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## VIII.—The apodemes of Apus and the endophragmal system of Astacus

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This species cannot well be confused with any other of the Australian *Melampsaltæ*. By the prominent subapical spotting of the tegmina it is somewhat allied to *M. umbrimargo*, Walk., and *M. convergens*, Walk., but with both these species it has nothing else in common.

# SYNONYMICAL NOTES.

## *Tympanoterpes sodalis*.

*Cicada sodalis*, Walk. List Hom. i. p. 108. n. 9 (1850), = *Fidicina vultur*, Walk. Ins. Saund. Hom. p. 10 (1858).

*Melampsalta mangu*, B. White, Ent. Month. Mag. vol. xv. p. 214. n. 63 (1879), = *Melampsalta nervosa*, Walk. List Hom. i. p. 213. n. 166 (1850).

*Tibicina lacteipennis*, Puton, Rev. d'Ent. ii. p. 45 (1883).  
N. Persia.

This name is already preoccupied in the genus *Tibicen* by *T. (Cephaloxys) lacteipennis*, Walk. List Hom. i. p. 237. n. 8 (1850), described from North India. I therefore propose to rename the Persian species as *T. Putoni*.

## VIII.—*The Apodemes of Apus and the Endophragmal System of Astacus*. By HENRY M. BERNARD, M.A. Cantab.

[Plate V.]

THE endophragmal system of *Astacus* has been a considerable puzzle to all who have studied the subject. Though the elements of which it is made up are clearly seen to be folds of the outer skin, in some way connected with segmental constrictions, it has never been understood how they arose. No muscles are apparent which could have drawn them in; indeed, some of those attached to them, *e. g.* the coxal muscles, pull in the opposite direction, *i. e.* tend to straighten the skin and not to draw it into folds.

When attempting lately to show \* that *Apus* is a primitive Crustacean nearly related to the Annelids, I was many times struck with the close resemblance between it and the Macrurous Decapod Crustaceans, and could not refrain from

\* "The Apodidæ." Macmillan, 1892.

hoping that some one would attempt a detailed deduction of *Astacus* from the Apodidæ. As a contribution to such an attempt, I propose here to show how *Apus* supplies us with a full explanation of the endophragmal system of *Astacus*.

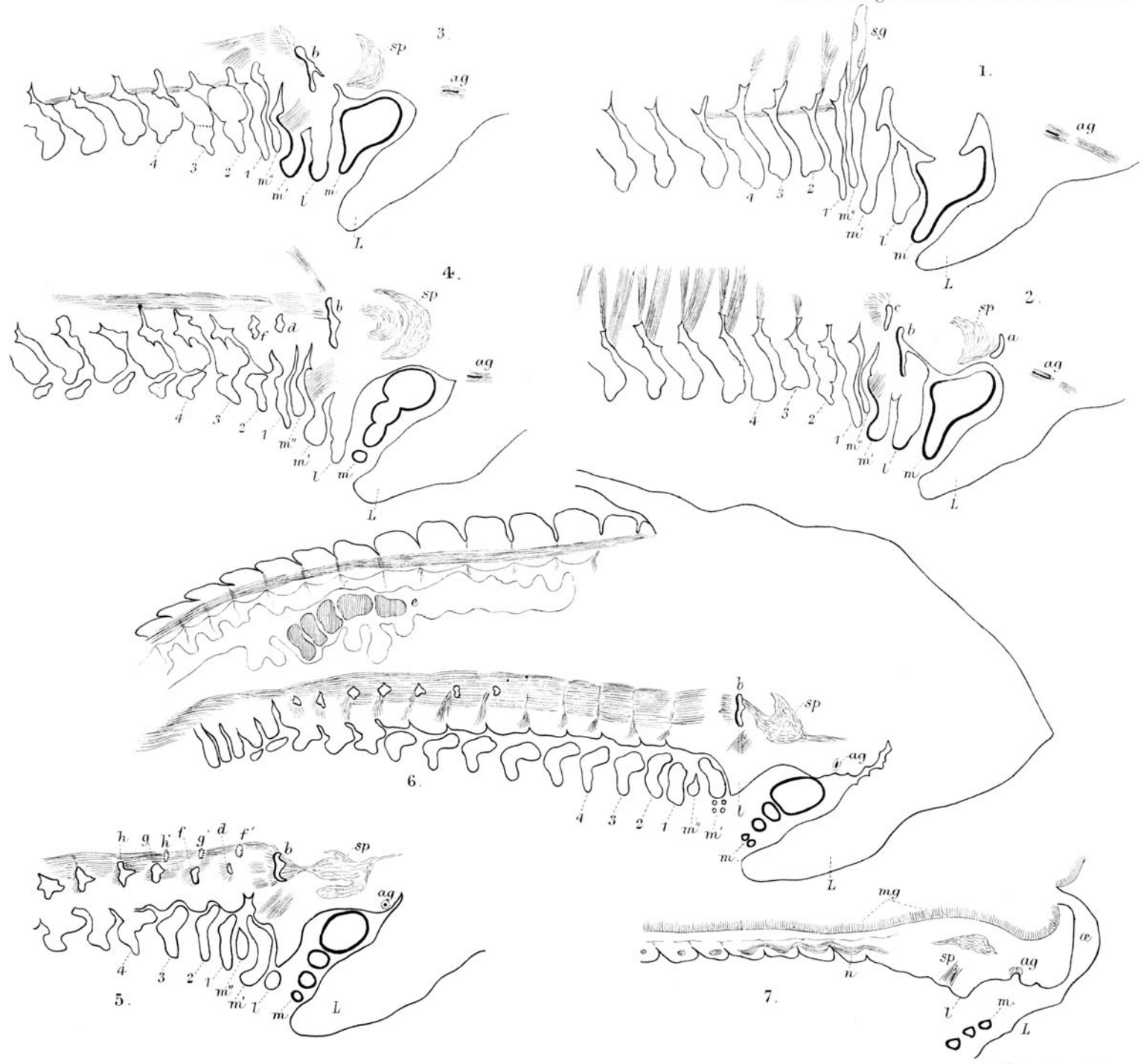
Apodemes, or inward foldings of the skin, are very plentiful in *Apus*, and their origin is in all cases clear.

We have, first of all, the segmental constrictions, which are naturally obliterated in the stretched regions of the body, but very marked in longitudinally compressed regions. For our present purpose we confine our attention to the constrictions on the ventral surface anteriorly. In some specimens, according to the state of contraction at death, these are very deep and throw the ventral cord into a series of waves (*cf.* Pl. V. fig. 7).

In *Astacus* the moving forward of the anterior trunk-limbs to function as mouth-parts or maxillipedes, and the consequent longitudinal compression of this region of the body, necessarily caused these constrictions to form high fixed barriers across the inner ventral surface. Over these barriers the ventral cord had at first either to stretch, or to form a series of arches. Each barrier has, however, in time been cut down in the middle line, so that the cord has come to lie in a groove along the ventral surface, known as the sternal canal. The subsequent arching over of the canal by sinewy matter is a secondary arrangement which also receives its explanation in *Apus*, as we shall presently see.

So far, this explanation of the origin of the endosternites (as the two halves of these constrictions are called) is simple enough. The origin of the endopleurites (or endotergites as they are sometimes called) is not quite so evident.

Taking first the endopleurites between the trunk-limbs, we find that in *Apus*, in the anterior part of the body, where the limbs are developed, the two ventral longitudinal muscle-bands are attached to the segmental folds between the limbs. These points of attachment naturally tend to be drawn inwards by the action of these muscle-bands. Further, as the pulls of the muscles are in the longitudinal direction, the folds naturally acquire the diamond-shape shown in the tangential sections (figs. 5, 6). In these apodemes the dorso-ventral diagonal is the natural direction of the segmental constriction; the longitudinal diagonal is due to the pulls of the muscle-bands. By comparing the sections we find that each of these apodemes in *Apus* is pulled backwards as far as the segmental constriction posterior to that to which it really belongs. This is easy to understand; the length of the posterior region in *Apus* and the use made of it for sudden



diving movements make it probable that the prevailing pulls of these muscle-bands are for the bending of the abdominal region. But although the greater part of the apodeme thus slopes backwards, there are indications of a slight anterior pull in its diamond form.

Turning now to *Astacus*, we find very pronounced apodemes dorsally to the limbs, and in the line between them. These are clearly homologous with the apodemes of *Apus*, and originate as part of the segmental constriction between the limbs. How they came to be drawn in we have learnt from *Apus*; they were originally the points of attachment of the segmental constrictions to the ventral longitudinal muscle-bands inherited from the original Chætopod Annelid, and retained in *Apus*. This origin is no longer apparent in *Astacus*. Internally these endopleurites give off two branches, one running posteriorly to the endosternite belonging to the next posterior constriction, and one running in towards its own endosternite. The former alone of these is, as above described, developed in *Apus*, and has been handed on to *Astacus*; but whence came the anterior branch?

A trace of this anterior branch is, as we have seen, present in *Apus*, and might be easily developed if it were to be submitted to any strong anterior pulls of the longitudinal muscle-bands. This is clearly what has happened in *Astacus*, and we have abundant evidence of such persistent anterior pulls in the compression of the anterior ventral region. The effort to bring forward the four anterior pairs of legs as maxillipedes and forceps must have meant, for many generations, a strong contraction of the ventral longitudinal muscles connecting the somites to which these limbs belong. To this, then, I attribute the development of the anterior branch of the endopleurite.

The parallel between *Apus* and *Astacus* is, however, by no means complete. The most anterior of the folds forming the endophragmal system of *Astacus* cannot be called either an endopleurite or an endosternite, because it is one deep continuous furrow only interrupted by the sternal canal. It occurs between the 2nd maxillæ posteriorly and the paragnatha and mandibles anteriorly. So capacious is it that the 1st maxillæ may be said almost to spring from the bottom of it. It is, in fact, nothing more than the sinking in of the region of insertion of these limbs.

*Apus* again supplies us with a complete explanation of this phenomenon. The Sections 1-7 show us a very deep fold behind the underlip, which runs in above the insertion of the 1st maxilla. It is so pronounced that it forms one of

the principal supports of the "sternal plate"\*. It runs in further than any of the other lateral apodemes of *Apus*. I consider the fold of some importance, and due not so much to the bending round of the five annelidan segments to form the crustacean head†, as to the forcing back of the underlip in order to bring the mandibles in front of it. The counterpart of this fold may be seen in a small apodeme in front of the mandible, due to the forcing forward of the latter in front of the underlip (fig. 2 a).

This very pronounced fold behind the underlip in *Apus* very nearly coalesces with another less pronounced apodeme between the 1st and 2nd maxillæ. The fold between these limbs is very deep, as is also that between the 1st trunk-limb and the 2nd maxilla (Section 1). I am inclined to attribute these to the bending round of the segments to form the head.

It is clear, therefore, that we have in *Apus*, just behind the underlip around the insertion of the 1st maxilla, an area of subsidence, which, if it sank, would infallibly draw this limb down with it, so that it would then spring from the base of the fold.

In *Astacus* this subsidence has actually taken place, and the cause of it is not far to seek. The bringing forward of the anterior trunk-limbs as maxillipedes necessarily compressed the region of the body between these limbs and the mouth, with the natural result that any tendency of the skin to form folds in this region would at once be taken advantage of, and the fold would become deeper. That this is the true account of the origin of this fold in *Astacus* can still be made out from an examination of its structure. It shows its composition out of two apodemes, the anterior of which, as in *Apus*, is much the more pronounced, bending forward at its proximal end into a strong horn-like prolongation, which is clearly the homologue of the stout apodeme marked *b* in the sections. If this is the case, then the sinewy tissue joining the folds of the two sides across the middle line and thus bridging over the sternal canal is the rudiment of a sternal plate like that of *Apus* and *Limulus*.

Following on this first fold of the endophragmal system of *Astacus* is a somewhat complicated arrangement of folds and ridges. The chief complication seems to be due to the fact that the endopleurite between the first and second trunk-legs (or

\* This is commonly called the endosternite, but, having already (following Huxley) used that term for the ventral apodemes, I here use an alternative term for the sinewy mass to which the ventral longitudinal bands are attached anteriorly.

† *Vide* 'The Apodidæ,' pp. 10 *et seq.*

maxillipedes) has been drawn forward dorsally to, and a little in front of, that between the 1st maxillipede and the 2nd maxilla. We can only explain this by supposing that the muscle-pull on the first endopleurite was very small, while it was very strong on the second and following endopleurites. This explanation is borne out by the fact that, in *Astacus*, no anterior branch of the first endopleurite is developed. This is easy to understand if we refer to Section 5. In this we see the change that has to take place to give us the transposition of the 1st and 2nd endopleurites in the endophragmal system of *Astacus*. In order to bring up the trunk-limbs to act as maxillipedes, the muscular contraction must act on the apodemes behind them, not in front of them. Hence we find that, while the endopleurite marked *d* has nearly retained its original position, the endopleurites *f, g, h*, &c. have been drawn into positions *f', g', h'*, &c. indicated on the Section (5) by dotted lines. The endosternites have been also affected, those corresponding to *d* and *f* having been drawn very close together.

In addition to the longitudinal compression repeatedly referred to above, the anterior part of the thorax of *Astacus* has been subjected to considerable lateral compression, also due to the transformation of trunk-legs into mouth-parts. This has naturally forced the transverse segmental constrictions into folds, which are still visible in the buttress-like backward prolongations of the endosternites, and perhaps also in the sternal canal. This lateral compression of the thorax in *Astacus*, forming a keel along the sternum, very marked in the lobster, is in interesting contrast to what has taken place in *Branchipus*, where the sternum is bent in exactly the opposite manner, *i. e.* upwards, leading to a separation of the two longitudinal halves of the ventral cord.

Tempting as it is, it is hardly necessary to show how the posterior portions of the endophragmal system of *Astacus* may be accounted for. They afford abundant evidence of the strong muscular contractions which originally compressed the thoracic somites.

I have thus, I think, made it very clear that *Apus*, with its powerful ventral longitudinal muscle-bands and its flexible skin, supplies us with a complete explanation of the endophragmal system of *Astacus*, in which the ventral muscle-bands, except those specialized for moving the tail, have almost entirely disappeared, and in which the deep folds of the skin which the now vanished ventral muscles once called into existence have become permanent calcified ridges, fastened together by sinewy connective tissue.

We have now, lastly, to explain the changes which have taken place in the ventral longitudinal bands of *Apus* and their attachments, to form the flexor muscles of *Astacus* with their somewhat different attachments.

In *Apus* the muscle-bands are attached solely to the endopleurites. Anteriorly they are attached to the large apodeme behind the underlip, and run backward in a band until they gradually widen out to form, in the limbless segments, a dermo-muscular tube.

In *Astacus* a great change has taken place. As above described, the anterior part of the thorax has undergone lateral as well as longitudinal compression, due to the transformation of legs into maxillipedes. The *lateral* compression caused the longitudinal bands of the two sides to meet in the middle line, with a consequent fusing of the sinewy segmental partitions of the one band with those of the other. The *longitudinal* compression caused the ventral segmental constrictions to become the fixed permanent endosternites, which were pressed up till their inner edges fused with these same sinewy partitions.

When it was no longer necessary further to compress the thorax, in order to turn the anterior trunk-limbs into maxillipedes, the greater part of the muscles degenerated, leaving, however, the branches of the endopleurites bound to the endosternites by the sinewy tissue which persisted after the muscle elements disappeared. The most important parts of the ventral longitudinal bands which were retained were those which ran either downward into the limbs or backward into the abdomen. Of the former, we find the coxal muscles in *Astacus* attached to the sinewy capitals of the pillar-like endosternites. We have, in fact, muscles pulling outwards attached to each side of a fold of the skin! It is evident that this must have been a secondary arrangement, as no fold of the skin could possibly have arisen under these circumstances. There is, however, no difficulty if we refer to *Apus*. There we find these coxal muscles springing from the sinewy partitions in the ventral muscle-bands. By the longitudinal compression of the thorax already mentioned, the segmental constrictions in *Astacus* were forced up until their inner edges fused with these sinewy partitions. Hence the coxal muscles naturally come to descend from the upper edges of the segmental constrictions or capitals of the endosternites.

The abdominal muscles require little notice. The order of their attachments to the endosternites of the thorax is just what we should have expected from their origin. As we go



backward we find the continually thickening flexor muscle of the abdomen with which we are all familiar.

Owing to the comparatively undifferentiated character of the long muscle-bands of *Apus*, treated as a primitive crustacean, it is probable that no part of the band contracted without leading to a partial contraction of the rest. We accordingly find the ventral curve of the body much more pronounced in the *Brachyura* than in the *Macrura*. In the former, while there seems to have been no lateral compression, the longitudinal compression of the thorax has been much greater than in the latter, and the maxillipedes are far more pronounced as mouth-parts than they are in *Astacus*.

There are other points in the anatomy of *Astacus* which can be shown to have been modified from a more primitive condition, such as we find in *Apus*. But we must pass over these for the present and conclude with a few descriptive notes on the sections of *Apus glacialis* given in the drawings.

#### EXPLANATION OF PLATE V.

##### *Description of Sections.*

These are all from camera lucida outlines. The detail of the inner organization is somewhat simplified, *e. g.*, the sections through the branchings of the liver and the genital glands are omitted in 6.

*Fig. 1.* Sagittal section through the right side of a specimen of *Apus glacialis*, Kröyer.

*ag*, the salivary gland, attached to the body-wall by muscle-bands, like a typical acicular gland. This may be followed through the sections till it opens in a transverse groove shown in Section 7.

*sg*, the shell-gland, which is here seen running out laterally towards the dorsal parapodium of the 2nd maxilla (*m'*).

*L*, labrum, or large upper lip.

*m*, mandible.

*l*, metastoma or underlip, which is here seen projecting laterally.

*m'*, *m''*, 1st and 2nd maxillæ.

1, 2, 3, first three trunk-limbs which, in *Astacus*, were forced forward towards the mouth as maxillipedes.

4, the 4th limb which, in *Astacus*, becomes the forceps.

*Fig. 2.* The same, six sections further on.

*a*, the apodeme in front of the mandible, probably due to the forcing of the latter forward.

*sp*, the sternal plate, which first comes in view as a *strongly curved mass*. This is of interest in connexion with my attempted deduction of *Apus* from an Annelid with the first five segments bent round to form the new head. The curve is very pronounced in Sections 2, 3, 4, and partly in 5. In Sections 6 and 7, which lie nearer the middle line, we have only the posterior portions of the sternal plate, which naturally lie straight.

*b* is the large fold behind the underlip, due, I think, to the forcing of the lip backward.

*c* is the apodeme behind the 1st maxilla; *b* and *c* together form the area of subsidence described in the text which gives rise to the great fold commencing the endophragmal system of *Astacus* anteriorly.

*Fig. 3.* The same, four sections further in towards the median plane.

*Fig. 4.* The same, three sections further in than 3.

*d* and *f*, apodemes between *m'* and the 1st trunk-limb, and between the 1st and 2nd trunk-limbs. In *Astacus f* has been drawn to the position marked *f'*, as shown in:—

*Fig. 5.* The same, five sections further in than 4.

*Fig. 6.* Seven sections further in than 5. The gnathobases are seen as distinct appendages; the anterior trunk apodemes are no longer visible, only the large one, behind the underlip, which forms the support of the sternal plate and the anterior attachment for the longitudinal musculature, remains. In the specimen these muscles had been torn from the apodeme, as shown in the drawings. The apodemes which are still visible in the posterior segments are clearly seen to have travelled backward so as to come nearly over the segmental constrictions posterior to those to which they properly belong. This gives us the posterior branch of the endopleurite of *Astacus* (*cf.* text).

*e*, eggs in the genital tube.

*Fig. 7.* A nearly median section.

*n*, the ventral cord thrown into slight waves by the ventral constrictions.

*m*, teeth of the mandibles.

*α*, the œsophagus.

*mg*, the wall of midgut.

*sp*, the median portion of the sternal plate which binds the two apodemes behind the underlip across the middle line. The underlip is represented by the ridge *l*. It is to be noticed that no muscles run into the underlip excepting here, close to the median plane. These bands may have originally formed the true anterior ends of the ventral longitudinal muscles.

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IX.—On a new Genus of *Oligochæta*, comprising Five new Species, belonging to the Family *Ocneroдрilidæ*. By FRANK E. BEDDARD, M.A., F.R.S., Prosector to the Zoological Society of London.

[Plates VI. & VII.]

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- III. Diagnoses of Genus and Species, p. 93.
- IV. Affinities of the Genus *Gordiodrilus*, p. 96.
- V. Explanation of Plates, p. 97.

I. INTRODUCTORY.

THE material upon which the present paper is based consisted of a large number of living worms, all of which I received, through the kindness of the Director of the Royal