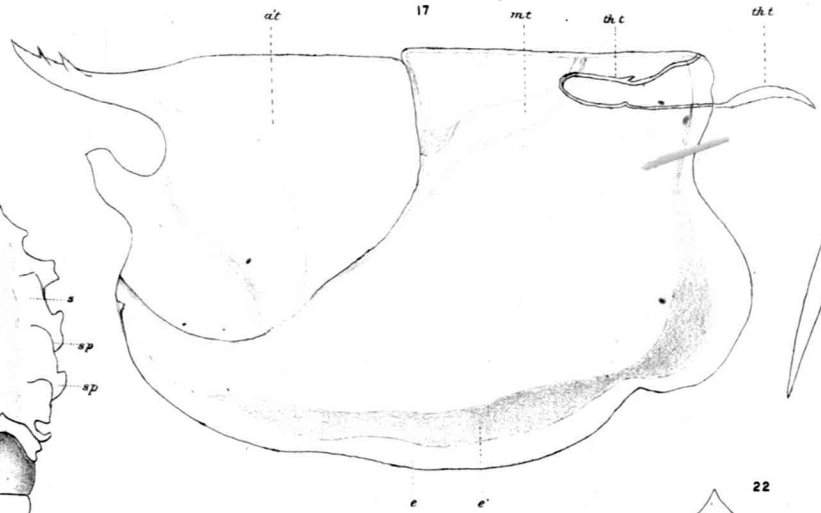

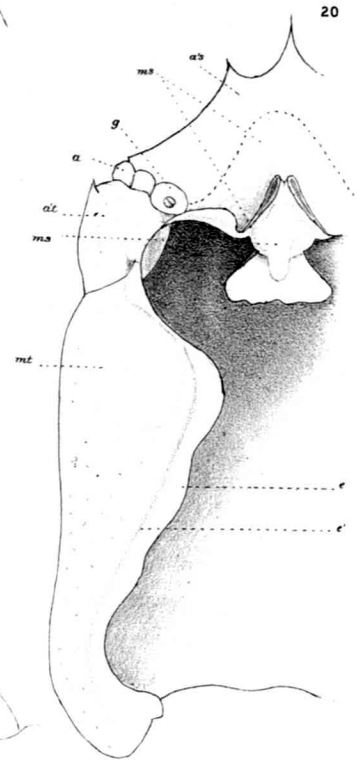

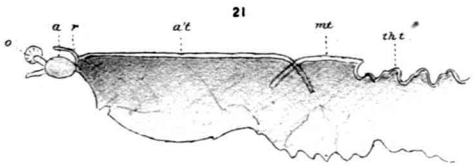

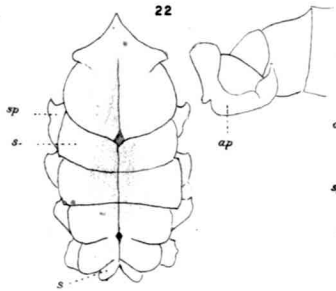

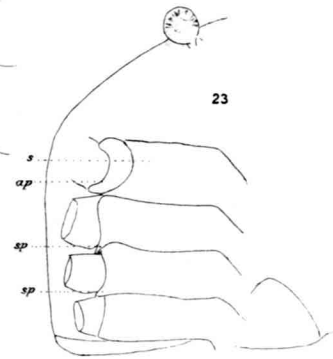

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