Crustacea Phyllopoda and Malacostraca: a reappraisal of cephalic and thoracic shield and fold systems and their evolutionary significance

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SUMMARY

In 1909 Calman presented the carapace hypothesis, according to which all Crustacea possess or once possessed a carapace fold, formed from the posterior margin of the cephalon. In those Crustacea which have no such free fold but a cephalothoracic shield covering the cephalon and part or the whole of the thorax, this shield was interpreted as a carapace fold fused to the dorsum of the thorax and often overhanging its sides, for example, in lobsters and natantians.

When a carapace fold or carapace shield is missing, as, for example, in Anostraca or Syncarida and behind the maxilliped segment in amphipods and isopods, this has been understood to imply that a carapace fold or shield has been lost.

The carapace hypothesis has been universally accepted and has influenced the interpretation of Crustacean evolution and inter-relationships.

Phil. Trans. R. Soc. Lond. B (1991) **334**, 1–26
Printed in Great Britain

Vol. 334. B 1269 (Published 29 October 1991)

A re-examination of numerous Crustacea, including embryos and larvae, with the application of a variety of histological standard techniques, proved that no cephalic carapace fold is formed in any malacostracan presumed to possess it, or in any notostracan, spinicaudate or laevicaudate branchiopod examined. In the Branchiopoda, when a dorsal fold is formed, it is always attached to a trunk segment.

Free dorsal folds in the Malacostraca are always attached to the posterior margin of a thoracic segment, and dorsal cephalothoracic shields are never formed as a result of the fusion of a cephalic carapace fold to the dorsum of the thorax. Instead, the formation of a cephalothoracic shield in the Malacostraca is always due: (i) to the fusion of the 1st thoracic segment to the cephalon in connection with the differentiation of maxillipeds; and (ii) to the obliteration of lateral and dorsal external segment borders in the whole or part of the dorsum of the thorax apparently because of the formation of continuous and unsegmented branchiostegal folds. These folds are always continuous with those of the maxilliped segment and the cephalon. In the Anaspidacea, Amphipoda and Isopoda, which have no branchiostegal folds behind the maxilliped segment, the external segmentation is retained in all segments behind it, and the same is the case with the segments behind the cephalothoracic shield in, for example, mysids and cumaceans.

The rule that the number of thoracic malacostracan segments covered by a cephalothoracic shield is identical to the number of segments contributing to the formation of branchiostegal folds has no exceptions.

In the light of the failure of the carapace hypothesis, the retention of an external thoracic segmentation represents a plesiomorphic condition and the formation of an only partly segmented or an unsegmented thorax a derived one. The Syncarida, with up to eight free thoracic segments in the Palaeocaridacea and Bathynellacea, then appear to reflect an ancestral condition and are possibly not too far removed from malacostracan ancestors. This permits a new approach to eumalacostracan phylogeny and higher systematics.

The reason for many misunderstandings concerning dorsal folds and shields appears to be technical. Observations leading to claims that a carapace fold *sensu* Calman exists, or existed, in all Crustacea were to a large extent based on studies of wholemounts, often made after maceration in potassium hydroxyde solutions. This leads to the dissolution of soft tissues so that the dorsal integument comes to consist of only a single sheet of cuticle attached anteriorly to the cephalic region. This may easily give the false impression of representing a true carapace fold. An examination of serial sections of the intact cephalothorax reveals the true topographic inter-relationships.

LIST OF ABBREVIATIONS USED ON FIGURES

a	antenna
abd	abdomen
al	antennule
ap	apodeme
br	brain
brf	branchiostegal fold
bw	body wall
c	cephalon
ce,cer	compound eye rudiment
cpf	carapace fold
cts	cephalothoracic shield
cplf	cephalic pleural fold
df	dorsal fold
dfr	dorsal fold rudiment
dfatt	dorsal fold attachment
div	diverticle
h	heart
hep	hepatopancreas
l	labrum
lm	longitudinal muscle
m	mandible
mg	midgut
mo	mouth opening
mx	maxilla
mxgl	maxillary gland
mxglp	maxillary gland pore
mxl	maxillula
mxldm	maxillular dorsal muscle
mxp	maxilliped
oe	oesophagus
pg	paragnath
pl	pleon
plf	pleural fold
plt	pleon tergal shield
r	rostrum
st	stomodaeum
t	telson
th	thorax
thdf	thoracic dorsal fold
thp	thoracopod
thplf	thoracic pleural fold
thpr	thoracopod rudiments
trl	trunk limb
trs	trunk segment
v	ventricle
vg	ventral ganglion
y	yolk

1. THE CARAPACE HYPOTHESIS

Many Crustacean taxa possess dorsal or dorsolateral cephalothoracic shields or folds which often have important roles in their various functional systems. These structures have long attracted the attention of carcinologists (see, for example, Milne Edwards 1834) and under the collective name of 'carapace' have figured prominently in discussions concerning crustacean morphology, evolution and phylogeny. But it was not until this century that the classical carapace hypothesis found its final shape, presented by Calman (1909 p. 6) as follows: 'A structure which, from its occurrence in the most diverse groups of Crustacea, is probably a primitive attribute of the Class, is the dorsal shield or *carapace*, originating as a fold of the integument from the posterior margin of the cephalic region. In its simplest form, as seen in *Apus* [= *Triops*] among the Branchiopoda, the carapace loosely envelops more or less of the trunk.... In many cases among the Malacostraca the carapace coalesces with the tergites of some or all of the thoracic somites, though it may project freely at the sides, overhanging, as in the Decapoda, the branchial chambers.' A corollary to the carapace hypothesis is that the absence of the carapace in certain taxa must be due to its having been lost secondarily.

With the same contents, but with variations in its actual formulation, the definition of the carapace introduced by Calman (1909) has been repeated in handbooks and textbooks up to the present time, for example, by Zimmer (1926), Moore & McCormick (1969) and McLaughlin (1980), and it appears to be universally accepted by contemporary carcinologists.

As seen from the definition, the basic postulate of the carapace hypothesis is the presence, originally in all Crustacea, of a carapace fold attached to the posterior margin of the cephalon. This implies that the whole thorax behind the attachment of the fold should be normally segmented, and this is generally presumed to represent the situation found, for example, in notostracan branchiopods and in leptostracans. But when, as in many Malacostraca, the dorsum of the thorax is covered by a shield, this shield was presumed by Calman (1909) to represent the whole or part of a carapace fold fused to the dorsum of the thorax. In mysids, where the anterior part of the thorax is covered by a shield, to the posterior margin of which a free fold is attached, this fold should then, logically, represent the terminal portion of a partly fused carapace fold.

In some papers published before and after the formulation of the carapace hypothesis, observations have been described that appear to contradict it. It is surprising that even clearly relevant cases of this kind do not figure at all in more recent discussions concerning problems bearing upon the carapace hypothesis. Perhaps because some of them come from the fields of embryology and microscopical anatomy, they appear to have escaped being noted by carcinologists concerned with systematics and phylogeny. Conversely, embryologists and microanatomists have, in recent years, shown little interest in evolutionary and phylogenetic problems in the fields covered by the carapace hypothesis. Particularly in the last 30–40 years the result has been a lack of information exchange between different branches of carcinology. Examples will be given below in their proper contexts.

It is now time for a re-evaluation of the foundations upon which the carapace hypothesis was built. Brief references to some aspects of the problems involved were included in previous papers (Dahl 1983*a*, *b*) but because those papers were mainly concerned with other aspects, space did not permit a full presentation of the evidence then available. Many new observations have since been added, which shed new light upon the problems involved.

In the study of primary material, which is presented below, interest has been focused upon the Malacostraca and the Branchiopoda, for the following reasons. The Notostraca, Spinicaudata and Laevicaudata have long been considered to provide classical examples of primitive Crustacea with carapace folds attached to the posterior margin of the cephalon. At the other extreme the Malacostraca, including the most advanced Crustacea, have been fundamental to the carapace hypothesis because some of their less derived taxa have been reported to possess cephalic carapace folds during the whole or part of their life cycles. In others, as noted above, characteristic dorsal shields have been considered to represent such carapace folds fused to the dorsum of the thorax and overhanging its sides.

It appears reasonable to presume that if the Branchiopoda and Malacostraca could be proved to possess a cephalic carapace fold, the general validity of the carapace hypothesis could be regarded as established, even if certain representatives of the two taxa no longer have a carapace *sensu* Calman. If, however, a cephalic carapace fold cannot be found within these two taxa, a carapace fold cannot be accepted as a basic element of the crustacean structural plan.

In accordance with the considerations presented above, cephalothoracic and thoracic fold and shield structures and their formation were studied in those higher branchiopod and malacostracan taxa which have been presumed to possess structures of this kind. These studies led to a reconsideration of the formation of dorsal shields and folds and their bearing upon, in the first place, malacostracan evolution and interrelationships. The Maxillopoda, including the remarkable maxillopod members of the Upper Cambrian Orsten fauna (Müller & Walossek 1985, 1988), were not included in the present study.

2. MATERIAL AND METHODS

To a limited extent this investigation could be based on published records. Wherever possible, however, primary material was examined. The main source was the collection of sectioned Crustacea in the Department of Zoology of the University of Lund, which was founded in the 1920s by the eminent carcinological morphologist Professor Bertil Hanström and has been added to by generations of zoologists. It is of historical interest that most of Hanström's slides, in part more than 60 years old, are still in a very good condition. I estimate that the collection now comprises about 20000 slides of Crustacea, sectioned and stained with the application of a wide variety of techniques. Although there are gaps and also considerable variations with respect to quality, most higher taxa are quite well represented. In the course of this investigation substantial additions have been made. This collection is probably unique with respect to both volume and diversity. Where desirable, microanatomical methods were supplemented with dissections of larger forms and the study of stained and cleared wholemounts. More detailed information concerning material and techniques used in specific cases will be given in connection with the treatment of the various taxa and in figure legends.

3. TERMINOLOGY

(*a*) *Previous applications of the term 'carapace'*

The definition of a carapace given by Calman (1909) and quoted above appears clear enough, but in the course of the present study I encountered the term 'carapace' applied in a wider sense than compatible with this definition (for instances cf. Schram 1986 pp. 5–6). For this reason in the present paper the term 'carapace' has been used only when referring to the specific sense in which it has been applied by the respective authors.

(*b*) *Shield and fold terminology used in this paper*

To avoid the difficulties referred to above, the terms used in this paper and defined below are purely descriptive and without evolutionary or phylogenetic implications. They are explained in figure 1.

(i) *Cephalothoracic shield* (Calmon 1904) in the Malacostraca. A shield covering dorsally the cephalon and one, several or all thoracic segments. In a previous paper (Dahl 1983*a*) I referred to the thoracic part of this type of shield as a 'postcephalic shield'. However, considering the fact that this thoracic part of the shield is always a direct continuation of the cephalic dorsal shield, I find the term 'cephalothoracic shield' more adequate.

(ii) *Dorsal fold.* A fold formed from, and attached to, the trunk behind the cephalon, in the Malacostraca always to the posterior margin of a cephalothoracic shield, in the Branchiopoda to a trunk segment.

(iii) *Cephalic pleural fold* (in the Malacostraca). A more or less distinct lateroventral fold comprising the fused pleura of the cephalic segments.

(iv) *Segmental pleural folds* (in the Malacostraca). Separate segmental folds formed from the ventrolateral margins of free trunk segments (thoracic or abdominal).

(v) *Branchiostegal folds* (in the Malacostraca). Ventrolateral folds formed by the fusion of one, several or all thoracic pleural folds to the cephalic pleural fold and, when more than one, to each other. Branchiostegal folds, when present, form the boundary between the dorsal and ventral parts of the thorax, covering its ventrolateral sides, including the more proximal parts of the thoracopods and the whole or part of the branchiae which may be attached to them.

(vi) *Branchiostegal flaps* (in the Malacostraca). Lateral folds growing out from the posterior margin of branchiostegal folds, when large generally held together and in place by a free thoracic dorsal fold (for example, in the Mysida).

4. DORSAL FOLDS IN THE BRANCHIOPODA

(*a*) *General remarks*

Many branchiopod taxa possess simple or bivalved dorsal folds, which, in less derived forms, are attached

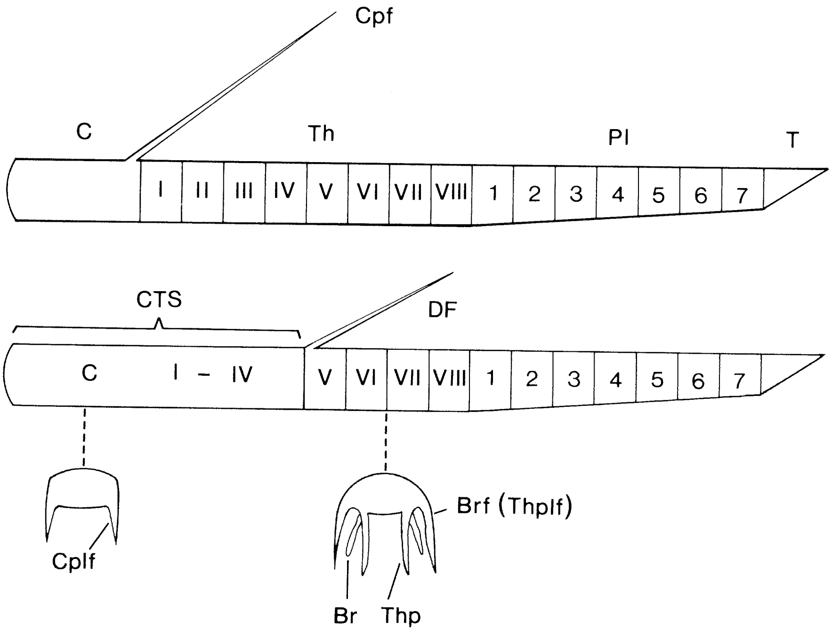


Figure 1. Diagrammatic sketch explaining certain terms in the list of abbreviations used on figures.

anteriorly and loosely cover part of the trunk and the appendages. In comparison with the thoracic exoskeletons of some Malacostraca, those of the Branchiopoda are comparatively simple structures.

It has been accepted as axiomatic that the dorsal folds of the Notostraca, Spinicaudata and Laevicaudata (*sensu* Fryer 1987) are formed from and remain attached to the posterior margin of the maxillary segment and that, consequently, they are true carapace folds in the sense postulated by the carapace hypothesis. Before the present investigation I saw no reason to doubt that this was the case (Dahl 1983*b*). Note, however, that Lang (1888), in his textbook on invertebrate comparative anatomy, stated that the carapace fold in *Triops* is attached to the anterior trunk segments, but this statement attracted no attention, and I have found no reference to it in carcinological literature.

(*b*) *Notostraca*

The notostracan material at my disposal consists of numerous series of sectioned specimens of *Triops cancriformis*, both larvae and juveniles reared in the laboratory and adults collected in the field, as well as numerous series of sections of the South African species *T. namaquensis*, of which many specimens fixed in freshwater Bouin and stored in alcohol were also available for dissection.

In sagittal sections of a recently hatched matanauplius of *Triops cancriformis* about 0.3 mm in length (figure 2) most cells, except those of the brain, contained yolk granules. The stomodaeum is open, but the proctodaeum is still closed, and the midgut is empty. There is no sign of any dorsal fold.

A series of sagittal sections through a bottom-feeding juvenile 3.10 mm in length provides evidence that more mediad a dorsal fold is attached both to the 1st and the 2nd trunk segments, whereas more laterad only the 1st trunk segment is involved (figures 3–9).

Study of the adult condition was based mainly upon comprehensive sectioned material of *T. namaquensis*, particularly upon a number of specimens fixed in aquatic Bouin, embedded in celloidin, cut at 100 μm and stained in Mallory's phosphotungstic acid haematoxylin as described by Wingstrand (1951), who also produced the sections. These series constitute superb material for the study of the topography of the cephalon and the trunk.

The topography of the cephalon of the Notostraca was described by Fryer (1988), and here only aspects concerning the formation and attachment of the dorsal fold will be dealt with.

Behind the cephalon the segmental arrangement of the trunk musculature of the adult is very distinct. As seen from figures 8 and 9, the dorsal fold is attached to the posterior margin of the 1st trunk segment, including the part forming a deep cleft between the dorsal parts of the musculature of the 1st and 2nd trunk segments, and thus also to the anterior margin of the 2nd segment. It is a dorsal fold as defined above and not a carapace fold.

In summing up the evidence presented above it can be stated that the Notostraca do not possess a cephalic carapace fold during any part of their life cycle. The dorsal fold is formed ontogenetically from the anterior part of the trunk of the postnaupliar larva. In both juveniles and adults the attachment of the dorsal fold is primarily to the 1st trunk segment, although the 2nd trunk segment is also involved. Throughout life the attachment of the dorsal fold lies behind the cephalon.

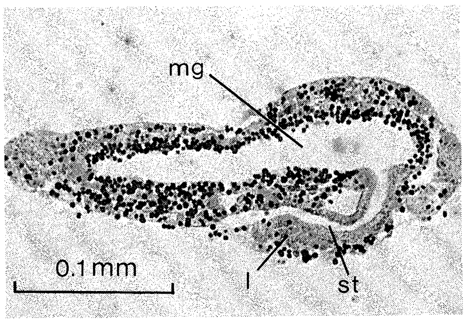
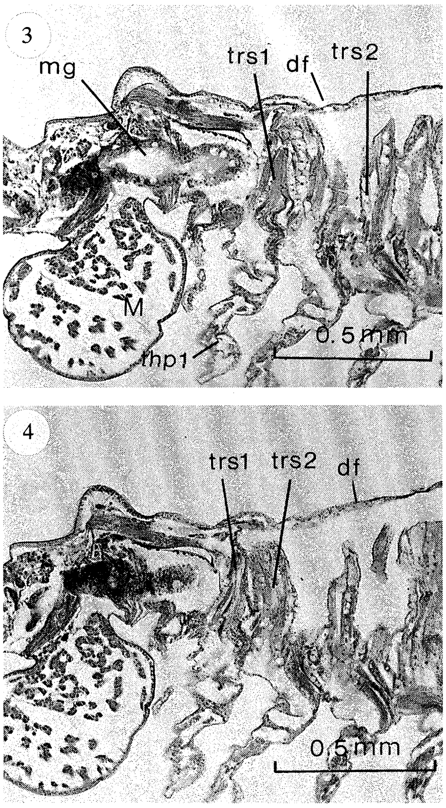


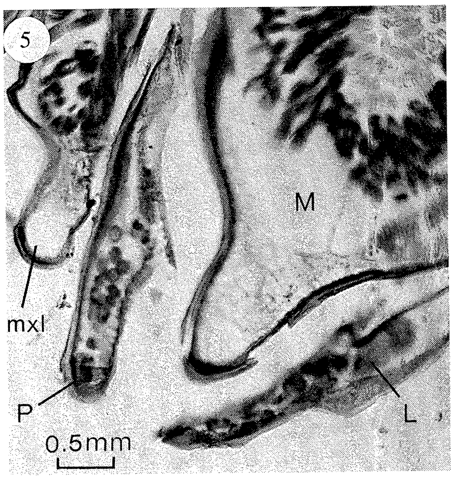
Figure 2. Sagittal section through early metanauplius of *Triops cancriformis*, length 0.3 mm. All tissues full of yolk granules. Stomodaeum open but proctodaeum still closed, no sign of fold formation.



Figures 3, 4. Parasagittal sections through cephalon and anterior part of trunk of early benthic juvenile of *T. cancriformis*, total length 3.10 mm. Figure 4, lying slightly more laterad than figure 3, shows attachment of the dorsal fold (df) only to the 1st trunk segment, whereas in figure 3 the fold is attached both to the 1st and 2nd trunk segments.

(*c*) *Spinicaudata and Laevicaudata*

The ontogeny and early larval development of *Estheria packardi* was studied by Sars (1896*a*), that of



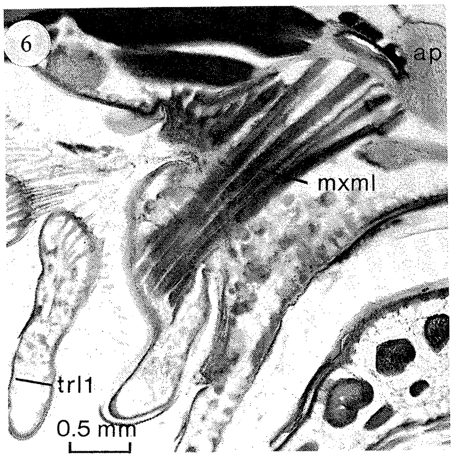
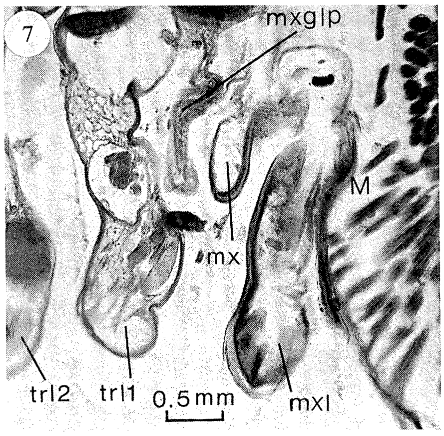
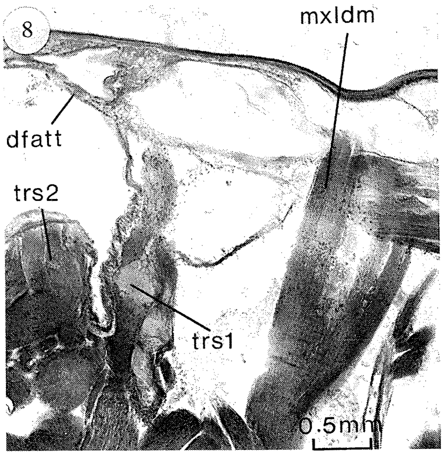


Figure 5. Parasagittal section through ventral parts of limbs in the mouth region of an adult *Triops namaquensis*.
Figure 6. *T. namaquensis*, parasagittal section showing strong muscle attachment of maxillula to apodeme below the ventral nerve chord.





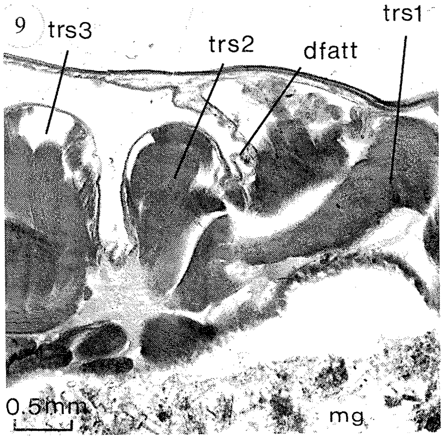


Figure 7. More lateral parasagittal section through *T. namaquensis* showing maxilla and outlet of maxillary gland.
Figure 8. Parasagittal section of *T. namaquensis* showing dorsal fold attachment to posterior margin of 1st trunk segment. More anteriad the attachment: of the maxillular dorsal muscle to the roof of the cephalon, and the muscles of trunk segments 1 and 2.
Figure 9. Parasagittal section through the lateral part of the anterior trunk segments of *T. namaquensis* and the attachment of the dorsal fold.

Estheria sp. by Cannon (1924), and that of *Limnadia stanleyana* by Anderson (1967). The following brief account of the ontogeny of the bivalve folds enclosing the body of the adult is based mainly on these sources. My own primary material consists only of a series of sagittal sections of an adult *Limnadia lenticularis* and dissections of an adult specimen of an Australian *Estheria* species (s. lat.).

In *E. packardi*, Sars (1986*a*) found the earliest fold rudiments as small bulges in the anterior part of the trunk region of the 3rd nauplius. Anderson (1967) noted similar bulges in the 3rd nauplius of *L. stanleyana*. In a somewhat older nauplius of *Estheria* sp. a transverse section through the 1st trunk segment showed the presence of deep lateral folds attached to the sides of the trunk but no carapace fold (Cannon 1924, cf. figure 10). This suggests that at this stage the attachment of the free dorsal folds could not lie anteriad of the posterior margin of the 1st trunk segment. This is consistent with the results of Anderson (1967, fig. 6), who showed that small dorsal folds were present in the region of the 1st trunk segment, and with those of Sars (1986*a*) who, in his drawings of lateral views of the various stages of *E. packardi* from the last nauplius to the adult, showed that the attachment of the bivalved dorsal folds lies at the posterior margin of the 1st trunk segment.

My observations confirm that the situation is similar in the adult *Limnadia lenticularis*. In the region where the long axis of the body of the adult bends abruptly ventrad at nearly right angles to the posterior part of

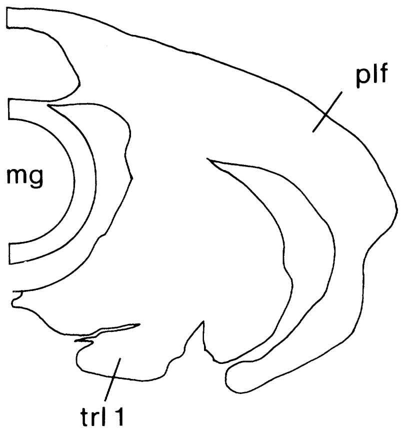


Figure 10. Transverse section through the anterior part of the post-cephalic trunk in larva of *Estheria* sp., showing, *i.a.*, the well-developed pleural fold behind the cephalon, but no indication of a formation of a free dorsal cephalic fold. (After Cannon (1924, figure 18), redrawn and much simplified.)

the trunk, the dorsal body wall forms a pair of bulges to which the shell valves are attached (cf. Calman 1909, fig. 17). This attachment area lies behind that of a pair of strong obliquely longitudinal muscles, referred to by Hessler (1964) as trunk adjustor muscles. In *L. lenticularis* most of the musculature forming these large muscles is contributed by well-defined muscle bundles running dorsad from the four anterior trunk segments. In the same species, Nowikoff (1905) found a small muscle from the maxillary segment attached to the dorsal integument just at the anterior margin of the large oblique muscle attachment (cf. Nowikoff 1905, plate 19). This does not justify his referring to this entire muscle complex as maxillary. An arrangement similar to that found in *Limnadia* was shown by Hessler (1964) to exist also in *Lynceus*, where, however, the oblique muscle complex is much less voluminous.

Summing up the situation in the Spinicaudata and Laevicaudata it can be stated that no cephalic carapace fold is formed in the investigated species. The paired shell valves grow out in the larva at the posterior margin of the 1st trunk segment. In the juveniles and adults these valves increase in size and finally envelop the body and most of the trunk limbs.

(*d*) **'*Cladocera*'**

In the case of the Cladocera it has been known for a long time that the dorsal folds are formed from the trunk behind the cephalon, sometimes, particularly in *Leptodora*, far behind it (cf. Calman 1909).

(*e*) ***Conclusions concerning the Branchiopoda***

Despite previous statements to the contrary, a survey of relevant literature supplemented by studies based on microanatomical techniques have shown that cephalic carapace folds do not occur in any of the higher branchiopod taxa investigated. When present, dorsal folds are formed from and attached to the anterior part of the trunk and not to the cephalon.

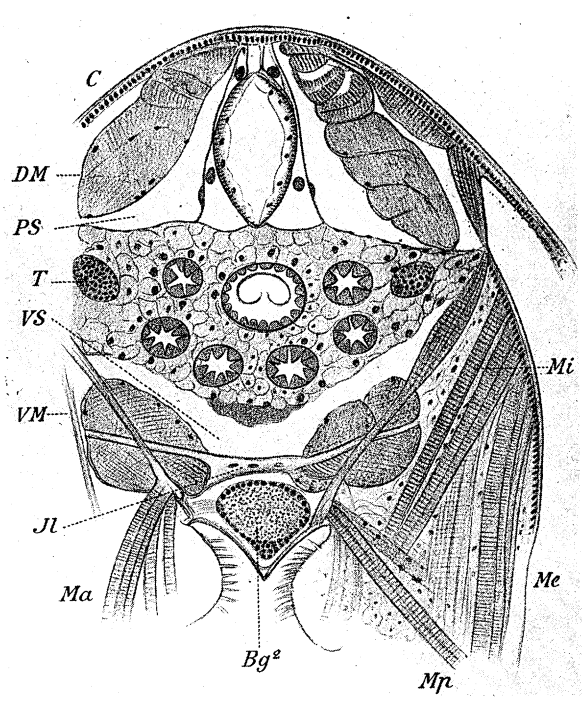


Figure 11. Transverse section through the 2nd thoracic segment of *Nebalia strausi* showing the broad attachment of the cephalothoracic shield to the dorsum of the thorax, the heart and the large longitudinal muscles. In the centre the midgut, the six hepatopancreatic tubuli, and the testes. Ventrolaterally the muscles of the 2nd thoracopod and, midventrally, the ganglion of the 2nd thoracic segment (after Claus 1887, plate IX, figure 8).

5. CEPHALOTHORACIC SHIELDS AND FOLDS IN THE MALACOSTRACA

(*a*) ***Phyllocarida***

(i) *Background*

The Phyllocarida possess a very large fold system which envelops the cephalon and thorax, except for the distal parts of some appendages, and also a part of the abdomen.

It appears to be universally accepted that the Leptostraca, the only Recent order of the subclass Phyllocarida, possess a cephalic carapace fold *sensu* Calman (1909). As early as 1887 Claus stated that in *Nebalia* a fold emanating from the cephalon covers the thorax without being attached to it. Many subsequent writers have agreed, more recent ones including Lauterbach (1975).

Nevertheless, examination of the literature reveals much ambiguity. Claus himself was first to doubt his own statement concerning the presence of a free carapace fold in *Nebalia*. This was done indirectly and without comments in a drawing (Claus 1887, plate IX figure 8, reproduced here as figure 11), which shows a transverse section through the 2nd thoracic segment of a specimen of *Nebalia*. This can, with the aid of a habitus drawing in another plate, (plate I), be identified as *N. strausi* Risso (Dahl 1985). This transverse section shows a cephalothoracic shield broadly attached to the dorsum of the segment and flanked by well-developed pleural (branchiostegal) folds. No explanation of the discrepancy between the statement and the drawing was offered. As seen from figure 11 the drawing is very detailed. It is consistent in all respects with observations on other species of *Nebalia* (cf. section 5 (*a*) (iii)).

Independently of Claus, Sars (1887) included a small cephalothoracic shield, covering part of the dorsum of the 1st thoracic segment, in his drawings of the two new genera *Paranebalia* and *Nebaliopsis*, but stated in the text that the carapace is attached to the cephalon. Later, however, Sars (1896*b*), after showing a corresponding cephalothoracic shield to be present in *Nebalia*, revised his opinion concerning the attachment of the carapace fold in stating that 'the carapace forms, only within a very limited space quite in front and above, the immediate wall of the body'. Hessler (1964, plate 46) also showed that in *N. pugettensis* a small cephalothoracic shield is present, interpreted as covering the 1st and possibly part of the 2nd thoracic segment (cf. figure 27). Calman (1909) in his chapter on the Leptostraca included both Claus (1887) and Sars (1896*b*) among his references but without mentioning their observations concerning the cephalothoracic shield.

In the Archaeostraca, observations concerning the attachment of the dorsal fold or shield are extremely difficult, and few have dared to make any comments upon it. Rolfe (1962) thought that in the Silurian *Ceratiocaris papilio* the cephalon bears the carapace, which appeared not to be fused to the body. However, in the Devonian *Nahecaris stuerzi*, Bergström *et al.* (1987) found that the fold may be attached to the anterior part of the thorax, but in either case no definite conclusion is possible.

(ii) *Formation and topography of shield and fold systems in Nebalia*

Manton (1934), in her comprehensive report on the embryology of *Nebalia*, did not deal directly with the formation of the dorsal fold. Her drawings show, however, in embryos hatched from the vitelline membrane, the presence of a cephalothoracic shield covering the dorsal and lateral parts of the cephalon and the anterior parts of the thorax and delimited form the more posterior part of the trunk by a furrow or incipient fold. In somewhat more advanced embryos she demonstrated that a thoracic dorsal fold is attached to the thorax behind the cephalon. In her drawing of a lateral view of a whole embryo (Manton 1934, figure 4) and in a diagrammatic drawing of a sagittal section (Manton 1934, figure 7) it is not possible to state exactly how many trunk segments are covered by the cephalothoracic shield, but it is clear that it must be more than one.

Because of the uncertain information concerning shield and fold formation in the Leptostraca a re-examination became necessary. My investigation of the problem was based on embryo-carrying females of an undescribed North American species of *Nebalia*. These females, with embryos in various stages of development, were fixed in alcoholic Bouin (Duboscq-Brasil), embedded in polyester wax, cut transversely, horizontally, and sagittaly at 8 μm, impregnated with silver according to Bodian and counterstained with eosin. Some of the resulting series of sectioned embryos were of very good quality and provided the desired information concerning fold and shield formation. It is a great advantage that embryos at these stages, treated as noted above, are generally straight or only slightly curved, a condition that greatly facilitates the study and interpretation of sections and the necessary comparisons with more advanced stages.

A micrograph of a sagittal section through an embryo of *Nebalia* sp. at a somewhat earlier stage of development than that drawn by Manton (1934, figure 7) is shown here in figure 19. Part of the compound eye is seen in the lower left-hand corner of the micrograph. The anterior part of the midgut is dilated and filled with yolk. In the dorsal body wall of the anterior part of the thorax the dorsal fold is in the process of being formed by an accumulation of cells growing thin fibres which become attached to the dorsal integument. This fold is formed behind the cephalon in the anterior half of the thorax, but as in the drawing by Manton it is not possible, in a sagittal section, to see to which segment it is attached.

In this respect another embryo, cut transversely, provides definite information (figures 12–17). A section through the anterior part of the cephalon (figure 12) shows the rudiments of the compound eye (*ce*), the antennules (*Al*) and the rostrum (*R*). Figures 13–16 show transverse sections through the mouth opening and foregut and the three segments carrying the three anterior pairs of thoracic limb rudiments (*thp* 1–3) and, in figure 16, part of the small dorsal fold (*df*), attached to the posterior margin of the 3rd thoracic segment. Figure 17, a transverse section through the 4th thoracic segment, shows the rudiments of the 4th pair of thoracic limbs (*thp* 4), and also the absence of pleura in the segments behind the attachment of the dorsal fold. Figures 18 and 19, transverse sections through the border area between the 3rd and 4th thoracic segments in a slightly more advanced embryo from the brood pouch of another female, show a more developed fold than in the specimen shown in figures 13–17. The fold is only narrowly attached to the body, which means that only slightly more posteriad it will be free.

As shown by Manton (1934) the juvenile *Nebalia*, when leaving the brood-pouch of the mother, is, generally speaking, a miniature copy of the adult. My observations on species of *Paranebalia* and *Sarsinebalia* suggest that in these two genera the young leave the brood pouch at approximately the same stage of development. However, the status of the fold system in early free-living stages of Leptostraca has never been studied, and therefore some information will be presented below, based on two juveniles of *Nebalia borealis*, dredged in the Skagerrak off the Swedish west coast and measuring 1.2 mm and 2.3 mm in total body length. The specimens were fixed in seawater Bouin, embedded in Araldite, cut transversely and stained in methylene blue. In the juvenile 1.2 mm long the pigment of the compound eye is still poorly developed, and the tissues, particularly in the posterior part of the trunk and in the posterior thoracopods, are still partly embryonic. The four anterior pleopods, though not yet fully developed, were functional, permitting the speci-

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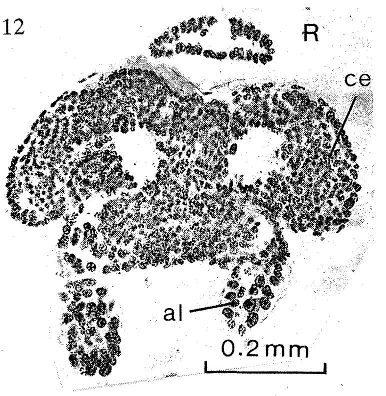

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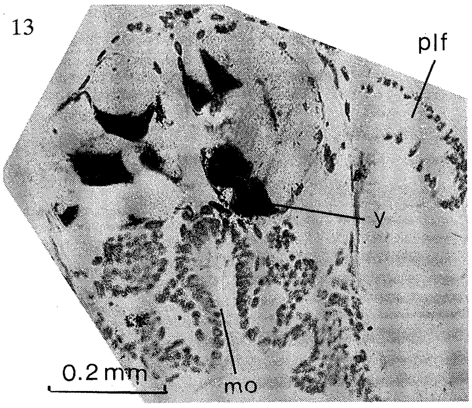
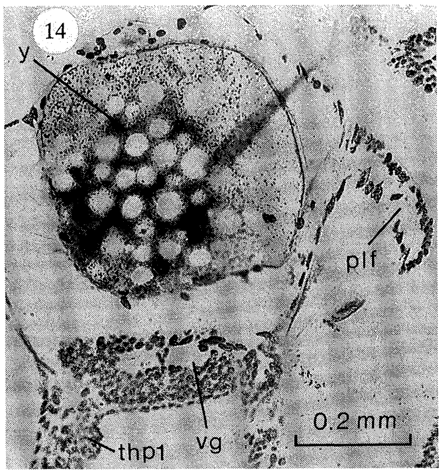




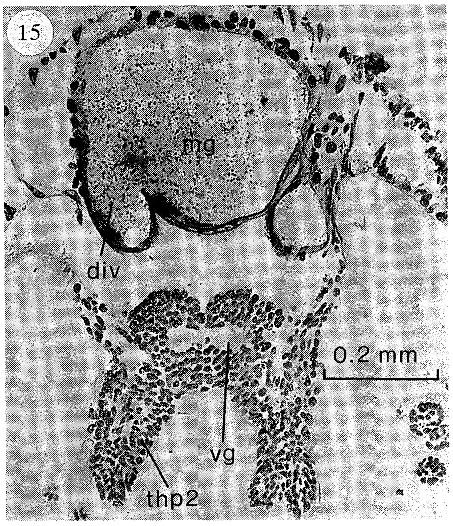


Figure 12. Transverse section through the anterior part of the cephalon of an embryo of *Nebalia*, showing rudiments of rostrum, compound eyes and antennule.

Figure 13. Same embryo as figure 12. Transverse section through the mouth region, showing yolk in the anterior part of the midgut and comparatively well-developed cephalic pleural fold rudiments.

Figure 14. Same embryo as figure 12. Transverse section through the 1st thoracic segment, with much yolk in the anterior part of the midgut and rudiments of the 1st pair of thoracopods.

Figure 15. Same embryo as figure 12. Transverse section through the 2nd thoracic segment with incipient formation of midgut diverticles, the ventral ganglion chain and the 2nd thoracopods

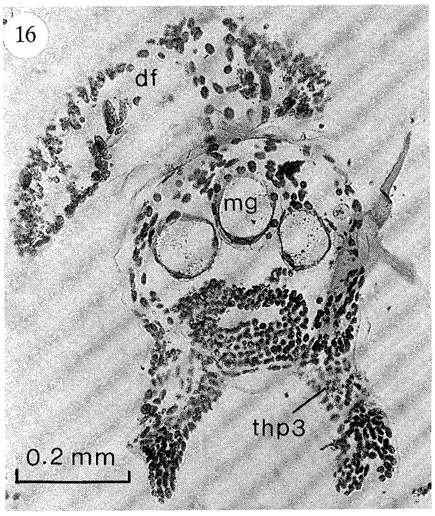
men, when caught on the surface film, to swim rapidly over it. In the specimen 2.3 mm long the tissues in the posterior thoracic legs were losing their embryonic character, the appendages approaching the pattern found in the adult.

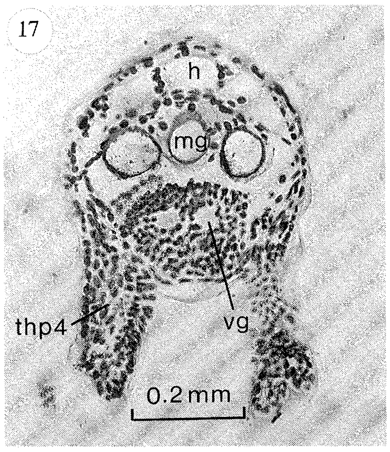
Immersion in the fixative caused a distortion of the dorsal cuticle. In both specimens the cuticle covering the dorsal and lateral part of the cephalothoracic shield and the pleura became separated from the underlying integument everywhere except along the margins of the fold system, to which the cuticle remained firmly attached (figure 20). The pleural margins were also pulled dorsad, but the attachment of the pleura to the lateral body wall remained intact (cf. arrows).

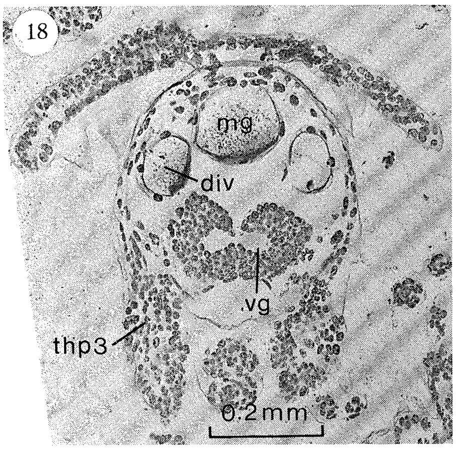
As shown in figures 21–24, the cephalothoracic shield and fold system is arranged in the same way as in the embryos described above, a cephalothoracic shield covering the cephalon and the three anterior thoracic segments, with a small free fold attached to the posterior margin of the 3rd thoracic segment.

The distortion of the cephalothoracic cuticle described above is produced much more easily in juveniles than in adults, in which strong muscle attachments within the fold system tends to keep the cuticle in place. Thus, in *Nebalia*, in the 1st thoracic segment particularly strong apodemes are formed as invaginations from the body wall in the angle between the pleural folds and the sides of the body (see, for example, figure 21). These invaginations later become drawn into the body. In the adult they form internal cavities, surrounded by a very strong cuticular wall to which powerful muscles from the dorsal integument, the base of the 1st thoracopod and the midventral integument are attached (figures 25 and 26). Also in the 2nd thoracic segment there are very strong muscle attachments on which the large longitudinal dorsal trunk muscles end (cf. figure 11).

Concerning *Nebalia* there is an argument that, as a result of curvature of the anterior part of the body, transversal sections through the thorax of *Nebalia* should easily become oblique and hit more than one segment. This is an exaggeration as it is generally not







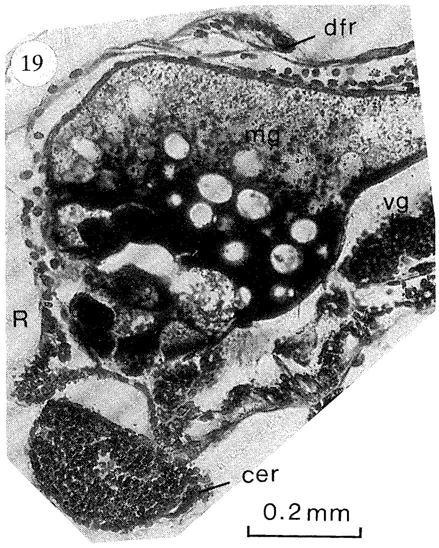


Figure 16. Same embryo as figure 12. Transverse section through posterior part of 3rd thoracic segment showing the beginning formation of a small dorsal fold.

Figure 17. Same embryo as figure 12. Transverse section through the 4th thoracic segment, behind the small dorsal thoracic fold formed from the posterior part of the 3rd segment.

Figure 18. Transverse section through the border area between the 3rd and 4th thoracic segment of a somewhat more advanced embryo with a dorsal fold separating from the body.

Figure 19. Sagittal section through embryo of *Nebalia* sp. at approximately the same level of development as shown in figures 12–17, showing the compound eye rudiment and a group of dorsal cells forming the dorsal fold rudiment.

difficult to find specimens in which the thorax, or at least its anterior part, is straight. Moreover, the curvature of the body tends to be deceptive, for as shown by Hessler (1964, figure 46, reproduced here as figure 27), in *N. pugettensis* the row of thoracic segments (figure 34) form a practically straight line, this despite the fact that the dorsal outline of the thorax is somewhat curved, as a result of the arrangement of its very strong longitudinal and oblique trunk musculature, and the cephalon curving ventrad. With due caution it is not difficult to obtain good transverse sections of the thoracic segments of *Nebalia*.

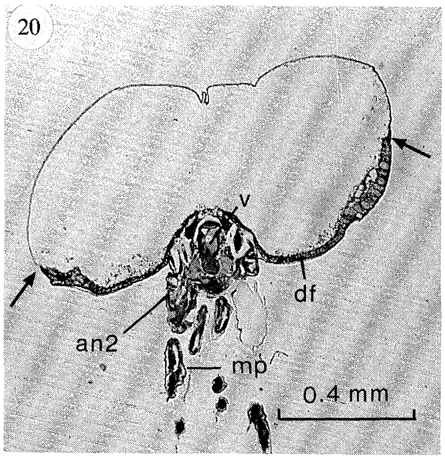
(iii) *The shield and fold system in Dahlella*

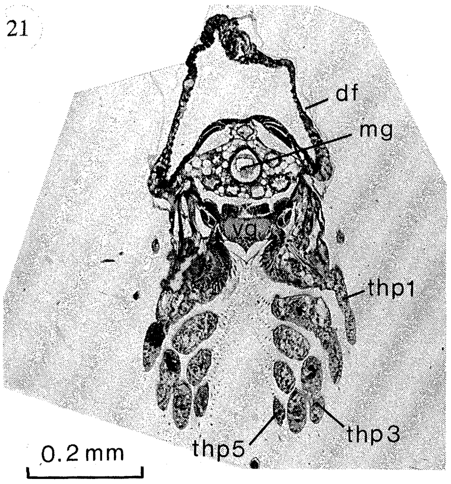
In *Dahlella caldariensis* from the Pacific deep sea thermal vents, specimens of which (fixed in formalin) were kindly placed at my disposal by Professor R. R. Hessler, the fold and shield system resembles that of *Nebalia*, the main difference being tht the cephalothoracic shield in *Dahlella* covers the five anterior thoracic segments (figure 34), that of *Nebalia* covers three segments. In both genera a short free dorsal fold is formed at the posterior margin of the shield, in *Dahlella* at the posterior margin of the 5th thoracic segment (figures 28–33).

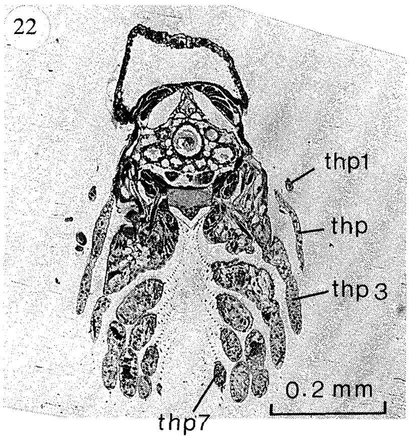
The sections through the thorax illustrating the situation found in *Dahlella* are transversal, as seen from their proportions and the position of the midgut in relation to the position of the thoracopod attachments, even if the down-hanging thoracopod endopods may give a false impression of obliguity.

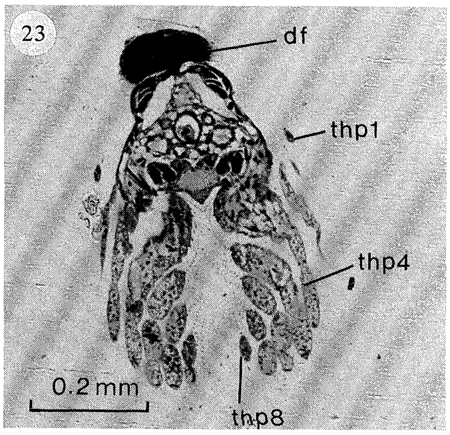
(iv) *Conclusions concerning leptostracan thoracic shields and folds*

In *Nebalia*, the only leptostracan genus in which the ontogeny has been studied, the origin and development of the cephalothoracic shield and fold system differs from the traditional concepts based on the carapace hypothesis. In *Nebalia*, instead of being a fold growing out from the posterior margin of the cephalon, the rudiment of the future cephalothoracic shield and fold









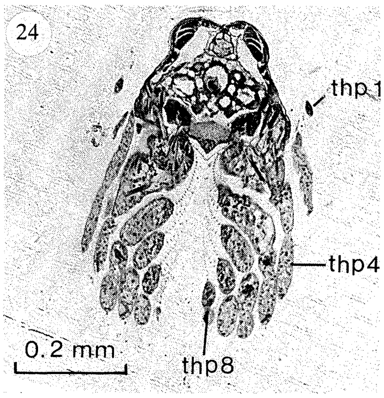


Figure 20. Juvenile of *Nebalia borealis*, total body length 1.2 mm, transverse section through maxillary segment showing distorsion of cephalothoracic shield due to the immersion in salt-water Bouin. The pleural folds have been pulled dorsad, and the cuticle of the dorsal shield and fold system has lost its attachment to the underlying tissues everywhere except along its margins (arrows).

Figure 21. Same specimen as figure 20. Transverse section through 1st thoracic segment showing broad attachment of cephalothoracic shield. thp. 1, 1st thoracopod, thp. 3 advanced rudiment of 3rd thoracopod. In upper lefthand corner a very distorted part of the dorsal fold has been cut off.

Figure 22. Same specimen as figure 20. Transverse section through 2nd thoracic segment. The oblique orientation of the thoracopods in relation to the length axis of the body result in their being visible in several subsequent sections.

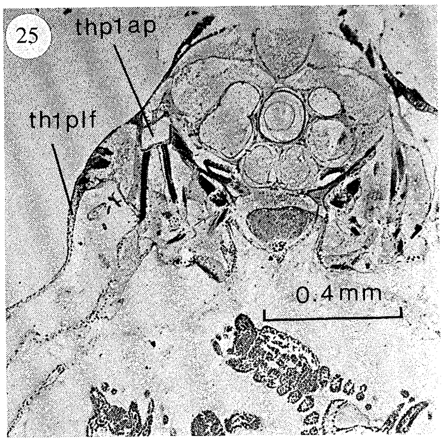
Figure 23. Same specimen as in figure 20. Transverse section through 3rd thoracic segment, near posterior margin where small discoloured fold can be seen.

Figure 24. Same specimen as in figure 20. Transverse section through 4th thoracic segment behind the dorsal fold.

system is first indicated in comparatively late embryos by the formation of a furrow encircling the cephalon and anterior part of the body (cf. Manton 1934). This furrow later comes to form the pleural folds of the anterior thoracic segments and the rudiment of a free dorsal fold attached to the posterior margin of the 3rd thoracic segment. In juveniles, before leaving the brood chamber, this fold system has developed further and resembles that of the adult (Manton 1934; this paper, §5*a*(ii).

In *Dahlella*, of which only adults are known, the cephalothoracic shield covers the five anterior thoracic segments, and a free fold is formed only in the border region between the 5th and 6th thoracic segments.

Claims by previous writers that the Leptostraca possess a free carapace fold *sensu* Calman (1909) were based on unsuitable techniques and led to misunderstandings, which for a long time have obscured the issues concerning the leptostracan shield and fold topography. The application of microanatomical methods has revealed the true situation. The sides of the cephalon and the three to five anterior thoracic segments are flanked by deep folds representing the fused pleura of the corresponding cephalic and thoracic



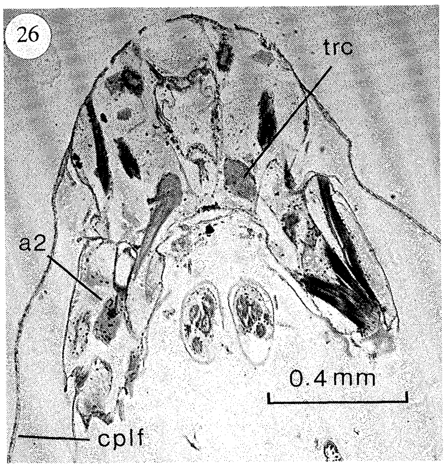


Figure 25. Transverse section through adult *Nebalia* sp. showing the very strong internal apodeme near the left body wall (thp1 ap), originally formed in the juvenile in the angle between the pleural fold in the 1st thoracic segment and the body wall.

Figure 26. Transverse section through the tritocerebral region of adult *Nebalia* sp. showing the very deep cephalic pleura.

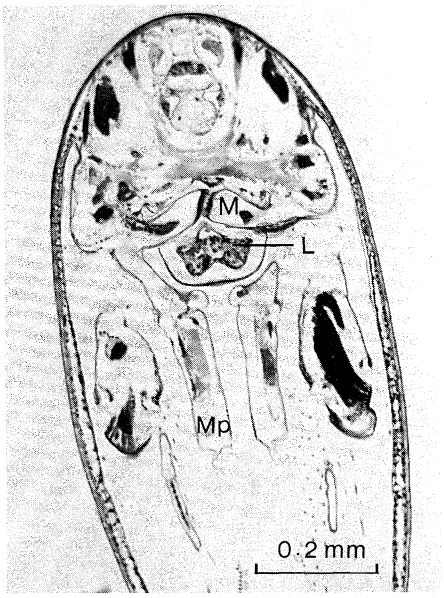


Figure 28. *Dahlella caldariensis*, adult Transversal section through mandibular segment.

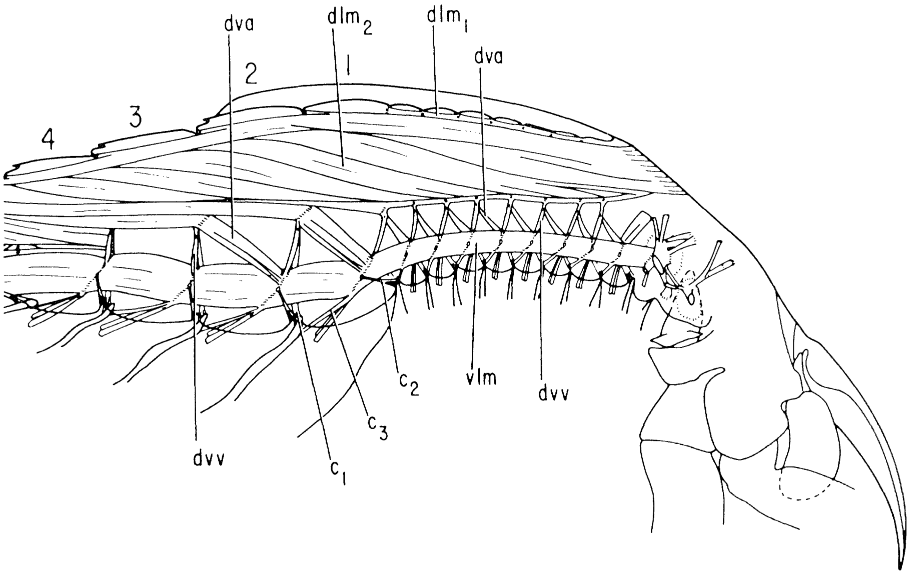


Figure 27. Drawing of parasagittal section of *Nebalia pugettensis*, showing topography of trunk musculature. Despite the dorsal curvature of the dorsal body wall and the cephalon the ventral segmental structures form a practically straight line. *c*, connecting ligaments; *dlm*, dorsal longitudinal muscles; *dva*, anteriorly descending dorsoventral trunk muscle; *dvv*, vertical dorsoventral trunk muscle; *vlm*, ventral longitudinal muscle; 1–4 pleon segments (Courtesy of Professor R. R. Hessler and the Connecticut Academy of Arts and Sciences.)

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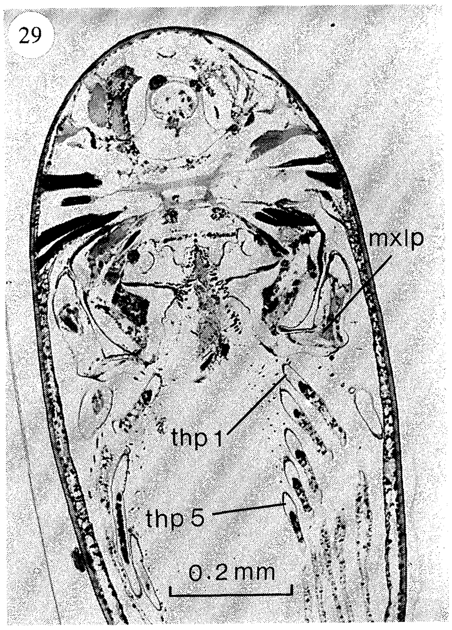

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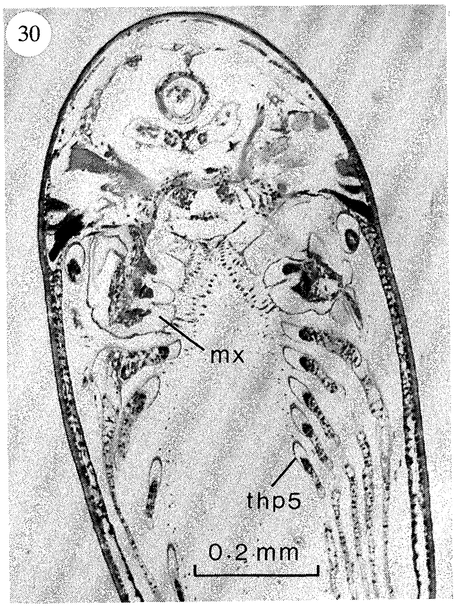

Figure 29. Same specimen as figure 28. Transverse section through maxillular segment.

Figure 30. Same specimen as in figure 28. Transverse section through 2nd maxillar segment. As a result the oblique arrangement of the thoracopods in relation to the length axis of the body, different parts of the same thoracopod may be seen in more than one transverse section.

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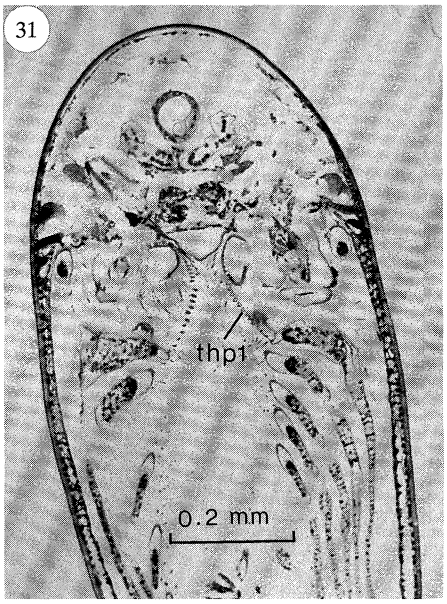

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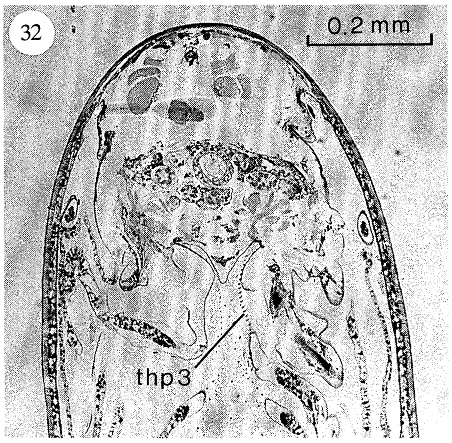


Figure 31. Same specimen as in figure 28. Transverse section through 1st thoracic segment.

Figure 32. Same specimen as in figure 28. Transverse section through 4th thoracic segment. Note the narrowing of the connection between the cephalothoracic shield and the body.

segments (figure 30). These fused thoracic pleura are homologous with the eumalacostracan branchiostegal folds, a term which can also be applied to them. Obviously they fulfil many of the corresponding functions, in containing and to a certain extent canalizing the currents produced by thoracopod and pleopod activity.

(*b*) *Eucarida*

Within the Eucarida well-defined thoracic dorsal folds occur in larvae of euphausiids and dendrobranchiate decapods. Small transient dorsal folds can also appear in other decapod mysis larvae, for example in the genus *Pandalus*. It has long been known that the dorsal folds of the euphausiid larvae are thoracic (Gurney 1942), those of the dendrobranchiate larvae are generally accepted as being true cephalic carapace folds (Gurney 1942; Williamson 1982).

The following brief account of the formation and topography of dorsal folds in the Euphausiacea is based on Sars (1898) and Gurney (1942), and on the study of serial sections of calyptopis and early furcilia stages of *Meganyctiphanes norvegica*. For comparison, whole mounts of calyptopis larvae of *Thysanoessa* and of furcilia larvae of *M. norvegica* were examined.

In *M. norvegica* a small dorsal fold first appears in the metanauplius, which has rudiments of three post-mandibular pairs of appendages (Sars 1898). The fold is attached to the posterior margin of the 1st thoracic segment. In the 1st calyptopis of *M. norvegica* the fold has grown (figure 35). Small pleural folds are present in the antennal segment (figure 36). In the 1st thoracic segment the pleural folds are deeper, enveloping the

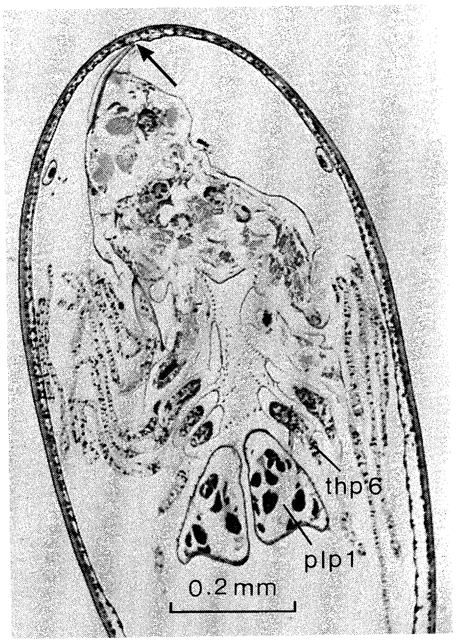


Figure 33. Same specimen as in figure 28. Transverse section through posterior margin of 5th thoracic segment, showing the separation of the cephalothoracic shield from the body (arrow).

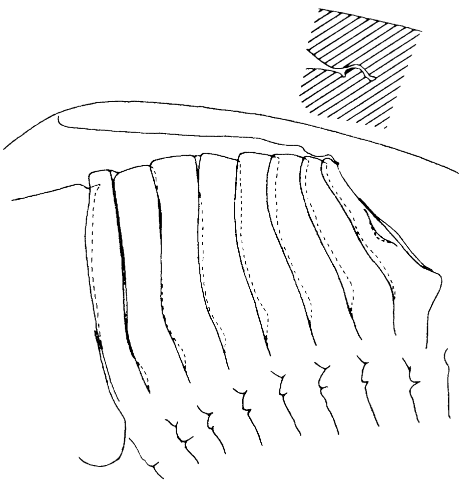


Figure 34. Lateral view of whole mount of *Dahlella caldariensis*, showing the thoracic exo- and endoskeleton after treatment with potassium hydroxide solution. The soft tissues of the dorsal integument to which the cephalothoracic shield of the intact specimen were attached up to and including the 5th thoracic segment have been dissolved and the endo- and exoskeletons are free. (Courtesy of Professor R. R. Hessler.)

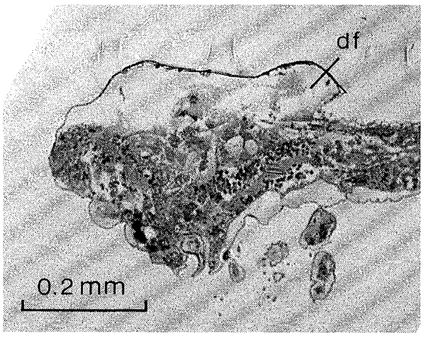


Figure 35. *Meganyctiphanes norvegica*, parasagittal section through calyptopis larva showing a small dorsal fold.

sides of the thorax and part of the rudiments of the 1st thoracopods (figure 37). The dorsal fold is attached to the posterior margin of the segment and produced over the dorsum of the 2nd segment (figure 38). In furcilia stages, in which the cephalothoracic shield does not yet cover the whole dorsum of the thorax, a small fold may be present at its posterior margin, leaving several narrow thoracic segments free behind it in front of the comparatively well-developed abdomen (figure 39). This gap later becomes closed by the extension posteriad of the cephalothoracic shield.

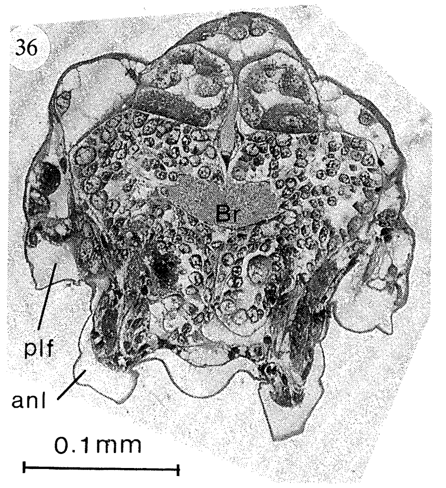
The dendrobranchiate decapods hatch as nauplii and pass through several naupliar stages and three protozoean stages. The protozoea larvae possess a free dorsal fold. Other decapods hatch as zoea larvae *sensu* Williamson (1982), with a more developed cephalothoracic shield.

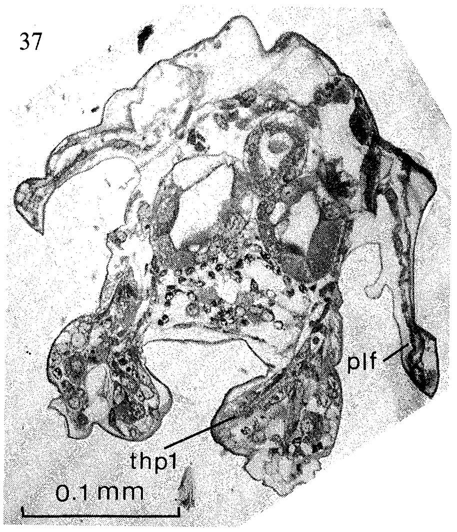
In the dendrobranchiate larvae, as noted above, the dorsal fold has been presumed to be a true carapace fold formed from the maxillary segment. Gurney (1942, p. 112) stated that 'the carapace of the 1st protozoea of the Penaeida is a simple head-fold without rostrum which is not fused to the thoracic terga'. Gurney also stated (p. 180) 'the Protozoea differs from the Nauplius in having a carapace developed as a fold from the somite of the maxilla free from the thoracic somites'.

Some confusion was introduced by a reference by Gurney (1943) to the presence of a praemaxillary carapace in the nauplii of *Sicyonia*. From the drawings it appears, however, as if Gurney in this case let the term 'carapace' include also the cephalic pleural folds. In the two passages quoted above, however, Gurney obviously referred to a carapace fold *sensu* Calman.

When, in a previous paper (Dahl 1983*a*), I expressed doubts concerning the general validity of the carapace concept they did not include the situation in the dendrobranchiate larvae. It was only in the light of the results from the investigation of the 'carapace' of the Branchiopoda and Leptostraca, presented above, that a re-investigation of the nature of the dorsal larval fold of the Dendrobranchiata appeared desirable. Larval material, of *Penaeus duorarum* (superfamily Penaeoidea) and *Sergestes similis*, was kindly placed at my disposal by Professor Rolf Elofsson and Professor W. A. Newman respectively. Thus one representative of each of the two dendrobranchiate superfamilies could be examined. In both cases the state of preservation was poor, part of the internal organs having disappeared, but fortunately remnants of the transitory maxillary glands were present providing reliable points of reference for the segment count.

In *P. duorarum*, of which a series of nauplius stages was available, it was found that the first rudiment of the dorsal fold became visible in a late nauplius, in which the rudiments of three pairs of postmandibular appendages were present, thus confirming observations by Cook & Murphy (1965). At this stage the rudiment of the dorsal fold forms a slightly elevated band of cells along the posterior margin of the 1st thoracic segment (figure 40). In the first protozoea the 1st thoracic segment is covered by a cephalothoracic shield, from the posterior margin of which a free dorsal fold has been formed (figures 41–43).





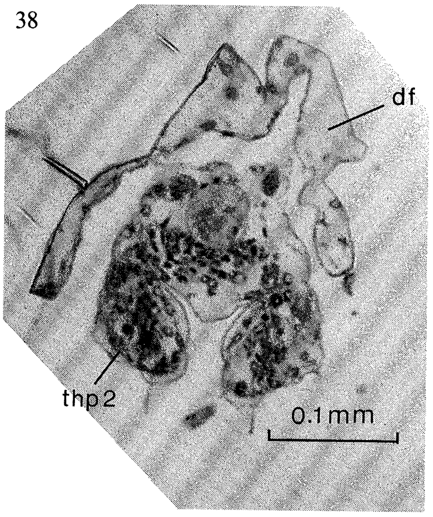


Figure 36. *M. norvegica*, transverse section through cephalon of early calyptopis larva with small cephalic pleural fold rudiments of antennule and brain.
Figure 37. Same specimen as in figure 36. Transverse section through 1st thoracic segment showing deep pleural folds and rudiments of 1st pair of thoracopods.
Figure 38. Same specimen as in figure 36. Transverse section through anterior part of 2nd thoracic segment showing a free dorsal fold and rudiments of 2nd thoracopods.

No naupliar stages were present in the material of *S. similis* but all three protozoean stages were represented. In all of these a cephalthoracic shield covers the cephalon and the 1st thoracic segment, and a free dorsal fold is attached to the posterior margin of the 1st thoracic segment (figures 44–45).

This examination of dendrobranchiate larvae by means of histological techniques proved that in the protozoean stages of representatives of both dendrobranchiate superfamilies a dorsal fold is formed at the posterior margin of the cephalothoracic shield covering the 1st thoracic segment. Consequently this is not a carapace fold *sensu* Calman. No such fold has been proved to exist in any eucarid taxon.

(*c*) ***Peracarida and Thermosbaenacea***

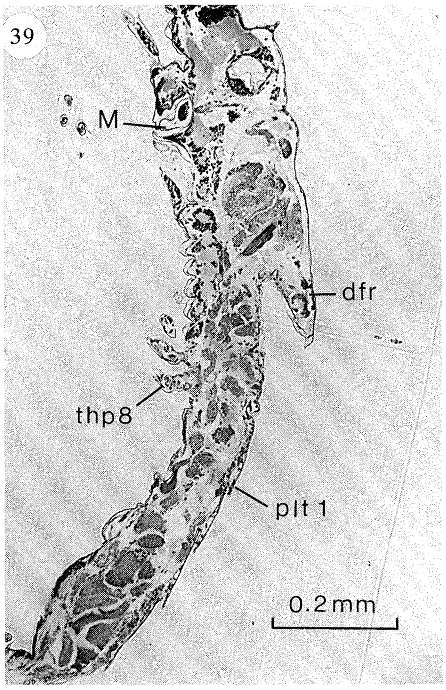
In all Peracarida, one or more thoracic segments are always fused to the cephalon, forming a cephalothoracic shield. In those taxa in which a free dorsal fold is present, i.e. in the Mysidacea and the Spelaeogriphacea, it is always a thoracic fold, attached to the posterior margin of a cephalothoracic shield.

No indication of the formation of a cephalic carapace fold has ever been reported from any stage of peracarid ontogeny.

In the Thermosbaenacea the situation is essentially similar, although the specialization of the thoracic dorsal fold, attached to the 1st thoracic segment and functioning as a brood chamber, makes the topographical relations less obvious. Zilch (1974), in his paper on the embryology of *Thermosbaena mirabilis*, reported no indication of a formation of a cephalic dorsal fold.

(*d*) ***Hoplocarida***

No adequate hoplocarid larval or embryological material has been at my disposal so the following survey is based on literature records, mainly on the



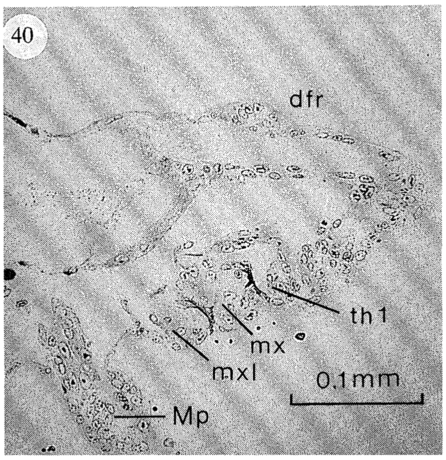


Figure 39. Parasagittal section through young furcilia of *M. norvegica* with small dorsal fold rudiment. Below and behind the fold narrow thoracic segment rudiments, further posteriad pleon with well-developed terga.

Figure 40. *Penaeus duorarum*, parasagittal section through last nauplius, 1st thoracic segment with transversal dorsal ridge of cells forming the rudiment of the dorsal fold.

comprehensive report on the ontogeny of *Squilla oratoria* by Shiino (1942), supplemented by observations by Komai (1924) and Nair (1941).

Drawings of hoplocarid larvae in Gurney (1942, 1945) and elsewhere give the impression that in the early hoplocarid larvae a dorsal fold is attached to the cephalon and therefore is to be regarded as a cephalic carapace fold. This interpretation appears to have been generally accepted by recent writers, myself included (cf. Williamson 1982; Dahl 1983*a*). The new results recorded above concerning the Branchiopoda, Leptostraca and Eucarida appeared, however, to call for a closer re-examination of previous reports dealing with the early development of the Hoplocarida.

The externally visible aspects of hoplocarid embryogenesis and early ontogenesis were studied by Komai (1924) in *Squilla oratoria*, and a more detailed study, including later stages of the same species, was published by Shiino (1942). Both these writers, particularly Shiino, presented interesting and highly relevant information concerning the derivation and further development of the dorsal fold.

Komai (1924), working with whole mounts, noted that a dorsal fold was formed 'on the antero-dorsal side of the thorax' at a stage when all eight segments of the thorax could be recognized. Shiino (1942), using histological techniques, observed the first signs of a dorsal fold formation in embryos with seven thoracic segments. Considering that the technique applied by Shiino generally permits more exact observations, the agreement between the two writers concerning the stage at which formation of the dorsal fold begins can be regarded as very good. They both found that the dorsal fold is formed from the anterior part of the thorax, which makes it possible to identify it as a thoracic and not a cephalic fold. Judging from Shiino (1942, figure 105) it appears likely that the fold appears in the posterior part of the 1st or, possibly, in the 2nd thoracic segment.

The process of fold formation was described by Shiino as follows. Within the thoracic area mentioned, four rows of nuclei form a semicircular band. The more posterior rows move to a position below the anterior rows, thus forming what Shiino described as an ectodermal fold. At a later stage within the fold a

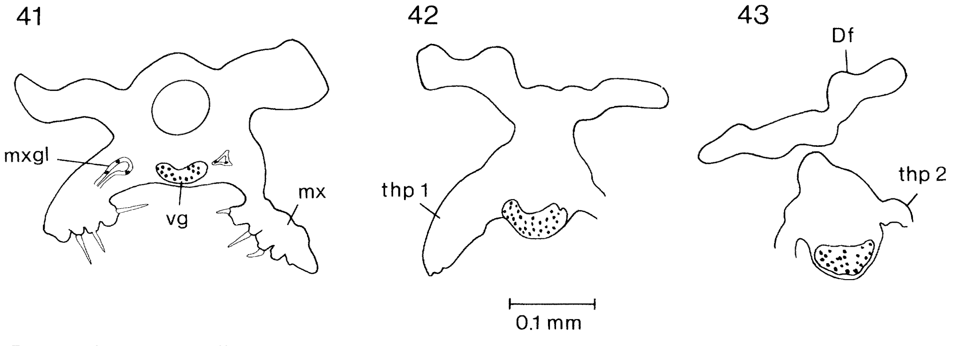


Figure 41. *Penaeus duorarum*, outline drawing of transverse section through maxillary segment of 1st protozoea with transient maxillary gland rudiment, ventral ganglion and part of 2nd maxilla.

Figure 42. Same specimen, transverse section through 1st thoracic segment, attachment of dorsal fold to cephalon narrowing.

Figure 43. Same specimen, transverse section through 2nd thoracic segment, showing free dorsal fold.

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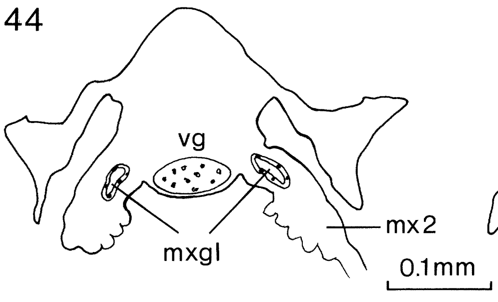

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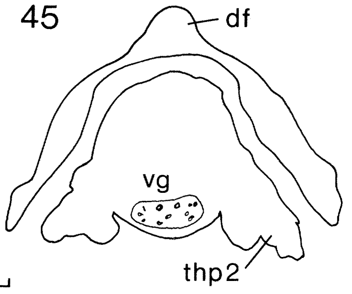

Figure 44. *Sergestes similis*, transverse section through maxillary segment of protozoea with rudiments of maxillary gland in basal part of 2nd maxilla.

Figure 45. *Sergestes similis*, same specimen as in figure 44. Transverse section through anterior part of 2nd thoracic segment with free dorsal fold.

hollow space appeared which became gradually invaded by connective tissue forming a system of lacunae. During the last phase of embryonic development Shiino noted that the attachment of the fold shifted forward so that it came to lie near the antero-dorsal margin of the segment but still within the thorax.

Nair (1941), working with other species of *Squilla*, gave no account of the earliest development of the dorsal fold but reported that, in the late embryo, mesoderm from the maxillary and 1st thoracic segments grows dorsad to form 'the musculature of the carapace'. Thoracic dorsal folds of other malacostracans have no intrinsic musculature (cf. Shiino 1942). It appears probable therefore that the muscles referred to by Nair were extrinsic muscles of the maxilla and the 1st thoracopod becoming attached to the cephalothoracic shield. This has been seen to happen in *Nebalia*.

Summing up the evidence from the three investigations reviewed above it can be concluded that the dorsal fold in *Squilla* is formed from the anterior part of the thorax and that it is attached to the 1st thoracic segment. In adult hoplocarids the two anterior thoracic segments are covered by a cephalothoracic shield (Calman 1909). A free thoracic fold is attached to the posterior margin of this shield.

6. THE FAILURE OF THE CARAPACE HYPOTHESIS

For 80 years the carapace hypothesis, as formulated by Calman (1909), has exerted a profound influence upon ideas concerning crustacean evolution and interrelationships, and it is surprising that in all these years its validity has never been seriously in doubt. This appears even more remarkable considering the cautious way in which Calman referred to the carapace fold as 'probably a primitive attribute of the class'.

Here the presumed presence of a cephalic carapace fold has been tested with respect to those representatives of two crustacean classes, the Branchiopoda and the Malacostraca, in which a carapace fold has been generally presumed to exist in its most typical form.

No cephalic carapace fold could be found in any stage of the life cycle of the notostracan genus *Triops*, or in larvae and adults of the order Spinicaudata or adults of the Laevicaudata. Nor could the presence of a free cephalic carapace fold be proved in any stage of the life cycle of any of the malacostracan taxa where it has been presumed to exist. It is particularly important to note that this includes also the Phyllocarida, for which special efforts have been made to elucidate the ontogeny and morphology of the thoracic fold and shield systems, and for which various recent writers have claimed to confirm the presence of a true carapace fold.

In his presentation of the carapace hypothesis Calman (1909) also introduced a second postulate according to which the absence of a free carapace fold is due to its having fused to the dorsum of the thorax. When the hypothesis of a ubiquitous carapace fold is proved untenable, the postulate concerning a fused carapace fold also automatically loses its foundations. Nevertheless, to obtain independent evidence, cephalothoracic shields of many Malacostraca, embryos, larvae and adults, were examined for signs indicating an ontogenetic fusion of a dorsal fold to the thorax.

As well as all available stages of species dealt with in section 5, material of sectioned specimens of the following species were examined: Decapoda: *Pasiphae tarda*, adults; *Eualus gaimardi*, zoea and adults; *Crangon allmani*, zoea and adults. Mysidacea: *Lophogaster typicus*, adults; *Boreomysis arctica*, adults; *Praunus flexuosus*, embryos and adults; *Neomysis integer*, adults. Hoplocarida: *Squilla armata*, adults.

In all these Malacostraca it was found that the cephalothoracic shield consists of a single integument layer, covered by a simple continuous cuticle, forming a direct continuation of the cephalic integument and cuticle and posteriorly directly continuous with the integument and cuticle behind the cephalothoracic shield. No indication of anything that could be interpreted as signifying a fusion of a carapace fold to the thoracic dorsum was discovered. This is consistent with the conclusions of Milne Edwards (1834). The second postulate of the carapace hypothesis must, like the first, be rejected.

Observations casting doubts on the validity of the carapace hypothesis have existed for a long time, some well before the formulation of the hypothesis by Calman (1909). Lang (1888), in his text-book on invertebrate anatomy, presented the correct conclusion that the dorsal fold in the Notostraca is produced from the trunk. Sars (1896*a*) showed that the same is the case in the Spinicaudata, and in two papers Sars (1887, 1896*b*) presented evidence showing that the dorsal fold in the Leptostraca is thoracic. Of these papers, only Sars (1896*b*) was referred to by Calman, who does not appear to have realized its significance with respect to the interpretation of the dorsal fold. The information contained in the papers mentioned above, like that of Claus (1887), has also been overlooked by subsequent writers.

Later Manton (1934) showed that the dorsal fold in *Nebalia* is formed ontogenetically from the trunk behind the cephalon, but her paper, like those mentioned above, was not even mentioned by recent writers dealing with the formation of the dorsal fold in the Leptostraca. Shiino (1942) gave a detailed account of the formation of the dorsal fold from the thorax in *Squilla* but it appears never to have been referred to by more recent writers dealing with the carapace hypothesis.

The conclusion drawn from the results produced by previous writers, in combination with the new observations presented above, must be that the carapace hypothesis formulated by Calman (1909) has to be declared invalid because it lacks a factual basis and has been contradicted by results obtained by a number of writers dealing with various crustacean taxa. This does not necessarily mean that there could not exist a crustacean with a dorsal fold derived from the cephalon, but this would hardly have any deeper evolutionary or phylogenetic significance. As will be shown below (section 7) there are other and apparently more realistic alternatives for the formation of dorsal thoracic shields, at least in the Malacostraca.

7. BRANCHIOSTEGAL FOLDS AND VENTILATORY-RESPIRATORY MECHANISMS IN THE MALACOSTRACA

(*a*) *Leptostraca*

The main respiratory organs of most Leptostraca are the flattened thoracic epipods (Siewing 1956) although the large and richly vascularized pleural folds also contribute. Ventilation is provided by endopod and pleopod beating.

(*b*) *Eumalacostraca*

The primary respiratory organs of the Eumalacostraca are the thoracic epipods, which occur in practically all orders. They may be supplemented or, in a few taxa, even replaced by other respiratory surfaces, but can be said to play a dominating part.

The respiratory system of the anaspidacean syncarids can be regarded as the least modified of any eumalacostracan. In the Anaspidacea all thoracopods except the 8th pair carry two leaf-shaped and uncomplicated epipods, fully exposed to the surrounding water. According to Brooks (1962), epipods of this type were also present in the Paleocaridacea. When the anaspidacean is resting on the bottom the epipods are ventilated by autochtonous vibration and by slow beating of the thoracic exopods and the anterior pleopods. When the animal is moving, increased ventilation is automatically achieved by means of accelerated endopod, exopod and pleopod activity. There are no specialized ventilatory mechanisms.

From this simple type of respiratory system those of all eumalacostracans could have evolved. In most cases specialized ventilatory mechanisms have been added.

In most eucarids and peracarids the respiratory thoracic epipods are semi-enclosed in branchial chambers. The lateral walls of these chambers are formed by the fused pleural folds (branchiostegia) of the segments involved. When present they always include the pleura of the 1st thoracic segment and are also always continuous with the cephalic pleural folds.

Shiino (1942) studied the earliest phases of branchiostegal and pleural fold formation in *Squilla oratoria*. He found that in stages with six distinct abdominal segments the space lateral to the ventral nerve chord in the thoracic segments is crossed by fibres running more or less vertically and anchored ventrally and laterodorsally in the integument. When the body wall continued to grow these fibres were said to contract. It appears more likely that their growth rate is reduced relative to that of the other parts involved. In that way the lateral and the medial wall of the pleural fold remain close to each other and room for a branchial chamber between the pleural fold and the body wall is created.

This interpretation gains strength from observations made in the course of the present investigation. In late embryos of *Nebalia* sp. the three anterior thoracic segments are covered by a shield flanked by continuous pleural folds. Particularly in the part of the fold nearest to the body wall a great number of fibres growing out from cells below the integument are attached to the opposite pleural wall (figure 46). In the more distal part of the folds similar fibres also occur but not in the same numbers.

Similar connecting fibres, although in comparatively small numbers, have been seen in the part of the

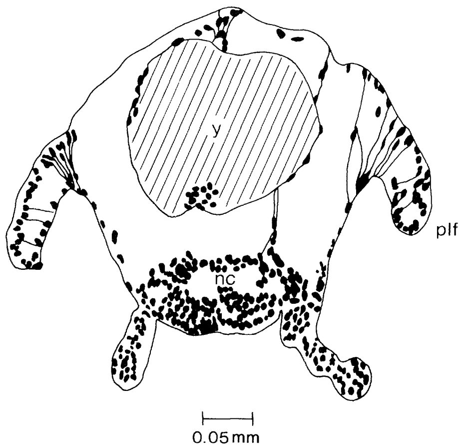

Figure 46. Pleural fold formation in embryo of *Nebalia* sp. due to production of fibres attached to the body wall. Composite drawing based on three consecutive sections.

pleural fold close to the body wall in calyptopis larvae of *Meganyctiphanes norvegica*. In later furcilia larvae, and in the adults of the same species, the loose groups of fibres have been replaced by muscles attached to the dorsal and ventral body walls and to sheaths of adjacent muscles (figure 47). More or less identical patterns of connections occur in zoea larvae of *Crangon allmani* (figures 48–50) and *Pandalus borealis*. A study of serial sections proved that in the two decapod genera these muscles are arranged segmentally.

As shown by this survey the early phases of branchiostegal fold formation are practically identical in the Leptostraca, Euphausiacea, Decapoda and Hoplocarida, and therefore it can apparently be concluded that this is the basic malacostracan pattern of pleural fold formation.

In later developmental stages of Euphausiacea and Decapoda, however, divergences occur in the growth of the pleural folds. In both taxa branchiostegal folds are formed along the whole length of the thorax. In the calyptopis of the Euphausicea and the protozoea of the Dendrobranchiata the cephalic and the thoracic branchiostegia envelop the posterior part of the cephalon and the sides of the thorax including the thoracopod bases and the branchial rudiments. This is also the case in later stages of Dendrobranchiata and Caridea. But in more advanced furcilia stages of the Euphausiacea branchiostegia gradually stop growing and cover less and less of the thoracopods, and in adult Euphausiacea the thoracopod bases and the branchiae are fully exposed, whereas in the Decapoda they are enclosed in branchial chambers.

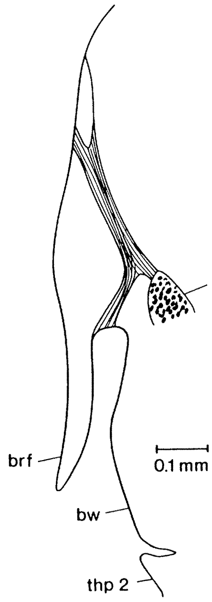

Figure 47. *Meganyctiphanes norvegica*, adult. Attachment of roof of thoracic pleural fold to dorsoventral and longitudinal muscles.

(*c*) **Peracarida**

In the Peracarida the situation with respect to the branchial chambers is much less homogeneous. In the Lophogastrida and the Mysida, branchiostegal folds are formed in one to four anterior thoracic segments, but they are supplemented by free dorsal folds and branchiostegal flaps more or less completely covering the dorsum and the sides of the more posterior parts of the thorax. In this way branchial chambers are formed, which, in the Lophogastrida, where the dorsal fold is strongly built and, at least in *Lophogaster*, non-respiratory, provide effective protection for at least part of the branchiae. In the Mysida the fold itself has taken over the respiratory function and epipodial branchiae are lacking.

In the Spelaeogriphacea only the first, in the Tanaidacea the two anterior, and in the Cumacea the three or four anterior thoracic segments form branchial chambers, enclosing epipodial branchiae.

In the Thermosbaenacea only the 1st thoracic segment forms a small branchial chamber, which also functions as a respiratory organ.

In the Mictacea the posterior cephalic pleural folds and the pleural fold of the maxilliped segment form what in the terminology of Bowman & Iliffe (1985) is 'a lateral carapace fold' covering the bases of the maxillae and the maxilliped. A small, thin-walled area

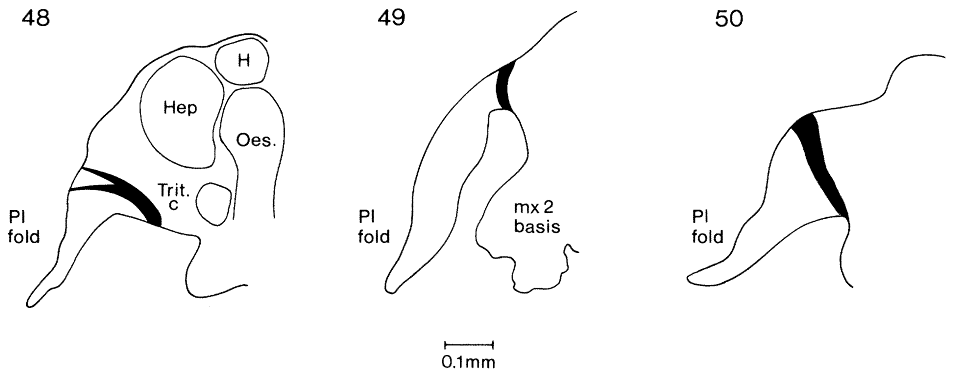

Figure 48. *Crangon allmani*, mysis larva. Transverse section of trito-cerebral segment, showing arrangement of pleural fold muscles.

Figure 49. *Crangon allmani*, same specimen as in figure 48, transverse section through 2nd maxillary segment with 2nd maxilla and deep pleural fold.

Figure 50. *Crangon allmani*, same specimen as in figure 48, transverse section through pleura of 1st thoracic segment.

above the fold is presumed to be respiratory. However, no respiratory epipods have been seen either in *Hirsuta* (Sanders *et al.* 1985) or in *Mictocaris* (Bowman & Iliffe, 1985). Epipods found on thoracopod bases in both genera have been interpreted as oostegites.

The Amphipoda and Isopoda have no branchial chambers.

Finally, in the subclass Hoplocarida, the epipods of the two anterior thoracopods lie inside branchial chambers and those of the three subsequent thoracopods below the lateral parts of the thoracic dorsal folds.

(*d*) ***Eumalacostracan ventilatory mechanisms***

To fulfil their respiratory function branchiae, semi-enclosed within branchial chambers, must be served by ventilatory devices. Highly specialized mechanisms producing currents passing through the branchial chambers are present in the Decapoda and most Peracarida, including the Thermosbaenacea, of somewhat doubtful peracarid affinities. In comparison with the simple type of ventilation found in the Anaspidacea these ventilatory systems are much more advanced. Effective ventilatory mechanisms producing currents passing over respiratory surfaces increase the metabolic efficiency and thereby probably improve the evolutionary potential. They have undoubtedly contributed to the success and diversification of the more advanced malacostracan taxa.

In the Decapoda the ventilatory current is produced by the beating of the scaphognathite, a long and narrow process formed from the exopod of the maxilla. Epipodial branchiae are often supplemented by accessory respiratory outgrowths from the body wall inside the branchial chamber.

In the other eucarid order, Euphausiacea, there are no branchial chambers and there are no specialized ventilatory mechanisms. The branchiae are fully exposed, ventilation is achieved by perpetual pleopod swimming, and, as shown by Kils (1981), in these holopelagic animals this is sufficient for keeping metabolism at the necessary level.

Perpetual swimming, however, has probably imposed restrictions upon behavioural patterns and may have reduced evolutionary flexibility. As also shown by Kils (1981) for *Euphausia superba*, a euphausiid will start sinking as soon as pleopod beating is interrupted. By assuming a horizontal position and spreading appendages *E. superba* can reduce the rate of sinking, but cannot prevent it. Whereas in a decapod or in a pericarid the ventilatory apparatus can provide the necessary oxygenation irrespective of the activity or inactivity of the animal, the euphausiid is literally compelled to swim for life. It is possibly this demand which has imposed upon the Euphausiacea a great rigidity with respect to the basic morphological and functional patterns, resulting in a low rate of speciation and the absence of a diversification at higher systematic level.

In most Peracarida (provisionally including the *Thermosbaenacea*, cf. below), the specialized ventilatory organ is the maxilliped palp. In the Lophogastrida and Mysida its function is purely ventilatory, but in the Spelaeogriphacea, Tanaidacea and Cumacea, and also in the Thermosbaenacea, the maxilliped palp acting within the small branchial chamber is a more or less complicated respiratory organ. Two orders of Peracarida remain to be discussed, viz. the Amphipoda and Isopoda, in which ventilatory mechanisms different from those described above have evolved.

In the Amphipoda the maxilliped segment is fused to the cephalon and has no pleural fold. In the four subsequent segments vestigial pleura can be found at least in certain genera, for example, *Gammarus*, but functionally they have been replaced by the enlarged coxae, which cover the maxilliped and the basal part of the four subsequent thoracopods. In the thoracic segments six to eight pleura are lacking and the coxa are smaller than in the anterior segments, but in most cases the 2nd thoracopod article is strikingly enlarged. In the abdomen the three anterior segments have large pleura. Because of secondary specialization only the three anterior pairs of limbs are typical natatory pleopods with flagellate rami, the three posterior ones uropods.

Respiratory epipodial branchiae are present on most thoracopods. They are curved in below the body and ventilated by the perpetual beating of the three anterior pleopods. On some thoracopods in the female the proximal epipod has been transformed into an oostegite. As seen from this brief description no branchial chamber in the stricter sense is formed, but the unique amphipod arrangement with four pairs of deep anterior coxae, followed by three legs with generally broad coxa and much enlarged basal articles and three anterior pairs of deep abdominal pleural folds creates a trough guiding a respiratory current (for details see Dahl (1977)).

The Isopoda, having no branchial chambers, have evolved another unique respiratory–ventilatory system with pleopods acting as respiratory, ventilatory and in most cases also natatory organs.

(*e*) ***Summary of alternatives in eumalacostracan respiratory systems***

As shown in the survey presented above, the morphological basis of eumalacostracan respiratory systems is in most cases provided by the thoracic epipods. Exceptions are found in the Mysida and the Thermosbaenacea, in which the dorsal thoracic fold is the main respiratory organ, and in the Isopoda, in which the pleopods are both ventilatory and respiratory.

The ventilatory mechanisms show a wider spectrum of alternatives. The least specialized is found in the Anaspidacea, in which literally any kind of thoracopod or epipod activity contributes to the ventilation of the exposed epipods. In the Decapoda and most Peracarida the respiratory branchiae are enclosed in ventilated branchial chambers. In the Euphausiacea the epipodial branchiae are exposed and ventilated by pleopod beating. Ventilation in the Decapoda is effected by the maxillary scaphognathite and in most Peracarida by the ventilatory maxilliped epipod.

Amphipoda and Isopoda have independently evolved unique respiratory–ventilatory mechanisms. In the case of the Mictacea, definite proof concerning the presence of specialized respiratory organs is still lacking (cf. Bowman & Iliffe 1985).

8. ORIGIN OF CEPHALOTHORACIC SHIELDS AND FOLDS IN THE MALACOSTRACA

(*a*) *Cephalization of maxilliped segments*

In the Malacostraca there is a tendency for one or more pair of thoracopods to become included into the mouthpart apparatus and transformed into maxillipeds. This can be seen as a continuation of the same process that led to the cephalization of the maxillae, still incomplete in the Cephalocarida and possibly also reflected in the presence of a cervical groove between the mandibular and maxillary regions of the cephalon in certain Malacostraca (Calman 1909; cf. figure 53). In this respect the Leptostraca constitute a special case, as despite the fact that, as shown above, the 1st thoracic segment is fused to the cephalon, the 1st thoracopod, though smaller than the subsequent ones, remains a typical thoracopod without any masticatory devices.

Among the Eumalacostraca there are only two higher taxa in which a fusion of the 1st thoracic segment to the cephalon has not taken place, namely the two syncarid orders Palaeocaridacea and Bathynellacea, which both have eight free thoracic segments. In the third syncarid order, the Anaspidacea (*sensu* Schminke 1974, i.e. including the Stygocarididae), the 1st thoracic segment is fused to the cephalon, thus forming a narrow cephalothoracic shield.

The 1st thoracopod of the Palaeocaridacea was shorter than the subsequent ones. The endopod had a full number of articles, but in these extinct forms nothing is known concerning the possible occurrence of endites (Brooks 1962). In the Bathynellacea the 1st thoracopod is similar to the subsequent ones and has no endites. Among the Anaspidacea the genera *Anaspides*, *Paranaspides*, *Allanaspides* and *Stygocaris* have endites on the 1st thoracopod coxa, whereas in *Koonunga* and *Psammides* they are missing (Smith 1909; Siewing 1959; Noodt 1970; Swain *et al.* 1970; Schminke 1978).

Thus within the Syncarida only some of the Anaspidacea are known to have a 1st thoracopod showing some of the modifications of a maxilliped, although in a somewhat imperfect form, and it is only the Anaspidacea that have the 1st thoracic segment fused to the cephalon, forming a small cephalothoracic shield. The Anaspidacea appear to be in the process of developing an effective masticatory maxilliped.

In the Malacostraca there exists a correlation between the transformation of the 1st thoracopod into a maxilliped and the formation of a cephalothoracic shield produced by the fusion of the 1st thoracic segment to the cephalon, possibly in response to a demand of increased stability of the exoskeleton of the mouthpart region. There are no instances of a true maxilliped being present without such a fusion.

This cephalic-maxilliped segment shield is the only kind of cephalothoracic shield existing in the Anaspidacea, Amphipoda, Isopoda, Spelaeogriphacea and Mictacea. The respiratory system of the Mictacea is not known, but the other four orders represent four different solutions of the problem of respiration and ventilation, all except the Spelaeogriphacea without branchial chambers with specialized ventilatory systems.

However, larger cephalothoracic shields are present in the Hoplocarida and Euphausiacea, which have no masticatory maxillipeds, and in many other malacostracans such shields cover segments following behind the fused maxilliped segment. Thus there appears to exist, in the Eumalacostraca, a correlation between the presence of cephalothoracic shields covering the maxilliped segment and segments behind, and the development of branchiostegal folds and advanced respiratory and ventilatory systems. These apparent correlations and their implications will be discussed below.

(*b*) *Branchiostegal folds and cephalothoracic shields in the Malacostraca*

As demonstrated above (§6), the traditional concept of cephalothoracic shield formation as a result of the fusion of a carapace fold to the dorsum of the thorax was founded on false premises. Obviously another explanation has to be found.

There are indications that the presence of continuous cephalothoracic shields may be a result of the formation of continuous branchiostegal folds along the sides of the thorax. Below, the degree of coincidence between cephalothoracic shields and branchiostegal folds will be reviewed.

The phyllocarid dorsal fold, previously believed to be cephalic, has never been discussed in the terms of pleural and branchiostegal folds. Nevertheless, such a discussion appears to be highly relevant. Exceptionally deep and continuous pleural folds are formed from the margin of the cephalon and the anterior thoracic segments of *Dahlella* and *Nebalia* (cf. above, §5*a* (ii, iii)). A cephalothoracic shield covers the dorsum of these thoracic segments. The folds are homologous with the pleural and branchiostegal folds of the Eumalacostraca and fulfil similar functions. At the posterior margin of the cephalothoracic shield a free dorsal fold is formed, corresponding to that occurring in the Mysidacea.

The major functional difference between the leptostracan and mysidacean respiratory systems lies in the mode of ventilation, which is effected by thoracopod and pleopod beating in the Leptostraca and maxilliped palp beating in the Mysidacea.

In the present context the early development of the Euphausiacea and the dendrobranchiate Decapoda is very instructive, and in somewhat later phases also very similar to that of the Caridea. The earliest phases of the development of the cephalothoracic shield and fold of the two first-mentioned taxa was described in §5*b*. In the protozoea and zoea stages differentiation of the thorax proceeds posteriad, the formation of the cephalothoracic shield and branchiostegia keeping in step. On the posterior dorsal margin of the growing cephalothoracic shield there is a small fold and behind it several narrow segment rudiments. In later larval stages these segments become longer and covered by the shield. The dorsal fold disappears. It is possible that its main function has been that of an integumental reserve. After ecdysis, soft tissues grow very rapidly, mainly as a result of water uptake (Gersch 1964). Then the cuticle gradually hardens and prevents further growth in length. Stretching and fusing to underlying tissue an integumental fold with an upper and lower surface the combined length of which is longer than the corresponding part of the dorsum of the previous instar might constitute an advantage. Observations by Newman & Knight (1984) suggest that this kind of stretching actually occurs, for they stated that 'the dorsal surface of the thorax becomes covered by the outer cuticular surface of the carapace'. This appears convincing, for the dorsal fold is part of the dorsal thoracic integument, and it is only natural that it should contribute to the coverage of the growing thorax. This view gains further support from the study of sagittal sections of a young furcilia of *Meganyctiphanes norvegica* as reported in §5*b*.

It is interesting that in the yolky eggs of *Pilumnus* spp. Wear (1967) could show that the first thoracic exoskeletal element to be formed in the embryo is an unsegmented branchiostegal fold and that the laterodorsal part of the cephalothoracic shield is gradually formed as a dorsal extension of this lateral exoskeleton.

In the Hoplocarida the embryos form branchiostegal folds along the anterior thoracic segments, which are the only ones covered by a cephalothoracic shield (cf. Balss 1938; Shiino 1942).

The Peracarida are particularly interesting because some of the taxa have branchiostegal folds, cephalothoracic shields and respiratory–ventilatory systems based on the activity of the maxilliped epipod, whereas in others both branchiostegal folds and cephalothoracic ventilatory mechanisms are missing.

The rule that branchiostegal folds and cephalothoracic shields, when present, are formed very early holds also for the Peracarida. As shown by Manton (1928) in *Hemymysis lamornae*, branchiostegal folds are already present at a stage when the dorsal mesoderm has formed the floor but not yet the roof of the heart (Manton 1928, text-figure 15*a*). In *Boreomysis arctica* Jepsen (1967) showed that the branchiostegal folds and the cephalothoracic shield covering the same segments appear in what she termed the 2nd embryonic stage, i.e. after the embryo has become free from the egg membrane but before the 1st moult. Segmental borders are formed behind but not within the part of the body where branchiostegal folds are present.

The development of the external morphology of the cumacean *Diastylis lucifera* was studied by Sars (1900). At a stage when the pleon is still turned dorsad and no thoracic segmental borders are visible, the rudiment of a branchiostegal fold is formed in the body wall above the bases of the four anterior thoracopods (figure 51). At a later stage, when the pleon has turned ventrad, this fold has grown down to cover the proximal parts of the four anterior thoracopods. Segmental borders have developed between the four thoracic segments lying behind the branchiostegal folds. However, in the four anterior thoracic segments, where a branchiostegal fold is present, no segmental borders appear, and this part of the thorax remains covered by a continuous cephalothoracic shield, ventrally continuous with the branchiostegal folds, throughout life (figure 52). The enlargement of the maxilliped epipod, which later comes to function as a ventilator, commences at the same time as the formation of the branchiostegal folds.

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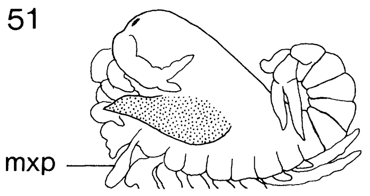

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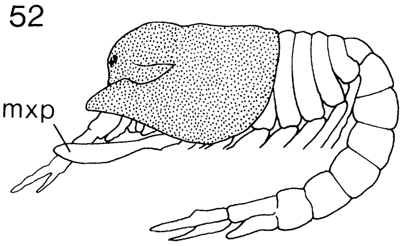

Figure 51. Early phase of formation of branchiostegal fold in *Diastylis*. (After Sars 1900.)
Figure 52. Later stage in formation of branchiostegal fold and cephalothoracic shield in *Diastylis*. (After Sars 1900.)

In the tanaidacean *Heterotanais oerstedi*, a branchial chamber flanked by a lateral fold first appears within the mandibular and maxillary region (Scholl 1963). Later an extension of the branchial chamber to include the two anterior thoracic segments takes place. This conforms to the statement by Sars (1899) according to which the branchial chambers are formed from the cephalon and the two anterior thoracic segments. A cephalothoracic shield covers the cephalon and the two anterior thoracic segments, but behind the branchiostegal folds the 3rd to 8th thoracic segments are separated by segmental borders.

In *Spelaeogriphus* the 1st thoracic (maxilliped) segment is fused to the cephalon but forms a small branchiostegal fold within which the enlarged and complicated palp of the maxilliped acts as ventilatory and respiratory organ. The exopods of thoracopods five to seven are also respiratory. Grindley & Hessler (1971) found that the exopods of thoracopods two and four, presumed by Gordon (1957) to be natatory, are ventilatory. The embryology of *Spelaeogriphus* is unknown. In the Thermosbaeanacea, Zilch (1974) showed that the rudiment of the pleural fold of the 1st thoracic segment appears in the last stage before the hatching from the egg membrane and is continuous with the cephalic pleural folds. Siewing (1958) showed that in the Thermosbaenacea, as in the Mysidacea, the respiratory organs are the branchiostegal folds themselves (referred to as 'Carapax'), and that ventilation,

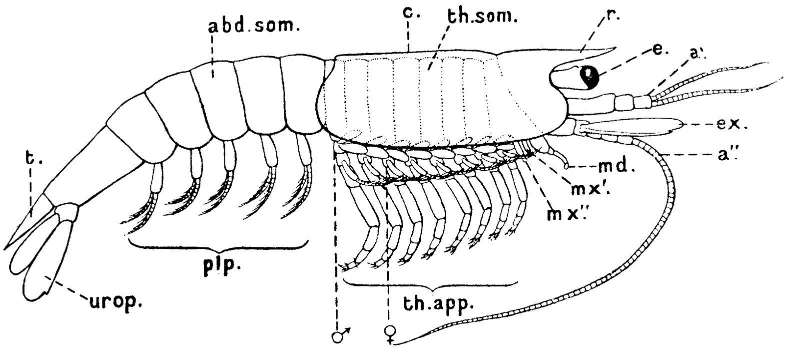

Figure 53. Drawing of 'generalized type of Malacostraca', (after Calman 1906.)

as in the peracarid orders dealt with above, is provided by the beating of the maxilliped epipod. The cephalothoracic shield in *Thermosbaena mirabilis* covers only the 1st thoracic segment but is continued by a free dorsal fold lying over the 2nd and 3rd thoracic segments (Zilch 1972).

In the Amphipoda and Isopoda, which have no thoracic branchiostegal folds, only the maxilliped segment is fused to the cephalon and all thoracic segments behind it are free.

This survey of pleural-branchiostegal fold and cephalothoracic shield formation shows that in all Malacostraca, the respiratory system of which includes branchiostegal chambers, the branchiostegal folds are formed at an early ontogenetic stage. At a time when external segmental borders appear elsewhere in the thorax, the parts possessing branchiostegia are covered by a continuous cephalothoracic shield, sometimes with a free terminal dorsal fold. In eucarid and euphausiid zoea larvae, external thoracic segment borders disappear in those parts where branchiostegal fold formation proceeds.

In Malacostraca without branchiostegal folds, or with folds only along part of the thorax, segmental borders are present in the entire thorax of the two syncarid orders Palaeocaridacea and Bathynellacea, which lack both functional maxillipeds and branchiostegal folds, and also in the part of the thorax behind the fused maxilliped segment of Anaspidacea, Isopoda, Amphipoda and Mictacea and behind the branchiostegal folds in Mysidacea, Cumacea and Spelaeogriphacea.

(*c*) *Conclusions concerning malacostracan dorsal shield and fold formation*

The conclusions concerning cephalothoracic fold and shield formation in the Malacostraca can be summarized as follows.

1. The classical concept of cephalothoracic shield formation as a result of fusion of a carapace fold to the dorsum of the thorax was founded upon false premises and no evidence can be found to support it.

2. In all recent Malacostraca, except those belonging to the syncarid orders Palaeocaridacea and Bathynellacea, at least one thoracic segment is fused to the cephalon, thereby contributing to the formation of a cephalothoracic shield.

3. The formation of branchiostegal folds leads to the disappearance of external segmental borders not only within the folds themselves but also in the dorsal part of the segments involved, resulting in the formation of a cephalothoracic shield, composed of elements from the cephalon, the maxilliped segment and the respective thoracic segments.

This last conclusion is supported by four sets of observations, namely: (i) the complete coincidence between the development of branchiostegal folds and cephalothoracic shields in all taxa studied; (ii) the incorporation in euphausiid, dendrobranchiate and caridoid larvae of further thoracic terga into the cephalothoracic shield in step with the extension posteriad of the branchiostegal folds; (iii) the absence of cephalothoracic shields except, in most cases, those of the maxillipedal segment, in those taxa in which no postmaxillipedal branchiostegal folds are formed (Syncarida, Amphipoda, Isopoda, Spelaeogriphacea, Mictacea); (iv) the presence, in cases where external dorsolateral segmentation has been replaced by the formation of cephalothoracic shields, of segmentally arranged endoskeletal elements below the cephalothoracic shield.

Thus it can be concluded that a cephalothoracic shield is no basic ingredient in the malacostracan structural plan and that, when present, these shields can be regarded as features resulting from the formation of masticatory, or at least food-handling, maxipilleds and the formation of branchiostegal folds.

9. SOME GENERAL CONCLUSIONS

Some of the results obtained in this investigation appear to contribute to a better understanding of certain aspects of the structural and functional morphology of the Crustacea and to elucidate aspects of the evolution and differentiation of the Eumalacostraca.

It could be shown that the carapace hypothesis formulated by Calman (1909) is based on false premises. A free or fused cephalic carapace fold of the type postulated by Calman does not exist in any Malacostraca or in any of the Branchiopoda investigated.

It could be concluded that the configuration and function of the ventilatory and respiratory mechanisms and the formation of maxillipeds have profoundly influenced the modelling of the eumalacostracan thoracic exoskeleton. The formation of continuous pleural-branchiostegal folds along parts of or in the whole cephalothoracic lateral margin apparently inhibits the formation of external dorsal and lateral segment borders between the segments involved. This results in the formation of the cephalothoracic shield. This interpretation is supported by the fact that the number of segments taking part in the formation of cephalothoracic shields and branchiostegal folds is always the same.

As a result of the invalidation of the carapace hypothesis, the absence of a carapace in the Syncarida can be recognized as primary and not secondary. This permits the conclusion that in this respect the structural and functional morphology of the Syncarida is truly primitive. This calls for a re-evaluation of various aspects of eumalacostracan evolution. It indicates *i.a.* that the presence of eight free thoracic segments in the Bathynellacea and the extinct Palaeocaridacea reflects the original malacostracan structural plan. The first indication of the formation of a eumalacostracan cephalothoracic shield, as seen in the Anaspidacea, is due to the fusion of the 1st thoracic segment to the cephalon in connection with the transformation of the 1st thoracopod into an incipient maxilliped.

The syncarid type of organization probably represents a basic eumalacostracan pattern. The progressive differentiation of this system can have been the result of an elaboration of ventilatory–respiratory systems and feeding mechanisms. This could have led to the evolution and differentiation of a wide spectrum of Eucarida and directly or indirectly to the evolution of the Peracarida (cf. Schminke 1978).

The results presented here support the conclusion drawn by Calman (1909) and further explored by Hessler (1983) that the original malacostracan structural plan was that of a caridoid. However, as shown above the failure of the carapace hypothesis makes it improbable that this ancestral caridoid possessed a carapace fold or even a cephalothoracic shield. It appears more likely that it had a segmented thorax, and the formation of a cephalothoracic shield, with or without a free terminal fold, could have come later in connection with the formation of a maxilliped and branchiostegia.

The conclusions concerning the higher systematics of the Eumalacostraca drawn by Hansen (1893) and Calman (1904, 1909) are not affected by the results and suggestions presented here, and the three higher taxa proposed by Calman, i.e. the 'Divisions' Syncarida, Eucarida and Peracarida, retain their validity as the highest systematic units within the Eumalacostraca.

The Peracarida show a much higher degree of morphological radiation than the Syncarida and Eucarida but they are held together as a natural taxon by two unique synapomorhies, namely a ventilatory maxilliped epipod and a brood pouch derived from thoracic epipods. Most peracarid taxa possess both these features, and the rest have one of them. All peracarids except the Thermosbaenacea, of somewhat doubtful peracarid affinities, have an epipodial brood pouch, and all except the Amphipoda, Isopoda and Mictacea have a ventilatory maxilliped epipod. Neither of these features occur in any Recent taxon outside the Peracarida, but the presence of oostegites has been recorded in Carboniferous Eocarida (Brooks 1969).

The Mysidacea are clearly caridoid and may be the closest surviving peracaridan relatives of the Syncarida and Eucarida, but they possess both the diagnostic peracaridan synapomorhies. Therefore I find it difficult to support the proposal by Watling (1983) according to which the Mysidacea should be transferred from the Peracarida to the Eucarida. An acceptance would lead to the breaking up of the taxon Peracarida, well defined and covering the largest and most highly diversified assemblage of Eumalacostraca. It would also tend to conceal a probably early separation of the syncarid–eucarid and peracarid lines of evolution with respect to two vital functional systems, namely those responsible for ventilation–respiration and brood care, which, in the case of the Peracarida, has obviously contributed to evolutionary success and comprehensive radiation. In other respects I share the views held by Watling (1981, 1983) concerning the Peracarida.

This investigation was supported by grants from the Swedish Natural Science Research Council and the Royal Physiographic Society, Lund. The Faculty of Mathematics and Science of the University of Lund granted me working facilities at the Department of Zoology, where Professor Rolf Elofsson and his staff helped me in every possible way. Professor Jarl-Ove Strömberg granted me ship time and laboratory facilities at the Kristineberg Marine Biological Station of the Royal Swedish Academy of Sciences. I am indebted to Professor D. T. Andersson for great hospitality, for permitting me to use the facilities of the Department of Zoology of the University of Sydney and to profit from his great experience of Crustacean embryology and general biology. Dr Roy Swain of the Department of Zoology of the University of Tasmania guided me during a week of successful field work, when species of Syncarida were collected. Dr Janet Kunze, Sydney, advised me concerning the keeping of live Syncarida in the laboratory. For long and profitable discussions and constructive criticism I am indebted to Professor R. R. Hessler and Professor W. A. Newman, and to my wife, Professor Christine Dahl. For technical assistance in laboratory and office I wish to thank Miss Ylwa Andersson, Mrs Gunilla Bergh, Mrs Lina Hansén, Miss Inger Norling, Mrs Astrid Ulfstrand and Mrs Rita Wallén.

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Received 26 November 1990; revised 16 May 1991; accepted 4 July 1991

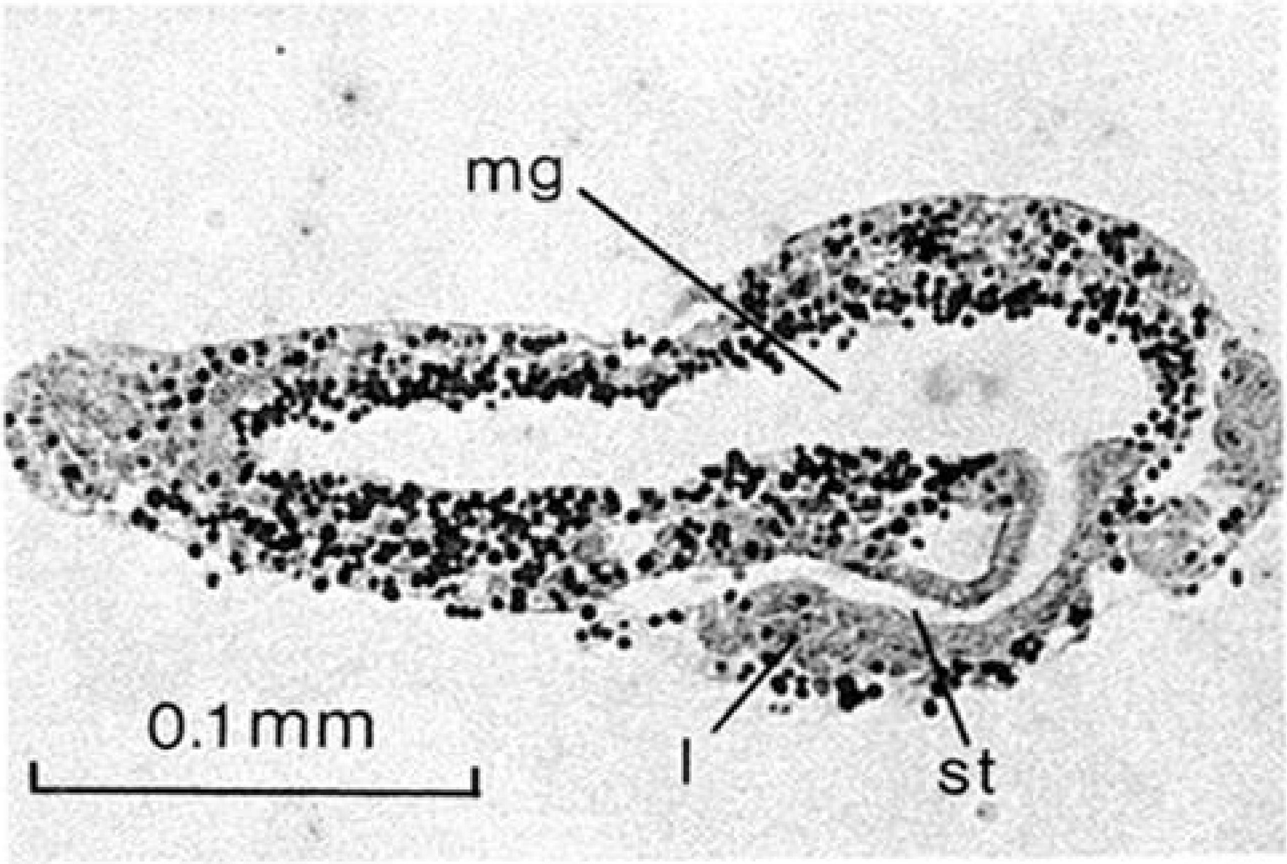
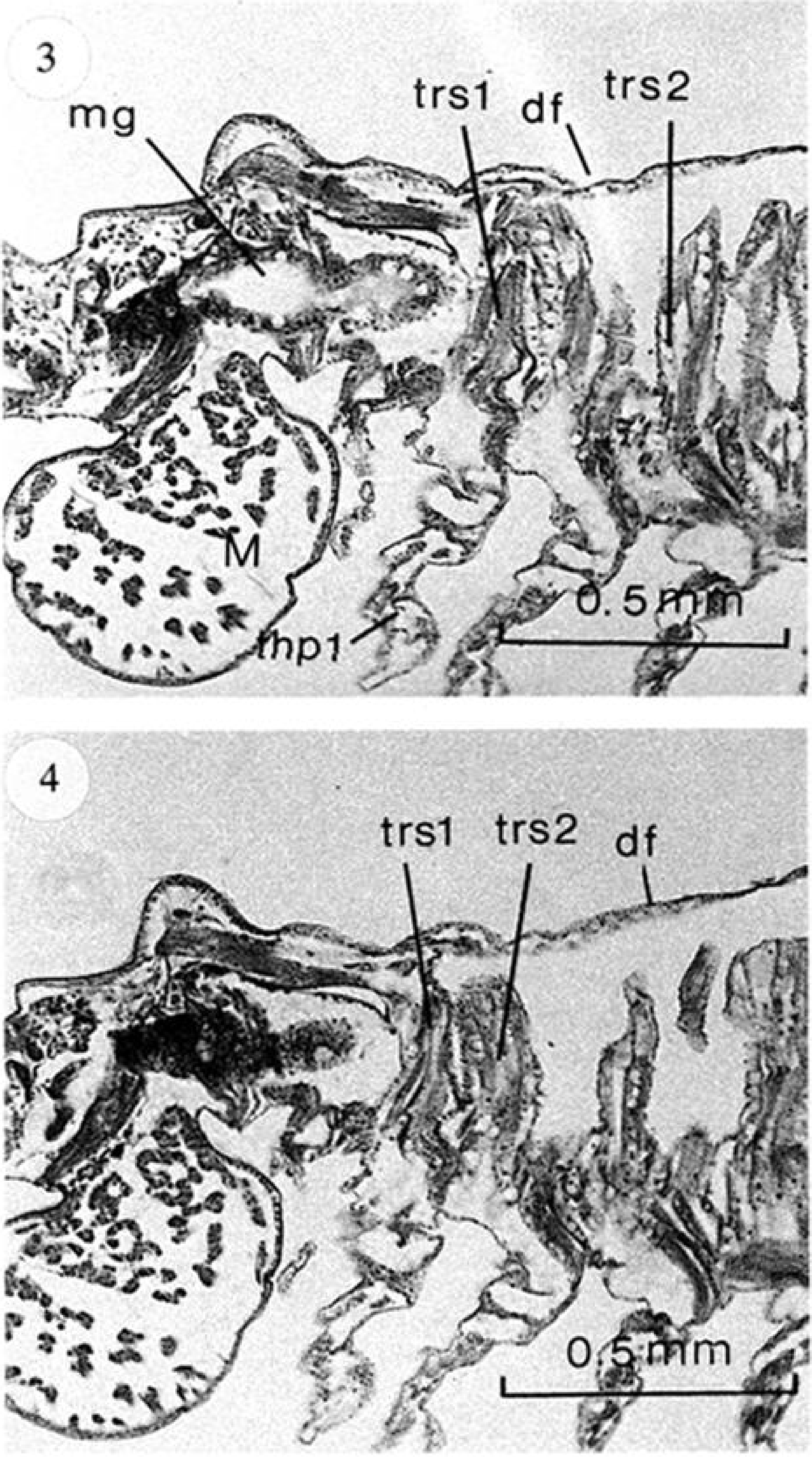
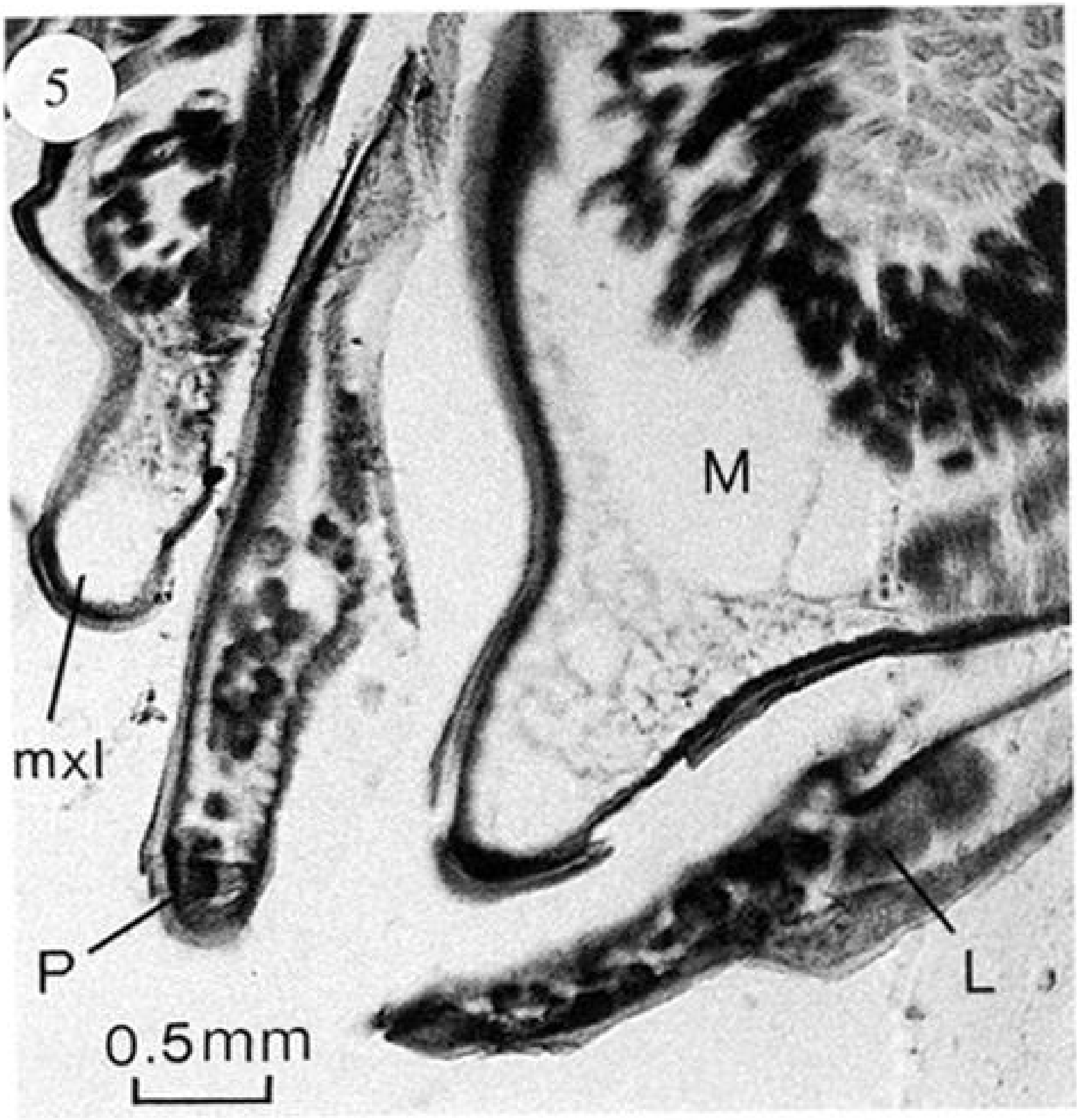


Figure 2. Sagittal section through early metanauplius of *Triops cancriformis*, length 0.3 mm. All tissues full of yolk granules. Stomodaeum open but proctodaeum still closed, no sign of fold formation.



Figures 3, 4. Parasagittal sections through cephalon and anterior part of trunk of early benthic juvenile of *T. cancriformis*, total length 3.10 mm. Figure 4, lying slightly more laterad than figure 3, shows attachment of the dorsal fold (df) only to the 1st trunk segment, whereas in figure 3 the fold is attached both to the 1st and 2nd trunk segments.



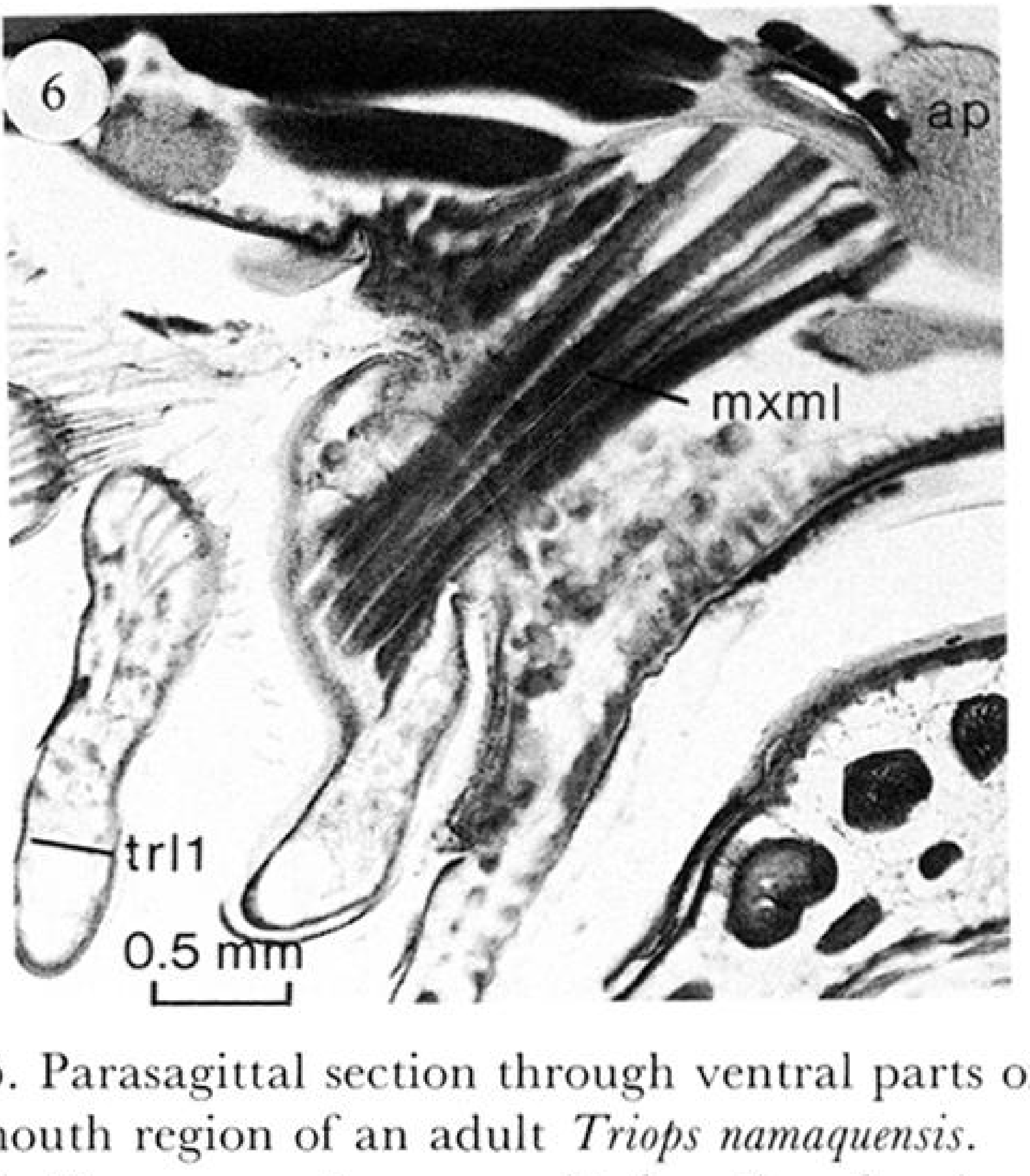
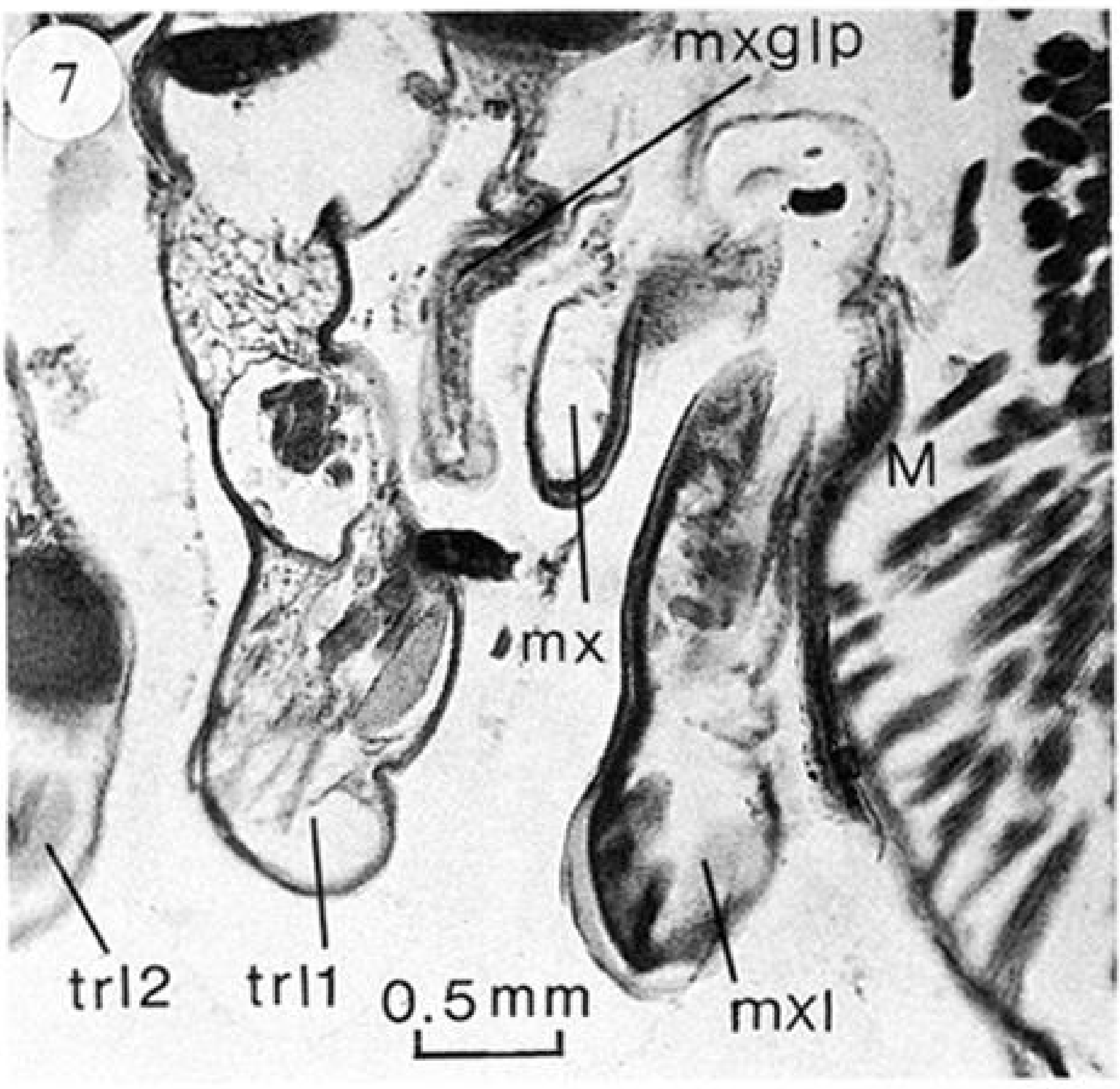
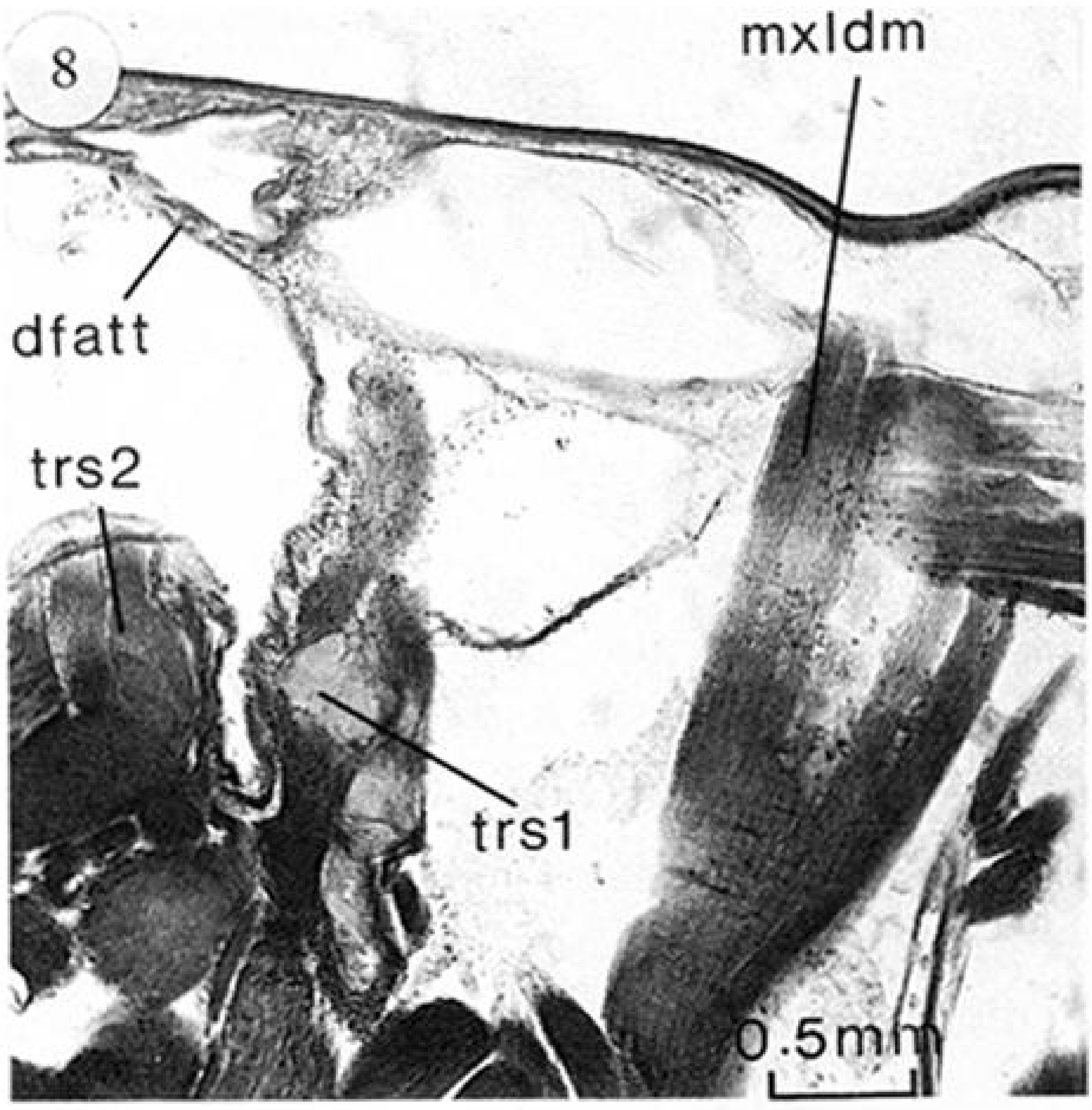


Figure 5. Parasagittal section through ventral parts of limbs in the mouth region of an adult *Triops namaquensis*.

Figure 6. *T. namaquensis*, parasagittal section showing strong muscle attachment of maxillula to apodeme below the ventral nerve chord.





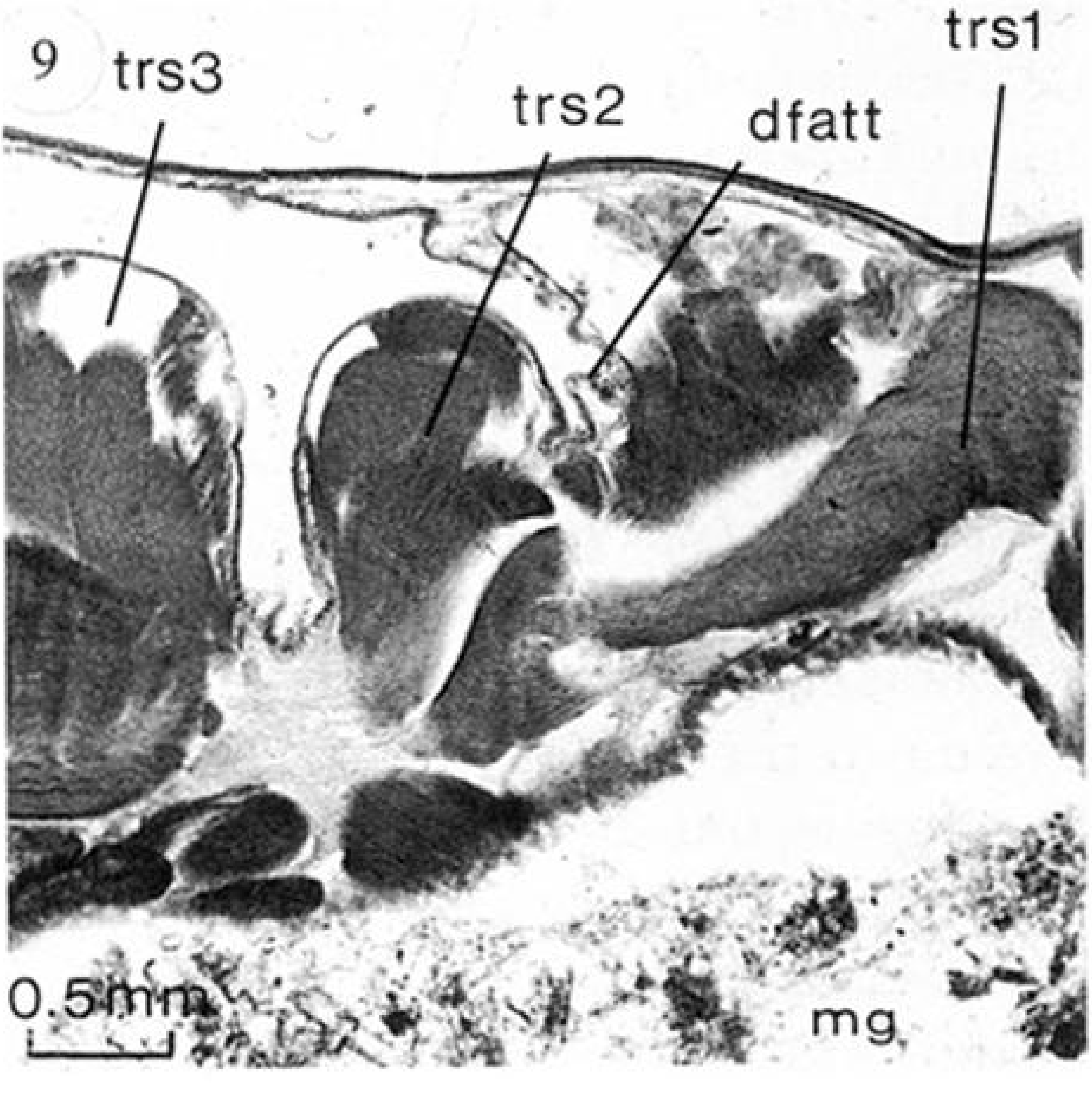


Figure 7. More lateral parasagittal section through *T. namaquensis* showing maxilla and outlet of maxillary gland.

Figure 8. Parasagittal section of *T. namaquensis* showing dorsal fold attachment to posterior margin of 1st trunk segment. More anteriad the attachment: of the maxillular dorsal muscle to the roof of the cephalon, and the muscles of trunk segments 1 and 2.

Figure 9. Parasagittal section through the lateral part of the anterior trunk segments of *T. namaquensis* and the attachment of the dorsal fold.

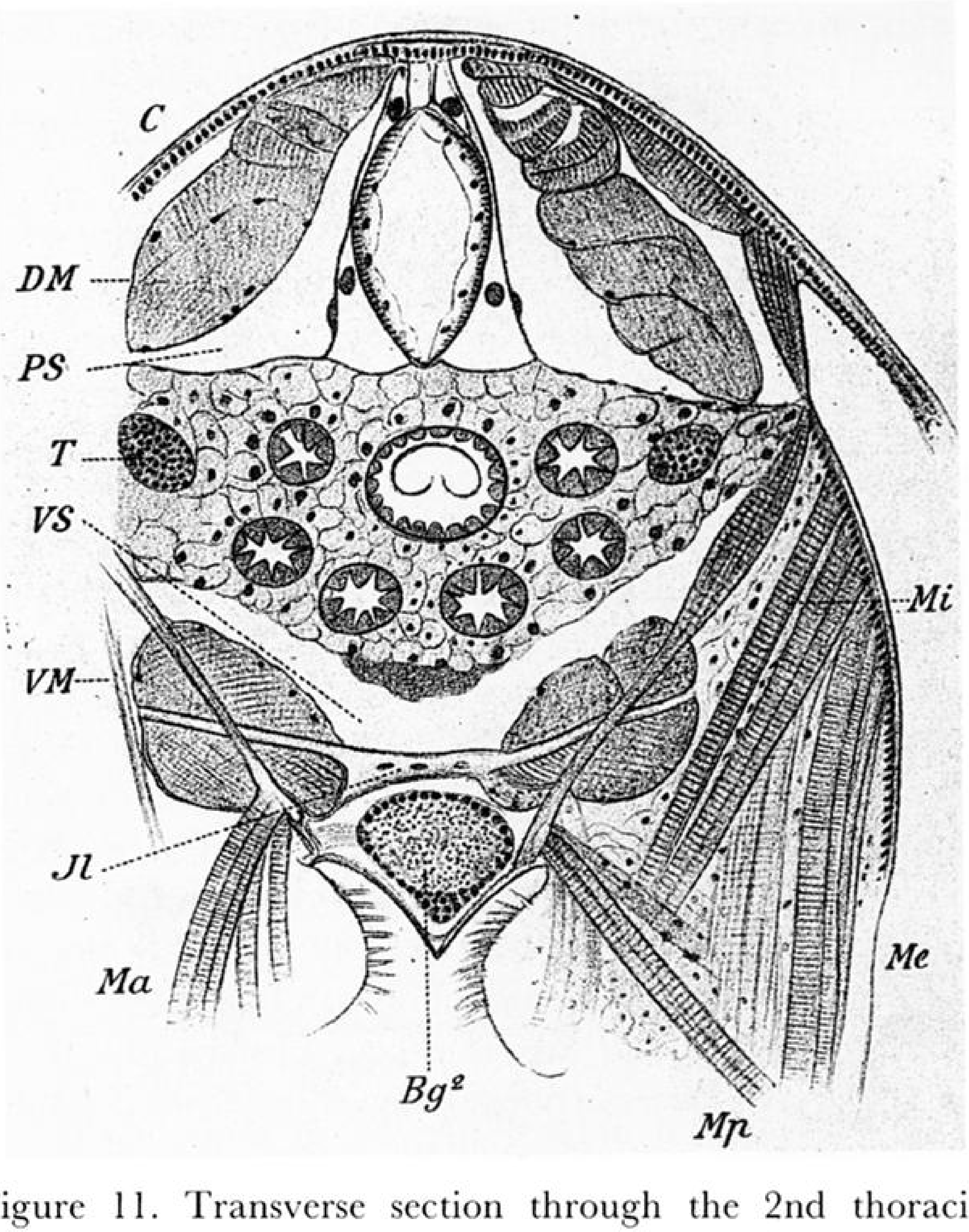


Figure 11. Transverse section through the 2nd thoracic segment of *Nebalia strausi* showing the broad attachment of the cephalothoracic shield to the dorsum of the thorax, the heart and the large longitudinal muscles. In the centre the midgut, the six hepatopancreatic tubuli, and the testes. Ventrolaterally the muscles of the 2nd thoracopod and, midventrally, the ganglion of the 2nd thoracic segment (after Claus 1887, plate IX, figure 8).

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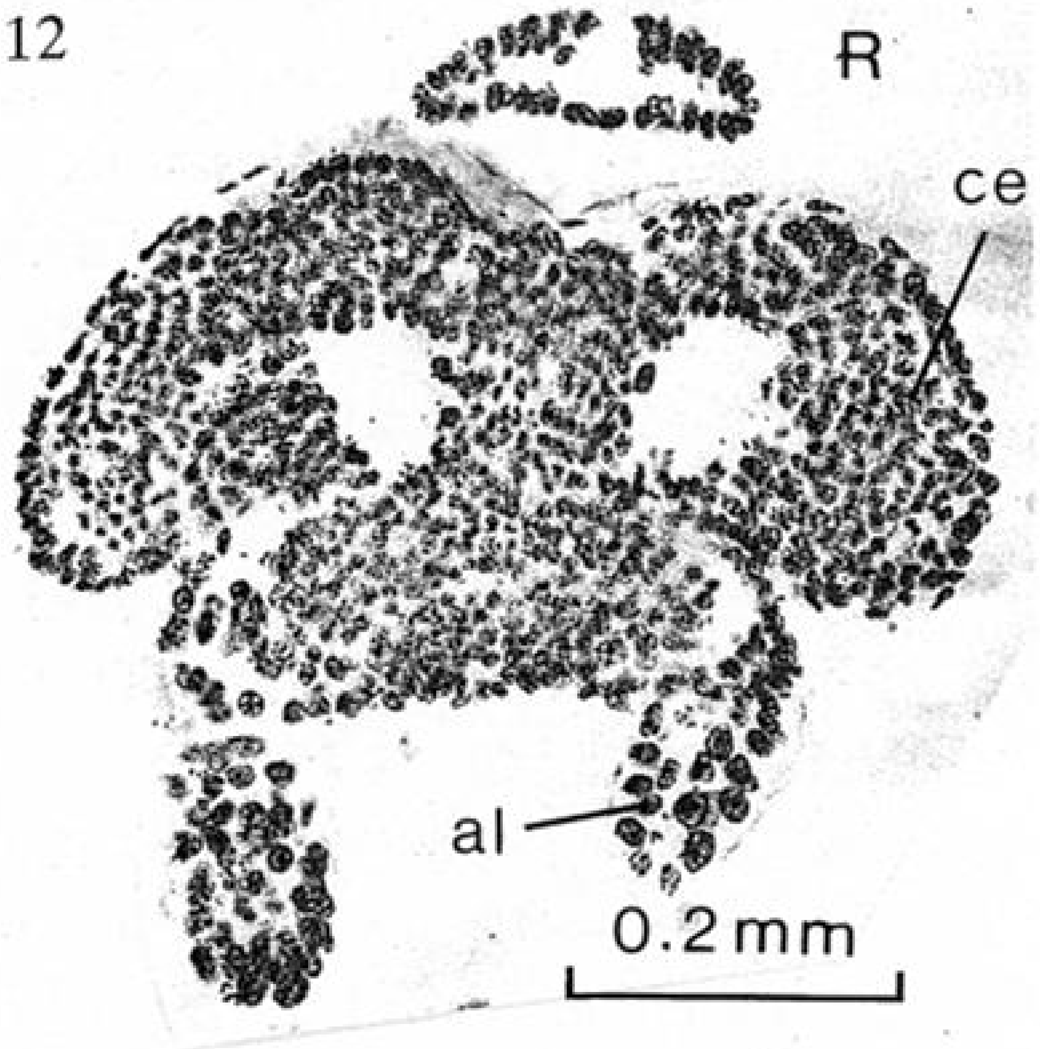

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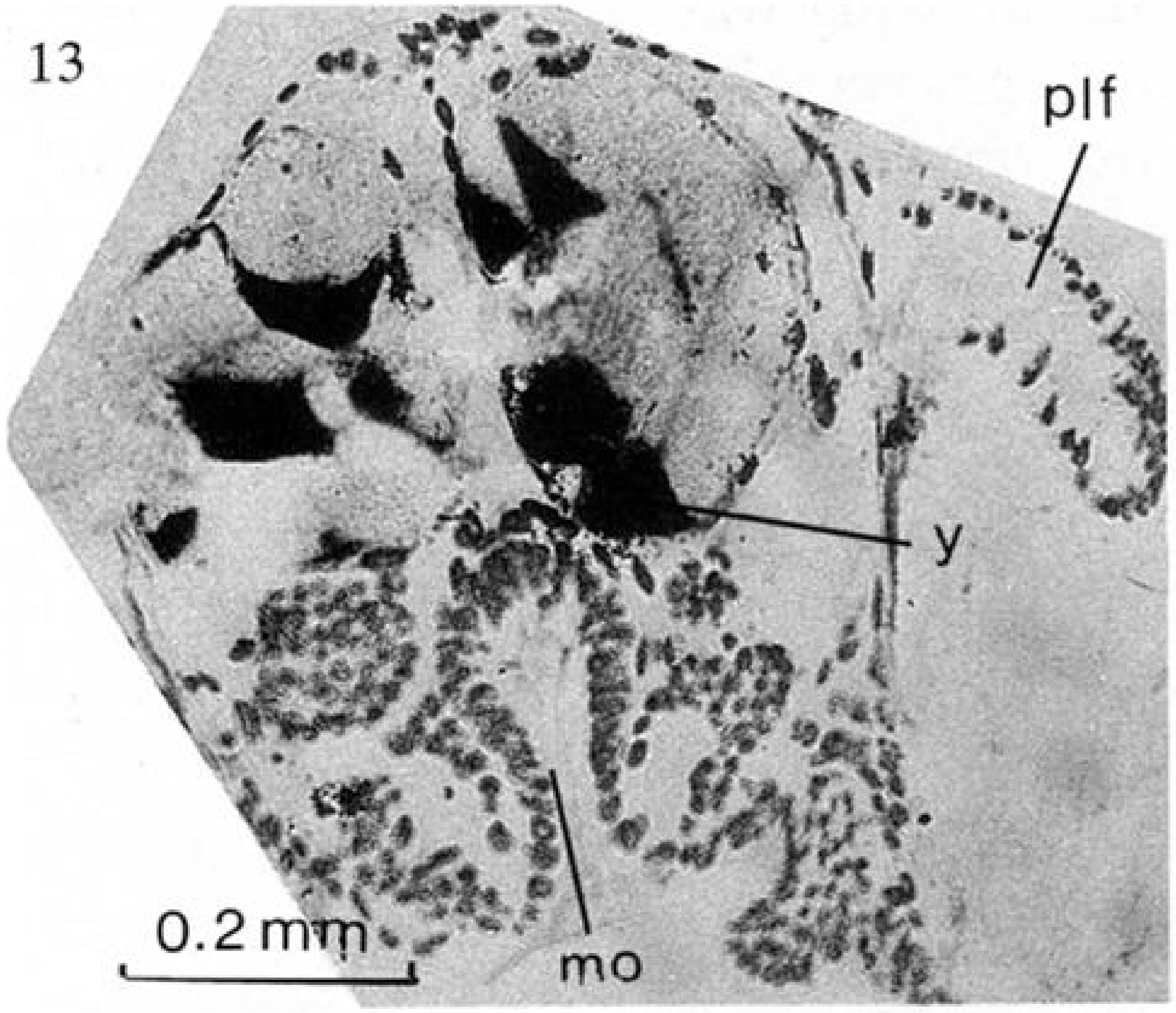
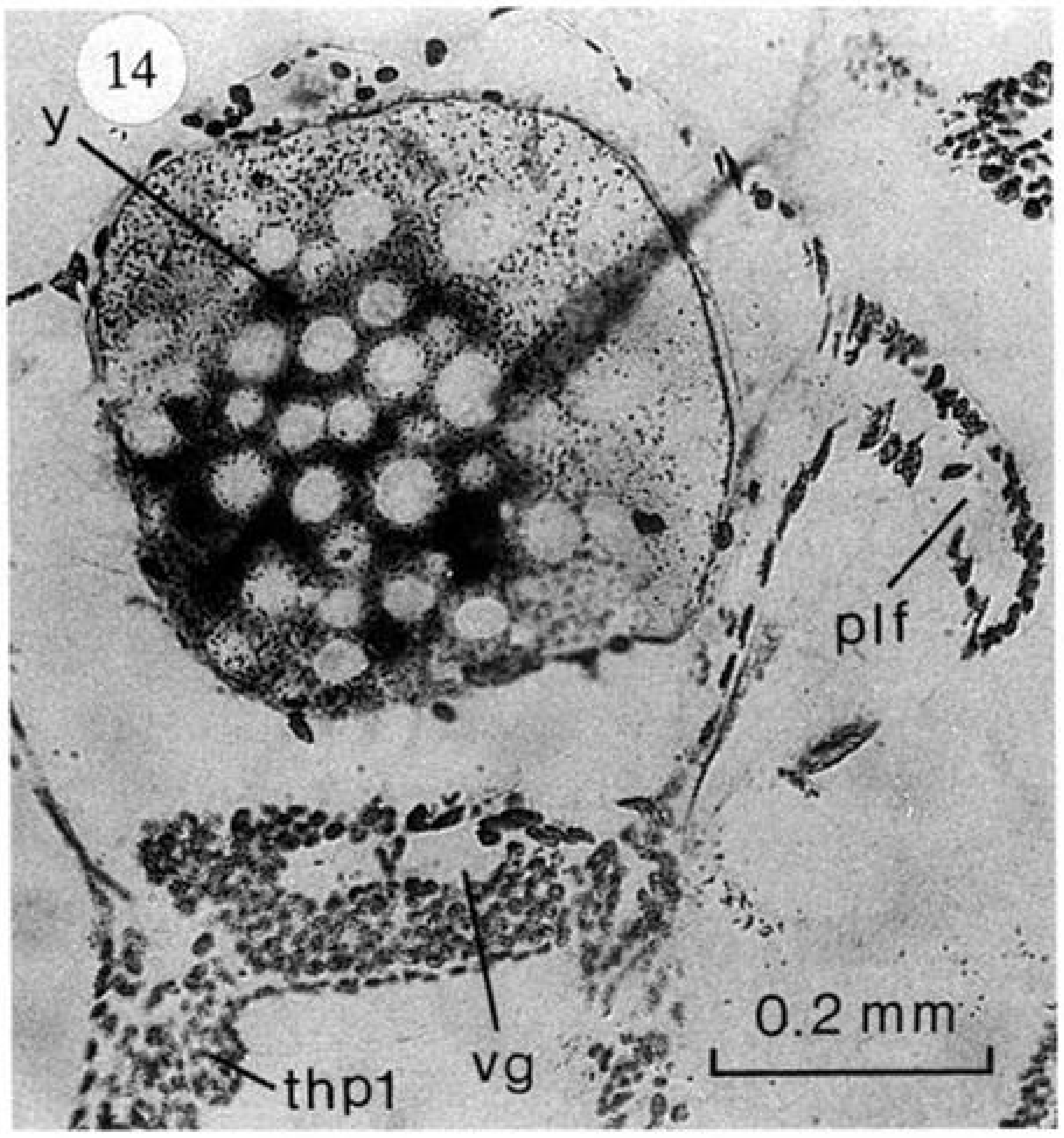




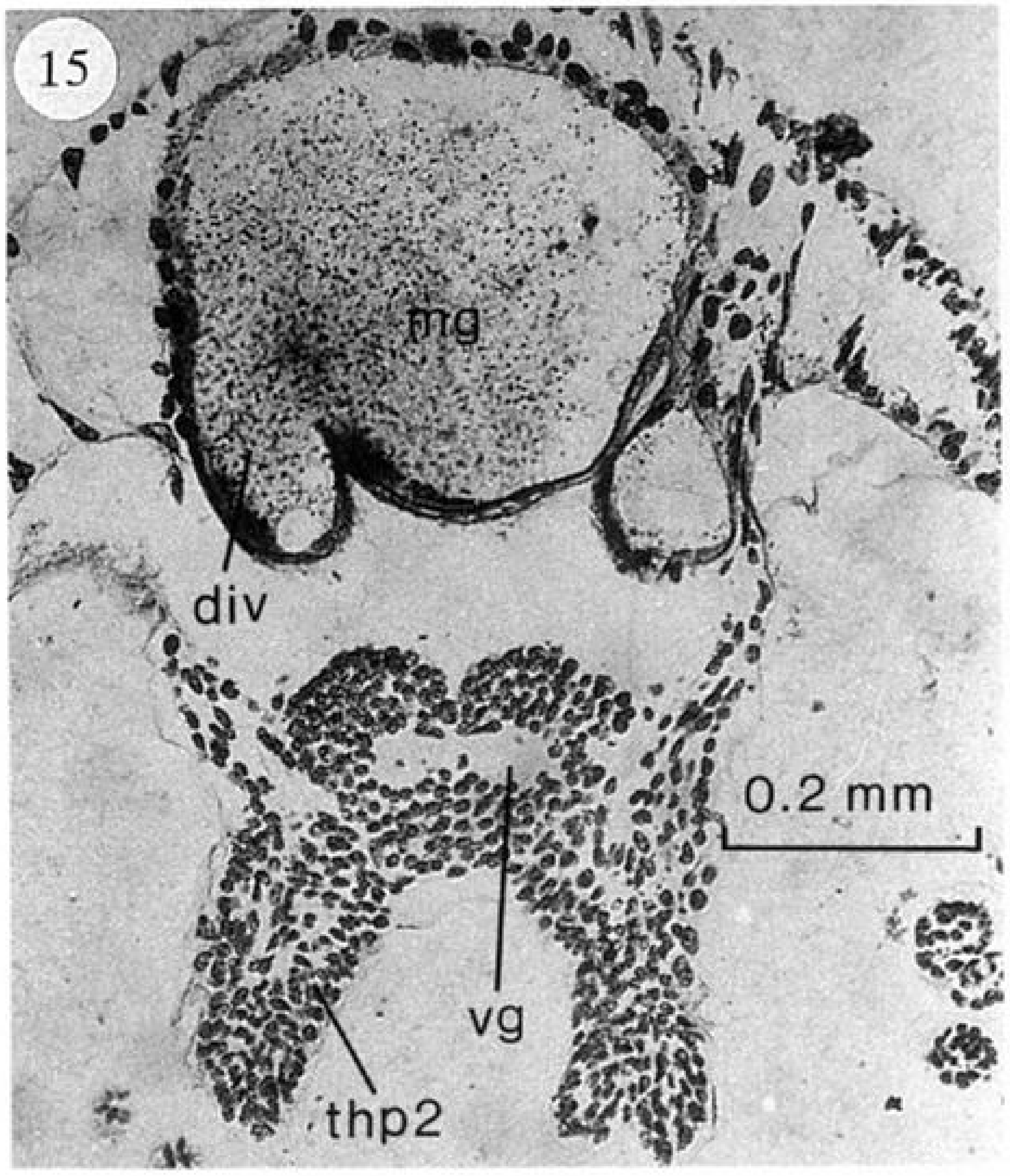
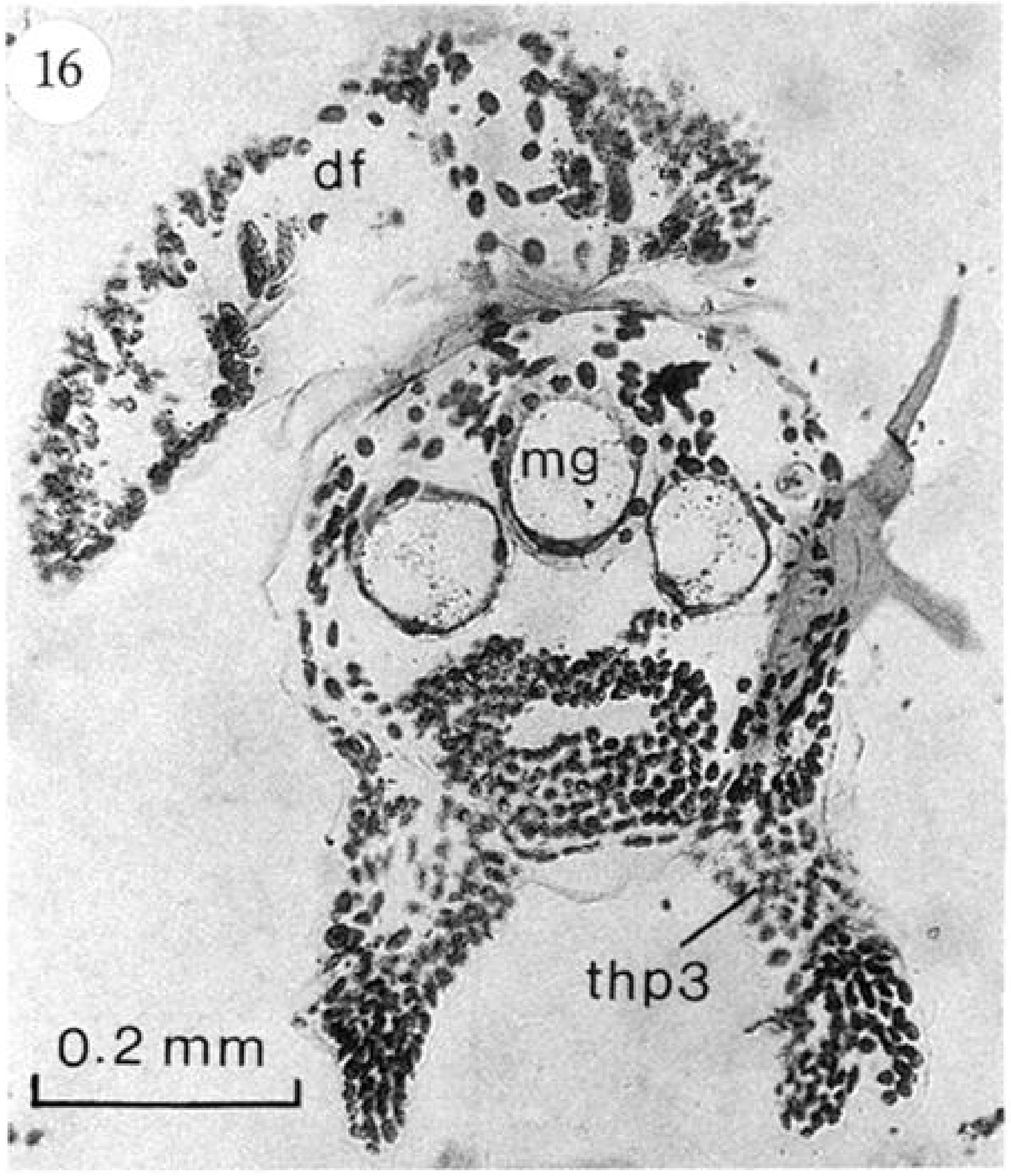


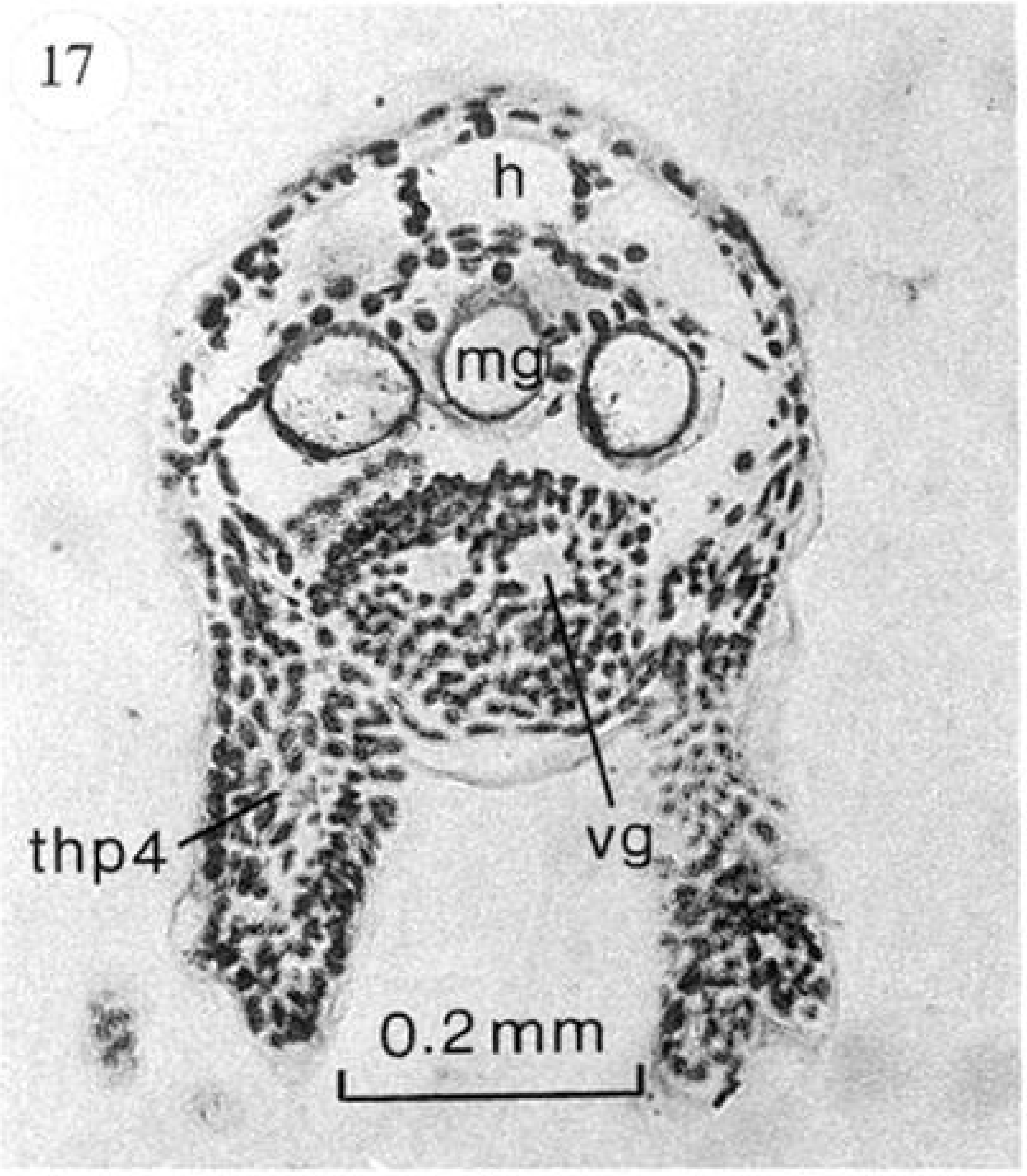
Figure 12. Transverse section through the anterior part of the cephalon of an embryo of *Nebalia*, showing rudiments of rostrum, compound eyes and antennule.

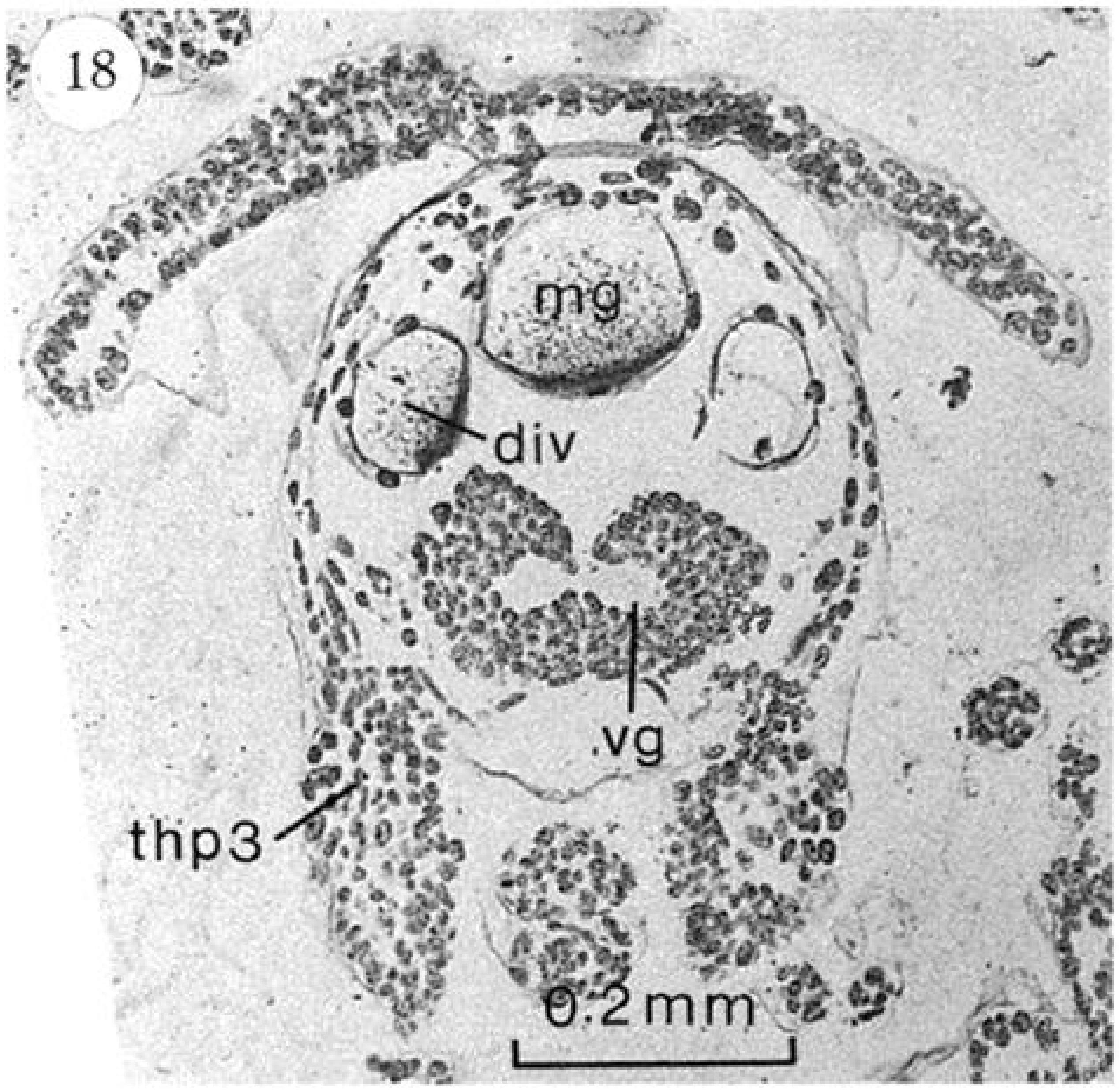
Figure 13. Same embryo as figure 12. Transverse section through the mouth region, showing yolk in the anterior part of the midgut and comparatively well-developed cephalic pleural fold rudiments.

Figure 14. Same embryo as figure 12. Transverse section through the 1st thoracic segment, with much yolk in the anterior part of the midgut and rudiments of the 1st pair of thoracopods.

Figure 15. Same embryo as figure 12. Transverse section through the 2nd thoracic segment with incipient formation of midgut diverticles, the ventral ganglion chain and the 2nd thoracopods







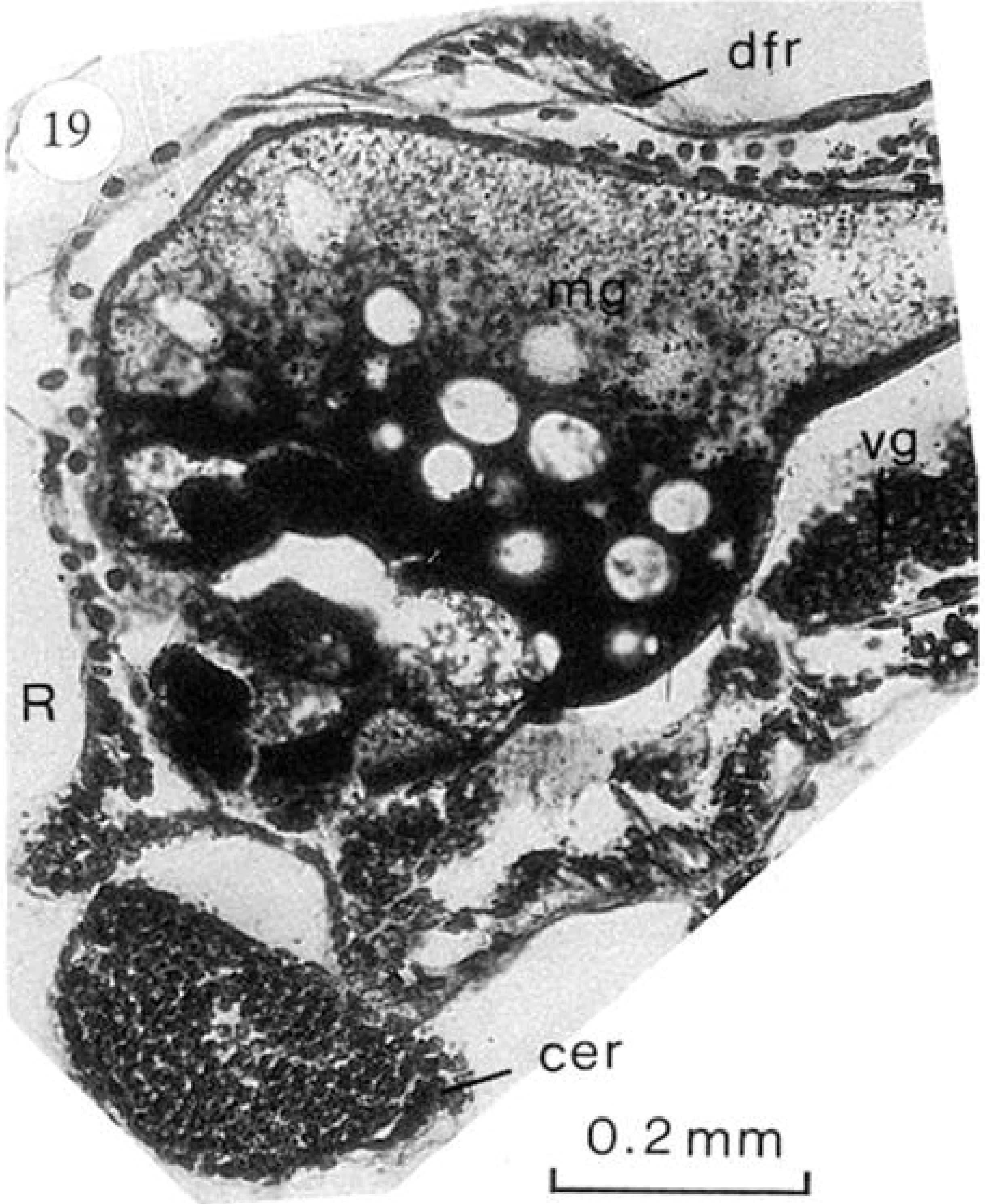
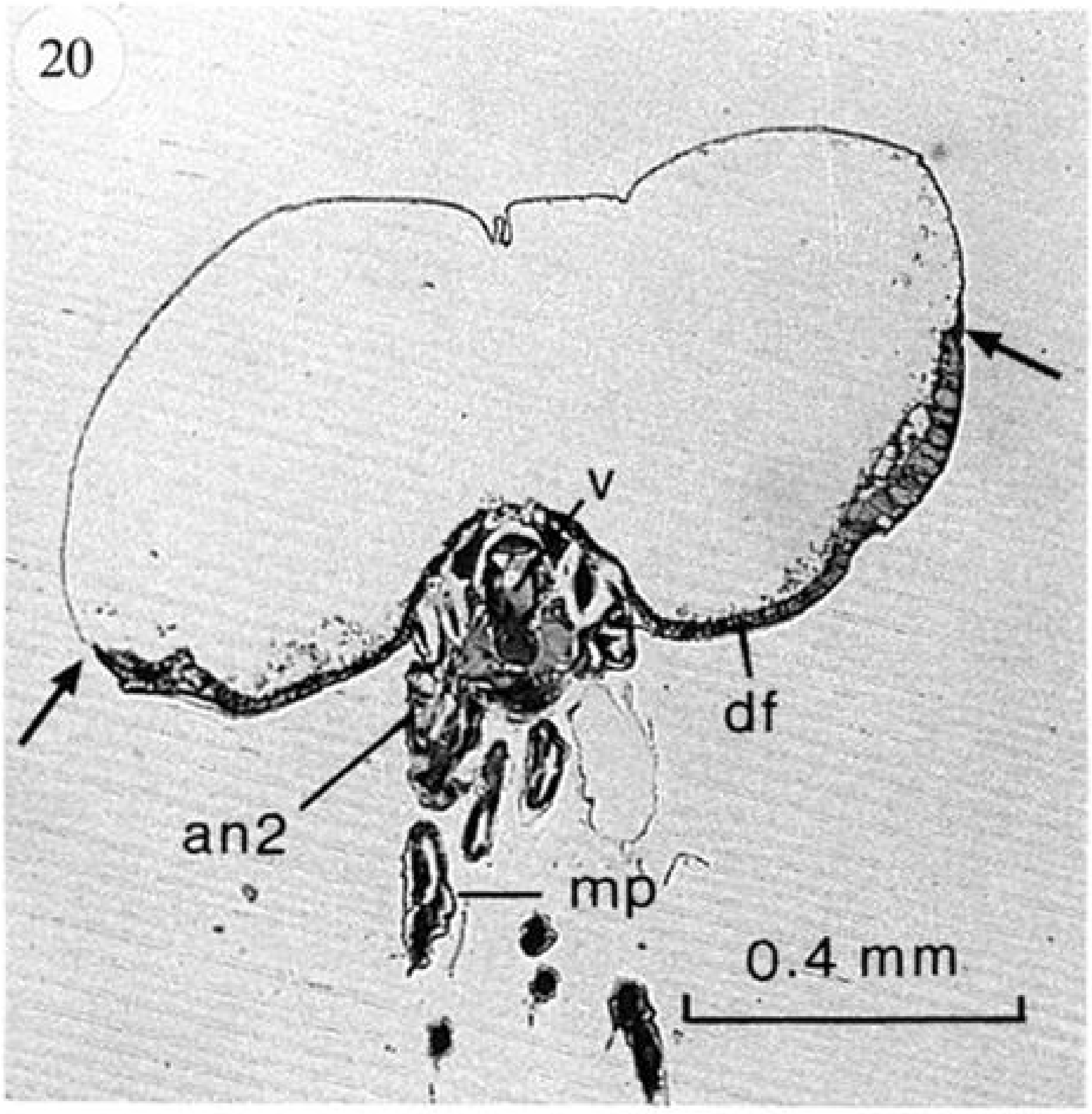


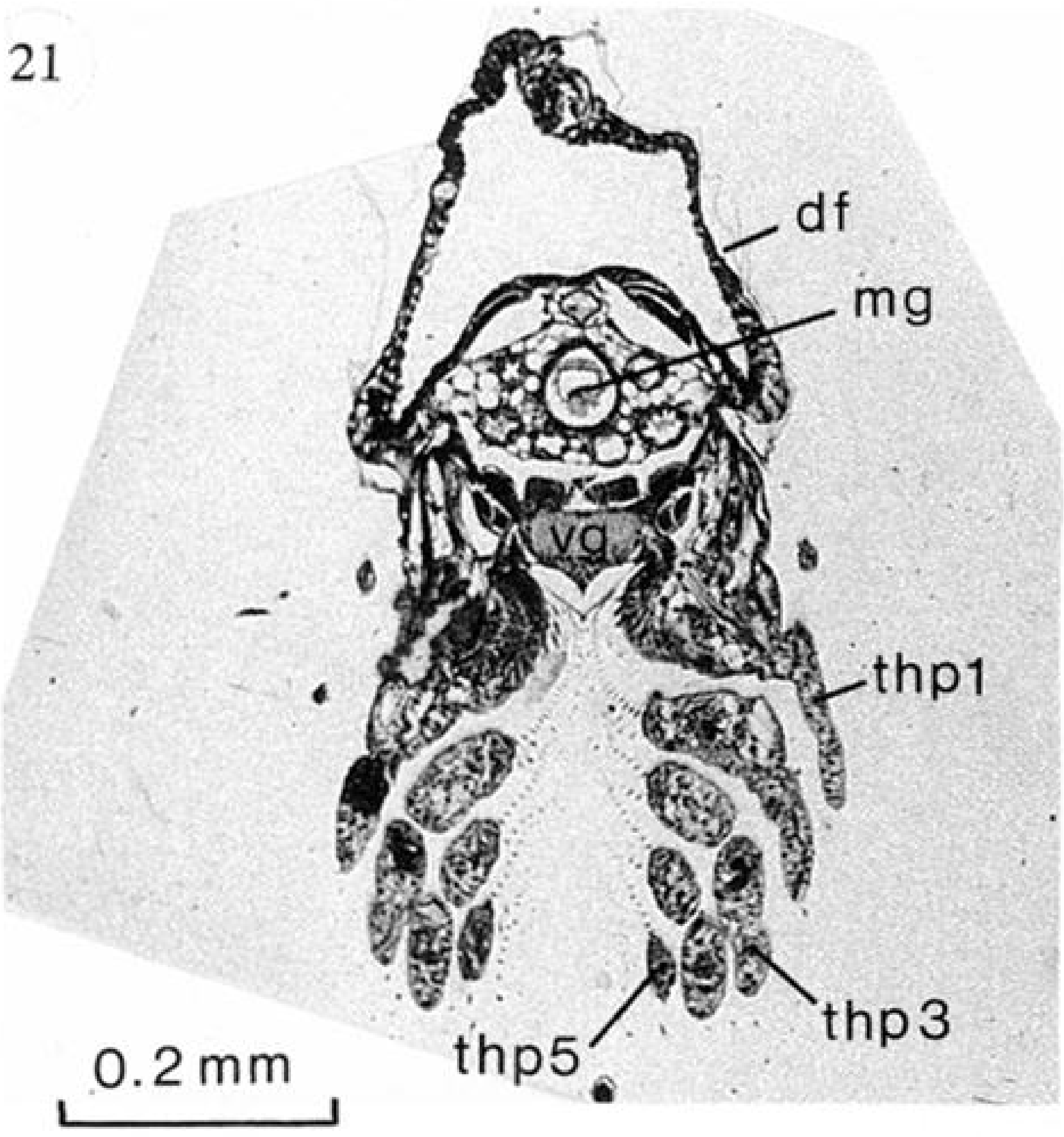
Figure 16. Same embryo as figure 12. Transverse section through posterior part of 3rd thoracic segment showing the beginning formation of a small dorsal fold.

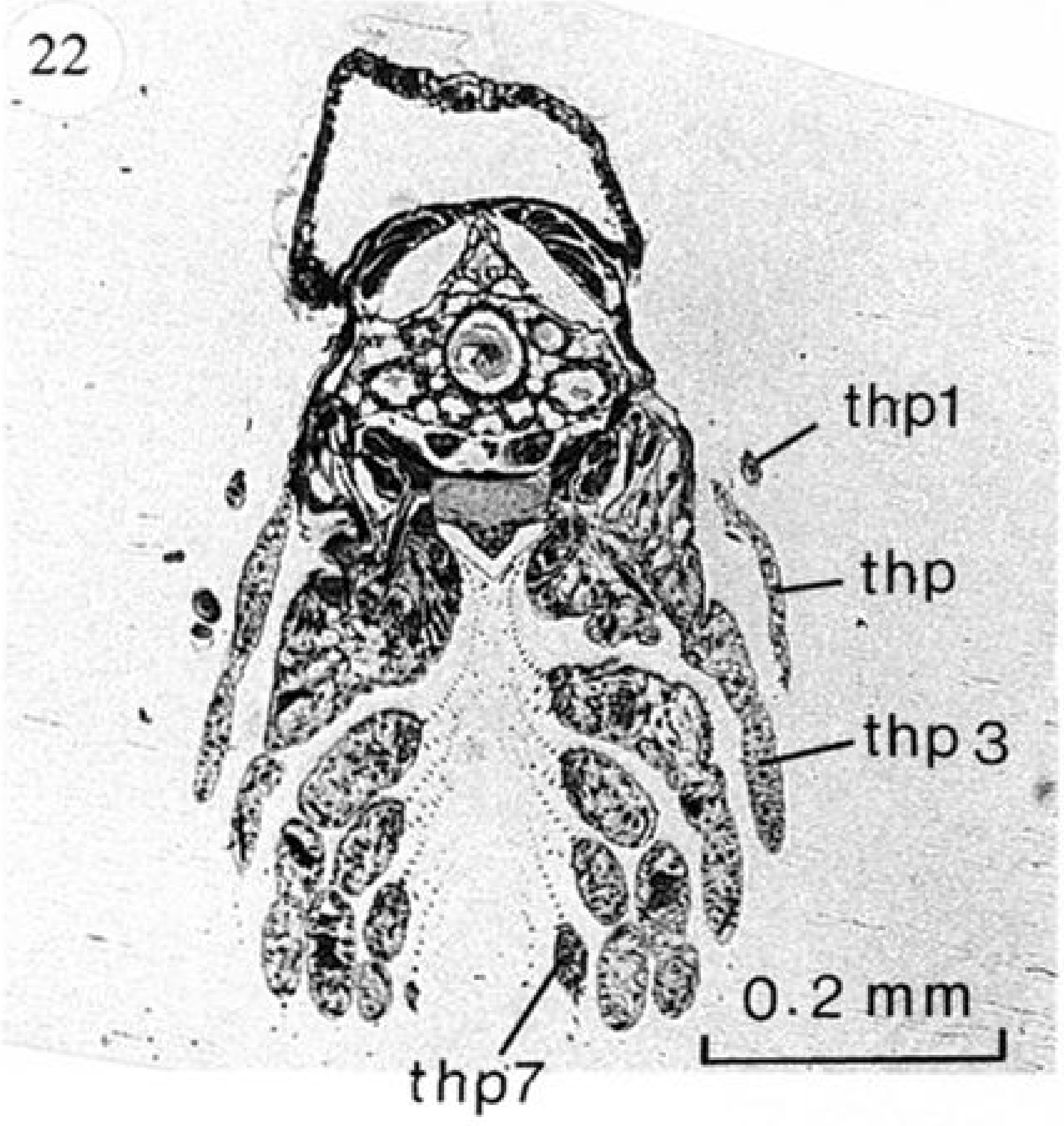
Figure 17. Same embryo as figure 12. Transverse section through the 4th thoracic segment, behind the small dorsal thoracic fold formed from the posterior part of the 3rd segment.

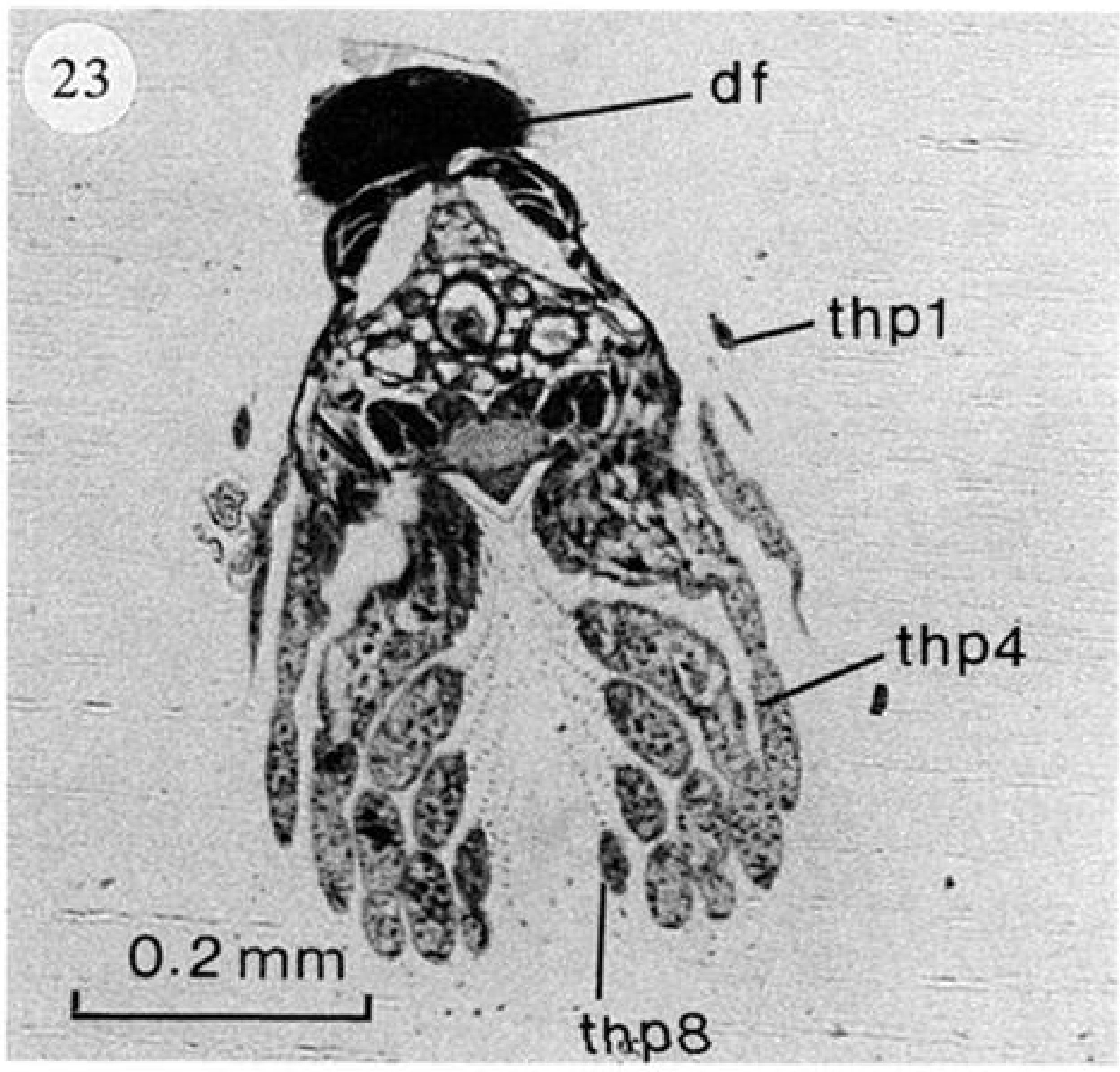
Figure 18. Transverse section through the border area between the 3rd and 4th thoracic segment of a somewhat more advanced embryo with a dorsal fold separating from the body.

Figure 19. Sagittal section through embryo of *Nebalia* sp. at approximately the same level of development as shown in figures 12–17, showing the compound eye rudiment and a group of dorsal cells forming the dorsal fold rudiment.









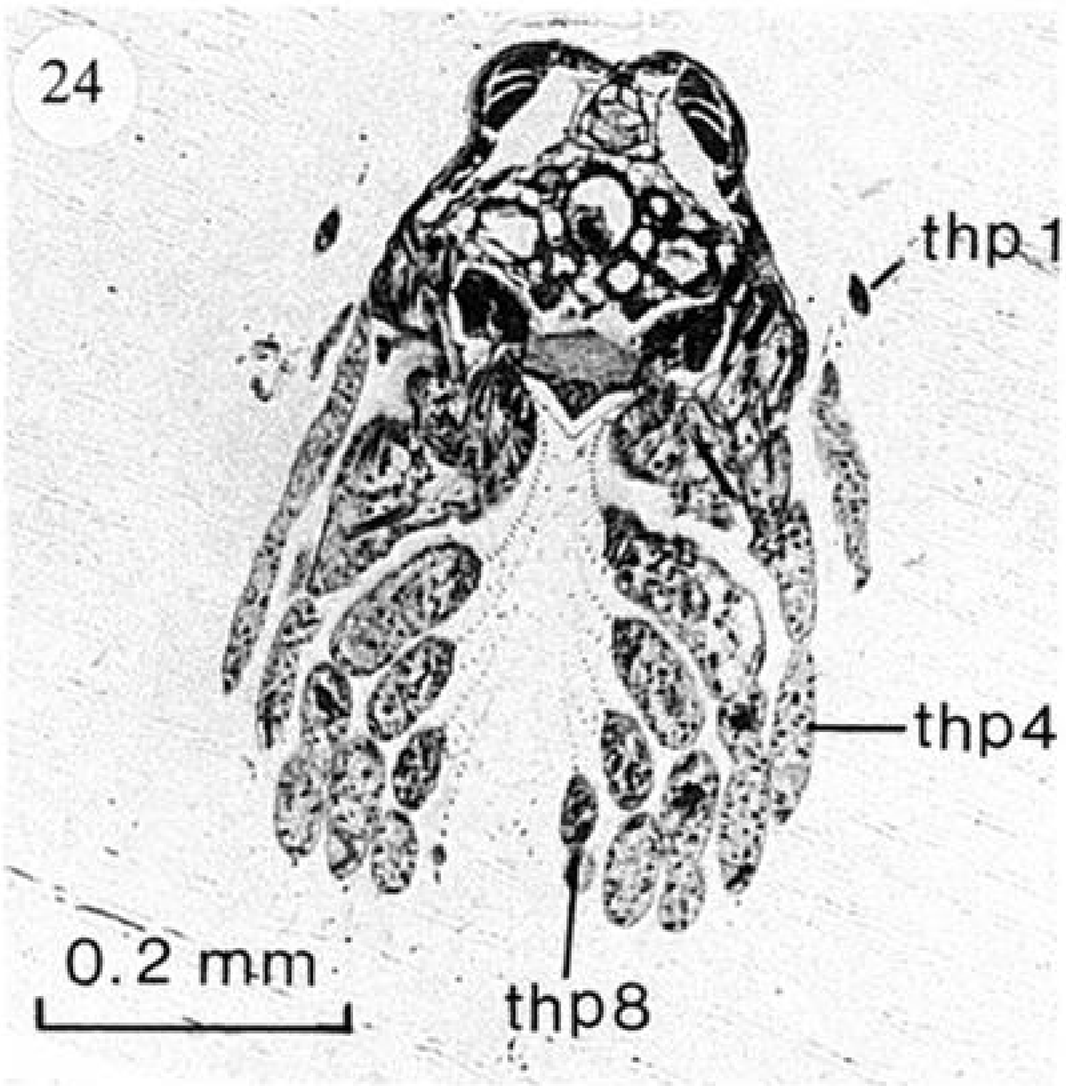


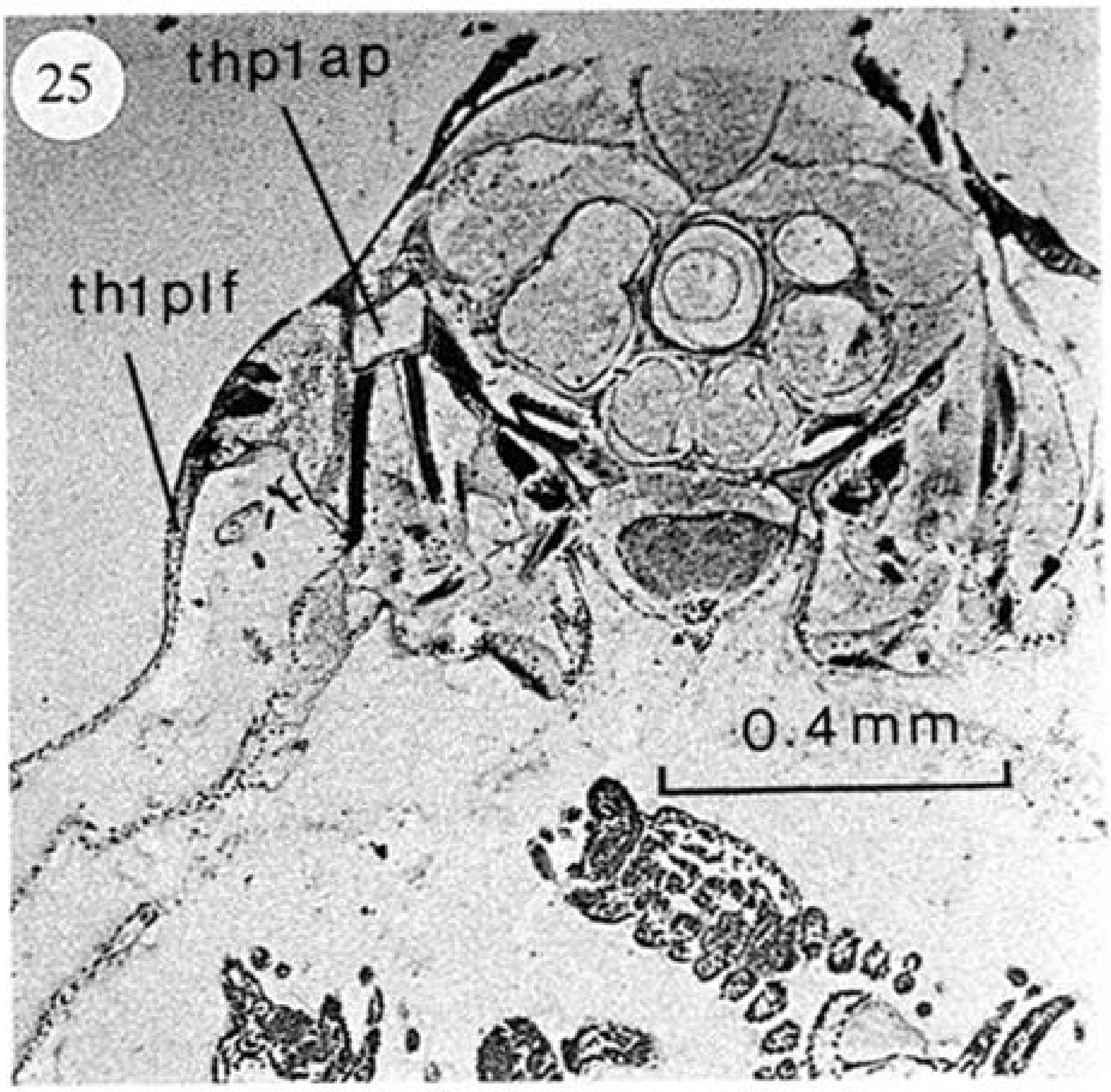
Figure 20. Juvenile of *Nebalia borealis*, total body length 1.2 mm, transverse section through maxillary segment showing distorsion of cephalothoracic shield due to the immersion in salt-water Bouin. The pleural folds have been pulled dorsad, and the cuticle of the dorsal shield and fold system has lost its attachment to the underlying tissues everywhere except along its margins (arrows).

Figure 21. Same specimen as figure 20. Transverse section through 1st thoracic segment showing broad attachment of cephalothoracic shield. thp. 1, 1st thoracopod, thp. 3 advanced rudiment of 3rd thoracopod. In upper lefthand corner a very distorted part of the dorsal fold has been cut off.

Figure 22. Same specimen as figure 20. Transverse section through 2nd thoracic segment. The oblique orientation of the thoracopods in relation to the length axis of the body result in their being visible in several subsequent sections.

Figure 23. Same specimen as in figure 20. Transverse section through 3rd thoracic segment, near posterior margin where small discoloured fold can be seen.

Figure 24. Same specimen as in figure 20. Transverse section through 4th thoracic segment behind the dorsal fold.



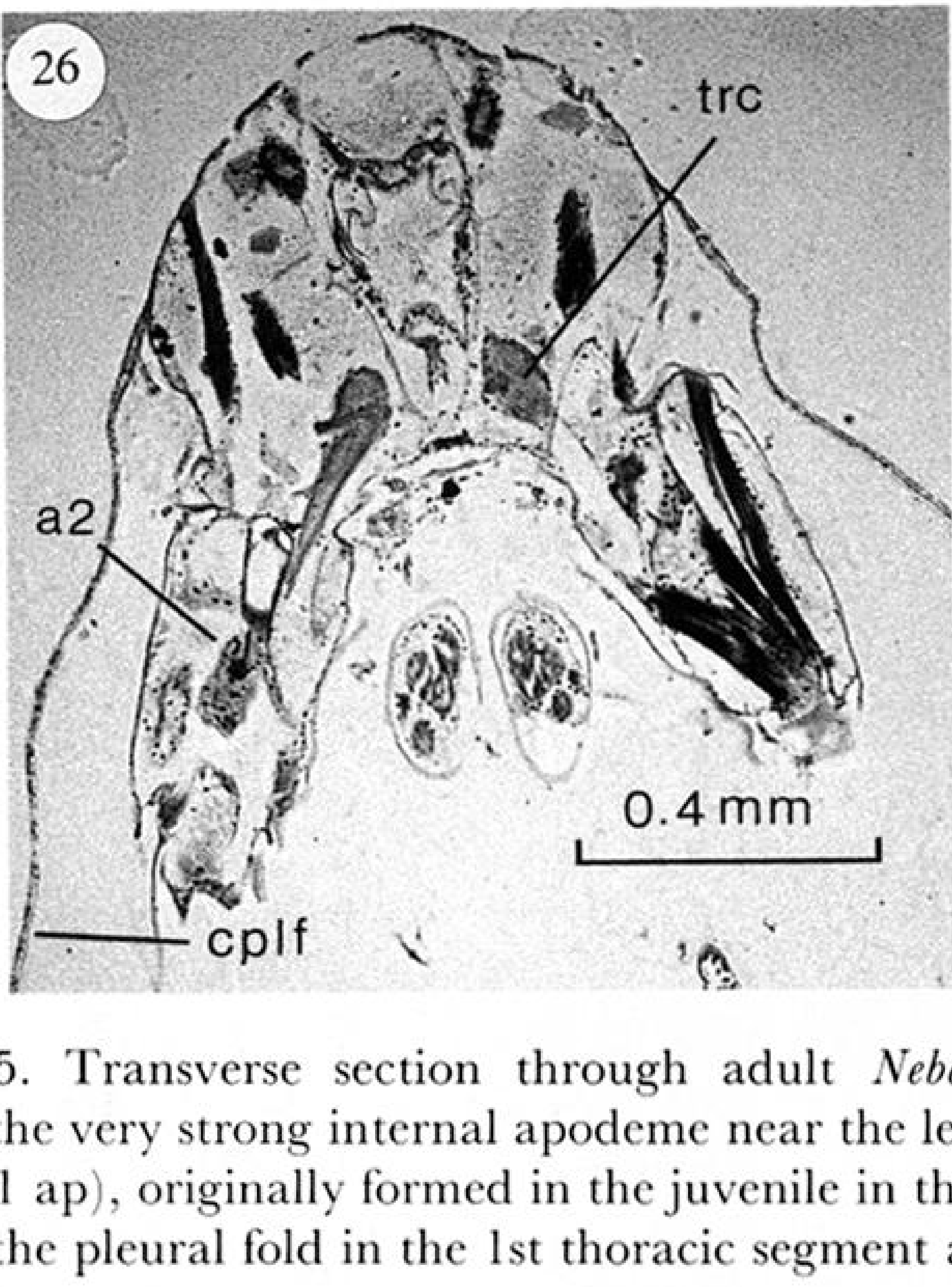


Figure 25. Transverse section through adult *Nebalia* sp. showing the very strong internal apodeme near the left body wall (thp1 ap), originally formed in the juvenile in the angle between the pleural fold in the 1st thoracic segment and the body wall.

Figure 26. Transverse section through the tritocerebral region of adult *Nebalia* sp. showing the very deep cephalic pleura.

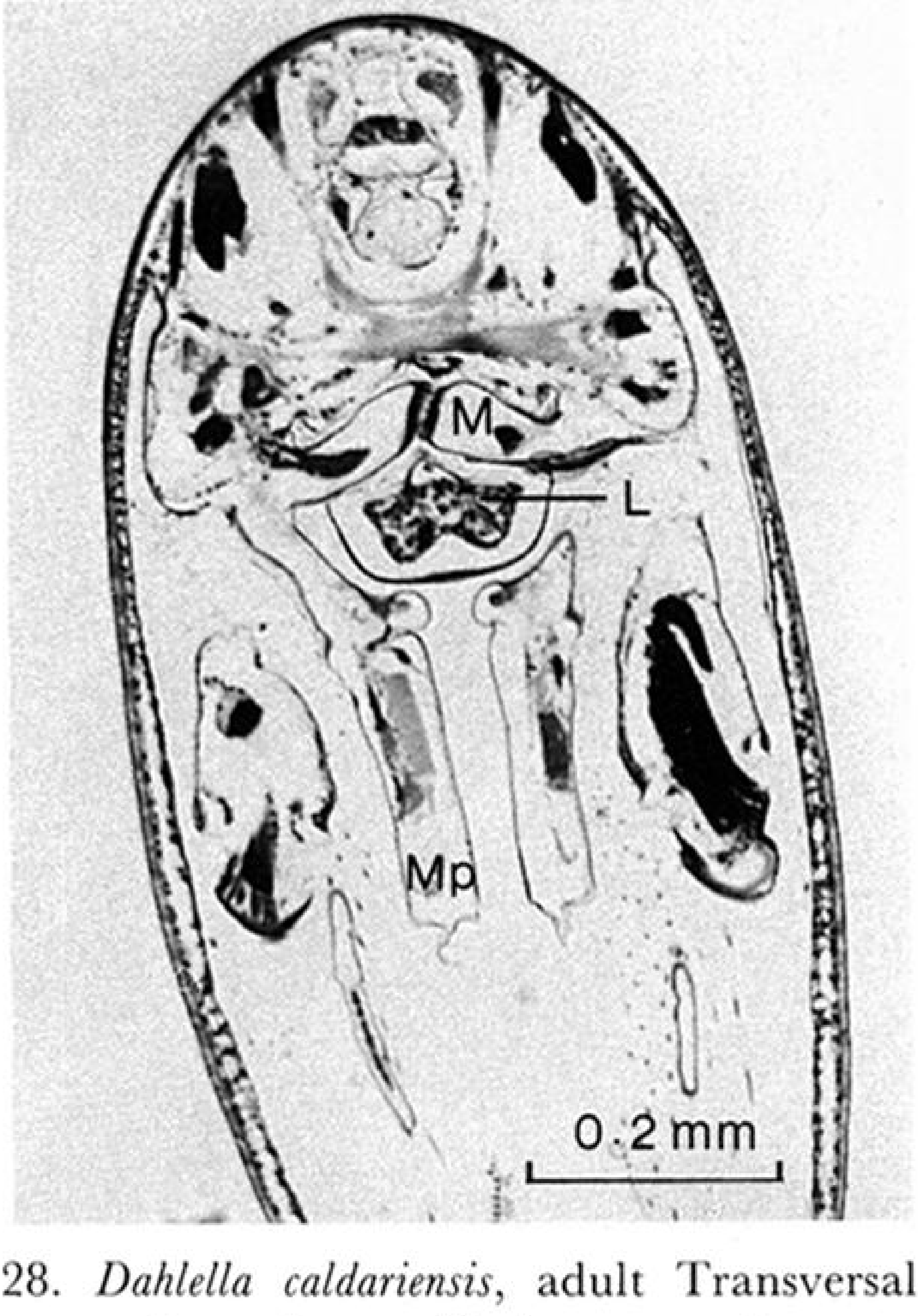
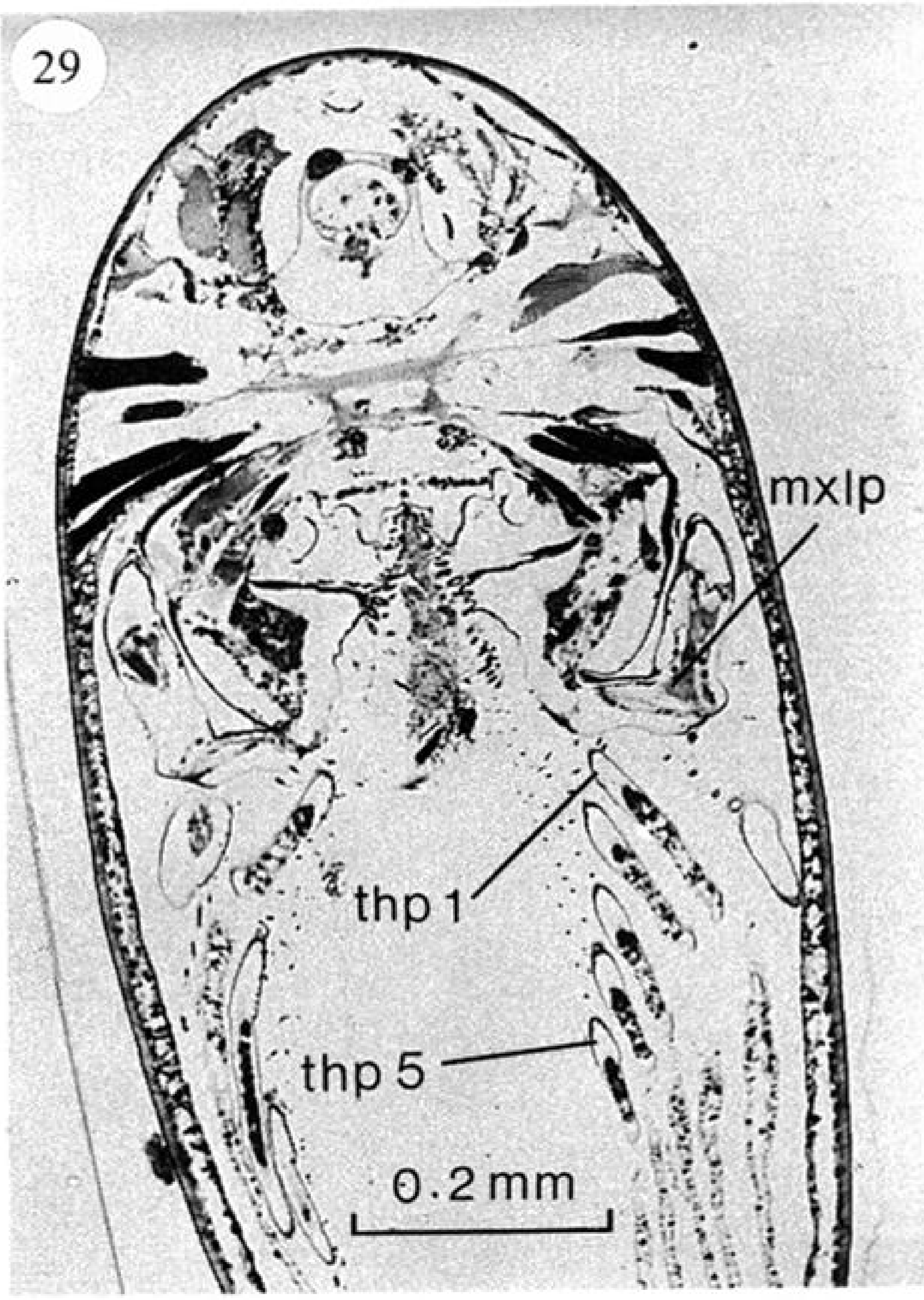


Figure 28. *Dahlella caldariensis*, adult Transversal section through mandibular segment.



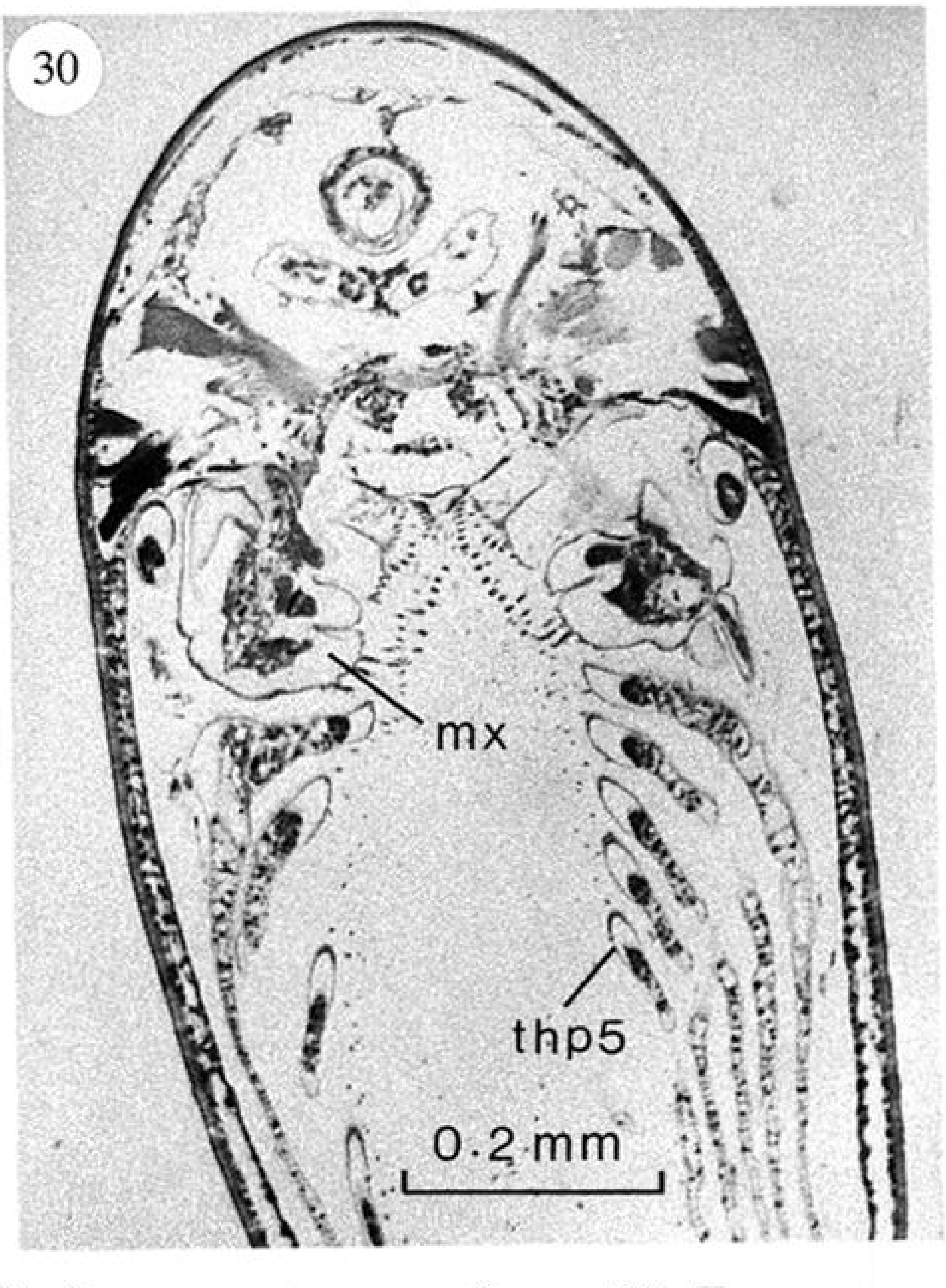
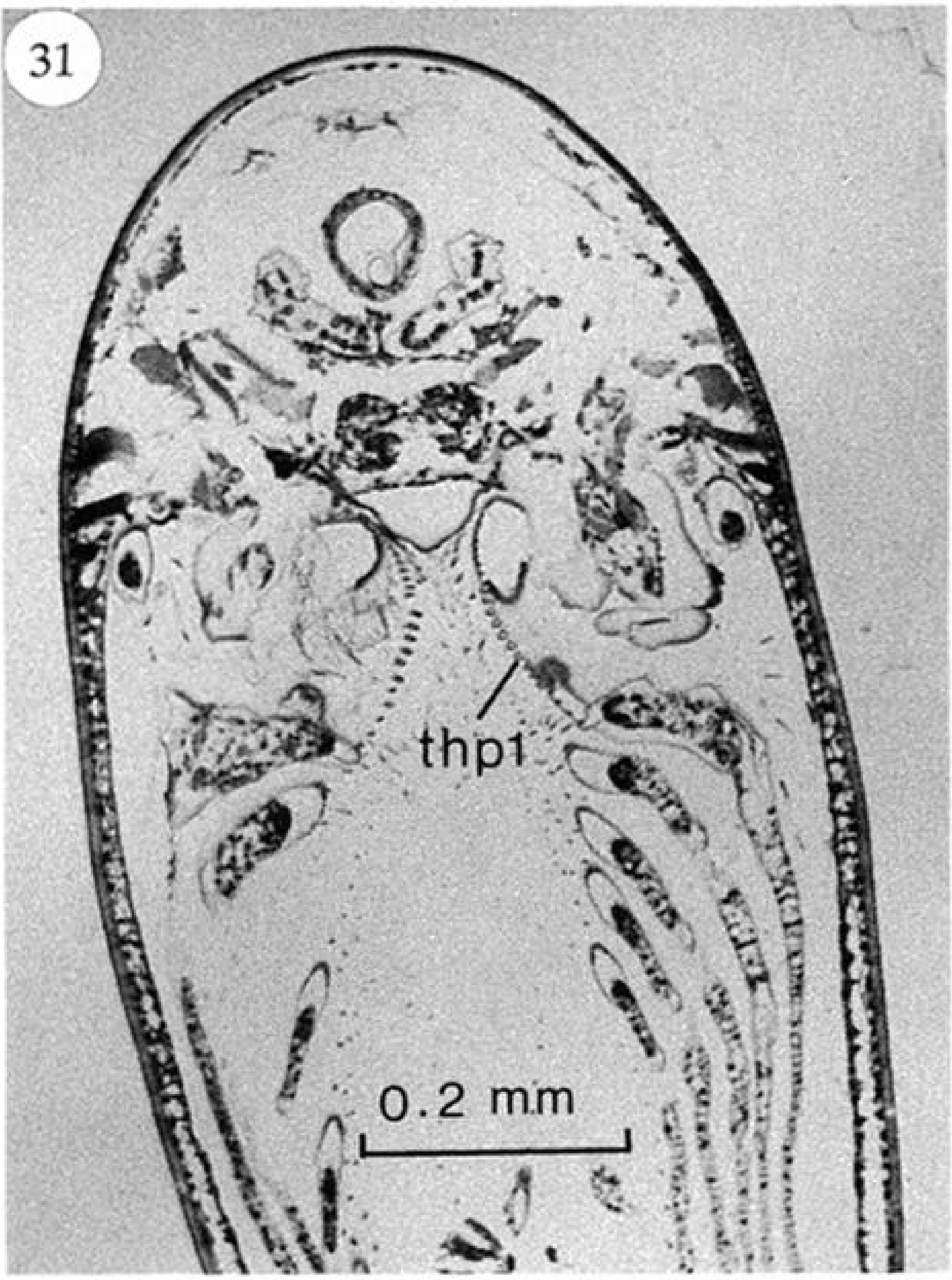


Figure 29. Same specimen as figure 28. Transverse section through maxillular segment.

Figure 30. Same specimen as in figure 28. Transverse section through 2nd maxillar segment. As a result the oblique arrangement of the thoracopods in relation to the length axis of the body, different parts of the same thoracopod may be seen in more than one transverse section.



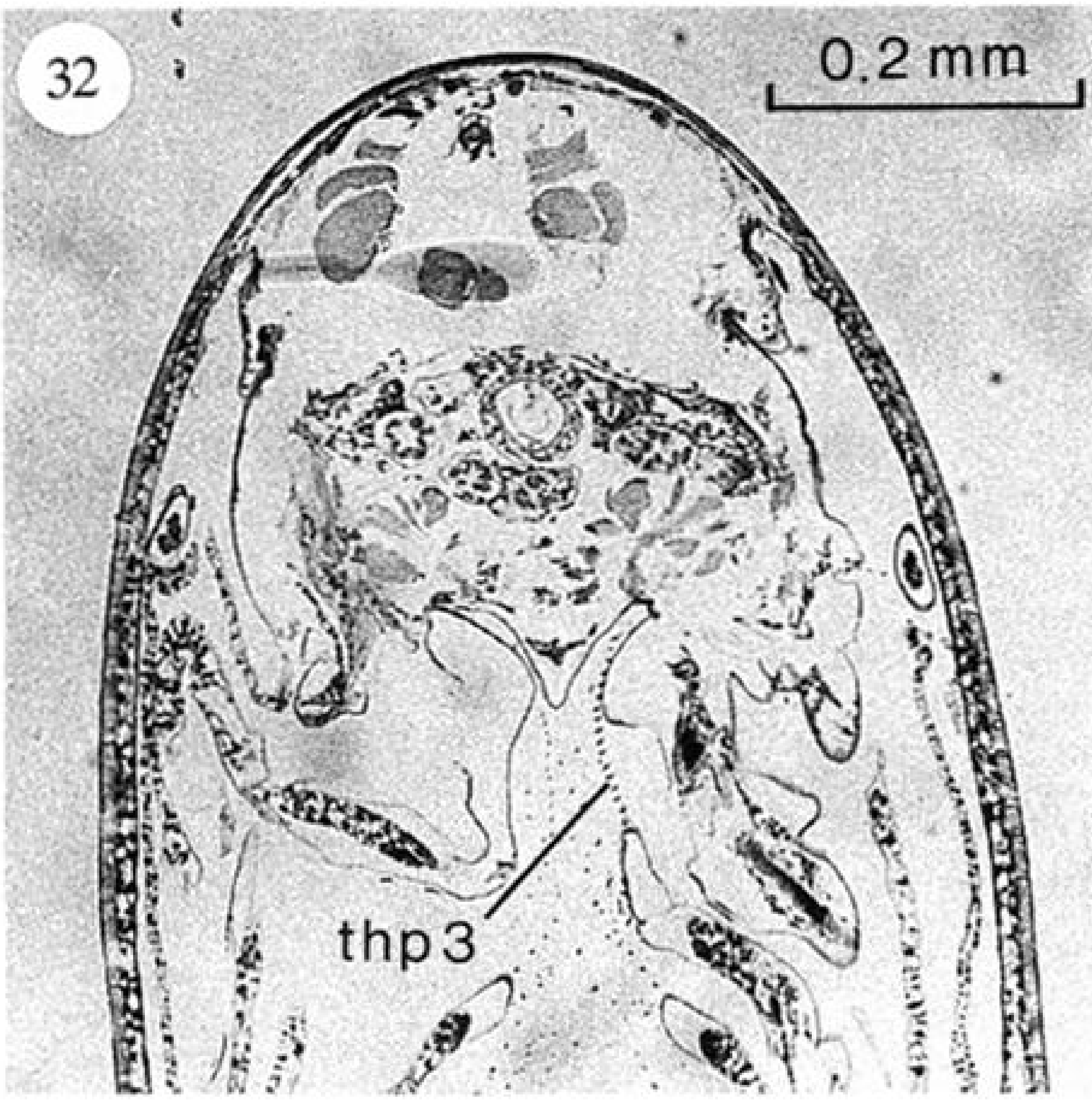


Figure 31. Same specimen as in figure 28. Transverse section through 1st thoracic segment.

Figure 32. Same specimen as in figure 28. Transverse section through 4th thoracic segment. Note the narrowing of the connection between the cephalothoracic shield and the body.

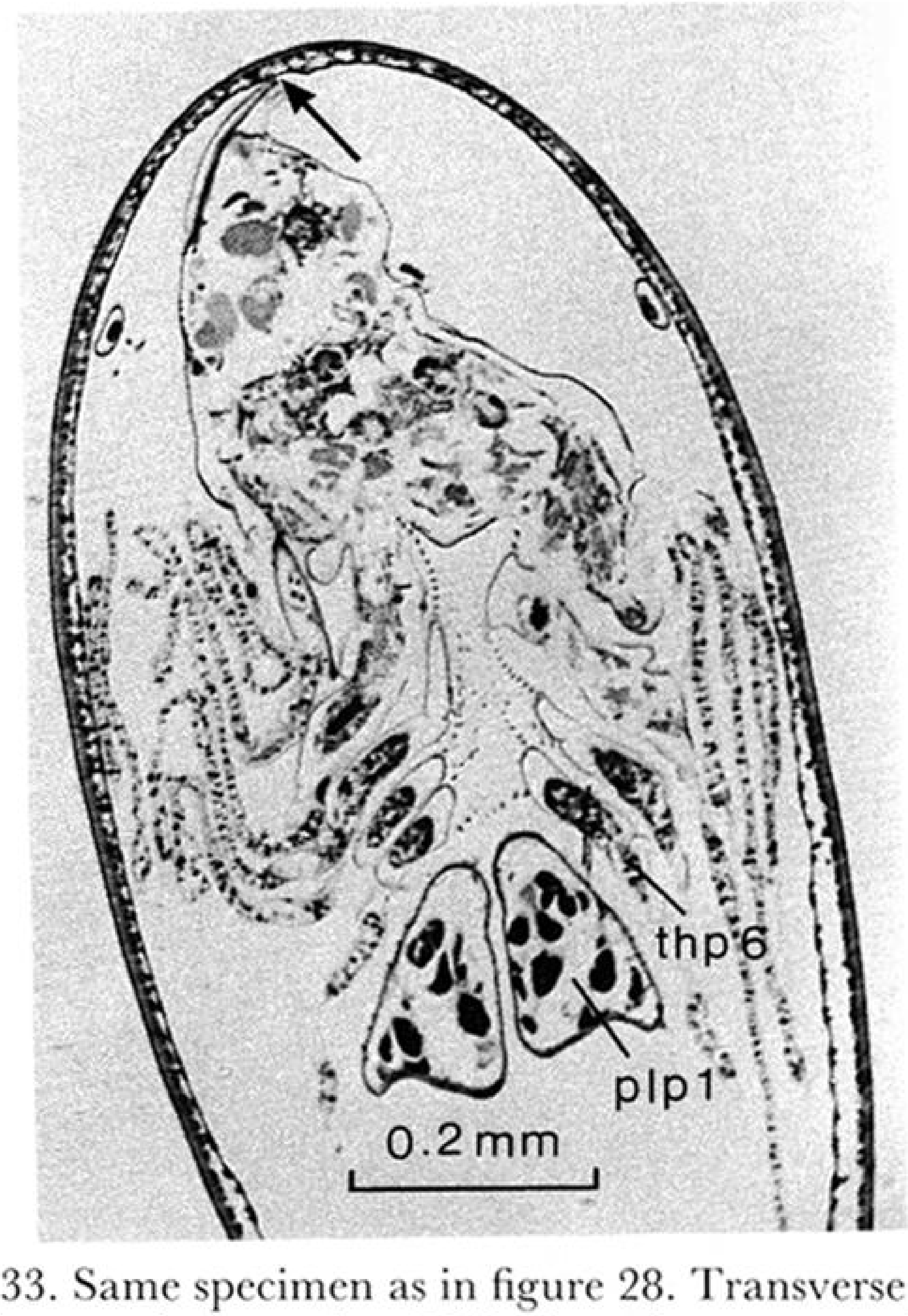


Figure 33. Same specimen as in figure 28. Transverse section through posterior margin of 5th thoracic segment, showing the separation of the cephalothoracic shield from the body (arrow).

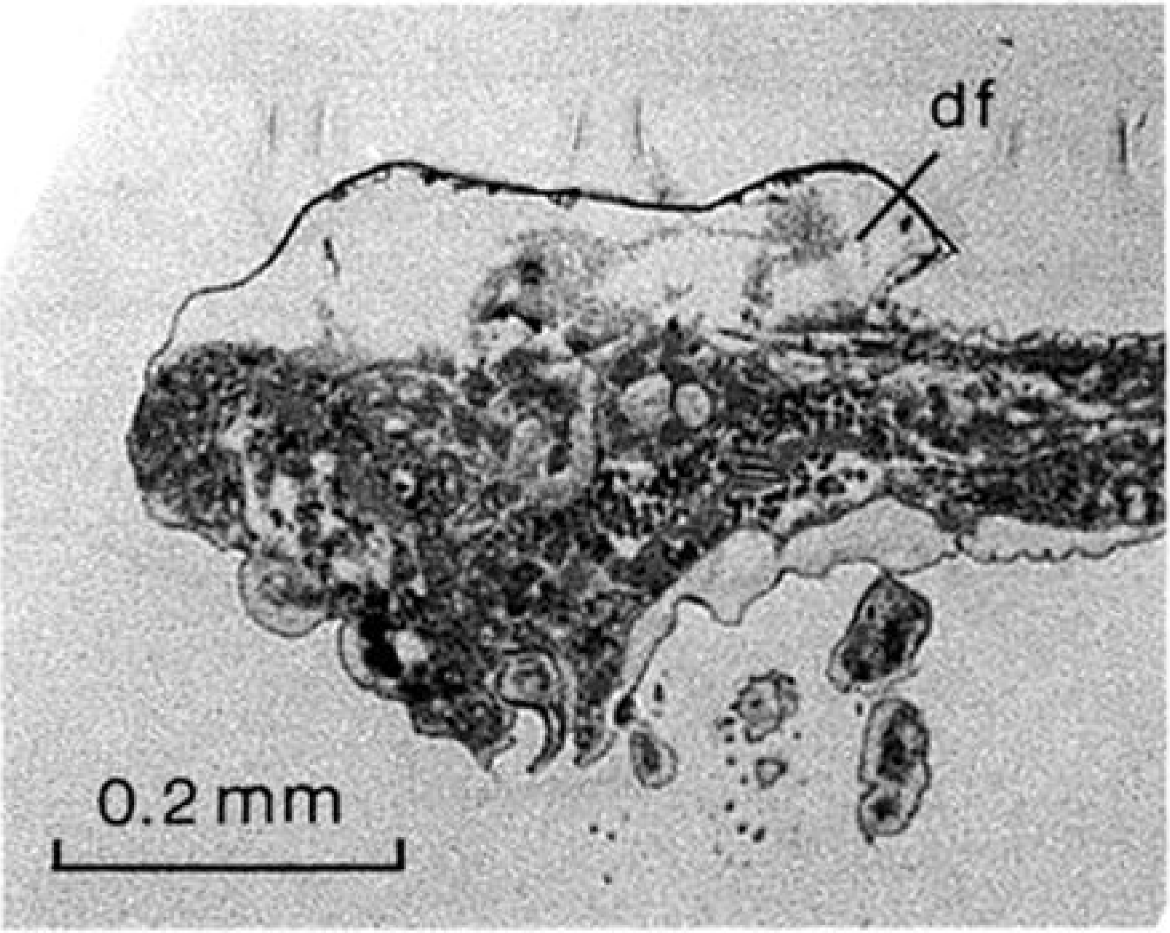


Figure 35. *Meganyctiphanes norvegica*, parasagittal section through calyptopis larva showing a small dorsal fold.

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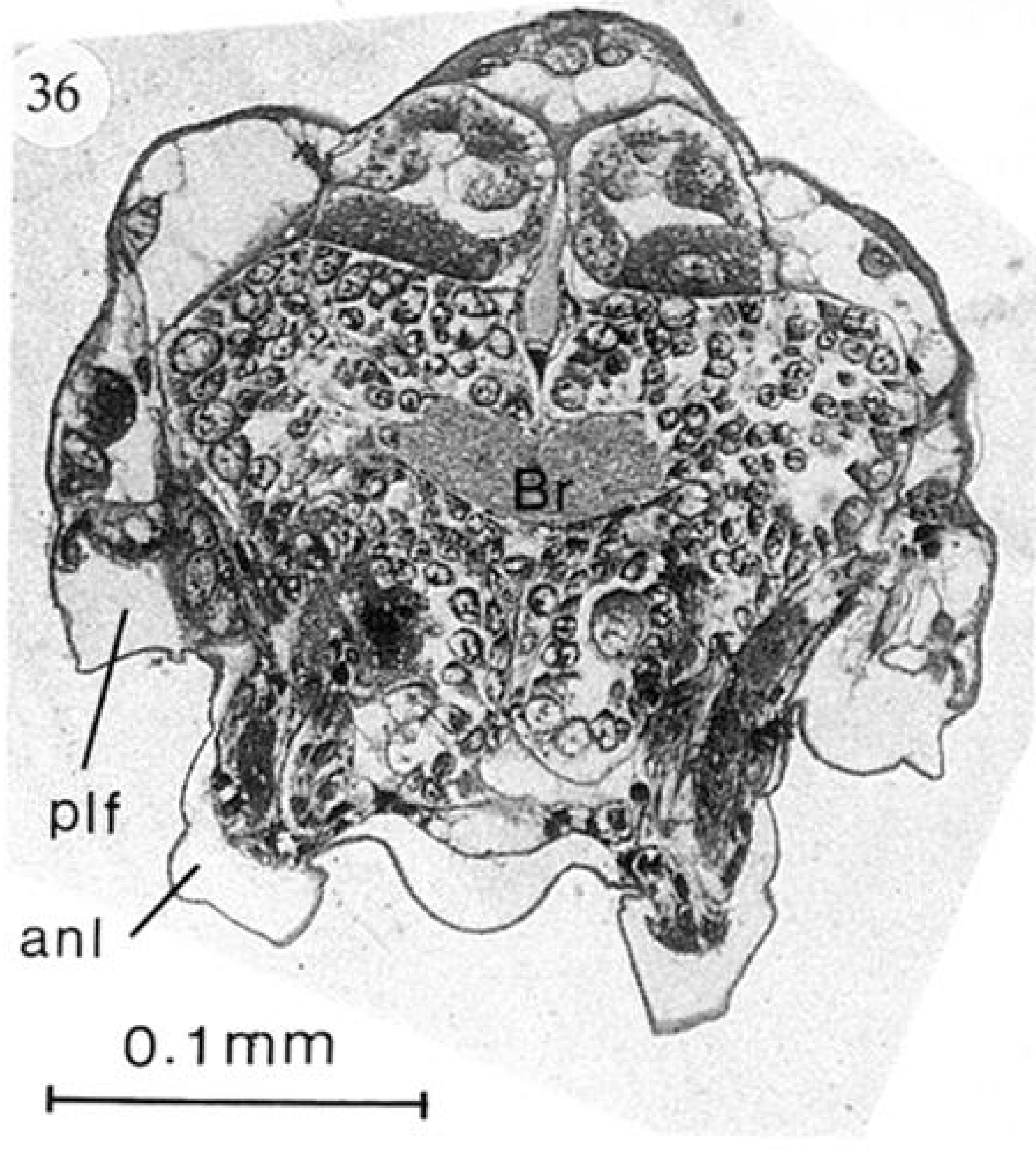

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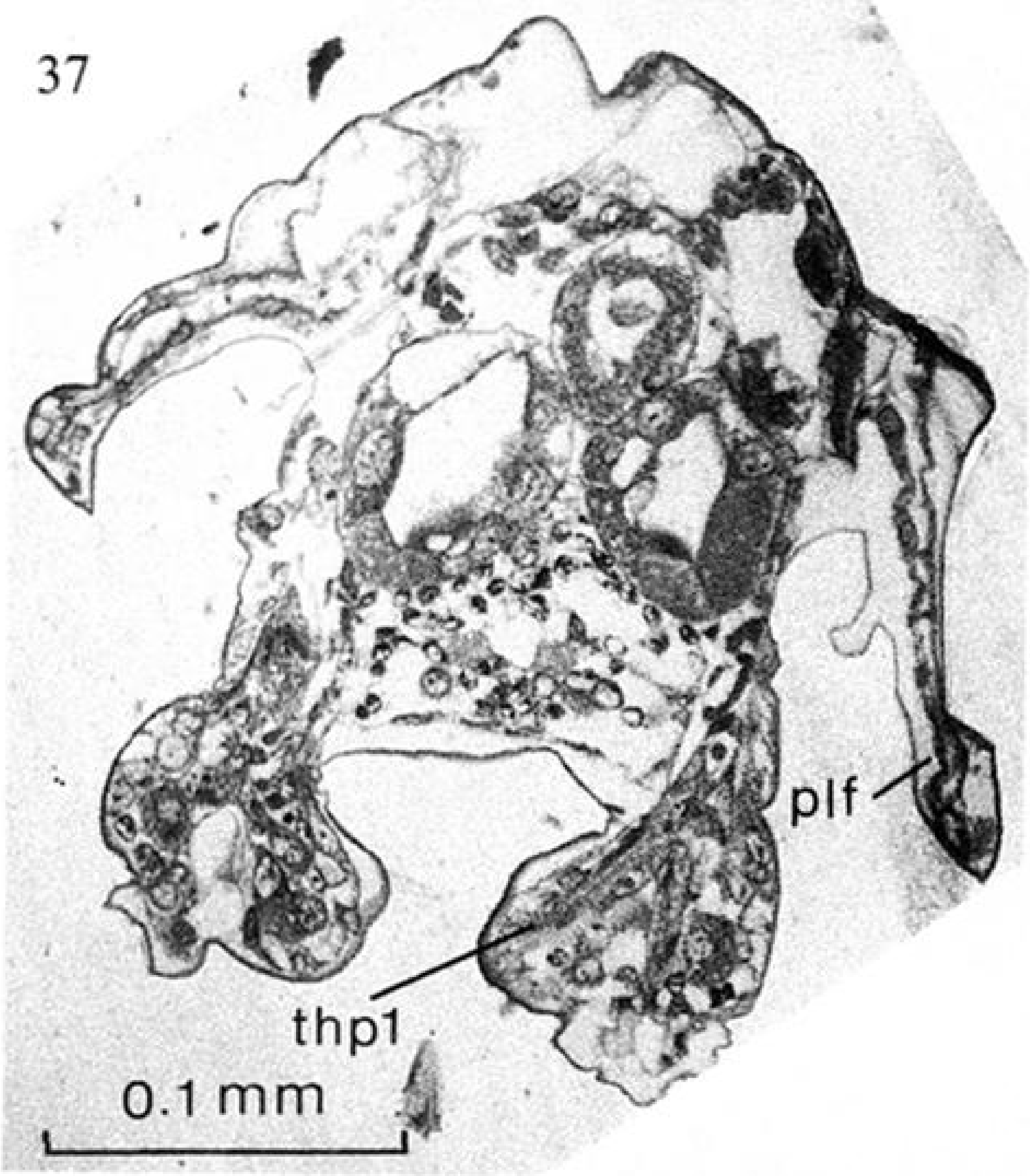

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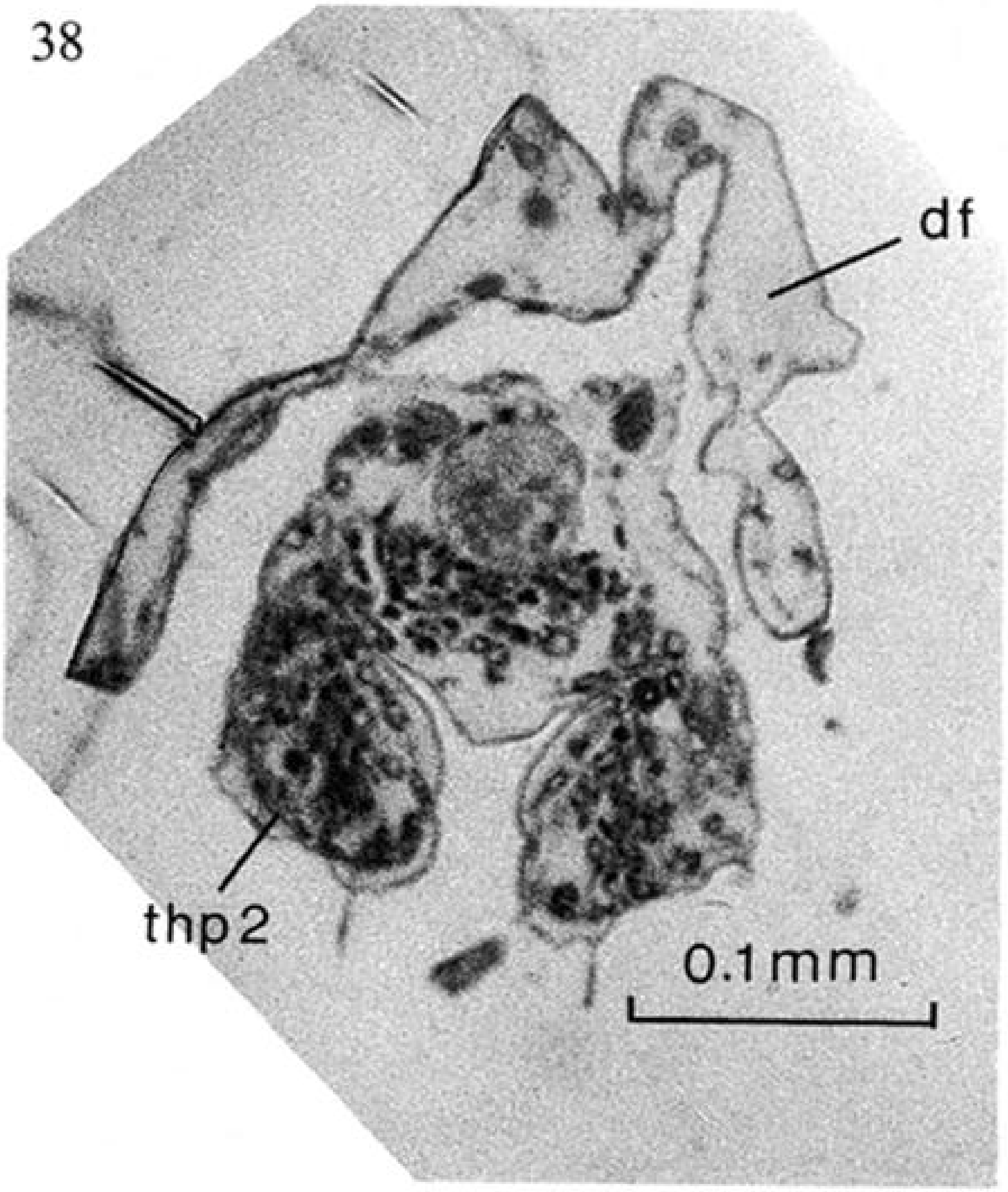

Figure 36. *M. norvegica*, transverse section through cephalon of early calyptopis larva with small cephalic pleural fold rudiments of antennule and brain.

Figure 37. Same specimen as in figure 36. Transverse section through 1st thoracic segment showing deep pleural folds and rudiments of 1st pair of thoracopods.

Figure 38. Same specimen as in figure 36. Transverse section through anterior part of 2nd thoracic segment showing a free dorsal fold and rudiments of 2nd thoracopods.

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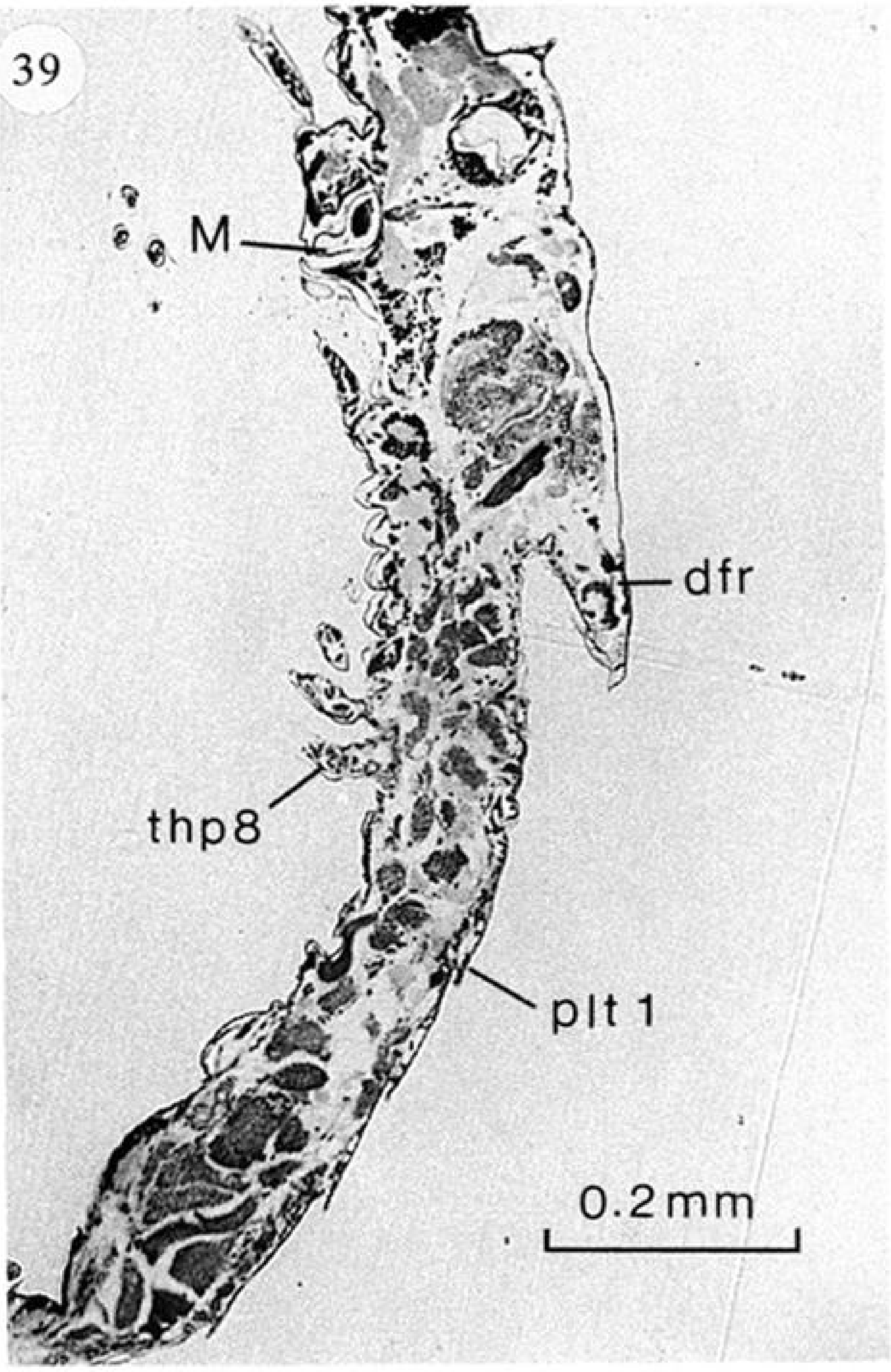

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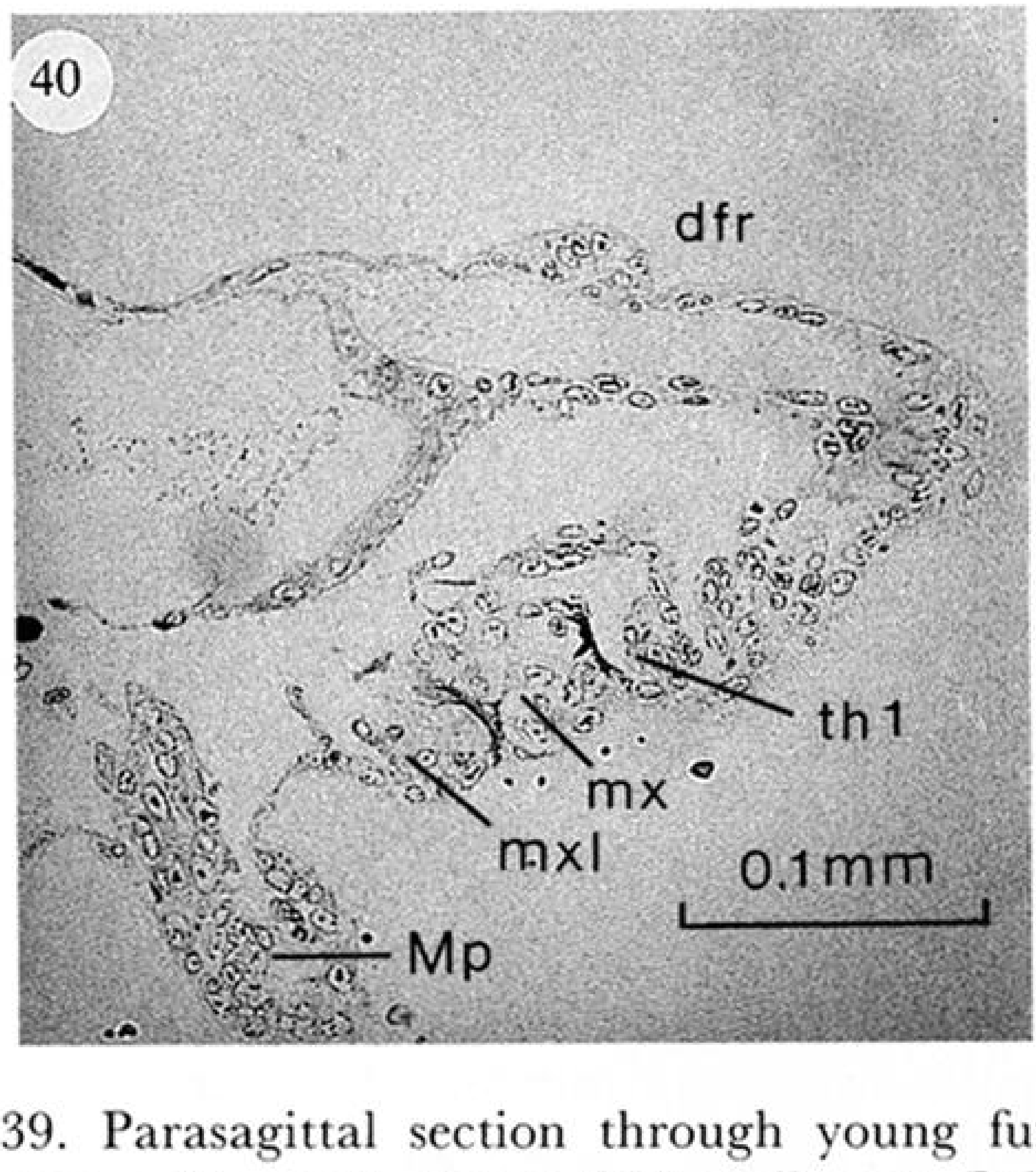

Figure 39. Parasagittal section through young furcilia of *M. norvegica* with small dorsal fold rudiment. Below and behind the fold narrow thoracic segment rudiments, further posteriad pleon with well-developed terga.

Figure 40. *Penaeus duorarum*, parasagittal section through last nauplius, 1st thoracic segment with transversal dorsal ridge of cells forming the rudiment of the dorsal fold.