THE FIRST LEG SEGMENTS IN THE CRUS-TACEA MALACOSTRACA AND THE INSECTS

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INTRODUCTION

One of the great services Dr. R. E. Snodgrass has rendered to our science is to have pointed out in several of his recent works the lack of coherence still prevailing between the data of insect morphologists and those of specialists in other classes of Arthropoda. In his fine treatise of 1952 (pp. 284-285), for instance, he observes that one does not know what can correspond in the inferior classes of Arthropoda to those sclerites at the leg bases that we have studied so thoroughly in the Apterygota.

We preferred not to try to settle this question before acquiring a sufficient knowledge of the said formations in the Apterygota themselves. Their diversity within this subclass is so great that what they can have in common remained unknown for a long time. Hard work was needed to make up for this lack of knowledge and to enable us to show within the limb base new guiding marks in which we only now have taken interest, namely, the ties of the endosternites. These are more or less numerous according to the morphological types under examination ; a great deal of experience was necessary to distinguish and recognize them in the various types.

As our attempts proved convincing, we set about gathering the elements of an answer to the question raised by our eminent American colleague. The Myriapoda [1] gave us little useful information ; their supracoxal structures are too specialized. The Crustacea Malacostraca turned out to be of far greater interest in this connection, and we have already published a short paper [2] on them. We are pleased to offer in the present article, as a tribute to R. E. Snodgrass, more complete explanations and some illustrations on the same subject.

It is known that we have observed in quite varied types of Apterygota the presence of two main overlying supracoxal zones : the ana-

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[1] *Scutigera, Lithobius, Cryptops, Scolopendra* (unpublished observations).
[2] Proc. 10th Internat. Congr. Ent., Montreal, 1956, vol. 1, pp. 489-490, 1958.

pleuron and the catapleuron. Furthermore, between the latter and the coxa, we have proved the presence of a trochantin certainly homologous with the trochantin of the Orthopteroidea (Carpentier, 1946, 1955), but this may be but a derivative of the coxa, in spite of the development and the individualization which it attains in certain orders.

Now, the question is, do all these formations exist in the Malacostraca as well, and if so, from what part of the leg do they start in a proximal direction?

To take a stand in this matter was to choose between two interpretations of the limb base which have been opposed to each other for a long time; one of them, advocated by Hansen (1893, 1925, 1930) and accepted by other writers including Vandel (1949), maintains that the insect coxa does not correspond morphologically to the coxopodite of the Crustacea but to the basipodite. Thus Hansen could homologize the coxal stylus of the Machilidae with an exopod. And on our part, we were tempted to see in the precoxopodite and coxopodite of the Crustacea the probable equivalents of the main supracoxal arcs of the Apterygota.[3]

However, the Crustacea Malacostraca compelled us to reject such homologizing. As we were trying to find to what part of the leg base the pleural region of the Apterygota corresponds, we had to acknowledge the accuracy of a former opinion, which regarded the coxa simply as homologous with the coxopodite; the correctness of this opinion will so be proved.

BASIPODITE AND COXOPODITE

Our researches on the Malacostraca concerned various species, particularly *Anaspides* [4] and *Penaeus*. We first studied *Anaspides,* which is the "most primitive" genus of the subclass. The thoracic limbs of this malacostracan, mainly the maxilliped, have been considered by Hansen and other morphologists as having best preserved the organization of the primitive biramous limb. Neither Hansen [5] nor Snodgrass,[6] who has lately taken up the study of these appendages, saw an independent precoxopodite. According to those authors the precoxopodite of these "primitive" legs would be imbedded in the lateral

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[3] Lameere (1935, p. 70) regarded these homologies as "probable."

[4] *Anaspides tasmaniae* Thoms., specimens of which were sent to us by Prof. E. Percival (Christchurch, New Zealand), thanks to the kind offices of our colleague Prof. H. Damas (Liège).

[5] Hansen, 1925, pp. 102-103 and pl. 5, fig. 3e, f, h.

[6] Snodgrass, 1952, p. 135, fig. C.

region of the thoracic segment in the shape of a rather reduced "laterotergal plate." It would be, after all, a "pleuron," the aspect of which would be quite different from that of a basal ring of the limb.

The only typical precoxopodite that Snodgrass observed in the arthropods in general is the "subcoxa" of *Strigamia*. This one completely encircles the coxa but remains a part of the body wall. *Strigamia* is a geophilomorphous chilopod, an arthropod the whole organization of which is far "less primitive" than *Anaspides*. Hence Snodgrass thinks (1952, p. 208) that, after all, there is no convincing evidence for a theory according to which a subcoxa, or primitive pleuron, would originally have made up the functional base of the limb of the arthropods.

However, we had to check whether the base of the maxilliped had been correctly described and figured. Snodgrass's data do not fit in very well with Hansen's (1925), and the results obtained by the latter have not been discussed. There is nothing astonishing in the fact that Snodgrass could not study with the same degree of care every detail which comes up in so vast and extensive a work as his. But here a greater accuracy is necessary.

We thought that the first point to check in *Anaspides* was to which segment of the limb the exopod is attached. Hansen regarded it as pertaining to a very short basipodite. Snodgrass, who neglected this last segment, saw the exopod attached, quite proximally, to the following segment, which is well developed and which Hansen named preischiopodite. We found that Snodgrass was right. Our figure 1c shows that the exopod mainly pertains to a differentiated region at the proximal end of the large segment of the leg. This "preischiopodite" is thus the true basipodite. Besides it is quite usual for the exopod of the thoracic limbs of the Malacostraca to pertain to the base of the basipodite.[7] These relations are the same as those we observed in a general way in the Malacostraca we studied (see for instance *Penaeus,* fig. 2). The exopod of the thoracic legs of *Eupagurus* which puzzled Hansen (1925, p. 143) and which we reexamined with care is at least as proximal as that of *Anaspides*. Besides, the Danish writer found that one could be tempted to refer it to the coxopodite as well as to the following segment.

Yet the reduced region of the maxilliped as well as of the legs of *Anaspides,* which Hansen regarded as a basipodite, remains for us equivalent to a segment. This one is indeed very short, so short that on the side toward the body of the crustacean one could see but a

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[7] The "base" of a segment we define as its proximal end.

mere border line between two successive segments. However, the dissection shows that we have to do with a true segment and that this segment is a coxopodite. Despite the imperfect preservation of our material, we saw that a group of muscles inserted in the insects near the point where the trochantin articulates with the coxa, is inserted in *Anaspides* on our coxopodite and not on the base of the coxopodite of the other authors.

The reduced segment is, on the other hand, not merely a trochantin, a skeletal element which had never before been found in crustaceans but which we had some reason to look for in these arthropods. If we
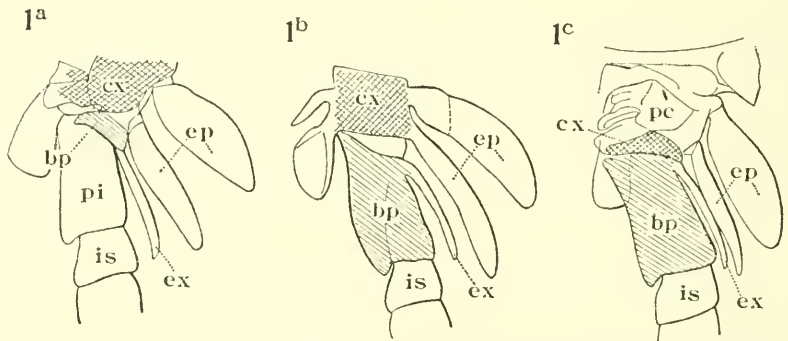

Fig. 1.—*a*, Basal part of the right maxilliped of *Anaspides tasmaniae* Thomson, posterior view, setae omitted. From Hansen, 1925. *b*, Idem. From Snodgrass, 1952. *c*, Idem. Original; new interpretation.

bp, basipodite; *cx*, coxopodite; *ep*, epipodite; *ex*, exopod; *is*, ischiopodite; *pi*, preischiopodite; *pc*, precoxopodite.

had to do only with a trochantin—the basipodite of Snodgrass and ours—it would be one that should possess at least some features of a coxa. But it actually resembles the insect trochanter by the extrinsic musculature which is inserted on its proximal end, opposite to the group of the levator and depressor muscles. In many insects the latter group contains muscles arising from the notum, the longest extrinsic muscles of the leg.[8] *Anaspides*, however, had only rather short depressor muscles. Since we raised the question of the trochantin of crustaceans, let us point out that in the species of crustaceans where it is found best differentiated, it still presents the appearance of a part of the superior border of the coxa. This is to be recalled and examined thoroughly when it comes to investigating the origin of the trochantin.

[8] See *Lepismachilis* (Barlet, 1946, fig. 2, TR-NT) ; but the said muscle does not exist except in the anterior leg of the machilid.

The "trochanteral" characteristics of the basipodite are particularly clear-cut in the Penaeids (figs. 2 and 4), primitive decapods. In each of the thoracic legs of a *Penaeus* [9] the proximal end of the basipodite forms with the preceding segment a typically trochantero-coxal articulation; this end of the basipodite is obliquely cut and bears two tendons. These tendons are opposite each other, and one of them bears a depressor muscle arising from the notal region. There is another similarity with the insects (fig. 4): beneath the tendon of the depressor muscle, a muscle (*bp-ca*) is attached on the wall of the basipodite of *Penaeus;* it runs along the ischiopodite and the meropodite to be eventually inserted on the proximal extremity of the carpopodite,[10] which is known to be homologous with the insect tibia. A similar tibio-trochanteral muscle can be found in the insects, *Periplaneta* [11] for instance. The facts we have just mentioned fit in with a homologization of the basipodite with the trochanter, a conception which, as we saw, has already been accepted by a number of authors but which it was useful to buttress with further arguments.[12]

PLEURAL CHARACTERISTICS OF THE PRECOXOPODITE

Thus the so-called coxopodite of *Anaspides* is actually a free precoxopodite, and this precoxopodite must correspond to the pleuron or to a part of the insect pleuron. Now let us see whether the malacostracan precoxopodite actually shows, especially on the inner side, at least some of the characteristics of a pleuron. We shall check, this time beginning with *Penaeus,* the precoxopodite of which, like an insect pleuron, has become a part of the lateral wall of the thoracic segments. We know [13] how this may have happened. The cylindrical

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[9] *Penaeus caramote* Risso of the Mediterranean.

[10] Hinton (1956, p. 11) wrongly denies the existence of this muscle in Crustacea.

[11] Original observation. Carbonell (1947) does not figure this muscle.

[12] Then the stylus on the coxa of the Machilidae cannot be homologous with an exopod. Besides it is attached rather distally on the posterior side of the coxa. This stylus is probably homologous with the epipodite which we see on the external side of the coxopodite of the penaeids and other Malacostraca.

[13] See Snodgrass, 1952, p. 146, fig. 41 D. The imbedding of the proximal segment of the leg of the decapods in the thoracic lateral wall has long since been accepted (Calman, 1909; Hansen, 1893) after observations of Claus (1885) on the shift of the pleurogills and arthrogills of *Penaeus* toward the end of the embryonic life. Yet Heegaard (1947, p. 192) made certain reservations about those observations of Claus although he never wanted to reject them completely. Let us remark that elsewhere Heegaard (op. cit., p. 188) sees only two segments in the sympod of the penaeids.

segment of the leg, drawing back into the lateral wall, shortened to such an extent that it almost disappeared, except on the side where it has formed, up to a certain level, the mesal wall of the gill chamber of the decapod.

Our figure 2 shows the internal side of this wall above the third right pereiopod of *Penaeus*.[14] From the direction of the lines which margin or run across the precoxopodian wall, we have the impression that it penetrated into the lateral wall like a wedge, pressing back the primitive wall more toward the middle of the segment than at the ends. Therefore, at these two extremities, the old wall could remain rather close to the coxa.[15] The coxa itself has grown like a wedge toward the lateral wall at its anterior angle (α) which is elevated compared with its posterior angle (β); a third angle (γ) exists on its proximal side; the upper frame of the coxa is thus triangular. The proximal side of the coxa is dihedral in keeping with a certain overlapping of the leg bases; it has an oblique anterior side against which the back of the coxa of the preceding leg can be moved and a posterior side which runs along the margin of the sternite.[16]

At each angle α and β of the coxa there is an articulation with the pleuron; it is a kind of "suspension" of the coxa which really resembles that of the last two pairs of coxae of the Machilidae (Carpentier, 1946, fig. 6). It is one more reason why we consider the Machilidae as having preserved certain resemblances with the Crustacea.

Above the articulation of the angle α an apodeme (ap), which we have every reason to homologize with the pleural apodeme of the insects, arises and bends backward in *Penaeus* as well as in the last two thoracic segments of the Machilidae. The apodeme does not present any process in *Penaeus,* but we find a rudimentary one in *Amalopenaeus*.[17] The apodeme divides the pleuron into two regions, anterior and posterior, which include the equivalents of the episternum and of the epimeron of the Pterygota. However, these regions are

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[14] We have chosen this third leg as typical; it is far from the head and it is the last one of those which, even at their base, are not influenced by the specialization of the genital region.

[15] This is only a general impression. We shall not be able to go into the details of the specialization which has affected the leg base, especially on the proximal side. Here we only suggest a few guiding marks.

[16] Compare with the tranversal sections of the coxae of a *Cambarus* on fig. 43 A of Snodgrass (1952).

[17] *Amalopenaeus valens* S. I. Smith (we used some of the well-preserved specimens which had been brought back years ago by Prof. D. Damas from his expedition with the *Armauer Hansen,* 1922).

very unequal and their upper limits are indistinct. The region anterior to the apodeme appears to have very little extension, but its lower precoxal part obviously proceeds proximally to the anterior angle of the coxa. Higher, the same anterior region of the lateral wall bears a winding ridge of a general direction parallel to that of the pleural apodeme. This ridge, which is about abreast of the intersegmental
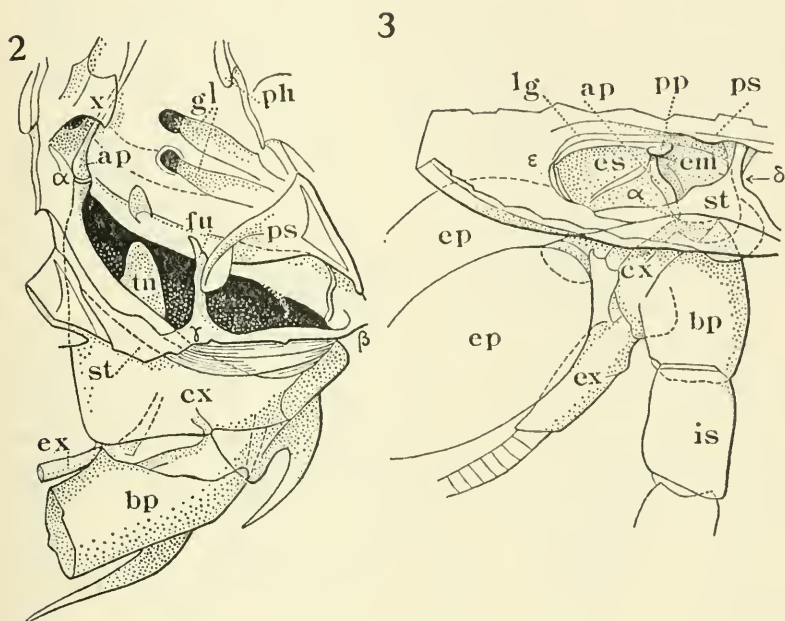
FIGS. 2 and 3.

Fig. 2.—Basal part of the 3d right pereiopod of *Penaeus caramote* Risso, seen from inside, setae omitted.

FIG. 3.—Basal part of 5th right thoracic limb (4th pereiopod) of *Anaspides tasmaniae* Thomson, seen from the front, setae omitted.

an, laterotergite, sclerite pertaining to a region which seems homologous with the anapleuron of the Apterygota; *ap,* pleural apodeme; *bp,* basipodite; *cx,* coxopodite; *e,* spot where the endosternal arm *e* is attached; *em,* epimeral region; *es,* episternal region; *ex,* exopod; *f,* spot where the endosternal arm *f* is attached; *fu,* furcal apophysis; *gl,* gill; *h,* spot where the endosternal tie *h* is attached; *is,* ischiopodite; *lg,* laterotergite; *ph,* phragm; *pp,* (medio)pleural process; *ps,* postpleural process; *st,* sternum; *tn,* trochantinal tendon; *x,* ax-shaped undetermined process.

α, antero-external angle and (idem) articulation of the coxopodite; *β,* postero-internal angle and (idem) articulation of the coxopodite; *γ,* internal angle; *δ,* internal articulation of the laterotergite; *ε,* external articulation of the latero-tergite.

phragm (ph), has given birth to an ax-shaped process x for which there is no equivalent among the insects. A branchial shaft (gl) is attached externally to the base of the process.

The region of the lateral wall posterior to the pleural apodeme is very large.[18] It bears externally two branchial shafts (gl); internally, in the back part of the segment, we find a strong infolding of the cuticle in the shape of a large triangular blade with a small terminal spatula. We call this large blade the postpleural process (ps). Does it proceed from the wall of the precoxopodite or does it pertain to the primitive lateral body wall, which locally is not pressed back? We cannot answer this question at the present time.

Near the proximal angle (γ) of the coxal margin a furcal apophysis (fu) arises. It takes its rise at the edge of the sternal plate, at the limit between this sternal plate and the membranous strip, the only remnant, proximally, of the precoxal wall. This spot corresponds to the spot which was pointed out by Weber (1928, p. 250) as typical of every furcal apophysis of the Pterygota.[19]

We have figured and described the postpleural process and the furcal apophysis of *Penaeus* as separated from each other, as they will be found after a specimen is treated with caustic potash. Without this treatment, these two internal formations of the cuticle would have appeared wrapped in a common subhypodermal sheath [20] pertaining to an endoskeletal scaffolding (fig. 4) which we shall analyze further on. In *Cambarus,* an American crayfish, Snodgrass (1952, p. 156) saw likewise a "pleural apodeme" united with a "sternal apodeme" by certain "interlocking fimbriations"; these parts become disconnected, he explains, if the preparation is left to dry.

We know that the schemes of the thorax depicted in general treatises

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[18] In going over the series of precoxopodites of *Penaeus,* we come across some of them in which the two regions of the lateral wall are less unequal.

[19] In a note written to do justice to all that may be valuable in Ferris's ideas, one of us (Carpentier, 1947, pp. 300-301) has maintained that in the insects, this one can pertain more to the proximal zone of the catapleural ring than to the sternum itself. Rendering an account of this note, Weber (1952, p. 110) unfortunately wrote that the basisternite is regarded in that note as a secondary formation. This is not correct.

[20] Let us keep in mind that we give this name to every endoskeletal scaffolding directly prolonging inward the basement membrane of the hypoderm. Muscles inserted on such an endoskeleton may be, of course, homologous with muscles inserted on cuticular infoldings encompassed with the hypoderm and thus with the basement membrane of the hypoderm (see Carpentier, 1946, pp. 171-172), whatever the chemical nature—not yet elucidated—of the subhypodermal formations.

on entomology do not show the furcal apophysis connected with a postpleural process but rather with the process of the (medio)pleural apodeme. However, the coexistence of the two kinds of processes has been observed in such insects as *Sialis* (Weber, 1928, fig. 14[b]; Czihak, 1953, fig. 7) and in Lepidoptera (Weber, 1928, figs. 1[a]
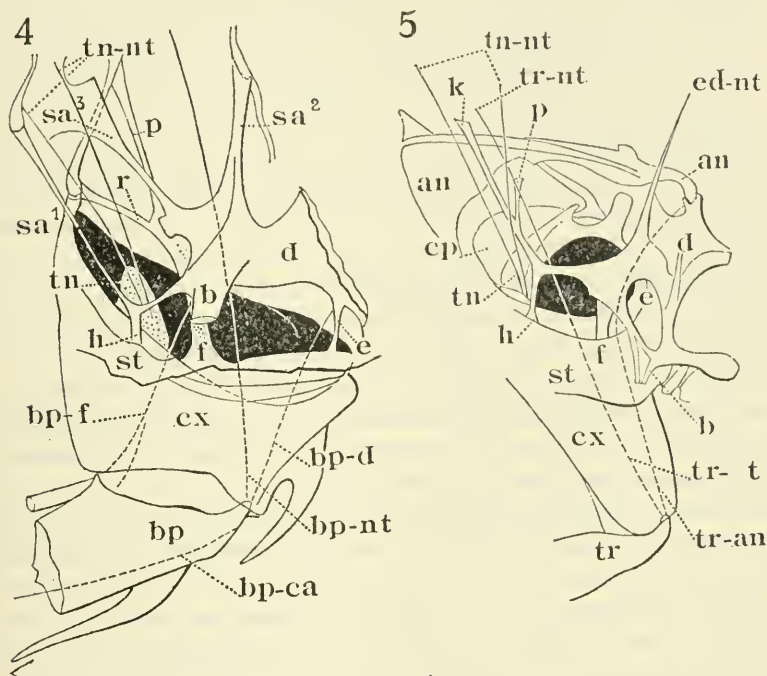
FIGS. 4 and 5.

FIG. 4.—Basal region of the 3d right thoracic limb of *Penaeus caramote* Risso, setae omitted.

FIG. 5.—Basal region of the prothoracic limb of a machilid. (Figure based especially on *Petrobius*.)

The two figures show the internal side, with the endosternite and some particularly interesting muscles (drawn with a single line).

an, anapleuron or anapleural pleurite; *ap*, pleural apodeme; *bp-ca*, muscle going to the carpopodite, homologous with a tibiatrochanter muscle in the insects; *bp-d*, other depressor of the basipodite; *bp-f*, levator muscle of the basipodite, homologous with a trochantero-furcal muscle of the insects; *bp-nt*, depressor of the basipodite, homologous with a trochantero-notal (epimeral) muscle in the insects; *cp*, catapleuron; *cx*, coxopodite or coxa; *d, e, f, h, k, p*, arms of the endosternite homologized in the Apterygota; *ed-nt*, endosterno-notal muscle; *sa*, superior arms (not homologized in the Apterygota); *st*, sternite; *tn*, trochantin or its tendon; *tn-nt*, trochantino-notal muscles; *tr*, trochanter; *tr-an*, trochantero-anapleural muscle; *tr-nt*, trochantero-notal muscle.

and 9ᵃ). The processes can be connected by muscular fibers or can be closely united. If the postpleuro-furcal complex has become somewhat voluminous, that with the (medio)pleural process can be found reduced or even lacking entirely. When we consider only the pterygotan insects, we might think that of the two ways in which the furca is united, that with the back is the more recent one. The Apterygota in which this way of union (fig. 5) is so widespread,[21] the Myriapoda [22] as well as the Crustacea, lead us to adopt the opposite opinion.

We have now to describe and to compare with what we have just seen the internal side of a precoxopodite of *Anaspides*. We shall use the fourth pereiopod (fig. 3), that is to say, the antepenultimate leg as in the previous species. The precoxopodite of this leg being free and uncovered, since *Anaspides* does not have a carapace, it is quite different from the preceding one in its orientation and in its shape. It is not imbedded in the side of the thoracic segment and keeps a certain mobility by means of two articulations (ϵ, δ) with a particular sclerite of the lateral wall (*an*). Hansen (1930) took this sclerite for a part of the precoxopodite; Snodgrass (1952) named it laterotergite (*lg*). The posterior articulation (δ), the only one seen by those authors, has been interpreted by them as representing β of our figure 2 (*Penaeus*). We see at once on figure 3 that there is no pleural apodeme on top of it but that this apodeme (*ap*) is actually a part of the wall of the so-called coxopodite of the authors. The curved pleural apodeme (*ap*) bears at the top of the precoxopodite a process (*pp*) which may be the pleural process; but, considering its position in comparison with that of the process of the penaeids, we cannot yet give a definite answer. The precoxal wall is divided into an episternal region (*es*) and an epimeral region (*em*) of about the same surface area. The episternum is barred almost horizontally with an apodeme which joins *ap* at the top. Two large blades, or epipodites, are attached externally on the episternal region of *Anaspides,* while in the same region we saw but a single epipodian gill in *Penaeus*. Finally the furcal apophysis of *Penaeus* is completely wanting in *Anaspides*. The thoracic lateral wall of the latter crustacean is thus rather different from that of the first one; but the comparative study of the endoskeletal scaffoldings

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[21] The subhypodermal endoskeleton is united with it, or connected by a tie (the postcoxal tie *d*) at the back of the anapleural arc. See Carpentier, 1946, figs. 4 and 5 (prothorax of the Machilidae), and fig. 2 (*Ctenolepisma*); Barlet, 1951, fig. 1 (*Lepisma*), Carpentier and Barlet, 1951, fig. 2 (*Campodea*); unpublished (*Japyx*).

[22] Unpublished observation.

and of their relations with the skin fortunately gives us better precision.

### ENDOSTERNITES OF PENAEUS AND ANASPIDES

We have seen that the postpleural and furcal formations of the cuticle of *Penaeus* are wrapped in a common subhypodermal endosternal sheath. This endosternite (fig. 6) is unified, that is to say the right and left parts of the scaffolding are medially united by a transverse strip (b) going over the nerve cord. Such were the endosternites studied in the Lepismatidae, in the prothorax and mesothorax of the Machilidae, etc. On each side of the body, the endosternite is connected with the skin by ties. There are three superior arms (sa); we do not name them with more accuracy because we have not found their homologues—at least their endoskeletal homologues—in the insects. The first arm (sa^1) is very thin and could be confused with the pleural "tigelle" k of the Apterygota[23]; but dorsally, instead of being connected with the notum, it is attached to the anterior phragm (fig. 2, ph). The upper arm (sa^2) is attached to the posterior phragm; it is double and each of its branches toward the phragm is enlarged into a blade serving as a support to longitudinal muscles. The arms sa^1 and sa^2 could respectively correspond to the oblique muscles 75 and 77 (prothorax of *Lepisma,* Barlet, 1951, fig. 1); sa^2 could also correspond to 85 (mesothorax, idem) and 92 (metathorax, idem). This is one possibility.[24] A third and last superior arm (sa^3) pertains to the lateral process (fig. 2, x), the morphological value of which we do not know.

All the other arms of *Penaeus* have been homologized and are designated therefore, on figure 6, by letters taken over from the notation system which was formerly adopted for the Apterygota. For instance the arm p, the identity of which is obvious; this arm connects the central part, g, of the endosternite with the pleural apodeme. The union is direct since there is no pleural process; in *Amalopenaeus* the union is achieved by means of a pleural process. Another lateral arm (r) pertains distally to the border between the precoxopodite and the coxa.

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[23] See Carpentier, 1946, fig. 2 (*Ctenolepisma*), fig. 5 (*Petrobius*); Carpentier, 1949, fig. 5 (*Tomocerus*); Barlet, 1951, fig. 1 (*Lepisma*).

[24] Back in 1927, Cannon (p. 413) examined in a phyllopod crustacean the muscularization of endoskeletal elements. See also Manton, 1928. Without knowing anything about these results, we came to conceive the substitution of "tigelles" for muscles (Barlet, 1946, p. 182; Carpentier, 1949, p. 46, note 7; Carpentier and Barlet, 1951, p. 4). Chadwick (1957) exploited this idea about the Pterygota.

Its homologue was seen in a collembolan, *Tomocerus* (Carpentier, 1949, fig. 5). A last lateral arm (*d*) corresponds to the postcoxal tie of the Apterygota, but here it is quite voluminous for it contains the postpleural process (fig. 2, *pu*) in a cavity which extends a little into the transverse strip *b*.
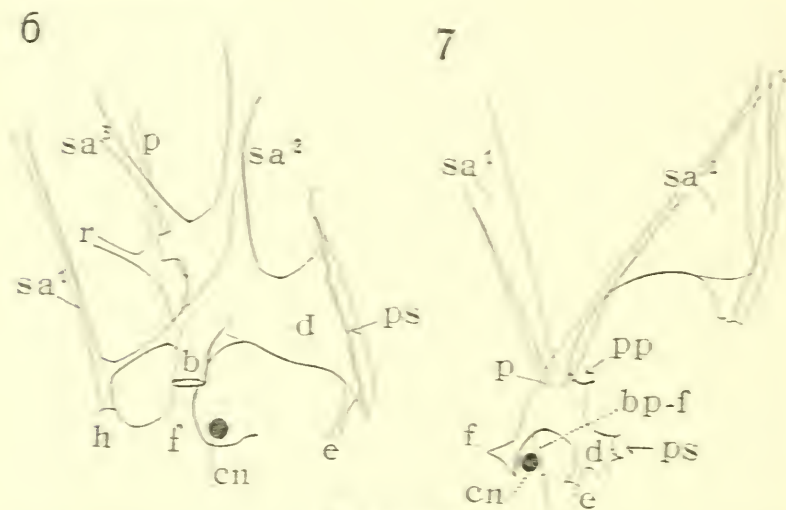
FIGS. 6 and 7.

FIG. 6.—Endosternite of the 7th thoracic segment (5d pereiopod) of *Penaeus* sp. (off the Brazilian coast), right half seen from inside. The transverse strip *b* has been cut.

FIG. 7.—Endosternite of the 5th thoracic segment of *Anurida maritima* Thomson, right part seen from inside.

b, d, e, f, g, h, p, r, arms homologized with those of the Apterygota, *bp-f,* levator muscle of the basipodite, homologous with *bp-f* of *Penaeus* (fig. 6) and with a trochantero-furcal muscle of the insects but missing in the Machilidae; *cn,* crural nerve, *ps,* pleural process; *pu,* postpleural process; *sa,* superior arms non-homologized in the Apterygota; *sa¹* could correspond to the muscle *od-ot* of the machilids (see fig. 3).

Finally, the endosternite is provided with three lower arms. Anteriorly we see *h* which proceeds in *sa¹* and contributes toward making this one similar to *h* of the Machilidae. Toward the middle lies *f* which contains the furcal apophysis (fig. 2, *fu*) in a separate pouch, a little more distal than that of the spatula of the postpleural apophysis. Posteriorly we find the lower arm *e*; it presents with *d* similar relationships to the ones we studied in the Lepismatidae.[28]

[28] Carpentier, 1946, fig. 2. The postcoxal tie of the Lepismatidae is thin and does not contain a cuticular process. In *Petrobius* (op. cit., figs. 5 and 6) *e* has

On the whole we see thus that the equivalents of the majority of the endosternal arms of the Apterygota and particularly those which had appeared the most consistent and typical, have been found in *Penaeus*. The importance of this result is obvious.

We have now to describe the subhypodermal scaffolding of *Anaspides* (fig. 7). In spite of the great differences which it displays at first sight from that of *Penaeus* and in spite of its relative simplicity, it furnishes us on many points valuable information for the interpretation of the cuticular skeleton to which it pertains. In *Anaspides,* the endoskeleton is not unified; no strip *b* connects the right formation with the left formation. Each of them contains two superior blade-shaped arms, one (sa^1) pertaining to the front of the tergal region, the other (sa^2) arising from the back of the same region and in the proximity of which it is particularly wide. The two arms do not pertain to phragms but to "pseudophragms" (subhypodermal).

There are two lateral arms, and these are the most interesting. One of them (p) connects the endosternite with what we have interpreted as the process of the pleural apodeme (pp). This arm is interesting, first because it confirms our interpretation, then because of its shape: it is a sheath of the process, a sheath of the same type as (although smaller than) the "fourreau" which fits the long pleural horn of the Machilidae (Carpentier, 1946, fig. 6, and 1949, fig. 1). The other lateral arm (d), no shorter than the preceding one, is attached to what was supposed to correspond to a postpleural process (ps). Our supposition becomes thus a certainty.

If we really have to do with a postpleural process, it becomes obvious that this formation does not pertain to the precoxopodite but to the upper sclerite, the laterotergite. It seems to us that this sclerite, already present in *Anaspides,* must represent the anapleural region of the Apterygota. In keeping with this opinion, we have to discuss the following facts: In *Penaeus* (fig. 4) and other Malacostraca we have found a muscle (bs-ps) of the basipodite (trochanter) coming from the under part of the postpleural process. In the Machilidae we have recently found out that in the prothorax (fig. 5) a few fibers (tr-an), very close to those of the depressor of the trochanter (Barlet, 1946, fig. 2, TR-ED), come from a sclerite (ibid., sp) to which the

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not been correctly located. Our researches after 1946 have shown that instead of "$f + e$" we should have written "f," and instead of "$i + d$" we should have written "$e + d$."

region d of the endosternite adheres and which must be anapleural.[26]
There are two inferior arms of the endosternite of *Anaspides:*
f and e. The arm f thus exists, but no furcal apophysis developed
within it. Our figures 6 and 7 show that in *Anaspides* as well as in
Penaeus the crural nerve cn passes between f and e. One will at once
object that in the Apterygota the crural nerve is not posterior to f
but anterior. This difficulty at first embarrassed us, but later we found
that the crural nerve can be connected with the ganglion by two roots,
one anterior to f (or fu), the other posterior. The two roots coexist
in *Amalopenaeus,* but quite often only the posterior root exists in the
Crustacea. In the insects it seems that it is always the anterior one.[27]
Thus our difficulty was only apparent.

We see that in spite of the difference of aspect and of composition
of the endosternites of *Anaspides* and of *Penaeus* we have been led
to locate in both crustaceans the homologues of the main lateral and
inferior arms of the Apterygota.

CONCLUSIONS CONCERNING THE LEG BASE AND THE PLEURON OF THE MALACOSTRACA

We have presented in this paper a comparative analysis of these
parts of the body only in two Malacostraca: that regarded as the most
"primitive" of all and a decapod particularly "primitive" too. We
have made a few references to other species which have also been
studied. Our present knowledge of the Malacostraca may seem insuffi-
cient, but one should bear in mind that our study has dealt with only
a very limited region of the body of the Crustacea and that this same
region had been previously studied for many years with the greatest
care and with exactly the same method on various Apterygota and
even (unpublished) on Myriapoda. The experience so acquired will
have kept us, let us hope, from making identifications based upon
coincidences rather than upon a real morphological kinship.

At any rate one result of our researches seems to be beyond all
question: the true pleural region of a malacostracon cannot contain

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[26] In the first of our works on the Apterygota (Carpentier, 1946, p. 177) we
indicated that this sclerite is "very ambiguous," but we thought that we could
refer it to the catapleuron. The preoccupation to classify the propleural sclerites
of the Machilidae according to two circles led to this interpretation, which
seemed to be supported by certain features of *Thermobia* (Lepismatidae). How-
ever, it must be false as we found out later in our studies.

[27] Constant, too, in the Pterygota. One would not think so upon examining
fig. 2 in Jösting's work (1942) concerning *Tenebrio;* but we were able to show
that his figure is in error.

a segment of the leg more distal than the precoxopodite. What we have found by carefully examining the exterior of the leg has been confirmed—we think, in a conclusive manner—by the inspection of the interior of the precoxopodite. Whether this segment has remained free or has been imbedded in the thorax, it has displayed in both cases features which correspond with those of an insect pleuron. It has displayed the most typical relationships with the ventral endoskeleton previously found in the Apterygota. *Anaspides* most resembles the latter by the predominance of its subhypodermal endoskeleton, whereas *Penaeus,* by the development of its cuticular infoldings, is more like a pterygote.

The precoxopodite is thus morphologically equivalent to a unilaterally developed pleuron; but is it the entire pleuron? Most likely not, for the precoxopodite does not directly articulate on the tergum of the thoracic segment but on a "laterotergal" plate. This laterotergite bears posteriorly a process which the comparison with the insects led us to call postpleural. The laterotergal plate seems to pertain to a region homologous with the anapleuron of the Apterygota.[28] On the proximal side we never saw it achieve a complete circle, but in these arthropods, the anapleuron, in certain points, remains difficult to analyze.

According to these new data, what must we think of the "subcoxal theory"? Of course it is beyond doubt that the originally basal ring of the leg has secondarily been imbedded in the thoracic wall, but this ring may very well have produced only a part of the pleuron.

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[28] A priori, we can hardly accept the idea of the distinction of an "anapleuron" and of a "catapleuron" (precoxopodite) starting with the Crustacea. Indeed in the nauplius of various Crustacea, the segments of the sympod appear distinctly only some time after the hatching (Heegaard, 1947); but for the phylogenist what does this order mean according to which morphological details appear in a larva such as a nauplius?

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