ON THE ANATOMY AND RELATIONSHIPS OF RECENT MONOPLACOPHORA

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ABSTRACT

The original description of monoplacophoran anatomy, which was based on two somewhat defective specimens of *Neopilina galatheae,* has been amended and checked on the basis of two immature *Vema ewingi* and one immature *Neopilina galatheae.* Some mistakes have been corrected: The evidence for a coiled larval shell has been found to be unreliable; the "dorsal coelomic sacs" are shown to be enlarged pharyngeal diverticula; it has not been possible to verify the presence of coelomostomes from the kidneys, except perhaps in the heart region. The repetition of pedal retractors, lateropedal connectives, nephridia, and other organs has been confirmed and compared in the two species. *Vema* has a more complete set of metameric organs, including six pairs of gills, seven pairs of nephridia, and three pairs of gonoducts (although one is vestigial), but it still has eight pairs of retractors.

The liver is connected with the stomach by a single, transverse, slitlike opening. The salivary glands of *Vema* are paired like those of chitons. Other points of the original description have been confirmed, supplied with new illustrations or notes on variation.

A comparison with other molluscs has been made, and the discussion in the literature inspired by the

To the memory of my late friend
HENNING LEMCHE

descriptions of *Neopilina* in 1957 and 1959 has been reviewed, with emhasis on the phylogenetical problems. The Monoplacophora are good Conchifera, and the Conchifera are accepted as a sister group of the Polyplacophora, within the Testaria. It is concluded that the eight-metameric retractor system of the Monoplacophora is homologous with the retractor groups of the Polyplacophora; the latter overlap the valve limits. This eight-metamerism is probably a ground-plan feature of ancestral Testaria, but has clearly been reduced in most descendent lines. It is maintained that similar eight-metamerism can have been present in other organ systems of the testarian ancestor and has been reduced in most lines in the same way as has clearly been the case with the muscle metamerism.

The origin of molluscs has been reconsidered. Their derivation from advanced oligomeric Spiralia ("prot-annelids" or "proto-articulates") with dorsal heart, oligomeric coelom, nephridia, gonads and gonoducts is still a possibility, although conclusions in the strict sense cannot be made at present.

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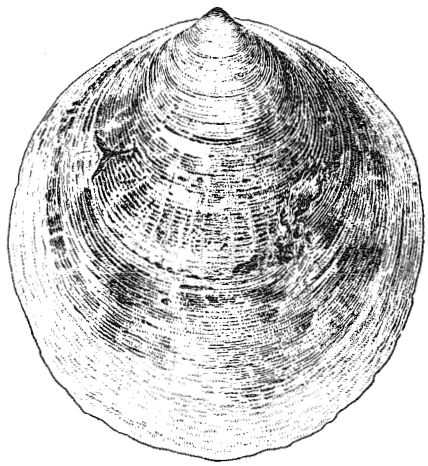

1. INTRODUCTION

After the anatomical description of *Neopilina galatheae* Lemche, 1957, had been completed (Lemche & Wingstrand 1959a, 1959b, 1960), Dr. Lemche and I received some additional material of monoplacophorans for further study. The technical work with this material, including also some reconstructions and drawings, was done in the early 1960's, but the publication of the results was unfortunately postponed several times. Not even a preliminary manuscript had been written when Dr.Lemche died in 1977. The material, including section series and reconstructions, is still in my laboratory, but most correspondance related to the material has unfortunately been lost.

Judging from numerous publications and letters the hitherto unpublished material is still of considerable interest, and I have therefore felt it as my duty to publish what I can get out of it.

I have chosen to concentrate on points where the original description was insufficient or directly wrong. I have also paid particular attention to the species *Vema ewingi* (Clarke & Menzies, 1959) which differs from *Neopilina galatheae* in the metameric repetition of organs.

Up to now very little original information has been added to the early anatomical accounts of the Monoplacophora which were published between 1957 and 1960. However, the theoretical discussion based on this same material has flourished and resulted in a large and in part confusing literature. Some themes of this discussion are summarized and commented below. Particular emphasis is given to comparisons between the Monoplacophora and Polyplacophora, because I feel that this important point has been somewhat neglected in the literature.

Acknowledgments

In addition to the new material of *Neopilina* and *Vema* provided by Dr. Robert Parker (Coastal Ecosystems Management Inc., Fort Worth, Texas), and the late Dr. Robert J. Menzies (formerly at Duke University, North Carolina), specimens of other molluscs were kindly provided by the Marine Biological Laboratory, Helsingør, Denmark, and by Drs. Jørgen Knudsen and Jean Just, Zoological Museum, University of Copenhagen.

The following colleagues have seen and critically commented on the entire manuscript or part of it: Drs. Jørgen Lützen, Arne Nørrevang and Bjarne Westergaard, Institute of Cell Biology and Anatomy (formerly the Institute of Comparative Anatomy), University of Copenhagen; and Drs. Claus Nielsen and Torben Wolff of the Zoological Museum. Dr. Mary E. Petersen, Zoological Museum, has revised the English text and provided useful criticism and suggestions. I am most grateful to all of the above for their help but take full responsibility for the final result.

To the named persons and institutions, plus several others not specifically mentioned, I express my sincere appreciation for their aid in bringing this manuscript to completion.

2. THE SPECIES OF RECENT MONOPLACOPHORA AND THEIR DISTRIBUTION

In the 27 years which have passed since Lemche's original description of *Neopilina galatheae* appeared in 1957, ten new recent species have been assigned to the class Monoplacophora (Wenz in Knight 1952) and have been included in the family Neopilinidae Knight & Yochelson, 1958. The number of recent species of Monoplacophora is thus brought up to eleven:

Neopilina galatheae Lemche, 1957
N. veleronis Menzies & Layton, 1962
N. adenensis Tebble, 1967
N. bruuni Menzies, 1968
N. oligotropha Rokop, 1972
N. zografi (Deutzenberg & Fischer, 1896)
N. (Lemchephyala) rebainsi Moskalev et al., 1983
Vema ewingi (Clarke & Menzies, 1959)
V. bacescui Menzies, 1968
V. (Laevipilina) hyalina McLean, 1979
Monoplacophorus zenkevitchi Moskalev et al., 1983

The species *zografi* was originally described as an archaeogastropod, *Acmaea zografi* Deutzenberg & Fischer, 1896, but a recent revision of the type material in the Monaco collections revealed that it was a neopilinid monoplacophoran (Bouchet, McLean & Warén, 1983). Bouchet et al. therefore transferred the species to the genus *Neopilina*. The type material of *Acmaea euglypta* Deutzenberg & Fischer, 1897, also present in the Monaco collections, was found to be conspecific with that of *A. zografi*, and the name *euglypta* is regarded a junior synonym, *zografi* being preserved by the rules of priority. This old material of monoplacophorans had been collected in the Azores area of the North Atlantic in 1888-1896 (see Fig. 1).

The distribution of the Monoplacophora appears to be worldwide (Fig. 1) although the records are still far apart. Only one species, *V. (Laevipilina) hyalina*, has been found in moderate depths (174-229 m). All other species are from greater depths, between 1800 and 6400 m.

All the finds and descriptions af recent Monoplacophora up to 1979 are carefully registered by Cesari & Guidastri (1976, 1979) to whom I refer the reader for details (in Italian, for an English text see McLean 1979). Moskalev et al. (1983) summarize all records up to 1983, including recent Russian contributions.

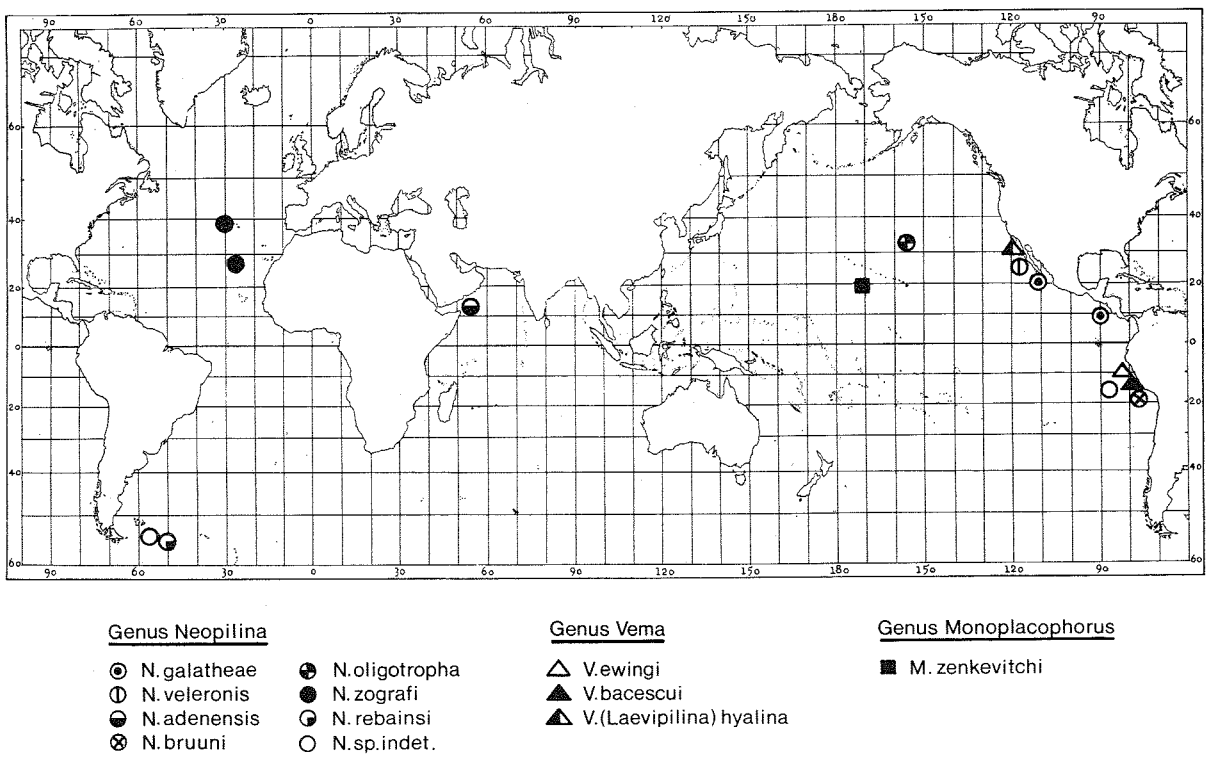

Fig. 1. Rcords of recent Monoplacophora. For details see Cesari & Guidastri 1976, 1979, Bouchet et al. 1983, and Moskalev et al. 1983.

3. MATERIAL AND METHODS

Neopilina galatheae Lemche, 1957

New Material

Specimen I. Label: VSS — 16.-22. Mar. 59. Off Cape San Lucas Canyon. Depth 1530-1535 fms. (2780-2810 m). Lat. 22° 32.5'N., Long. 109°40.8'W. R.H. Parker.

The specimen was immature, shell measuring 12×11 mm. Original fixation: 80% alcohol, 40% formalin and 100% acetic acid in the proportions 90:5:5. Stored in 90% alcohol. Decalcified in 90% alcohol with 2% hydrochloric acid for 2 days. Embedded in celloidin. 50 μm transverse sections stained in Friedländer-Ehrlich's hematoxylin.

The specimen was intact and fixation better than in other specimens seen up to now. However, hard matter in the intestine caused compression and scratching of several sections and made reconstruction of parts of the dorsal pharyngeal sacs ("dorsal coelom") somewhat difficult.

Older material

Specimens III and IV. The section series of an adult ♀ (specimen III) and one adult ♂ (specimen IV) used for the original description (Lemche & Wingstrand 1959a)[1] are still available for comparison. They are referred to as specimens III and IV as in the publication from 1959.

Specimen XIV. Remnants of a crushed and flattened specimen, recently found in the Galathea collections from 1952, are labelled *Neopilina galatheae* XIV. The intact radula ribbon of this specimen was used for scanning electron microscopy.

Vema ewingi (Clarke & Menzies, 1959).

New material

Specimen 2. Label: 7°30'S. Lat., 81°25'W. Long. 3195-3201 fms (corrected) (5911-5922 m). R/V Vema 15. Trawl 66, 6.-7. Dec. 1958.

The specimen was immature and was identical with the paratype drawn in fig. 1: A in Clarke & Menzies (1959). Size of shell 9.2×7.6 mm. Original fixation formalin. The specimen was refixed for some days in 80% alcohol, 40% formalin and 100% acetic acid (proportions 90:5:5), decalcified, sectioned (30μm) and stained as specimen 1. It was intact but for minor damage to the shell margin (Pl. 1). Histological preservation as in the original specimens of *N. galatheae* from 1952.

Specimen 3. One minute specimen. Label: Vema 17.XII.1958. South of Milne Edwards Trench. 2972-2976 fms (uncorr.) (5498-5505 m).

The minute specimen was about 1.8×1.3 mm. Original fixation was formalin. Refixed and decalcified in Bouin's solution, embedded in paraffin and sectioned transversely. The 8 μm sections were stained in Friedländer-Ehrlich's haematoxylin and eosin. The shell and dorsal parts had been crushed during capture, but the ventral parts with mouth, foot, radula apparatus, and 6 pairs of gills were almost intact.

Other molluscs

The collection of section series of the Institute of Comparative Anatomy, containing material of all major groups, was available. Dissection material of various molluscs was kindly supplied by the Zoological Museum, Copenhagen. The following species were used extensively:

Polyplacophora

Acanthopleura spiniger Sowerby. Alcohol material for dissection. Collected in the Red Sea by Th. Mortensen in 1937.

Cryptoplax sp. Alcohol material from Port Jackson, collected by Th. Mortensen in 1914.

Tonicella marmorea (Fabricius). Alcohol material from Upernavik, Greenland, collected by Ryder in 1887. For radula preparations.

Lepidopleurus asellus Spengler. Bouin's material from the Øresund, Denmark. Several section series in paraffin and celloidin. Material for dissection.

Lepidochiton cinereus (L.). Bouin's material from the Øresund. Some for dissection, some for section series in celloidin and paraffin, not all including entire animal.

Schizoplax sp. Two specimens alcohol, without locality data, both cut in continuous series in celloidin.

Gastropoda

Patella vulgata L. Formalin and alcohol-fixed material for dissection of radula apparatus and sections of the radula skeleton.

Reconstructions

All reconstructions were made on the basis of transverse continous sections. In most cases the structures and organs were projected vertically on to a horizontal plane in which each section was represented by a transverse line. The nerve cords, the rectum, parts of the pallial margin and foot margin served as reference lines from which measurements were taken. The general course of these reference lines was checked by comparing the reconstruction with photographs taken of the entire specimens, enlarged to the magnification of the reconstructions.

Reconstructions in which the animal is seen from the side and the structures are projected on to a sagittal plane are probably less precise, for the reference lines, mainly the ventral body surface, are not as easy to check critically. Some distortion of the reconstruction is therefore difficult to avoid.

The graphic reconstructions were used directly for illustrations in the present paper after some jagged lines had been smoothed and some shading had been added to facilitate understanding. Thus, if nothing else is said in the legends, the relative positions, shape and dimensions of the organs are as in the raw reconstructions.

Diagrams, i.e., simplified figures intending to illustrate structural principles and patterns at the cost of exactness in dimensions and form, involve a certain amount of interpretation. I have kept the number of such diagrams to a minimum in the present account in order to avoid discussions of the kind caused by the diagrams of the previous report (see p. 51). The legends of each figure in the present account indicate whether the figure is a direct graphic reconstruction or if simplifications or other didactic changes have been introduced, and if parts have been moved in order to visualize other organs or structures.

1. Lemche & Wingstrand 1959a/1959b/1960 is in the following abbreviated L. & W. 1959a/1959b/1960.

4. DESCRIPTIONS

4.1. The shell

The structure of the adult shell of *Neopilina galatheae* was described in detail by Lemche (1957) and L. & W. (1959a, 1960). Subsequent reports of this and other species of recent Monoplacophora have revealed some variation of the shell with regard to size, shape and surface sculpture, but in all cases the basic structure of the shell was found to be as in *Neopilina galatheae.* The most significant variation found seems to be the total absence or surface sculpture in the minute species *Vema (Laevipilina) hyalina.*

Information on shell structure can be found in the following publications:

Lemche (1957), L. & W. (1959a, 1959b, 1960) — On *Neopilina galatheae.*
Clarke & Menzies (1959) — On *Vema ewingi.*
Menzies & Robinson (1961) — On *Neopilina* sp.
Menzies & Layton (1962) — On *Neopilina veleronis.*
Menzies (1963) — On *Neopilina* sp.
Tebble (1967) — On *Neopilina adenensis.*
Menzies (1968) — On *Neopilina bruuni, Vema bacescui,* and *Vema ewingi.*
Filatova & al. (1968, 1969a, 1969b) — Species undetermined, see Moskalev et al., 1983.
Rosewater (1970) — On *Neopilina veleronis?*
Rokop (1972) — On *Neopilina oligotropha.*
Filatova & al. (1974, 1975) — On *Neopilina,* see Moskalev et al. 1983.
Lowenstam (1977, 1978), McLean (1976, 1979) — On *Vema (Laevipilina) hyalina.*
Bouchet et al. (1983) — On *Neopilina zografi.*
Moskalev et al. (1983) — On several species, including *Monoplacophorus zenkevitchi, Vema ewingi* and *Neopilina rebainski.*

The finer structure and histochemistry of the shell of recent Monoplacophora is now well known thanks to work of Schmidt (1959), Watabe et al. (1966), Erben et al. (1968), Meenakshi et al. (1970), and Poulicek & Jeuniaux (1981).

I have nothing to add to these descriptions of adult monoplacophoran shells but feel it is my duty to make some comments on the much-discussed larval shell or protoconch.

The larval shell

According to the original descriptions of *Neopilina galatheae,* the dextrally coiled larval shell lies flat on the apex with the aperture backwards (Lemche 1957, L. & W. 1959a, 1960). The figures indicate a diameter of about 0.1 mm. The coiling and the widely divergent axes of the larval shell and the adult shell forced us to assume that the larval shell had been tipped at metamorphosis as in some gastropods, and that the larva — if there is one — is asymmetrical. All this fits very poorly with the pronounced bilateral symmetry of the adult, in which the coiling of the intestine is the only distinct asymmetry.

A coiled larval shell was only reported from one specimen of *N. galatheae* and was supposed to have been lost in the other specimens. These had instead a somewhat convex apical shield with an oval to circular outline covering the apex (L. & W. 1959a, fig. 35). Such a smooth apical shield without coiling was present in all subsequently examined specimens of this and other species. It was particularly intriguing that small species such as *Neopilina veleronis, N. oligotropha,* and *Vema (Laevipilina) hyalina,* show no trace of a coiled protoconch, and that small juvenile animals like the minute specimen 3 of the present report (1.8×1.3 mm) only had a simple convex apical shield. It is therefore understandable that doubts have arisen about the existence of such a coiled larval shell, and I must admit that I soon shared these doubts.

The matter seemed to be decided when Menzies (1963, 1968) reported on a minute specimen of *Neopilina* sp. with a bulbous, uncoiled protoconch attached to the apex (Menzies 1968, fig. 2A). Menzies assumed that the apical shield of larger specimens is the protoconch scar which has healed up in some way when the protoconch is lost in early postlarval stages.

Already before learning of Menzies' discovery I critically examined the evidence for the presence of a coiled larval shell. According to Lemche (1972), Professor Gunnar Thorson was the one who originally discovered the coiled protoconch in a specimen of *Neopilina galatheae* in 1956, but when asked in the late 1960's Dr. Thorson had forgotten all about it.

In 1956 Lemche made a drawing of the presumed larval shell which he believed to be coiled, and this drawing was used for fig. 34 in L. & W. (1959a). I never saw this original specimen. It could not be refound later and we therefore believed that the protoconch had been destroyed together with specimen II, which fared badly in an attempt at decalcification.

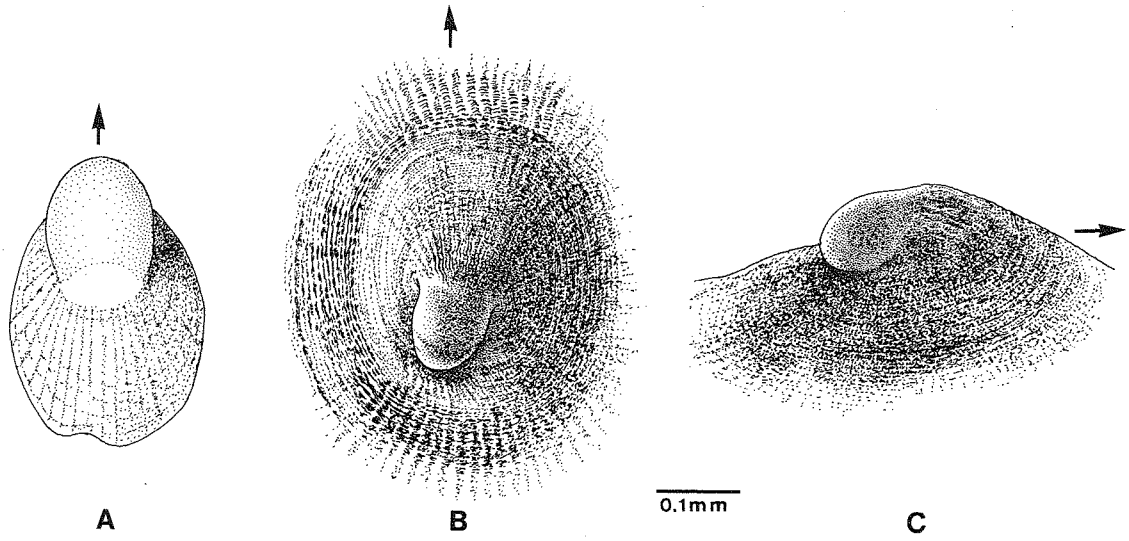

Fig. 2. A, symmetrical protoconch on the apex of minute mollusc, probably a newly metamorphosed *Neopilina*. Drawn after two photographs taken by W. Layton in Menzies (1968, pl. IV). B and C, protoconch on apex of 1.4 mm specimen of Patellid sp. from Thailand, coll. J. Just. Drawn after SEM pictures. Anterior direction marked by arrows. Magnification of Fig. A somewhat uncertain.

When searching for the original coiled protoconch we found a similar structure in specimen IV, which had been successfully decalcified and embedded in celloidin. The apex of this specimen was photographed and was used for fig. 49 in our monograph (1959a). The figure shows a spiral pattern on the apex, of similar dimensions as in the drawing, but it was realized that the picture was a poor piece of evidence. It did not show the third dimension and differed in details from the drawing. Several years later the small celloidin block with the apex of specimen IV was cut into sections and it could be seen that no three-dimensional coiled protoconch was present, only a spiral pattern caused by irregularities in staining of the periostracum. Specimen IV and the fig. 49 of the original account are therefore no evidence of a coiled larval shell.

The only piece of evidence remaining is therefore Dr. Lemche's drawing from 1956, which was reproduced several times (Lemche 1957, L. & W. 1959a, 1960). The drawing was made with a common dissection microscope, in which it may be difficult to see the third dimension in an object measuring about 0.1 mm. Dr. Lemche was a very able observer, but it can certainly not be excluded that he may have drawn a two-dimensional colour pattern like that photographed in specimen IV and believed it to be a protoconch. No control was possible afterwards, for the specimen could not be refound. I therefore suggest that all evidence in favour of a coiled larval shell is rejected. This is the only reasonable possibility after Menzies' description of the true, symmetrical larval shell in *Neopilina*.

The appearance of the apical shield in the new specimens of *Neopilina* and *Vema* was very much as described previously by L. & W. (1959a, fig. 35), Clarke & Menzies (1959) and Menzies (1968, fig 8C and D). Is is slightly convex, almost circular, and is delimited from the surrounding adult shell by the innermost (first) concentric ridges of the periostracum. These inner ridges are very low and less distinct. They mark a transitional zone in the underlying mineralized shell.

The microscopic structure was only well preserved in specimen 1 *(N. galatheae),* which had been cut in a suitable plane (Pl. 2). The apical shield differs from the surrounding shell in the absence of the prismatic layer. This begins to appear in the transitional zone and increases in thickness peripherally. The inner prisms near the margin of the apical shield are so low that they are hard to distinguish.

The shield proper thus consists of two layers only, an outer pigmented "periostracum" and an inner thick layer which has been mineralized in the intact specimen. The periostracum is thick and uneven on the surface of the shield, but suddenly becomes more even and thinner in the transitional zone along its margin.

The inner, mineralized zone of the shield differs from the nacreous layer in having a distinct radial striation in addition to tangential lamellae, which are directly continuous with the lamellae in the

nacreous layer in the surrounding adult shell. There is no obvious break or discontinuity in these lamellae when passing the transitional zone from the apical shield into the adult shell. Also the periostracum is continuous in the transitional region, but it is markedly thicker and more uneven within the shield proper (Pl. 2).

Comments. The available facts strongly indicate that the original description of a coiled larval shell was a mistake. No real evidence is left to support it, and I suggest that it should be completely forgotten. Menzies' description of a symmetrical bulbous larval shell in a minute specimen of *Neopilina* sp. appears convincing and so is his suggestion that this shell is shed in postmetamorphic specimens (Menzies 1963, 1968). The scar would then be closed by a regenerated wall, that forms the "apical shield" seen on the top of the apex of larger specimens. The appearance of the shield in sections is not incompatible with this interpretation, for its mineralized wall has a structure of its own, although continuous with the nacreous layer in the periphery. The continuity of the periostracum over the scar seems to speak against the theory for this would require contact with the epidermis when the new periostracum is regenerated. The dilemma is solved if it is supposed that the animal retracts from the larval shell prior to shedding of the protoconch and secretes a new periostracum as in *Patella* (Smith 1935, fig. 29b).

The remarkable similarity between protoconch of the supposed postalarval *Neopilina* and the bulbous protoconch of *Patella* should be noticed. The latter is of course asymmetrical and secondarily "endogastric" because of torsion (Figs. 2B and C).

4.2 The musculature of the body

In the description of *Vema ewingi,* Clark & Menzies (1959) report that this species has 6 pairs of gills (Pl. 1) in contrast to *Neopilina galatheae,* which has 5 pairs. A comparison of the two species with regard to metameric repetition of internal structures is therefore appropriate.

For such comparison I have at my disposal two specimens of *V. ewingi:* the almost full-grown specimen 2 and the minute and badly damaged specimen 3 (p. 12). In the former the pedal retractor system and the body muscles in general could be reliably reconstructed in most details. In the latter only a general check of pedal retractors and gills was possible, because the dorsal parts of the body were damaged.

For comparison with *N. galatheae* the old reconstructions of the large specimens III and IV were used (see L. & W. 1959a, fig. 121), but I also reconstructed the musculature of the immature specimen 1, partly because I wanted to check the old reconstruction, partly to check individual variation.

Both *N. galatheae* and *V. ewingi* have 8 pairs of pedal retractor muscles, which look similar in the two species (Figs 3, 4, 5 and 6). Each individual retractor originates in a single attachment area on the shell and consists of two portions with different fiber directions: 1) musculus mediopedalis, which passes dorsal to the pedal nerve cord and ramifies in the center of the foot, and 2) musculus lateropedalis which passes lateral to the pedal nerve cord and ramifies in the foot margin (L. & W. 1959a, figs 119-127). The two muscle portions of each retractor are visible in the new material (Pl. 6: 16), but are not kept apart in the reconstructions, for this would require a very large effort. The two portions, although characterized by different fiber directions, are somewhat intermingled both within the attachment area and during their further course, so their contours are difficult to reconstruct precisely in the new, smaller specimens. Instead I have concentrated on the attachment areas ("muscle scars"), which are sharply defined and suitable for objective reconstruction.

The small specimen of *V. ewingi* (specimen 3) has the same 8 pairs of pedal retractors as the larger specimens (Fig. 5).

Some irregularities were noted in the new specimen 1 of *N. galatheae.* The posterior retractor on the left side is exceptionally small, far smaller than the other retractors. Moreover, the 3rd retractor on the left side has a double head, corresponding to an unequal bipartition of the muscle itself. The 3rd muscle on the opposite, right side is normal, so this is clearly an accidental variation.

The irregularity of the 3rd muscle is not comparable to the variation seen in retractor G in the original large specimen III, which was interpreted as being bipartite by Salvini-Plawen (1969b, P. 200). In that case the mediopedalis portion had two heads, separated by the lateropedalis portion, but all three heads are within the same attachment area (L. & W. 1959a, p. 33, fig. 120, 121). The muscle is thus in fact tripartite with regard to fiber directions, and all heads originate close together within the same attachment area. This is not very different from other retractors, in which one lateropedalis and one mediopedalis portion originate within the same attachment area.

It should be remarked that the obvious asymmetrical situation of the pedal retractors in specimen 1 (Fig. 3) is in part an artifact for the shell can certainly be tilted and moved in relation to the foot and the body. This was seen in the living specimens of *Vema (Laevipilina) hyalina* by Lowenstam (1978). If the animal is fixed when the shell is tilted the muscles may of course be more contracted on one side than on the other, as in the posterior part of specimen 1 (Fig. 3).

If we disregard the obvious individual variations such as those mentioned above, all specimens of *V. ewingi* and *N. galatheae* have the same retractor pattern with regard to number, structure and relations of the individual retractors: 1) the first retractor on each side is assosiated with the m. oralis posterior (Figs 3 and 4); 2) the last muscle on each side is located just lateral to the rectum; and 3) the 6th muscle on each side marks the level at which the large pharyngeal diverticula end and the pericardium begins (Figs 10 and 11).

Many other identical relations to other organs

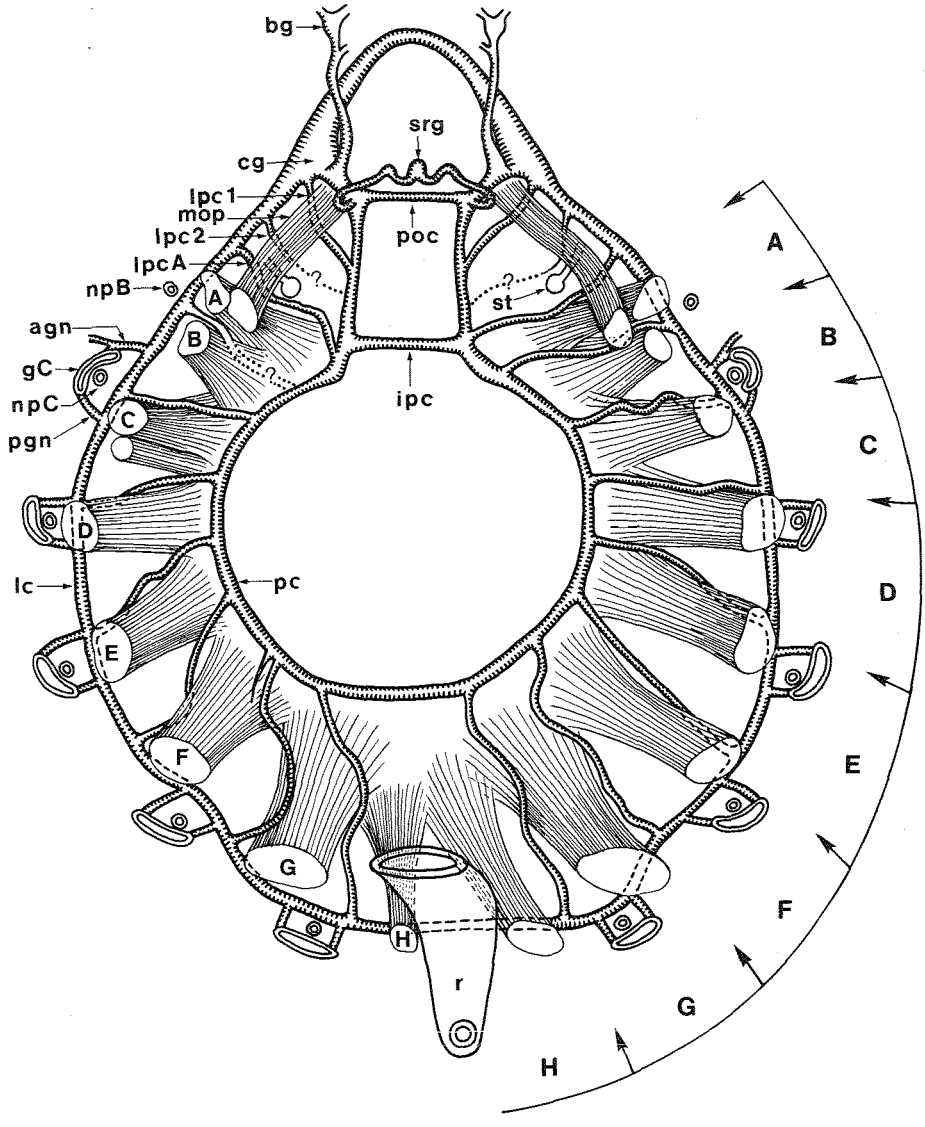

Fig. 3. *Neopilina galatheae,* specimen 1. Graphic reconstruction of pedal retractors, nervous system, gill bases and nephridiopores. The sector sequence (see Chapter 4. 2) is indicated to the right. Dorsal view.

A-H, pedal retractors A-H; agn, anterior gill nerve; bg, buccal ganglion: cg, cerebral ganglion; gC, gill C; ipc, interpedal commissure; lc, lateral nerve cord; lpc 1 and lpc 2, lateropedal connectives 1 and 2; lpc A, lateropedal connective A; mop, musculus oralis posterior; pc, pedal nerve cord; pgn, posterior gill nerve; poc, post oral commissure; np, nephridiopore; r, rectum; st, statocyst; srg, subradular ganglion.

(long radula muscles, atria of heart, gonads, crossing of anterior oblique muscles), help to identify single retractors in the two species. I therefore regard the retractor patterns in the two genera as homologous, and use the retractor pattern to indicate the situation of other structures, metameric or not, within the animal.

As in L. & W. (1959a) the eight retractors on each side are called "A" to "H", "A" being the foremost retractor, associated with the posterior oral muscle, and "H" being the last retractor, situated on the side of the rectum. Other metameric organs have been designated analogously in order to indicate the situation of the single units in relation to the metamerism of the retractors. Thus, in the nervous system, the lateropedal connective running immediately in front of each retractor is called connective A, B, C ... H.

In the figures I have also indicated the sectors which appear to contain similar sets of metameric organs and have given each sector a letter corresponding to the contained retractor (Figs 3-6,8-11). The limits of these sectors have been chosen so that, e.g., sector B contains retractor B and reaches from (including) connective B to (not including) connective C.

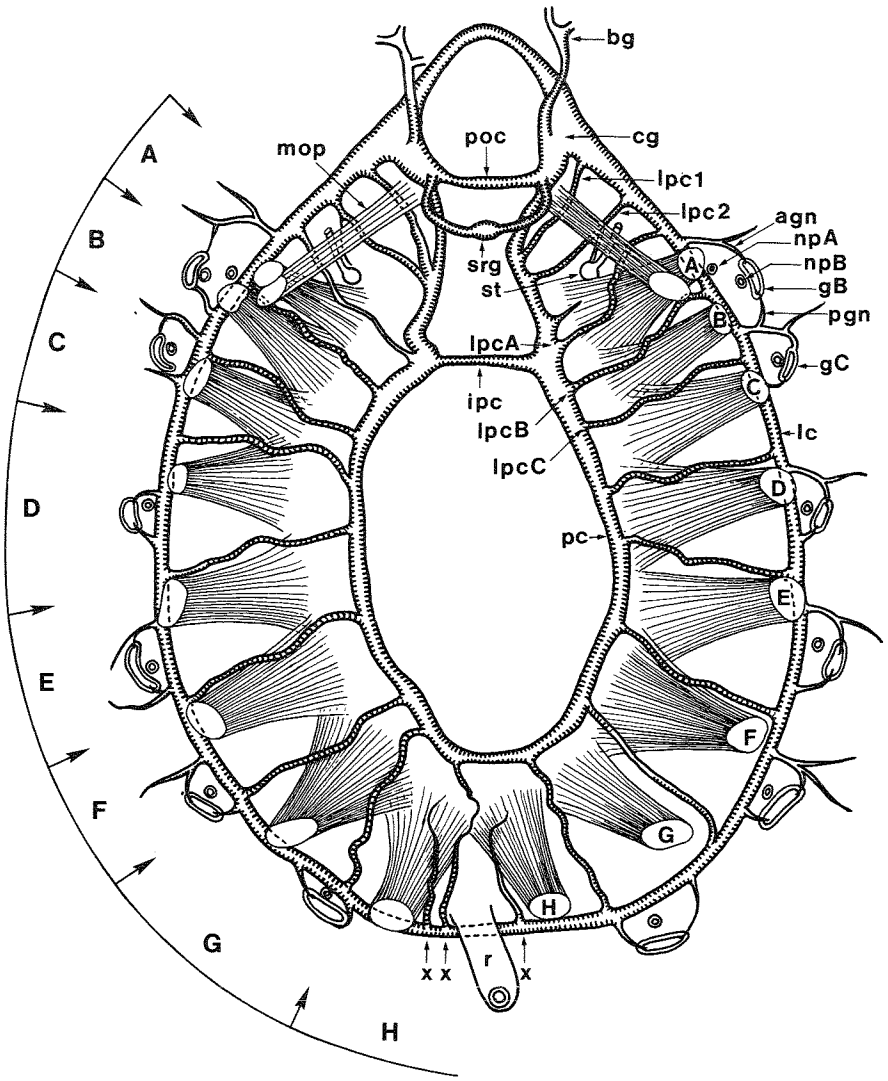

Fig. 4. *Vema ewingi*, specimen 2. Graphic reconstruction of muscles, nervous system, gill bases and nephridiopores. The sector sequence (see Chapter 4.2) is indicated to the left. Dorsal view.

A-H, pedal retractors A to H; agn, anterior gill nerve; bg, buccal ganglion; cg, cerebral ganglion; gB, gill B; gC, gill C; ipc, interpedal commissure; lc, lateral nerve cord; lpc 1, lpc 2, lateropedal connective 1 and 2; lpcA-lpcC, lateropedal connectives A to C; mop, musculus oralis posterior; pc, pedal nerve cord; pgn, posterior gill nerve; poc, postoral commissure; npA and npB, nephridiopore A and B; r, rectum; st, statocyst; srg, subradular ganglion; x, "extra" lateropedal connectives behind retractor H.

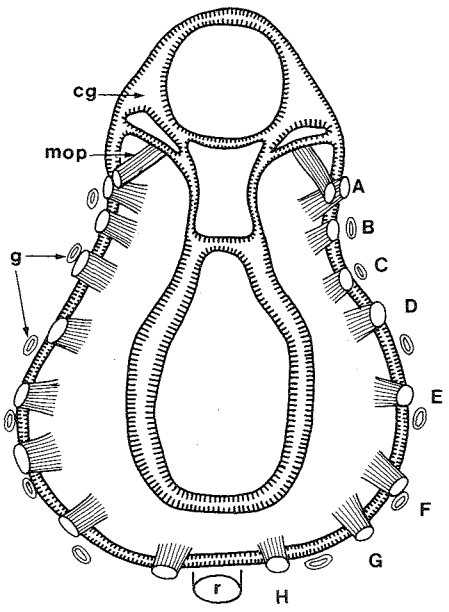

Fig. 5. *Vema ewingi,* specimen 3. Graphic reconstruction of pedal retractors, posterior oral muscles, nervous system, and gill bases. Only gross features could be reconstructed safely in this very small specimen (1.8 mm).
A-H, pedal retractors A to H; cg, cerebral ganglion; g, gill bases; mop, musculus oralis posterior; r, rectum.

It should be noted that the sector limits are arbitrarily chosen and that the introduction of sectors and their designations serves to facilitate comparison between genera. The sectors do not necessarily presuppose anything about segmental limits or about the nature of the metamerism in these animals.

The smaller body muscles such as anterior and posterior oblique muscles, gill retractors and pallial retractors were reconstructed in details in the large specimen III of *N. galatheae* (see L. & W. 1959a, fig. 121). Since a detailed comparison with *Vema* appeared of interest, I tried to reconstruct some of these smaller muscles also in specimen 2 *(V. ewingi)* and was succesful with the larger ones, but the smallest pallial muscles and some gill muscles had to be given up, as they are nearly invisible in the small specimen 2 and sometimes consist of a few fibers only.

The mm. obliquii anteriores were distinct in the larger of the new specimens (1 and 2) as well in the old material of *N. galatheae.* They were reconstructed completely in specimen 2 *(V. ewingi,* Fig. 6). As in *Neopilina,* there is a complete series of 8 obliquii anteriores on each side, one in each of the sectors A to H, and the muscles turned out to be practically identical in the two species (compare Fig. 6 with fig. 121 in L. & W. 1959a). Each obliquus anterior attaches to the shell peripheral to and somewhat behind the pedal retractor of the sector and passes forwards and medially under the pedal retractor to spread out in the circular foot musculature. The only irregularity in this strict metameric series is that m. obliquus anterior A passes transversely over to the opposite side before joining the foot musculature. In both species the attachment areas of these anterior oblique muscles are clearly separate from those of the foot retractors.

The mm. obliquii posteriores are not so well developed in any specimen. In the large specimen III of *N. galatheae* we found only two typical obliquii posteriores on each side, viz. in sectors E

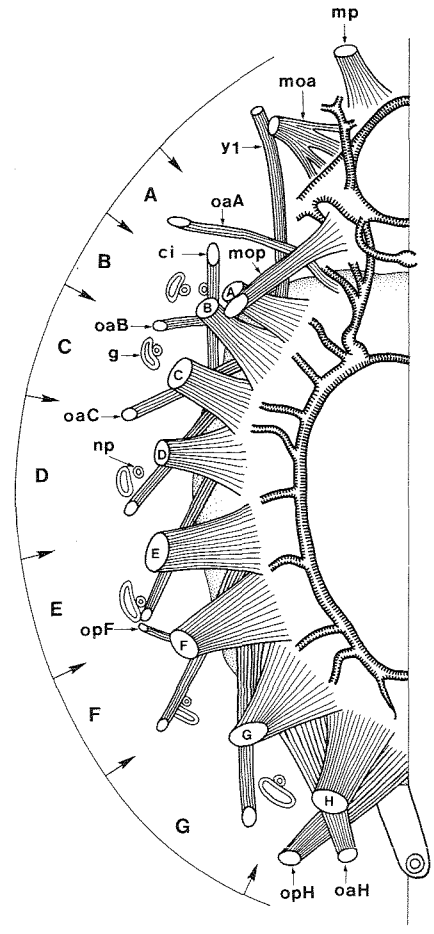

Fig. 6. *Vema ewingi,* specimen 2. Graphic reconstruction of left side with pedal retractors, oblique muscles and some oral muscles.
A-H, pedal retractors A to H; ci, anterior shell insertion of musculus circularis intermedius; g, gill; moa, musculus oralis anterior; mop, m. oralis posterior; mp, m. preoralis; np, nephridiopore; oaA-oaH, obliquus anterior A to H; opF and opH, obliquus posterior F and H; y_1, the muscle Y_1 (see text).

and F, but the two shell attachments of m. circularis intermedius in sectors A and H look similar and could be included in the series of obliquii posteriores (L. & W. 1959a, fig. 121). In *V. ewingi* a typical obliquus posterior was found only in sector F, as seen in the reconstruction of specimen 2 (Fig. 6). But as in *Neopilina* the two heads of the m. circularis intermedius were found in sectors A and H and look very similar to obliquii posteriores.

The gill retractors could be identified also in *V. ewingi* but were not reconstructed. In the better preserved gills of specimen 2 there are two in each gill, an outer one and an inner one, as in the large specimen III of *N. galatheae* (see L. & W. 1959a, figs 60, 61, 80, 121).

The circular foot muscles, which were analyzed in detail in the large *N. galatheae* III, are shown in L. & W. (1959a, figs 119 and 121). These muscles were also seen in *V. ewingi,* but were not reconstructed as the scattered bundles were difficult to delimit clearly in the smaller specimen 2. However, the shell attachments of this muscle system were distinct also in *Vema* and are included in the reconstruction (Fig. 6).

Muscle Y_1, connected with the m. circularis pedis and attaching to the shell far anteriorly in the "head region" (Figs 6, 7), is present in both species.

Retractor muscles of the anterior body region. With regard to these retractors, *Vema* appears nearly identical with *Neopilina.* The following muscles were found in both genera (Figs 6 and 7, compared with figs 121 and 137 in L. & W. 1959a):

a) musculus preoralis
b) m. oralis anterior
c) m. oralis posterior

All three muscles attach to the shell in the head region and pass down to the ventral body wall around the mouth, the velum, the lips and the postoral tentacles (Figs 6 and 7).

In addition, a previously unnoticed muscle is drawn in Fig. 7:

d) m. dilatator oris. It passses from the anterior shell wall to the anterior circumference of the mouth, all the way inside the ventral body wall. This muscle is fairly well defined in specimen 2 of *Vema,* but similar strands of muscle fibers are present also in the *Neopilina* specimens although not so clearly defined.

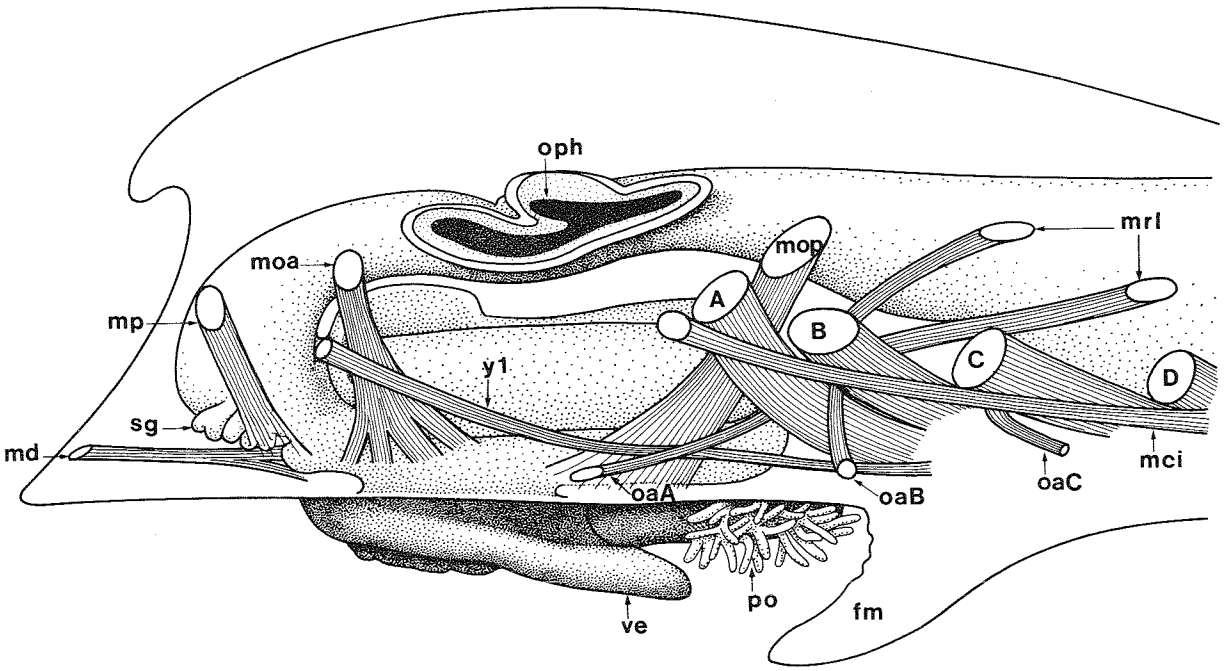

Fig. 7. *Vema ewingi* specimen 2. Parts of digestive tract and anterior musculature of left side, seen from the left. Graphic reconstruction on sagittal plane. Contour of shell added approximately for didactic purposes.
A-D, pedal retractors A to D; fm, foot margin; mci, shell attached branch of musculus circularis intermedius; md, dilatator muscle of mouth; moa, musculus oralis anterior; mop, m. oralis posterior; mp, m. praeoralis; mrl, m. radulae longus with its two heads; oaA, oaB and oaC, m. obliquus anterior A, B and C; oph, opening of pharyngeal diverticula of left side into the pharynx; po, postoral tentacles; sg, salivary glands; ve, velum; Y_1, the muscle Y_1.

4.3 The nervous system

The nervous system has been reconstructed in specimen 1 *(N. galatheae)* and specimen 2 *(V. ewingi)*. Together with the old reconstructions of the large *N. galatheae* III in L. & W. (1959a, figs 135-137), this should be a safe basis for a description.

As can be seen in the reconstructions, the nervous systems of *Vema* and *Neopilina* are very similar (Figs 3 and 4). In both there is a circumoral nerve ring with a brainlike swelling on each side. Each "cerebral ganglion" emits a buccal nerve and a subradular nerve. The latter passes up to the dorsal side of the subradular sac and ends in the unpaired subradular ganglion, the posititon of which varies with the degree of protraction or retraction of the subradular sac and organ.

The cerebral ganglion on each side contains two confluent cores of neuropile, surrounded by a common mass of ganglion cells (Pls 2, 4, 5). It emits the lateral and pedal nerve cords, both being bundles of nerve fibers with a continous layer of ganglion cells. The lateral nerve cord on each side follows the roof of the pallial groove, closely attached to the pallial epithelium, and passes medial to the gill bases to meet its contralateral partner between the foot and the anus, ventral to the rectum.

The pedal nerve cords run backwards to the anterior foot margin, where they are interconnected by a single pedal commissure, the only complete interpedal commissure present except for the one in the posterior region of the foot, where the two pedal cords meet. At the level of the anterior interpedal commissure the pedal cords have a large ganglionated swelling, but there is no circumscribed pedal ganglion: there is a continuous transition from the swelling to the ganglionated nerve cords in front and behind.

From the anterior interpedal commissure the pedal nerve cords lie in the periphery of the foot at some distance from the margin and fuse posteriorly to form a pedal nerve ring (Pls 5, 6).

The pedal nerve cords are embedded in the ramifications of the pedal retractor muscles. Actually the nerve cord lies in a blood sinus between the ramifications of the musculus mediopedalis and m. lateropedalis as originally described in *N. galatheae* by L. & W. (1959a, figs 119, 112, 167).

The small pedal and pallial nerves were not reconstructed in detail in the new material, but great efforts were made to follow the lateropedal connectives and the gill nerves, because these are important for the discussion on metamerism. Reconstruction of the lateropedal connectives was successfull in *V. ewingi* (specimen 2), but the new specimen 1 of *N. galatheae* proved difficult, and three of the anterior connectives could not be followed completely (hatched in Fig. 3).

The pattern of lateropedal connectives is essentially the same in the two genera (Figs 3 and 4). Two connectives on each side are situated in front of the foot. They are not associated with the pedal retractor muscles like the following ones and appear to be independent of other metameric structures. They do not seem to fit into the metameric series of connectives following behind them. I have therefore provisionally treated them as lying in a premetameric region and have not given them any sector letters.

On the other hand, the two anterior connectives are clearly homologous in *Neopilina* and *Vema*. In both genera the first connective is connected with the lateral parts of the cerebral ganglion and passes just behind the m. oralis postrior, whereas the 2nd connective is extraordinarily thin and emits a small branch to the statocyst. If there are fibres to the postoral tentacle tuft as in the original specimen III of *N. galatheae*, they cannot be followed in the new smaller specimens.

The statocyst, with a long open duct to the ventral body surface, is situated in the square between the 2nd and 3rd connectives and the lateral and pedal nerve cords. This was seen clearly in *V. ewingi* (Fig. 4) and in the old material of *N. galatheae* (see L. & W. 1959a, fig. 136).

The eight following lateropedal connectives (nos. 3-10) have an almost identical course in the two species, each connective being more or less closely attached to the anterior surface of a retractor muscle (Figs 3 and 4). Thus the connectives nos 3 to 10 belong to the pedal retractors A to H and have been named accordingly.

The larger specimen of *V. ewingi* is somewhat different from the *Neopilina* specimens in having one complete and two "incomplete" connectives behind the muscles H in the region of the rectum (Fig. 4). The complete extra connective is situated on the left side of the rectum and is not associated with a pedal retractor. The "incomplete" connectives are situated on either side of the rectum. They are very thin but their relations to the muscle ramification are similar to those of normal connectives and, like these, they are emitted from the inner side of the lateral nerve cord. Both these "incomplete" connectives were lost in the muscular parenchyma of the foot margin before making contact with the pedal

nerve cord. Such extra connectives, incomplete or complete, could not be discovered in the specimens of *Neopilina.*

4.4 The gills and the gill nerves

Neopilina galatheae has 5 pairs of gills, whereas *Vema ewingi,* even the minute specimen 3, has 6 pairs (Clarke & Menzies 1959). The situation of the gills is similar in the two specimens of *Vema* (Figs 4, 5, and Pl. 1).

In both genera the gills are unipectinate of the type described earlier (L. & W. 1959a, figs 58, 59). The number of filaments (lamellae) on each gill seems to vary with the size of the individual and also with the species. Thus, the gills of *N. galatheae* have 7-8 filaments each , both in the big specimen III (29 mm) and in the specimen 1 of the present material (12 mm long). Specimen 2 of *V. ewingi* is almost as long as the latter specimen (9.2 mm) but has only 4-5 filaments (Pl. 3), whereas the minute specimen 3 of *V. ewingi* (1.8 mm long) has but 2-3 indistinct filaments on each gill.

In the larger specimen of *V. ewingi* (2) the inner filament of each gill appears to be longer than the others and seems to have another direction (Pls 1 and 3). However, the appearance of the soft gills is so dependent upon fixation and handling that comparisons between the specimens with regard to gill form had to be given up.

In the large original specimens of *N. galatheae* each gill has a row of small vestigal gill filaments on the side of the gill stem opposite to the larger filaments, indicating that the gill is originally bipectinate (L. & W. 1959a, figs 58, 59). Similar vestigial lamellae could not be discovered in the new material, but the state of preservation of the gills is hardly good enough for such detailed studies.

The gills are attached to the roof of the pallial groove, and the "gill base" shown in the reconstructions is the line of fusion of the epithelium of the gill stem with the pallial epithelium. The spatial relations between the gill bases, nephridiopores and nerves as shown in the reconstructions are probably as in the living animals, for the nephridiopores open through the pallial epithelium, and the nerves are attached to its basement membrane. Artificial dislocation of gills, nephridiopores and nerves during fixation and handling is therefore hardly probable. The relations of the gill bases to the retractor muscles and the muscle attachments on the shell are far more dependent on artificial deformations and muscle contractions, for the shell can be tilted and rotated in relation to the ventral parts. Lowenstam (1978) observed this directly in living specimens of *Vema (Laevipilina) hyalina.*

As the reconstructions show, each gill is associated with a nephridiopore which opens just medial to the gill base. This metameric repetition of gills and associated nephridiopores is quite regular in sectors B to G *(Vema)* and C to G *(Neopilina)* (Figs 3, 4). However, in both forms there is in front of the first gill a supernumerary nephridiopore which opens independently into the pallial groove.

In *N. galatheae* the 5 gills on each side are located outside the muscle attachments C to G both in the large old specimens and in the new one (specimen 1). Gills D to G are directly outside or somewhat behind the muscle attachments, whereas gill C (the first gill) has a slightly more anterior location, just in front of muscle C and strictly taken within the posterior part of sector B as here defined. On the other hand, if the first gill is to be referred to a particular retractor, it must be retractor C, to which it is closest (Fig. 3). The somewhat exceptional position of gill C was noticed and described also in the old specimen III (L. & W. 1959a, p. 66, figs 121, 135) and is obviously characteristic of this species.

The aberrant situation of the first gill is also demonstrated by the origin of the two nerves belonging to this gill. In sectors D to G both gill nerves are emitted within the sector limits as chosen here (Fig. 3). The nerves of gill C are emitted in the border region between sectors C and B, one nerve falling in front of, the other falling behind, the lateropedal connective C, which is chosen as sector limit.

In *V. ewingi* the 6 pairs of gills are located in the sectors B to G, but in this species, as in *Neopilina,* there is a tendency for the anterior gills to be located more anteriorly in relation to the corresponding pedal retractors (Fig. 4). The 5 posterior gills of *Vema* have a situation which corresponds closely to that of the 5 gills (C to G) of *Neopilina.* As in this species, gill C is supplied by gill nerves which originate in front of and behind the lateropedal connective C, whereas the following gills have both their gill nerves inside the respective sectors. The first gill of *Vema* clearly lies within sector B and lacks a counterpart in *Neopilina.* Its gill nerves show the same aberrant origin as those of gill C, on each side of the corresponding lateropedal connective.

It is thus obvious that the extra gill characteristic of *Vema* is the gill of sector B. *Neopilina* lacks this

gill. The other gills (C to G) are clearly homologous in the two genera.

It should be remarked that the minute specimen 3 of *V. ewingi* has 6 pairs of gills situated in the same way as in the large specimen 2 (Figs 4, 5). Details such as gill nerves were impossible to reconstruct with certainty in this small specimen.

The internal structure of the gills in the new, immature specimens is remarkably loose and difficult to analyse (Pl. 4), not so compact as in the original large specimen III (L. & W. 1959a, figs 61, 63).

4.5 Nephridia and nephridiopores

The study of the nephridia is as difficult in the new

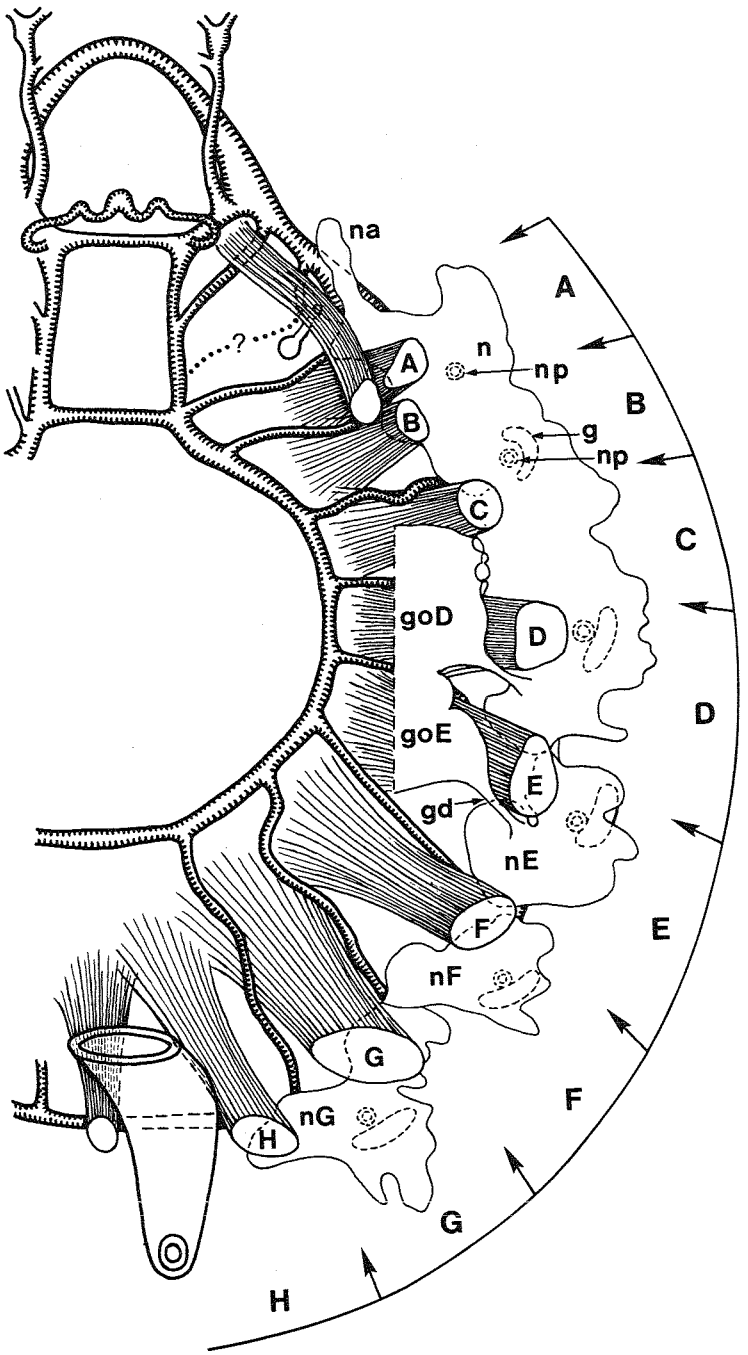

Fig. 8. *Neopilina galatheae,* specimen 1, dorsal view of right side, with pedal retractors, nervous system, outline of nephridial complex, nephridiopores, gonads and gill bases. Graphic reconstruction. Sectors indicated as in Fig. 3.
A-H, pedal retractors A to H; g, gill base; gd, gonoduct; goD and goE, gonads of sector D and E; n, nephridial sac complex; na, anterior nephridial diverticulum; np, nephridiopore; nE-nG, separate nephridial sacs of sectors E to G.

material as it was in the original specimens. The nephridial sacs and lobules consist of a single layer of very large vesicular cells which tend to collapse and stain indistinctly. This together with extensive interdigitation of lobules between adjacent nephridia makes it impossible to distinguish separate nephridia in many cases. Reconstruction therefore had to be restricted to the general outline of the nephridial complex and to the nephridiopores, which have a low, compact epithelium which is better defined (Pl. 4).

Both *Vema* and *Neopilina* have clearly separate nephridia in sectors E, F, and G (Figs 8, 9). The tangle of nephridial lobules in sectors B to D cannot be resolved into separate nephridia in any of the two genera. The anterior termination of the nephridial

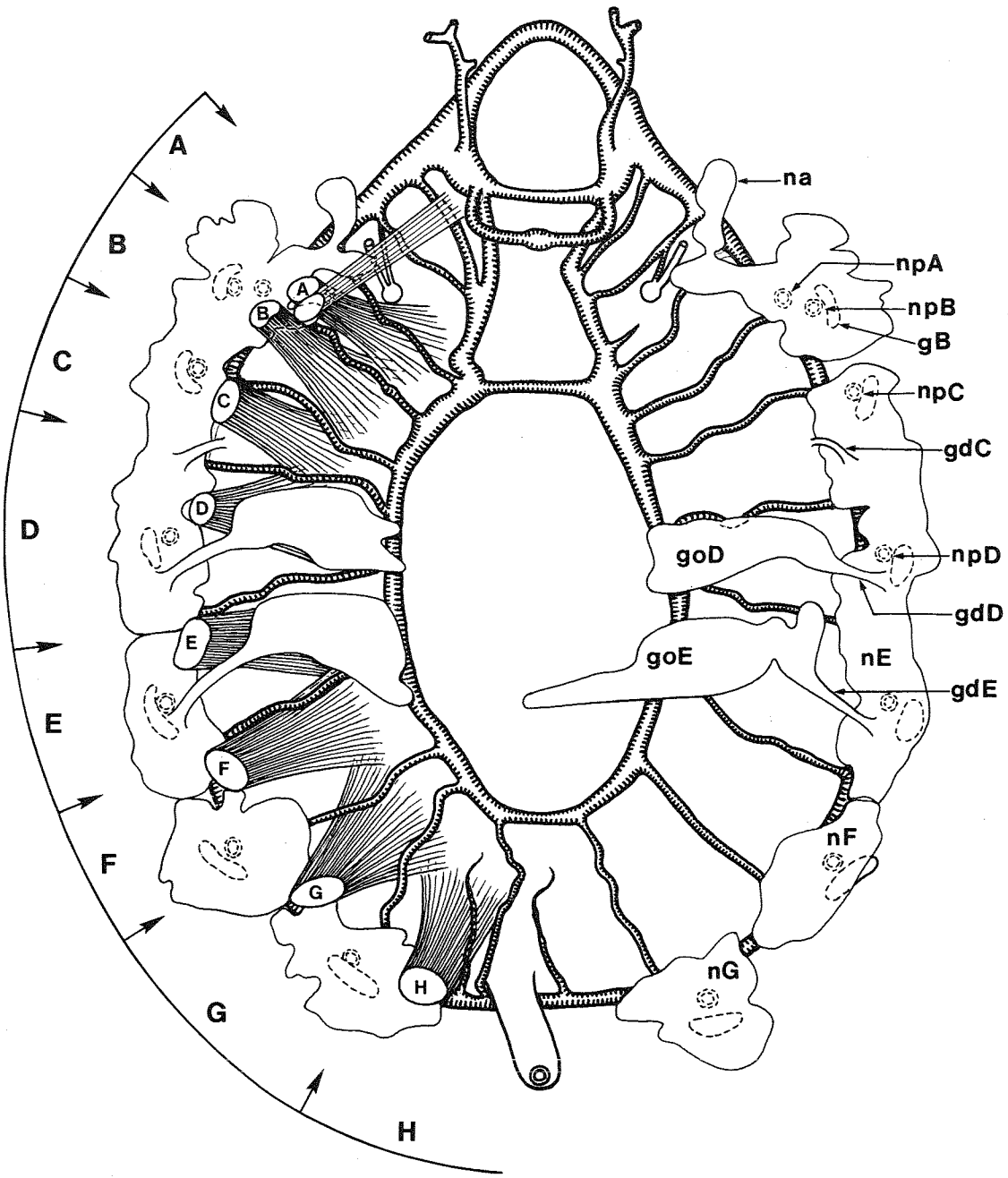

Fig. 9. *Vema ewingi,* specimen 2, dorsal view. Immature specimen. Graphic reconstruction of nephridial complex, nephridiopores, outline of immature gonads and gonoducts. Gill bases, nervous system and muscles added for orientation. Sectors indicated as in Fig. 4. A-H, pedal retractors A to H; gB, base of gill B; gdC-gdE, gonoducts of sectors C to E; goD and goE, gonads of sectors D and E; na, anterior nephridial diverticulum, probably referable to sector A; nE-nG, separate nephridial sacs of sectors E to G; npA-npD, nephridiopores A to D, those of E to G have no lettering.

complex is characteristic on both sides in all specimens, the old specimen III of *N. galatheae* included (L. & W. 1959a, figs 144, 145). A distinct branched lobule extends forwards in front of the first pedal retractor muscle and ends at the level of the cerebral ganglion (Figs 8, 9). This anterior lobule has a more medial position than the other nephridia and is partly medial in relation to the lateral nerve cord.

Each nephridial sac opens into a nephridiopore by a short duct. Both the duct and the pore are easily reconstructed because of their dark-staining, compact epithelium (Pl. 4). The series of nephridiopores in the reconstructions thus indicates how many independent nephridia can be expected in the nephridial series on each side. The nephridiopores are thus used for the comparison of metameric repetition in the nephridial system rather than the nephridial sacs, which are difficult to reconstruct precisely.

In *N. galatheae* there are 6 nephridiopores on each side, all opening into the pallial groove lateral to the lateral nerve cord. The five posterior nephridiopores are associated with gills C to G, each nephridiopore being attached to the medial margin of the gill base (Fig. 8). Nephridiopore C has the same exceptional anterior location in relation to retractor muscles and nerve commissures as gill C, to which it is associated. The first nephridiopore opens into the pallial groove independently of the gills. It is related to the limit between sectors B and A similar to the way in which nephridiopore C is related to the limit between sectors C and B, and it appears to precede nephridiopore C in the series. It is therefore called nephridiopore B, although situated on the very limit between the sectors. Comparison with *Vema* indicates that this is justified.

In *V. ewingi* there are 7 distinct nephridiopores on each side (Fig. 9). The six posterior ones are situated as nephridiopores B to G in *Neopilina,* with the exception that nephridiopore B has the expected association with gill base B, and that both these structures are clearly contained within sector B in *Vema.*

The supernumerary nephridiopore in *Vema* opens into the pallial groove independently of gills, medial to and a little in front of nephridiopore B, but still outside the lateral nerve cord (Pl. 4). Lying in front of nephridiopore B it would be expected to belong to sector A. Actually its situation is just on the limit between sectors B and A, but it is called nephridiopore A, for there is actually no alternative if it is a metameric structure, and also because it probably comes from the anterior nephridial complex in front of muscle A, where a nephridium A would be expected to lie. Actual communication between this anterior nephridial complex and nephridiopore A cannot be followed critically, but nephridiopore A connects with the base of the anterior nephridial complex (Fig. 9). The other nephridiopore in this region (nephridiopore B) is clearly associated with gill B and can be referred to the B sector.

It should be recalled that *N. galatheae* also has a nephridium A, although it lacks a nephridiopore of its own (Fig. 8). It was suspected in our original report on this species that the anterior nephridial lobules in the region of the musculus oralis posterior represent the nephridium of the A sector (L. & W. 1959a, pp. 57-58). This idea is supported by the finding of a separate nephridiopore in this region of *V. ewingi.*

The comparison between the nephridial systems of *Vema* and *Neopilina* thus shows that the supranumerary nephridiopore in *Vema* lies in front of the nephridiopore series seen in *Neopilina,* i.e., that the series extends forwards to sector B in *Neopilina* but to sector A in *Vema.* In this as well as in some other respects *Vema* has a more complete metamerism than *Neopilina.*

4.6 Gonads and gonoducts

The gonads of all the new specimens are immature, and those of the minute specimen 3 have not even been identified. In specimen 1 *(Neopilina galatheae)* and specimen 2 *(Vema ewingi)* gonadal rudiments are visible as dark masses of small germinal nuclei, situated along the bottom of the perivisceral cavity, below the intestine. The walls of the gonads are thin even in the large mature specimens III and IV, and are not discernible at all in the new small specimens. The reconstructions of the gonads in the new specimens therefore only show the outline of the clusters of dark germinal cells (Figs 8, 9).

The gonoducts with their low, cell-rich epithelium and darkly staining cells are distinct and could be reconstructed with full certainty in specimens 1 and 2 (Pl. 4). The gonoducts of the old, mature specimens III and IV of *N. galatheae* contain germ cells, but germ cells are naturally not present in the gonoducts of the immature specimens.

As in the mature specimens III and IV of *N. galatheae,* the immature specimen 1 has two pairs of gonadal rudiments in sectors D and E, and two pairs of gonoducts pass out to the pallial fold closely be-

hind the pedal retractors D and E, resp. In the pallial fold each gonoduct opens into the nephridium of the same sector: the duct widens into a funnel-like terminal part which fuses with the dorsal or dorsomedial wall of the nephridial sac.

The gonadal rudiments are seemingly confluent in the central part of the body of specimen 1 (Fig. 8) and resemble those of the adult female (specimen III, see L. & W. 1959a, fig. 145). However, this impression is probably caused in all cases by extensive interdigitation of the lobules of the gonads, for in the adult male the two strongly lobulated testes could be shown to be distinctly separate (L. & W. 1959a, fig. 123).

In the larger specimen of *V. ewingi* (2) the two pairs of gonadal rudiments are smaller and clearly separate. They are located in the same sectors as in specimen 1 (D and E, Fig. 9). Their gonoducts pass out to the pallial groove and open into the nephridial sacs as in *Neopilina.*

Thus far specimen 2 is as expected, but to my astonishment this specimen of *V. ewingi* has an additional pair of gonoducts connected with the nephridium C on each side (Fig. 9). The gonoducts of the C sector are somewhat thinner than those of the "normal" genital sectors D and E, but are no doubt correctly identified. These vestigial gonoducts in sector C connect with the dorsal wall of the nephridial sac in a quite typical way and can be followed medially to just behind the pedal retractor C, a course analogous to that shown by the gonoducts of the typically fertile sectors D and E. The vestigial gonoduct C tapers and becomes indistinct before making contact with the pedal retractor, where the rudiment of the gonad would be expected to appear. In the present material no gonad could be positively identified here, but the negative statement is made with reservations, for the 30 μm celloidin sections are too lightly stained to reveal small rudiments. It can only be concluded that gonadal rudiments in sector C, if present, must be less differentiated than those of sectors D and E, for the latter are readily identified in nearby slides of the same series.

Realizing the importance of this finding I rechecked several times the location and structure of the gonoducts of sector C, and critically examined the sequence of the sections on the slide. The sections were found in proper order and completely continuous although they are somewhat bleached 20 years after the original reconstruction was made.

No doubt, therefore, specimen 2 of *V. ewingi* has a third pair of gonoducts located in sector C, in front of the two "normal" pairs of gonoducts. Whether the extra gonoducts are connected with a functional gonad in the adult is not known, for no adult specimens of *V. ewingi* have been sectioned. The small, almost postlarval specimen 3 of the present investigation is hardly significant in this connection.

It should be remarked that no gonads or gonoducts have been discovered in sector C of *N. galatheae,* not even in the immature specimen 1 of the present investigation.

4.7 Are nephrostomes present?

The original descriptions of the nephridia of *Neopilina galatheae* included connections between each nephridium and the "dorsal coelom" or, in the posterior sectors, with the pericardium. These supposed connections were called nephrostomes and nephrostomic ducts (L. & W. 1959a, p. 58). Artifacts and poor fixation made a precise study difficult, and the observations were mentioned with some reservation.

Examination of a nearly intact specimen of *Vema* in 1959 made us realize that the "dorsal coelom" is a pair of enormouly enlarged pharyngeal diverticula (L. & W. 1959a, p. 56, and 1960, p. 1820). This made us reexamine the connections between the nephridia and the dorsal sacs, for nephrostomes are not expected to come from pharyngeal diverticula. It was obvious that some mistakes had been made in the original material because of poor preservation, but even the new material was not good enough for a definite revised description.

The new material, particularly specimen 1 of *Neopilina,* is better preserved, but artifacts confuse the interpretation in a similar way as in the original specimens. The "nephrostomes" originally described in the anterior parts (sectors C to E) are probably mistakes, but the posterior ones in sectors F and G seem to be present although interpretation is difficult even in the new material.

In the anterior sectors most nephridia emit one or several lobules in a medial direction, obtaining contact with the lateral margin of the dorsal pharyngeal sac (sectors A-E). In such contact areas the margin of the pharyngeal sac produces irregular pouches, often fairly long, with a low light-staining epithelium completely different from that of the sac proper. Such pouches were described as nephrostomes and nephrostomic ducts in the original paper. But real communications between such pouches and nephridial lobules were not observed in

the original material — except for one doubtful case (l. c., p. 58) — and are probably not present in the new material either.

In many cases the lateral margin of the dorsal pharyngeal sacs appears to have "exploded" and the pouches mentioned above have opened into the pallial fold (Pl. 4). This produces very confusing pictures, and such cases were obviously interpreted as open communactions between dorsal sacs and the ill-defined nephridial lobules. But in the new material the intact marginal pouches seem to be blind, and I have not seen a convincing case of open communication with a nephridium.

In the pericardial region (sectors F and G) the nephridia do not approach the dorsal sacs which only reach into the anterior part of sector F. Nephridia F and G each sends a long, medial diverticulum which attains contact with the pericardium, and actual continuity appears to exist in the new material of *Neopilina* and *Vema* between the epithelium of the nephridium and that of the pericardium. However, both the nephridial lobules and the pericardium are collapsed in these specimens and the lumen is difficult to follow in the thick sections. I therefore hesitate to make any statements about open communications in sectors F and G, although the picture is suggestive in the new specimens as well as in the old ones.

It should be mentioned that the histological appearance of the presumed nephrostomes and ducts adds to the difficulties, for, if present, they are loosely built and stain poorly, quite unlike the homologous structures in many other molluscs.

In view of all this uncertainty I suggest that the question of nephrostomes in the heart region is kept open until critically fixed material is available. But I suggest that the description of nephrostomes in the region in front of the heart be forgotten.

Lauterbach (1983a) proposed that the multiple excretory organ of *Neopilina* has evolved from a single, long sac on each side, lying inside the retractor muscles as in some Polyplacophora. The single sac may have been pressed out between the retractor muscles as diverticles, which have become isolated as separate nephridia and in some way aquired nephridiopores. It is even postulated that the original long nephridium may be preserved as a longitudinal duct medially of the retractor muscles but may have been overlooked in previous publications. Such a duct has been looked for in the large specimen III and IV and in the new material, with a negative result. If present, the duct should be seen in sections like that shown in Pl. 6:16. A related theory, in itself possible, was considered by Lemche and myself but was given up because of lack of evidence. On the other hand, the presence of separate nephridiopores regularly spaced and associated with gills, is a weak point of the theory since it requires additional assumptions. Also the uncertainty about the presence of medial connections from the nephridia ("nephrostomes") weakens the fundaments of the theory.

4.8 Pericardium, heart and blood vessels

The large specimens used in the original studies show the heart, the pericardium and the vessels much better than the new material, in which heart and pericardium are partly collapsed and many tissues have a more loose structure. The descriptions and the documentation given in the original account can therefore not be improved at present.

This is regrettable, for it is still unknown how the pericardial diverticula following the aorta on each side end anteriorly, i.e. whether they have some connection with gonads and nephridia or not. The principal structure of heart and pericard is well documented by the old material (L. & W. 1959a, figs 46-50).

4.9. The pharyngeal diverticula

In the original description of the anatomy of *Neopilina galatheae* (L. & W. 1959a, pp. 28 and 56) we described large, flattened "coelomic sacs", extending over most of the body under the shell. Other dorsally situated epithelial sacs in the anterior body region were called "pharyngeal diverticula" because their communication with the pharynx could be established. Interpretations and reconstructions were given with some reservation (stippling), for the appearance of the sacs in the region behind the apex was unknown because of damage to the specimens. The "coelomic sacs" were distinguished from the pharyngeal ones mainly because of their pigmented epithelium.

The new specimens 1 and 2 are intact in the postapical area and show that the original interpretation was wrong. The so-called coelomic sacs are in open communication with the pharyngeal diverticula and the pharynx, making the original interpretation as a coelem untenable. Unfortunately this information came too late to be included in the main text in the original papers and was only included as

short notes (L. & W. 1959a, p. 56, and 1960, p. 1820).

The system of dorsal sacs has been reconstructed graphically both in *N. galatheae* (Fig. 10) and *V. ewingi* (Fig. 11). The anterior parts of the complex including the communication with the pharynx were easily analyzed in the almost intact specimens, but the posterior parts of the sacs were so compressed that the lumen was difficult to see in some places. This appears to be an artifact caused by violent contraction of the pedal retractors when the animal was caught or fixed. Such compression may also be the reason why the lateral margins of the sacs appear to have "exploded" in some places (see Chapter 4.7 and Pl. 4). The small specimen 3 is too damaged in the dorsal regions to show anything about pharyngeal diverticula in the body behind the "head".

The system of pharyngeal diverticula is practically identical in *V. ewingi* and *N. galatheae* (Figs 10 and 11), and fits well with the incomplete picture obtained from the large specimen III (L. & W. 1959a, figs 86, 146). The sacs on each side form a communicating system, but there are no connections between the sacs across the midline. The sacs of each side communicate with the pharynx by a large, slitlike opening in the region behind and above the radula sheath, where the pharynx is dorsoventrally flattened and broad from side to side (Figs 13, 14, 16-18 and Pls 2 and 5). The opening from the pharynx leads into a kind of central lumen on each side, from which several flat sacs branch off in different directions. The constant situation of these secondary sacs in all three reconstructed specimens indicates that they are present in the living animal and not produced artificially as accidental wrinkles during fixation.

There are five pairs of sacs: four in the anterior body region and one in the posterior region. One anterior sac (I) has a ventral location and fills out the pallial fold in front of the pedal retractor A. This sac has a large open lumen in all the specimens. Another sac (II) is more dorsal and partly covers the first one (Figs 10 and 11). Both sacs extend into the region in front of the mouth and send branches in between the muscles of the radula and the oral apparatus (Pl. 7:22).

The dorsal wall of sac II is evaginated to form two smaller diverticula on each side, one of them situated medially and directed forwards (III), the other situated more laterally and directed backwards (IV).

The large flattened sacs which extend posteriorly under the shell (V) cover most of the body in sectors B to F and end abruptly at the anterior margin of the pericardial sacs. They cover most of the space between the midline and the row of pedal retractors, and their lateral margins tend to bulge out between the retractor muscles and approach the nephridia. The margin of sac V is deeply indented at the level of muscles A and C. This has an obvious reason, for the musculus oralis posterior inserts on the shell medial to muscle A and prevents the sac from extending laterally in this region, and the two heads of the long radula retractor insert medially of muscles C and D and cause an inward bulge of the margin of the sac in that region.

The lateral parts of the large posterior sacs (V) have a relatively low, pigmented epithelium, whereas the medial parts have little or no pigment in their higher, more prismatic cells. The limit between pigmented and unpigmented epithelium is often sharp and marked by a fold of the dorsal wall of the sac. Sometimes it looks as if pigmented and unpigmented parts of the sac are separated without communication, but this impression is probably artificially produced by the strong compression of the sacs. At other levels the epithelia are distinctly continuous, so I have been convinced that there is one large flat and strongly compressed sac on each side (pls 5:15, 6:26, 7:24, 27). Real subdivisions of these sacs have not been seeen with any certainty. The communication of sac V with the lumen of sac I on each side is beyond doubt in the new specimens.

Pigmented epithelium is also present in the ventral parts of sacs I and II in the anterior body region, particularly in the diverticula which penetrate between the radula muscles. Other parts of the sac system are nonpigmented, and there is no reason to use pigmentation to distinguish two classes of cavities as was done in our original report.

No doubt the sacs are much compressed in the fixed specimens. In the living animal they are probably filled with fluid, helping to lower the foot and extend it in a stalklike way below the level of the shell margin, so the animal can creep. That the foot is used in this way was shown by observations on living *Vema (Laevipilina) hyalina* by Lowenstam (1978). The sacs in the anterior region of the animal are perhaps also important when the mouth and the radula are brought into contact with the substrate.

4.10. Oral region, oral cavity, subradular organ, salivary glands

The new material mainly confirms the original

descriptions of the oral region, the velum, the postoral tentacles and the oral cavity of *Neopilina,* but some new observations on the preoral tentacles, the anterior jaw, the subradular sac, and the salivary glands call for some supplementary comments.

4.10.1. The preoral tentacles are poorly developed and hardly visible at all in the new, immature material.

In the large specimens III and IV from the Galathea Expedition the preoral tentacles are well developed, about 0.3 mm long, and could be seen with the dissection microscope as a pair of pear-shaped appendages raised above the surrounding body surface. Each preoral tentacle is situated in the groove between the velum and the body wall, ventrally to the cerebral ganglion, to which its small nerve is connected (L. & W. 1959a, figs 66-71, 136).

In the new, immature material, both of *Neopilina* (specimen 1) and *Vema* (specimens 2 and 3), the expected site of the preoral tentacles can be easily localized in the sections, but the tentacles themselves

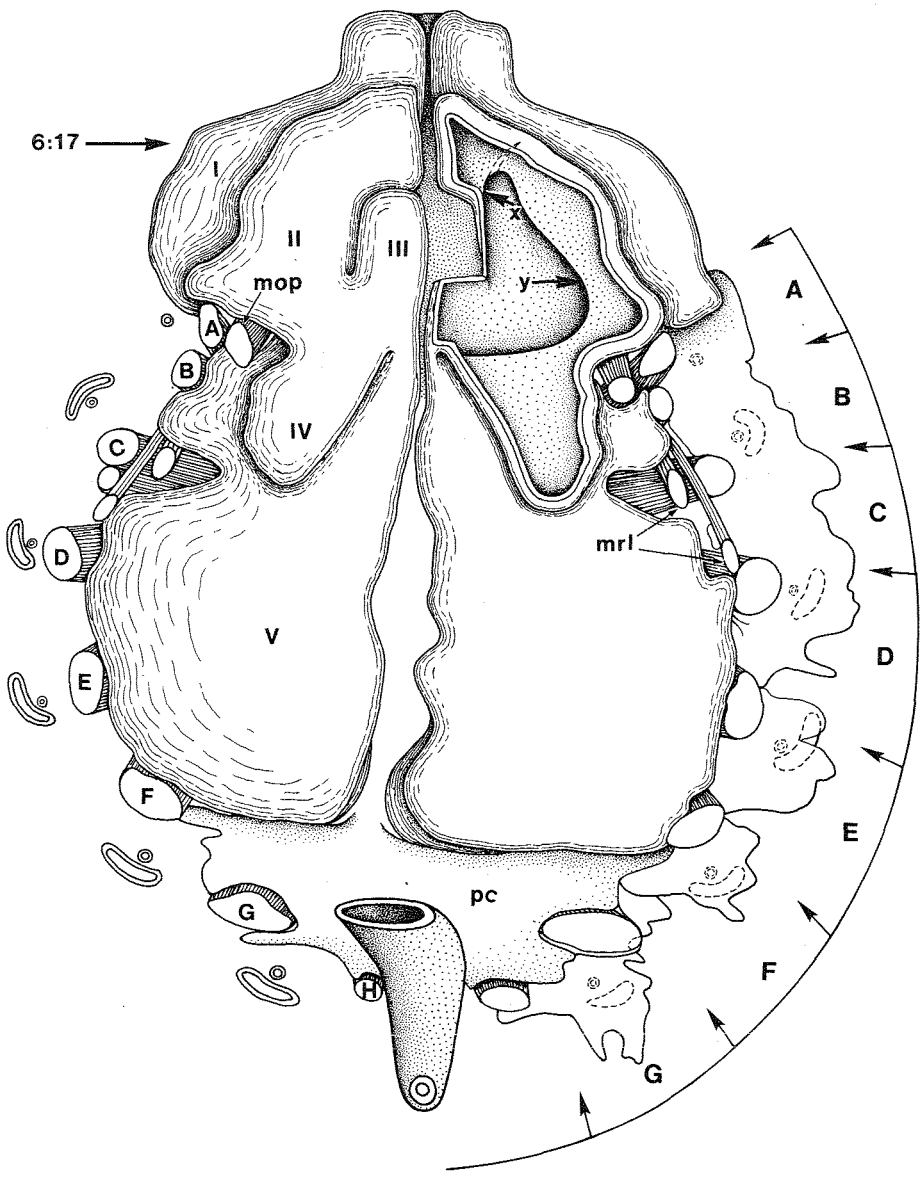

Fig. 10. *Neopilina galatheae,* specimen 1. Graphic reconstruction of the pharyngeal diverticula, previously mistaken for coelomic sacs. Dorsal view. The different parts of the sac complex are designed I to V. The roof of sacs II and IV is removed together with sac III on the right side. x indicates the communication with the pharynx, y indicates the communication between sacs I and II. The outline of the pericard (pc) is roughly indicated. For other structures see Figs 3 and 8. The level of section shown in Pl. 6: 17 is indicated.

are small and indistinct. They would probably escape detection among the wrinkles of the epithelium if their location were unknown. The tentacles of the large original specimens have a very high and characteristic epithelium, but in the new smaller specimens it is only little higher than that of the surrounding body wall (Pls 3, 4:7, 5:13). Unexpectedly, the preoral tentacles are easier to find in the minute and poorly fixed specimen 3 of *Vema* than in the almost mature specimens 1 and 2 *(Neopilina* and *Vema,* resp.).

4.10.2. The anterior jaw

There has been some uncertainty about the presence of a true anterior jaw in the Monoplacophora, particularly whether it can be homologized with a gastropod upper jaw or not. Some shrinkage and unsuitable planes of sectioning made the large original specimens difficult to interpret, and this resulted in a poor and imprecise description (L. & W. 1959a, p. 24, figs 75, 77). The new specimens (1, 2 and 3) are better preserved and are more satisfactory for description and illustration, also because individual variation in the material can be better checked.

In all three new specimens the anterior jaw is unpaired, developed as a well defined, U-shaped thickening of the cuticle of the anterior lip, which

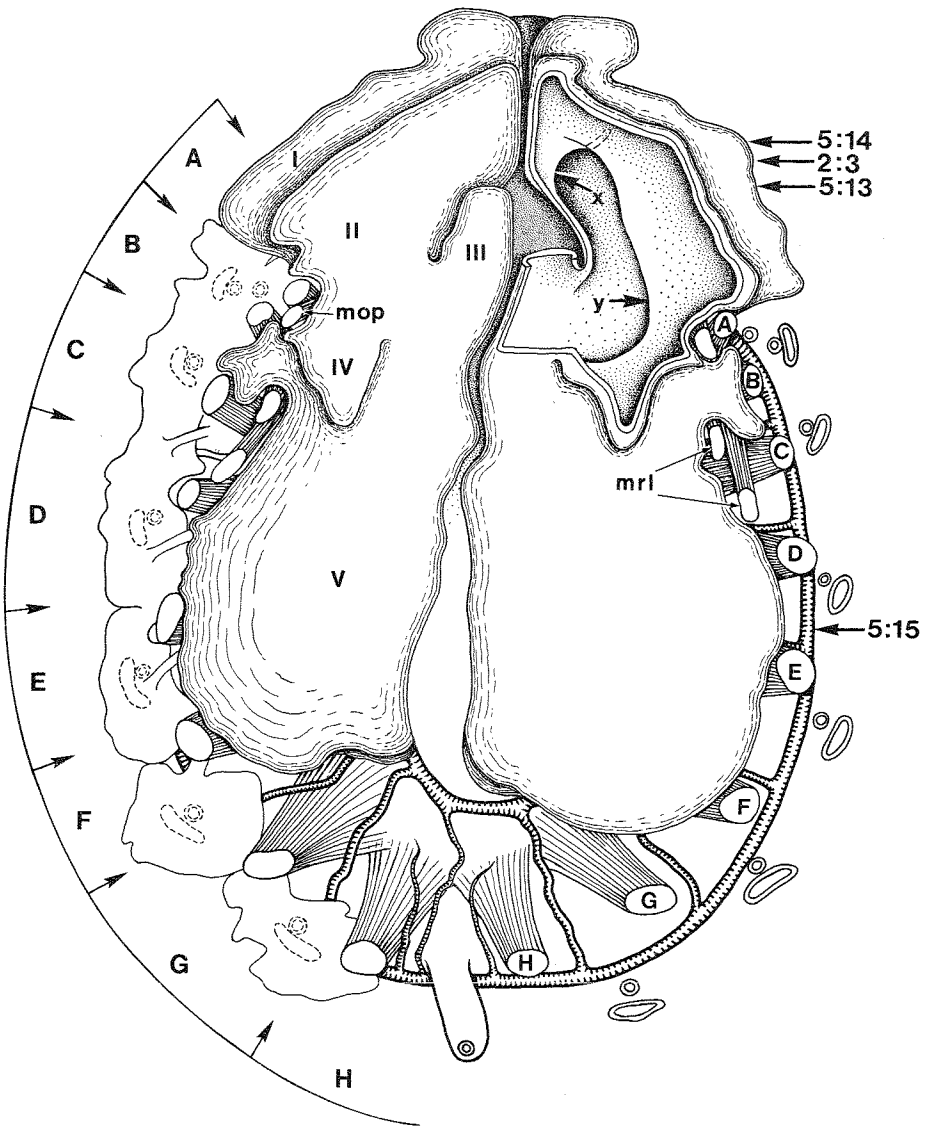

Fig. 11. *Vema ewingi,* specimen 2. Graphic reconstruction of the pharyngeal diverticula. The different parts of the sacs are designed I to V. The roof of sacs II and IV is removed together with sac III on the right side. x indicates the communication with the pharynx. y indicates communication between sacs II and I. For other structures see Figs 4 and 9. The level of sections shown in Pls 2: 3, 5: 13, 5: 14 and 5: 15 is indicated.

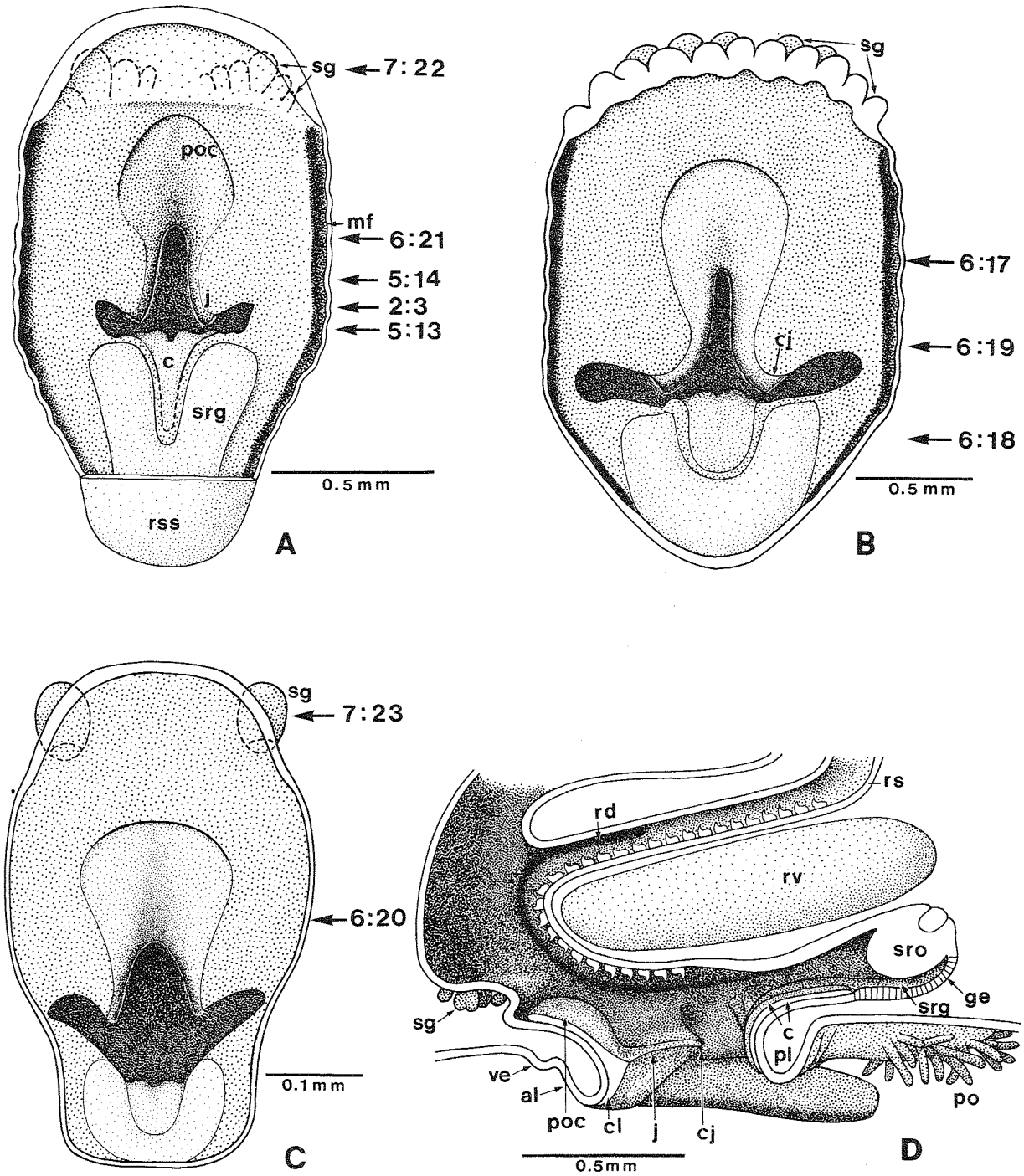

Fig. 12. Morphology of oral cavity, anterior jaw, salivary glands and subradular sac in recent Monoplacophora.
A-C, floor of oral cavity seen from above. Graphic reconstructions. A, *Vema ewingi,* specimen 2. B, *Neopilina galatheae,* specimen 1. C, *Vema ewingi,* the minute specimen 3. D, *Vema ewingi,* specimen 2. Right half of oral region, seen from the median plane. Graphic reconstruction. The relative site of radula sheath and radula vesicle somewhat changed to give a simpler picture. The level of some sections shown in plates are indicated.

al, anterior lip; c, cuticle on posterior lip and bottom of subradular sac; cj, pointed corner of anterior jaw; cl, cuticle on anterior lip, sectioned in the median line; ge, section of subradular glandular epithelium; j, anterior jaw; mf, marginal furrow between floor of mouth and subradular membrane, with thin epithelium allowing radula movements; pl, posterior lip; po, postoral tentacle tuft; poc, preoral cuticular plate on floor of pharynx; rss, retained roof over posterior end of subradular sac in A; rv, radula vesicle; sg, salivary glands; srg, subradular glandular epithelium; sro, subradular organ; ve, velum.

delimites the mouth anteriorly (Fig. 12: D). As described in the original paper from 1959, the anterior lip is crescent-shaped and separated from the posterior lip by a cleft on each side, through which the mouth cavity communicates with the "feeding furrow" (l.c., figs 66, 67, 71). The free ventral margin of the lip is only covered by thin cuticle and is wrinkled transversely in the preserved specimens.

The jaw is developed as a shelflike massive thickening of the cuticle on the posterior (oral) surface of the anterior lip (Fig. 12D, Pl. 6:19, 21). It protrudes into the anterior part of the oral cavity with a distinct concave cutting edge and ends laterally with a pointed corner in contact with the free lateral corner of the lip. The jaw is obviously fairly rigid, for in fixed specimens it has none of the small transverse wrinkles which characterize the free margin of the lip, where the cuticle is thin (Pl. 6).

On the other hand, the jaw can clearly be bent in the middle, forming an anteriorly directed angle, for the specimens differ strikingly with regard to the relative direction of the lateral arms of the jaws. In the small *Vema* (specimen 3) and the original *Neopilina* (specimen III) the angle is open so the jaw is crescent-shaped. In the new specimens 1 and 2 *(Neopilina* and *Vema,* resp.) the angle is much smaller, so the two arms of the jaw are nearly parallel, almost occluding the anterior part of the mouth opening (Fig. 12A-C).

At the anterior angle the anterior jaw is continous with the fairly thick cuticular plate which extends anterodorsally and covers the bottom of the anteriorly directed part of the pharynx (Fig. 12, Pl. 6). This plate is touched by the radula ribbon, which is presumed to move forwards and backwards in contact with the corresponding dorsal wall of the pharynx (Fig. 12D).

Histologically the anterior jaw is continuous with the thinner cuticle which covers the free margin of the anterior lip and the bottom of the pharynx. The transition from thin cuticle to jaw structure is so sudden that the outlines of the jaw are clearly demarcated.

The thick cuticle of the jaw can be seen to consist of densely packed, parallel fibers or prisms which are roughly perpendicular to the underlying epithelium. This striation can be seen in the light microscope at higher magnification.

The total thickness of the jaw from the free cutting edge to the basal epithelium varies with the size of the specimens: 30 μm in the minute specimen 3, 80-100 μm in specimens 1 and 2, and probably more than 150 μm in the large specimen III (which is difficult to measure precisely).

As described earlier (L. & W. 1959a, p. 24) the mouth is delimited posteriorly by a transverse wall (posterior lip) formed by median fusion of the two postoral tentacular ridges. This transverse wall is generally covered by a thin cuticle more laterally. In the large original specimens a median plate with somewhat thickened cuticle protrudes from the anterior (oral) surface of the posterior lip like an irregular shelf. This was called "lower jaw" in the original description, but after having seen the thin cuticle and the wrinkled appearance of this structure in the new specimens I realized that the term is an overstatement. There is at any rate no clearly demarcated postoral jaw with constant shape in the new specimens. However, it could be verified that the cuticle of the posterior lip continues as a thin cuticular plate over the central parts of the bottom of the subradular sac (Pl. 6:18, Fig. 12).

Comments: It appears to me that the anterior jaw of Monoplacophora, described above, is homologous with the upper jaw of the gastropods. It is developed by strengthening of the cuticle of an anterior lip and consequently situated in the (morphologically) anterior wall of the oral cavity, opposite to the radula ribbon. In most gastropods the jaw is paired, and consists of two rodlike structures, which meet with their anterior or anterodorsal ends (Hyman 1967, p. 211). In other gastropods the two jaws have fused medially as in the Monoplacophora. According to Fretter & Graham (1962, p. 168), Starmühlner (1952) and Nisbeth (1953) the most important role of the jaw in some gastropods is to work together with the radula and to guide and manipulate the radula ribbon. This may well be true in the Monoplacophora also, for in some specimens the radula has remained close to the jaw, and the radula teeth sometimes touch the jaw and the cuticular plate in the bottom of the anterior pharynx (Pl. 6:20, 21).

That the jaw in gastropods as well as Monoplacophora consists of packed chitinous rods may be taken as an additional structural criterion for homology. However, if this is a general way of producing thick cuticle in molluscs I feel that this support for homology has little weight.

In the Polyplacophora there is generally a cuticle lining the mouth opening and the oral cavity all the way round, and cuticular plates extend into the bottom of the pharynx and into the bottom of the

subradular sac. However, no discrete jaws have been found (Plate 1897, p. 19, Fretter 1937, pp 123-125, my own material of *Lepidopleurus, Lepidochiton* and *Schizoplax).*

Homologous anterior jaws thus appear to be present in the Monoplacophora, the Gastropoda and the Scaphopoda (Simroth 1892-94), possibly also the Cephalopoda (the "upper" jaw). I therefore suggest that the anterior jaw (or jaws) be listed among the synapomorphies of the Conchifera.

4.10.3. The subradular sac and the subradular glands

The new material allows some more details to be studied in the subradular complex, partly because of better fixation, partly because individual variation can be better checked.

The subradular sac of the recent Monoplacophora is a flat unpaired diverticulum of the oral cavity, extending backwards below the radula sheath (L. & W. 1959a, fig. 91). In the original specimen III the sac is strongly compressed and wrinkled. The new specimens give a more reliable picture, and the fact that the different specimens show varying states of protraction of the subradular organ indicates that it can function as in chitons (cf. Heath 1903): it can be protracted and exposed in the oral cavity each time the radula ribbon is retracted.

In specimen 1 *(Neopilina)* the subradular organ and ganglion is somewhat retracted but still at the posterior level of the oral cavity (Fig. 3). In specimen 2 *(Vema)* the organ and the ganglion are strongly retracted, far behind the level of the mouth (Figs 4, 12D), and the small specimen 3 of *Vema* has a completely protracted organ, stretched out in the roof of the oral cavity.

In all the new specimens the subradular organ is a cushion of high epithelium formed by the roof of the subradular sac. The lumen of the sac extends under this cushion as a narrow cleft and ends in the posterior blind end of the sac (Fig. 12D). The organ itself looks strictly unpaired in cross sections, not divided into two cushions as described in some Polyplacophora (Plate 1897, 1899; Haller 1883).

Particular attention was devoted to glandular structures in the subradular sac because of their suggested homologies with subradular glandular structures in different Conchifera, Polyplacophora and Aplacophora (Salvini-Plawen 1972, p. 277). The subradular sac has therefore been searched for the presence of glandular epithelia.

No distinct glandular epithelia could be identified in the roof of the subradular sac. The epithelium which connects the subradular organ with the epithelium supporting the posterior end of the subradular membrane is thin, in some places moderately thick, but does not look clearly glandular.

Areas with pronounced glandular epithelium are, however, found in the floor of the subradular sac. Just behind the posterior lip the central parts of this floor are covered by the cuticular plate which extends from this lip. The same is found in the Polyplacophora (Plate 1899, figs 172, 173). On each side of this cuticular plate there is a strip of high glandular epithelium (Pl. 6:18). More posteriorly where the cuticular plate ends the two glandular strips fuse and cover the entire floor of the sac (fig. 12). The glandular epithelium also extends into the blind posterior end of the sac and lines the cleftlike lumen there.

Thus, with the exception of the cuticularized plate in the anterior part of the subradular sac, the entire floor is glandular. This was easily observed because of the characteristic appearance of the glandular cells in all three specimens (1, 2 and 3). The cells look like mucous cells, but this could not be verified histochemically for the 30-50 μm sections of specimens 1 and 2 did not allow specific methods.

Comments: The distribution of glandular epithelium in the Monoplacophora appears to be almost identical with that found in the subradular sac of the Polyplacophora. In both the glandular epithelia cover the floor and the posterior end, but in the Polyplacophora the blind end may be produced into paired glandular branches or complicated in other ways (Plate 1897, fig. 17; 1899, figs 173-174; 1901, fig. 346). The situation of the subradular organ and of the cuticular plate adds to the similarity of this complex in the Mono- and Polyplacophora.

4.10.4. The salivary glands

L. & W. (1959a, p. 26) reported the salivary gland to be unpaired in *Neopilina galatheae.* The new and better preserved material of *Neopilina* (specimen 1) confirms this description but specimens 2 and 3 clearly show that *Vema* has paired salivary glands, more comparable to those of the Polyplacophora.

In all specimens at hand there are salivary glands developed from the anterior (dorsal) wall of the pharynx, at the level where the first, anteriorly directed pharyngeal part bends dorsally into the vertical part. The glands are situated in front of the margin of the cuticular plate which covers the pharyngeal bottom in front of the jaw (Fig. 12D).

Specimen 1 *(N. galatheae)* looks very like the original large specimens of this species (L. & W. 1959a, figs 81, 124). The anterior wall of the pharynx in front of the cuticular plate is a broad transverse zone of glandular epithelium, reaching from one side to the other across the midline. This glandular zone is folded into numerous deep parallel wrinkles (Fig. 12B).

It was surprising to find that the specimens of *V. ewingi* are completely different, having distinctly paired salivary glands in the same zone. In the small specimen 3 of *Vema* there are two globular glands, evaginated symmetrically on each side of the midline. The broad median wall between the two glandular complexes does not look glandular at all (Fig. 12C, Pl. 7:23).

The larger specimen (2) of *Vema* also has two complexes of glands, each consisting of 4-5 globular diverticula. The broad zone between the two groups of globular glands has a somewhat thickened epithelium but no diverticula of any kind. In each group are one or two particularly large diverticula, perhaps corresponding to the two which are present in the small specimen (Fig. 12A, Pl. 7:22).

Comments: The salivary glands of *Vema* are thus clearly homologous with the salivary glands or "buccal glands" of the Polyplacophora (see Plate 1897, figs 22, 23, 25, and Fretter 1937). In both cases they are paired structures, situated in front of the cuticular plate in a comparable and clearly homologous pharyngeal region. The most obvious difference is that the salivary glands of the Polyplacophora form the extreme ends of ciliated grooves, one on each side, which arise high up on the pharyngeal wall and pass down to the salivary gland on the same side.

The glands present in *N. galatheae* develop in the same zone and appear homologous with those of *Vema* and the Polyplacophora but are interconnected across the midline to form an unpaired complex. It is also possible that the dorsal pharyngeal glands of some gastropods and cephalopods, Solenagastres and Caudofoveata are homologous with these monoplacophoran salivary glands, but the criteria for homology are not equally strong because the location of the glands is less defined and somewhat different in the fairly variable pharynx (cf. Salvini-Plawen 1972, pp 244, 279).

4.11. The stomach, the liver and the crystalline style

The orginal description of the stomach and its adnexa was somewhat uncertain, for the material was deformed and partly disintegrated by crushing and autodigestion (L. & W. 1959a, pp 29-30). The new material is excellently preserved in these parts and allows some more precise descriptions.

4.11.1. The stomach was defined as the inflated part of the alimentary canal which is lined by the high prismatic gastric epithelium. Its shape in the "Galathea" animals was described as triangular when seen from above. This holds fairly good also for the new material, for in *N. galatheae* (1) and *V. ewingi* (2) it is pointed anteriorly and has a broad posterior contour (Figs 13, 14). The shape is certainly somewhat variable depending on the degree of filling. The oesophagus joins the stomach from an anterodorsal direction, above the attachment of the liver. It can be followed for some distance as a fold or ridge on the roof of the stomach. This could not be distinctly seen in the old material which was badly damaged in this region.

In the new material the stomach proper is nearly symmetrical but the intestine has an asymmetrical origin to the left of the midline from the ventrolateral wall (Figs 13, 14).

In the new specimen of *N. galatheae* (1) there is a voluminous and fairly well delimited style sac, evaginated from the dorsal part of the hind wall of the stomach. It contains what is believed to be a primitive crystalline style. In the original material (specimen III) such a sac was present but appeared to be approximately median, above the origin of the intestine. This certainly depended on artificial dislocations, for in the new and practically intact specimen (1) the style sac is clearly to the right of the midline and is clearly separated from the intestine on the left side (Fig. 13).

In *V. ewingi* (specimen 2) the style sac is not clearly delimited, but there is a shallow, approximately median evagination containing what seems to be a primitive style (Fig. 14). A small fold seen on the dorsal surface of this region may be a doubled part of the empty style sac but could also be a simple artifact.

4.11.2. The liver, attached to the stomach, is strongly lobulated in its peripheral parts. Its walls are characterized by the very high epithelial cells

with spherical secretion granules, described by L. & W. (1959a, p. 30, figs 107, 108). The communication between the liver and the stomach was originally described as "a long slit-like opening", which is correct, but several important features passed unnoticed in the badly preserved original material (1. c., figs 8, 108).

The new specimens 1 and 2 are practically intact in the liver region. They show clearly the following features:

1. The liver is, strictly speaking, unpaired. The liver complex of the right side is continous with that of the left, connected by an isthmus following the anterior contour of the stomach, below the entrance of the oesophagus. The liver has an extensive zone of contact with the anterolateral margins of the stomach, and the contact is uninterrupted anteriorly where the isthmus is attached to the anterior stomach wall (Figs 13, 14, Pl. 7:24).

2. Communication between the liver and the stomach is established by a long, cleftlike opening which extends from the anterolateral margin of the right side, below the entrance of the oesophagus to the anterolateral margin of the left side. The epithelium suddenly changes from the gastric type to the hepatic type, both in the dorsal and ventral walls of the cleft (Pl. 7:25).

3. The proximal parts of the liver, attached to the stomach, contain a continuous open lumen, which communicates with the stomach through the cleft. This vestibulum-like proximal lumen is continuous all the way round the anterior half of the stomach. No lobules start directly from the stomach or from the adjacent walls of the vestibulum. The numerous liver lobules grow out from the more peripheral walls of the vestibulum (Fig. 13B).

The sharp limit between gastric and hepatic epithelia excludes confusion of liver parts and of the stomach. Moreover, a furrow on the ventral surface marks the transition from stomach to liver, following the level of the communicating cleft (Fig. 13B).

Suspecting that the embryonic liver rudiment is paired as in the Polyplacophora I carefully checked the "isthmic" zone for signs of this, both in *Vema* and *Neopilina,* but found none. The lumen of the vestibulum can be followed from left to right side through the isthmic region, and the cleftlike communication with the stomach passes over the midline without interruption. This can even be seen in single sections (Pl. 7:24). In specimen 1 *(Neopilina)* two of

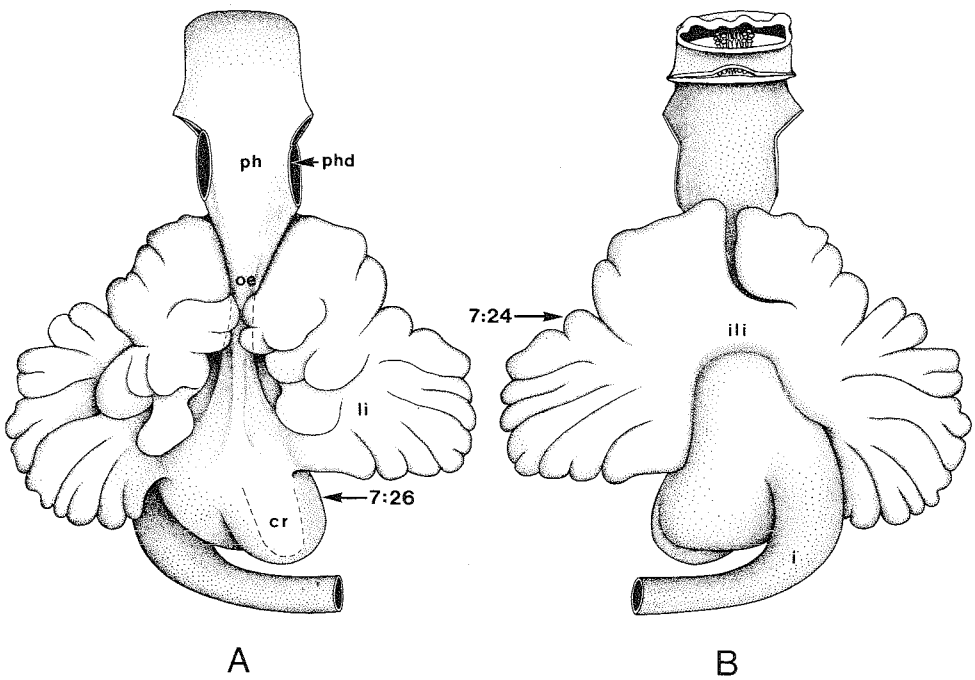

Fig. 13. *Neopilina galatheae,* specimen 1. Pharynx, oesophagus, stomach, liver and anterior intestine. Graphic reconstruction. Level of sections shown in plates are indicated.

A, dorsal view. B, ventral view. cr, crystalline style; i, intestine; ili, isthmus between right and left liver; li, liver; oe, oesophagus; ph, pharynx; phd; opening into pharynx of pharyngeal diverticula.

the medial lobules are separated by a fairly deep cleft, but this does not cut through to the stomach, so the vestibulum is uninterrupted medially (Fig. 13B). In specimen 2 *(Vema)* there are several shallow interlobular clefts in the same region but no interruption of the isthmus.

Comments: The liver of the Monoplacophora as found in *Vema* and *Neopilina* is unpaired but bilobed, actually appearing as a broad and flattened pouch from the whole anterior margin of the stomach, and the broad communication between the two organs is not constricted to form a "liver duct" but remains broad. The liver is - as far as can be seen, symmetrical.

The liver of the Polyplacophora, as described by Haller (1882), Plate (1901, pp 439-444) and Fretter (1937) is different in that it is clearly paired. In the adult the right and left liver parts are strongly asymmetrical with regard to size and localization, and their communication with the stomach is asymmetrical (or fused) and constricted to narrow pores. A symmetrical pair of liver rudiments is present in early ontogenetical stages of *Acanthochiton* (Hammarsten & Runnström 1925) and young *Ischnochiton* (Plate 1901). If embryonic Monoplacophora have paired, pouchlike liver rudiments like the Polyplacophora, one must assume that these rudiments fuse early across the midline below the oesophagus.

4.11.3. The crystalline style was originally described on the basis of material from a single specimen (L. & W. 1959a, pp 29-30), as the second specimen available at that time for some reason failed to show it. I have paid much attention to this structure in the new material for two reasons: 1) None of the specimens examined possesses a cuticular gastric shield or similar structure, although such a shield is correlated with the presence of a crystalline style in lamellibranchs and gastropos. 2) Graham (1959) suggested that the style originally described could in fact be a faecal string, for such strings can look like crystalline styles and are present in the same region of many primitive gastropods.

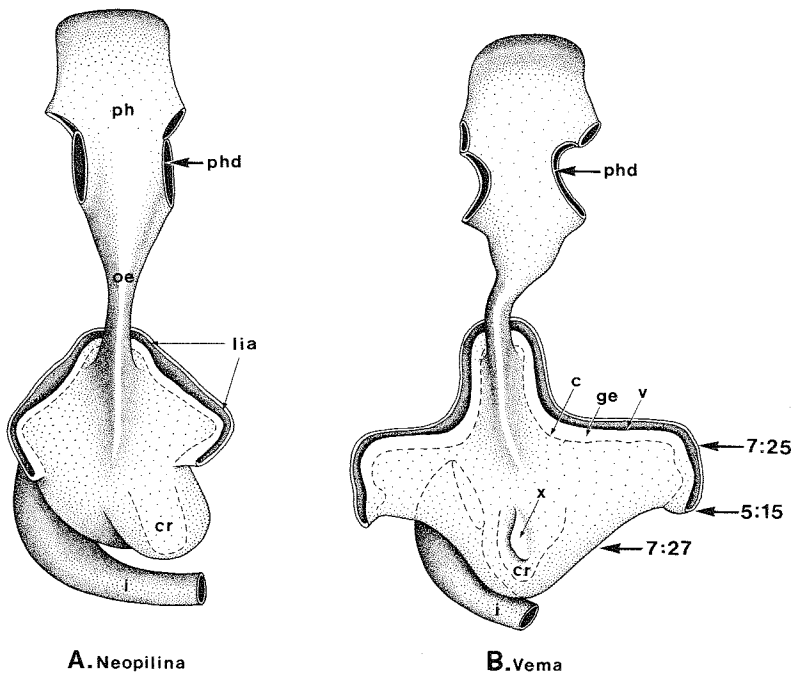

Fig. 14. Pharynx, oesophagus, stomach, and intestine. Dorsal view, reconstructed graphically, to show communication between liver and stomach. The liver is removed.

A, *Neopilina galatheae,* specimen 1. B. *Vema ewingi,* specimen 2.

c, the dotted line shows approximately the constriction of lumen between stomach and liver; cr, crystalline style; ge, gastric epithelium extending into the roof of the cleft between liver and stomach; i, intestine; lia, cleftlike attachment of liver along the antero-lateral aspects of the stomach, below the oesophagus; oe, oesophagus; ph, pharynx, phd, pharyngeal diverticula; v, vestibulum-like open lumen of liver communicating with the stomach; x, dorsal fold of stomach, artificial or remnant of top of style pouch.

None of the new specimens exhibits a crystalline style of the very distinct, strongly stainable type seen in the original specimen III. But a probably equivalent conelike body is present both in *N. galatheae* (1) and *V. ewingi* (2). The outlines and situations of the styles are shown in Figs 13 and 14. The styles of both new specimens have the appearance of somewhat irregular cones; that of specimen 1 distinctly has its narrow posterior end in the presumed style sac. The style of specimen 2 has a similar situation but the style sac is not clearly delimited. Cross sections show an indistinct concentric or spiralized internal structure (Pls 7:26 and 27).

As in the original specimen III, the style in each of the new specimens follows the roof of the stomach from the style sac in an anterior direction, but it becomes indistinct and disappears before reaching the level of the oesophagus. The anterior parts contain some food particles embedded between the layers of mucuslike matter.

The style is undoubtedly identical in the original specimen III and the two new specimens 1 and 2. The weaker staining in the new specimens can well be a consequence of the different staining techniques: Mallory's phosphotungstic acid hematoxylin and Friedländer-Ehrlich's alum hematoxylin, resp. The style of the new specimens is clearly separated from the exit of the intestine, which is on the left side, whereas the style sac with the style is middorsal or over on the right side (Fig. 14). The "style" can therefore not be a faecal string (cf. Graham 1959).

The anterior disintegrating part of the style is just behind the entrance of the oesophagus, as would be expected if it were a condensed mucus string from the oesophagus. But this does not explain why all styles seen up to now clearly disintegrate in their anterior ends, or why they are more solid and contain no food particles in their posterior end. The possibility that the style comes from the oesophagus is also contradicted by the fact that new mucus cornets seem to be added from behind in the strongly stained original specimen III (L. & W. 1959a, p. 29).

Studies of the well preserved gastric epithelium in the new specimens confirm that there is no gastric shield or comparable structure. The dorsal gastric wall, along which the style extends, has a particularly strong ciliation. Specimen 1 *(Neopilina)* which is particularly well fixed, seems to show that strong secretion is going on from the style sac epithelium at the level of the posterior end of the style. The peripheral ends of the cells are more stainable than in other parts of the stomach, and their distal ends bulge as if droplets were about to be detached. This could indicate that the mucuslike style material is secreted in the posterior part of the style sac as expected.

Comments: A mucoid body similar to the supposed crystalline style of the old specimen III was found also in the new specimens, situated with its posterior end in what seems to be a style sac (in specimen 1). The new well-preserved specimens show definitely that the cone-shaped mucus body is not a faecal string and make its interpretation as a food string from the oesophagus highly improbable. It is therefore probable that it is a true crystalline style, homologous with that of lamellibranchs and some gastropods. However, the absence of a gastric shield and the fact that the style is very short and irregular makes it look less perfected than the style apparatus of lamellibranchs and gastropods. Perhaps it is a primitive issue of a homologous enzyme-secreting apparatus.

4.12. The radula apparatus

The material for the original description of the radula apparatus in the Monoplacophora was deficient, particularly with regard to the radula vesicles, which had exploded and collapsed (L. & W. 1959a, pp 25-29, 39-42). Nevertheless the original description proved essentially correct when compared with the three new specimens, which have intact radula vesicles and well-preserved radula cartilages, radula sheaths and muscles (Pls 2, 5, 6).

The radula apparatus of *Neopilina* is identical in all essential respects with that of *Vema,* so I have found it unnecessary to repeat the verbal description for the latter species. Instead I present a series of figures showing the radula apparatus of *Vema,* with short comments and references to the original description of *Neopilina.* The new figures of *Vema* mostly show the radula apparatus in side view and supplement the original figures, which show dorsal views. Together the new and the original figures should give a better picture of the three dimensions.

4.12.1. The radula support ("odontophore", "tongue")

In all three new specimens the radula vesicles are elongate, ovoid bodies with converging anterior ends (Fig. 15A, B). Their walls consist of thin parallel lamellae, 7-9 in the larger specimens 1 and 2, but only 4 lamellae in the small specimen 3. Each of

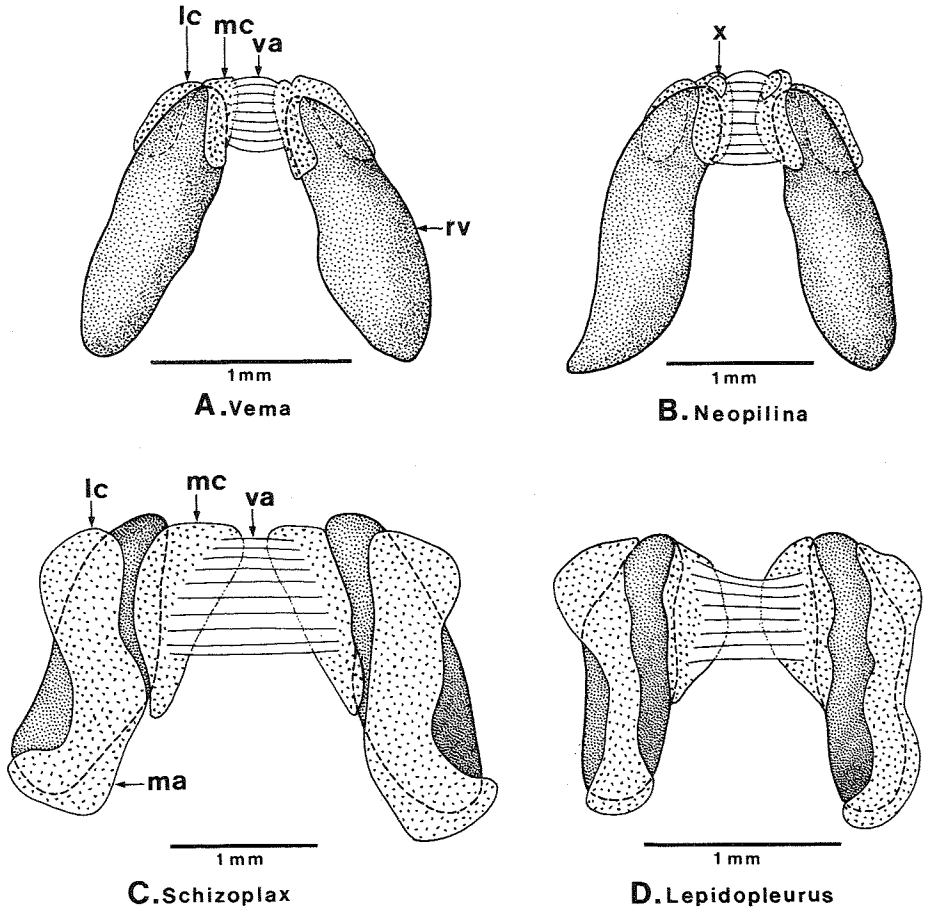

Fig. 15. Radula vesicles, radula cartilages and ventral approximator muscle (m. radulae impar) in A, *Vema ewingi,* specimen 2, B, *Neopilina galatheae,* specimen 1, C, *Schizoplax* sp., and D, *Lepidopleurus asellus.* Graphic reconstructions, seen from the ventral side. lc, lateral cartilage; mc, medial cartilage; rv, radula vesicle; va, ventral approximator muscle (m. radulae impar); x, small block of cartilage, partly separate from the medial cartilage.

these lamellae is about 1 μm thick, without apparent structure in the light microscope, and stains lightly with hematoxylin (Pl. 8:28). A few scattered cell bodies with nuclei attach to the surface of the lamellae, which are densely packed in some parts of the wall but more loosely arranged with large interspaces in others. The latter state may be an artifact. No distinct epithelium is seen lining the lumen of the vesicles, but several small nuclei attached to the innermost lamellae indicate that there is a very thin cellular sheath, although the plasm is invisibel with the staining used (hematoxylin) (Pl. 8: 28).

The anterior ends of the radula vesicles are partly covered by vesicular tissue resembling the "pseudocartilage" of mollusc odontophores. In all examined specimens of Monoplacophora this pseudocartilage is restricted to the anterior third of the radula vesicles and does not extend to the posterior ends as in the Polyplacophora (Fig. 15A, B). The morphology of these cartilages could be analyzed in the new specimens (1, 2 and 3) but was so badly preserved in the "Galathea" specimens that the original description could not include any details.

Each radula vesicle is associated with a medial and a lateral cartilage (Fig. 15, Pl. 6). Both are flattened, bandlike structures closely attached to the surface of the vesicle. The two cartilages meet at the anterior point of the vesicle, and in that region a small block is partly detached from the medial cartilage (Pl. 6:21). Near their margins the cartilages intermingle with some of the superficial lamellae of the wall, which spread into the vesicular tissue of the pseudocartilage (Pl. 8:28).

The radula vesicles are quite regular, oval, and seem to be completely empty in the sections. Like the homologous vesicles of chitons they probably con-

tain some fluid in the living animal and act as a kind of rigid skeleton: the turgor pressure of the contents making them hard (see L. & W. 1959a, p. 28).

The medial cartilages of left and right radula vesicles are interconnected over the midline of the animal by a short and strong muscle: musculus radulae impar (Fig. 15; Pl. 6:17). This muscle, the radula cartilages and the anteromedial ends of the radula vesicles form a transverse bar, over which the radula ribbon can slide. The bar is located in the angle between the radula sheath and the ascending pharynx, just above the anterior part of the oral cavity (Fig. 16).

Comments: The homology of the radula vesicles of the Mono- and Polyplacophora was suggested by L. & W. (1959a, p. 31) and seems to have been accepted. This similarity can now be extended to the entire radula support, for the medial and lateral cartilages of the Monoplacophora have their counterparts, in corresponding locations, in the Polyplacophora (Fig. 15; Pls 6, 8). The only significant difference is that these cartilages are larger in the examined Polyplacophora. In chitons the lateral cartilage even extends to the posterior end of the vesicle, which is covered by a cup-shaped layer of cartilage (Fig. 15C, D). This cartilaginous cup serves as origin of several important radula muscles, which appear to attach directly to the connective tissue of the vesicle in the Monoplacophora.

Except for the Polyplacophora, such a radula support with radula vesicles does not seem to have been reported from other molluscs. In searching for a homologous structure I paid particular attention to the radula of the docoglossan prosobranchs, which is similar to that of Mono- and Polyplacophora in several respects: docoglossan type of dentition, presence of comb-shaped teeth in the Lepetidae

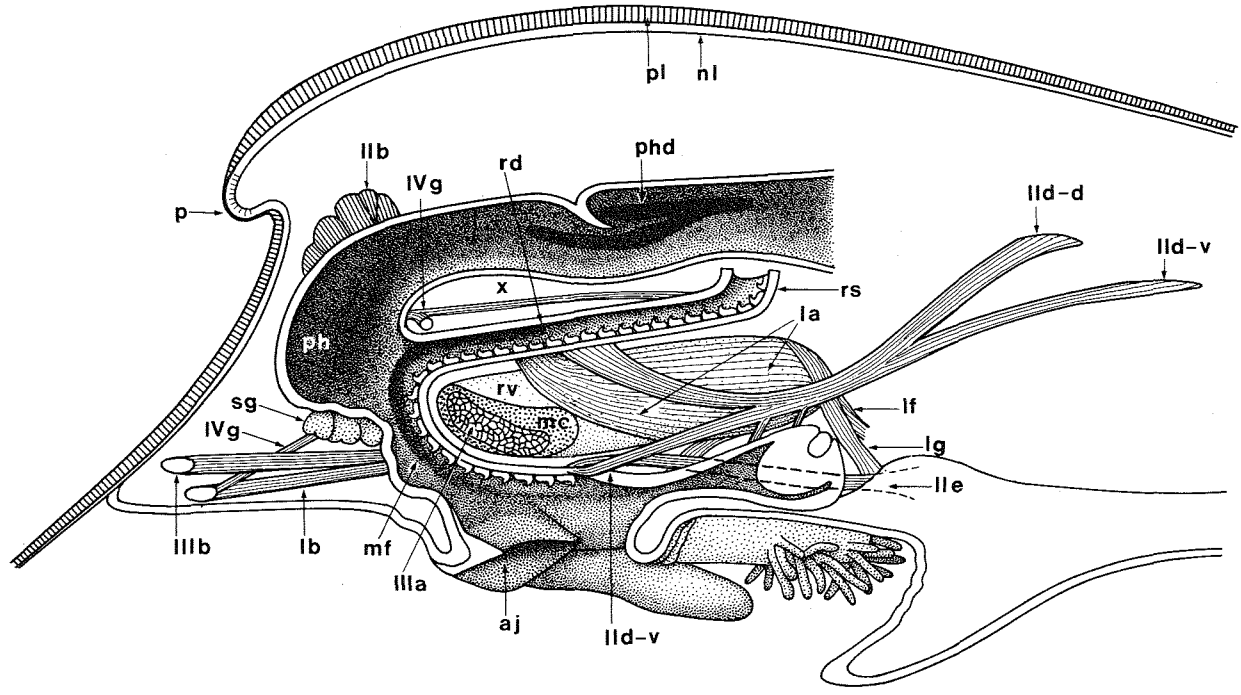

Fig. 16. *Vema ewingi*, specimen 2. Right half of anterior body, seen from the median section, to show the principal structure of the radula apparatus and the medially situated radula muscles. Based on graphic reconstruction, except for the shell which is added arbitrarily (partly destroyed by decalcification). The pharynx and radula sheath are elevated and separated in relation to the raw reconstruction, to give more space and avoid mutual covering of muscles and other structures.

aj, anterior jaw; mc, medial cartilage; mf, marginal furrow with thin walls along margin of subradular membrane; nl, nacreous layer of shell; p, protoconch scar; ph, pharynx; phd, opening of pharyngeal diverticula into the pharynx; pl, prismatic layer of shell; rd, inner end of radula diverticula; rs, radula sheath; rv, radula vesicle; sg, salivary gland. — *Muscles* (numbers refer to text): Ia, m. retractor radulae; Ib, m. protractor vesicae major; If, m. vesicae postero-lateralis; Ig, m. vesicae medialis; IIb, "m. protractor radulae"; IId-d, m. radulae longus pars dorsalis; IId-v, m. radulae longus pars ventralis; IIe, m. pharyngeus marginalis; IIIa, m. radulae impar (= ventral approximator); IIIb, m. protractor cartilaginis profundus; IVg, m. protractor diverticulorum; x, branches of muscle IVg on the dorsal side of the radula diverticula, equivalent to Plate's muscle 4 in the Polyplacophora.

(Troschel 1866-93), similar radula musculature (Graham 1964, 1973) and comparable radula cartilages. No really hollow radula vesicles were found in the docoglossan gastropods examined, but it is possible that the anterior cartilage of *Patella* includes the homologue of a radula vesicle as suggested by Graham (1964, p. 326). This will be further dealt with in chapter 5. 4. 3.

4.12.2. The radula ribbon

The radula ribbon, the radula diverticula, and the radula sheath were checked in the new material and found to be as described by L. & W. (1959a, pp 25-28). The gross structure of *Vema* (Fig. 16) was found to be very similar to that of *Neopilina.*

The morphology of the radula teeth of the Monoplacophora is now much better known thanks to McLean's comparisons of *N. galatheae* with his own whole mounts of the radulae of *N. veleronis, N. hyalina* and *Vema ewingi.* McLean found general agreement in the dentition of the species, but also some differences which may be used taxonomically (McLean 1979).

The radular ribbon was one of the few intact structures in the adult specimen XIV of *N. galatheae,* which had been completely crushed. Realizing the importance of the tooth morphology for taxonomic purposes I dissected the radula from this specimen free and cleaned it (in alcohol) by treatment with ultrasound. The part of the radula ribbon immediately behind the diverticula (rows 10-25) was then air dried and mounted for scanning electron microscopy, in order to control the drawing of the original report in L. & W. (1959a, figs 87, 88).

The SEM pictures (Pl. 9) generally confirm the original drawings, but a few new details can be added or better documented:

1. The middle tooth (rachidian) and the 1st lateral tooth are small with a slightly inflated point, which is raised but not really overhanging and reflexed. The rachidian is somewhat smaller than the 1st lateral and does not reach as far anteriorly (Pl. 9:36, 38).

2. The 2nd og 3rd laterals are the strongest teeth, with big, overhanging hooks. The 3rd bends medially so its hook is almost directly behind that of the 2nd. The hook of the 3rd tooth looks somewhat broader than that of the 2nd, but this is mainly because of its oblique orientation.

McLean was right when he suspected that we had partly missed the overhanging tip, so that the size and particularly the length of laterals 2 and 3 appear too small in our drawing (McLean 1979, p. 15). In the scanned material the hooks of these teeth were partly straightened out when the radula was dried (the process could be observed in the dissection microscope). It was therefore possible to get a SEM picture of the entire straight 2nd lateral (Pl. 9:38). Its length is 0.50 mm instead of 0.35 mm as it appears to be in the reflexed state. But even if this source of error is considered, the hooks of *Neopilina* appear shorter than those of *Vema ewingi* (compare McLean 1979, figs 22-25).

3. The combshape of the 1st marginal is even more striking in the SEM pictures than in the original drawing (Pl. 9:35, 37).

4. The 2nd marginal is triangular, with a fairly broad raised edge anteriorly, but there is no overhanging hook (Pl. 9:39).

Comments: The monoplacophoran radula was from the start found similar to that of the polyplacophorans and docoglossan prosobranchs (L. & W. 1959a, p. 31). In all these groups there is a rasplike radula ribbon with strong, hooked lateral teeth as the main mechanical component, and lateral movement of teeth is not pronounced. More specific features are also shared, e.g., the moderate development or reduction of the rachidian, and the small often platelike marginals.

The most important single feature is the comb-shaped inner marginals encountered in the Monoplacophora (Pl. 9:35, 37), some Polyplacophora (Plate 1899, p. 144: Troschel 1866-93, p. 389) and some lepetid docoglossan snails (Troschel 1866-93, pp 349-50). In the polyplacophorans *Tonicella* and *Nuttalochiton,* one of the marginals bends inwards behind the large hooks and bears a fringe of denticles very much like those on the 1st marginal of *Neopilina* (compare Pl. 9: 35, 37 with Pl. 10:4D). But the comb tooth is number 4 from the rachidian in the monoplacophorans and number 5 from the rachidian in the polyplacophorans, and the radula formula is 5 + r + 5 in the former, 8 + r + 8 in the latter.

Two comblike marginals are present on each side in some lepetids, viz. *Cryptobranchia alba* and *Pilidium fulvum,* but in this case the radula is strongly reduced (Troschel 1866-93, pp 349-50).

Comparisons between comblike teeth like those mentioned and the multiple teeth in rhipidoglossan radulae, e.g., *Pleurotomaria,* were attempted by L. & W. (1959a, p. 31) but appear fairly hypothetical.

4.12.3. The radula muscles

The radula muscles have been reconstructed as completely as possible in the larger specimen of *Vema*

ewingi (specimen 2), and nearly complete identity was found with the radula muscles of *Neopilina galatheae.* Also the minute specimen 3 of *Vema* was reconstructed, and all the important muscles were refound. Only some of the smallest muscles were missed — as could be expected in the small (1.8 mm) specimen.

In the following text the radula muscles of *Vema* are listed with short comments and reference to the drawings (Figs 16, 17, 18), and to the description of the muscles in *Neopilina* (L. & W. 1959a, pp 39-42). The nomenclature and the abbreviations are the same as in the original description so that the two species can be compared directly. The drawings are all based on lateral reconstructions and are intended to supplement the original description, which was based on dorso-ventral reconstructions only and, probably therefore, has been misunderstood on some points.

The designations of the muscles in the figures in the present paper refer to their place in the text. The muscle Ia is thus m. retractor radulae and is found under the head I, muscle IIc is m. tensor radulae and found under the head II.

I. Muscles inserting on the posterior tip of the radula vesicles (Figs 16, 17, 18)

Ia) m. retractor radulae (m. re. ra.) — Figs 16, 17

Ib) m. protractor vesicae major (m. pro. ve. ma.) — Fig. 18

Ic) m. protractor vesicae minor (m. pro. ve. mi.) — Figs 17, 18

Id) m. vesicae anterolateralis (m. ve. a-l.) — Figs 17, 18

Ie) m. vesicae anteromedialis (m. ve. a.-m.) — Not found in *Vema*

If) m. vesicae posterolateralis (m. ve. p-l.) — Figs 17, 18

Ig) m. vesicae posteromedialis (m. ve. p-m.) — Figs 16, 17, 18

Ih) m. vesicae ventralis (m. ve. v.) — Figs 17, 18.

With the single exception of muscle Ie, all these muscles were identified both in *Vema* and *Neopilina* and have a very similar course in the two species.

Muscle Ia, m. retractor radulae, inserts on the tip of the radula vesicle and follows a somewhat coiled course, passing as a flat membrane over the medial and lateral surface of the radula vesicle to the posterior margin of the radula diverticulum of the same side. It appears to be the most powerful retractor of the subradular membrane, homologous with that of the Polyplacophora and some gastropods (cf. Graham 1973).

The other muscles of the group appear to manipu-

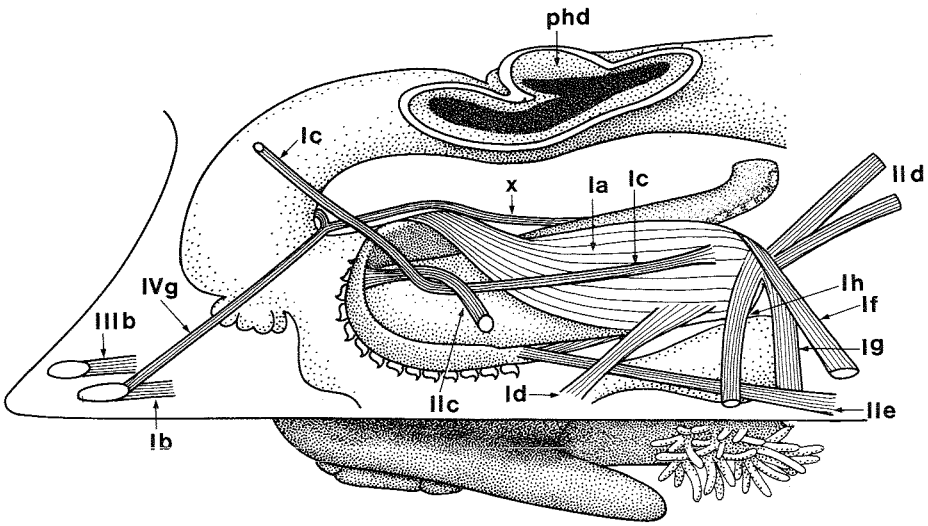

Fig. 17. *Vema ewingi,* specimen 2. Pharynx and radula apparatus, including radula vesicles, seen from the left. Some radula muscles of the left side are shown. The pharyngeal diverticula are removed but their opening into the pharynx is shown (phd). Graphic reconstruction with radula sheath in situ. *Muscles:* Ia, m. retractor radulae; Ib, m. protractor vesicae major; Ic, m. protractor vesicae minor; Id, m. vesicae anterolateralis; If, m. vesicae posterolateralis; Ig, m. vesicae posteromedialis; Ih, m. vesicae ventralis, IIc, m. tensor radulae; IId, m. radulae longus; IIe, m. pharyngeus marginalis; IIIb, m. protractor cartilaginis profundus; IVg, m. protractor diverticulorum; x, branches of IVg on the dorsal side of the radula diverticula.

late the tip of the radula vesicles (Id-Ih) and pull the vesicle forwards (Ib-Ic). Together these muscles seem to be able to control the angle between the radula vesicles and to control the inclination of the odontophore as a whole.

II. Muscles of the subradular membrane
(Figs 16, 17, 18)

IIa) m. retractor radulae (= Ia) mentioned above
IIb) m. protractor radulae (m. pro. ra.) — Fig. 18. Includes many heads on the shell, also two heads which were believed to end on the radula cartilage of *Neopilina* and were called m. protractor cartilaginis dorsalis. This was clearly wrong (see below!)
IIc) m. tensor radulae (m. te.ra.) — Figs 17, 18
IId) m. radulae longus (m. ra. l.) — Fig. 16
IIe) m. pharyngeus marginalis (m. ph. m.) — Figs 16, 17, 18.

All these muscles were refound also in *Vema ewingi,* but a correction is necessary with regard to the two ventrolateral heads of muscle IIb (m. protractor radulae). In the well preserved material of *Vema* these two muscles can be seen to attach under the margin of the subradular membrane and thus clearly belong to the series of heads of the m. protractor radulae. In the original *Neopilina* material these two heads were believed to pass to the surface of the cartilage and were called "m. protractor cartilaginis dorsalis". This was clearly a mistake caused by poor preservation of the specimen.

The most remarkable of these muscles is the IIb complex, called m. protractor radulae, which seems to lack a homologue in gastropods and polyplacophorans. It may act as a protractor of the subradular membrane when the odontophore is in a high situation as in Fig. 18 and the radula ribbon is retracted, whereas some of its bundles could retract the subradular membrane and the entire radula apparatus when the odontophore is depressed and the subradular membrane is protracted. Only experiments can solve this problem, and this is certainly hampered by difficulties involved in getting living material of the largesized species. Muscle IIb is one of the largest muscles of the Monoplacophora.

Muscle IId, m. radulae longus, consists of two almost independent portions, which are partially fused halfway between the origin and the insertion (Fig. 16). The dorsal portion (m. radulae longus pars

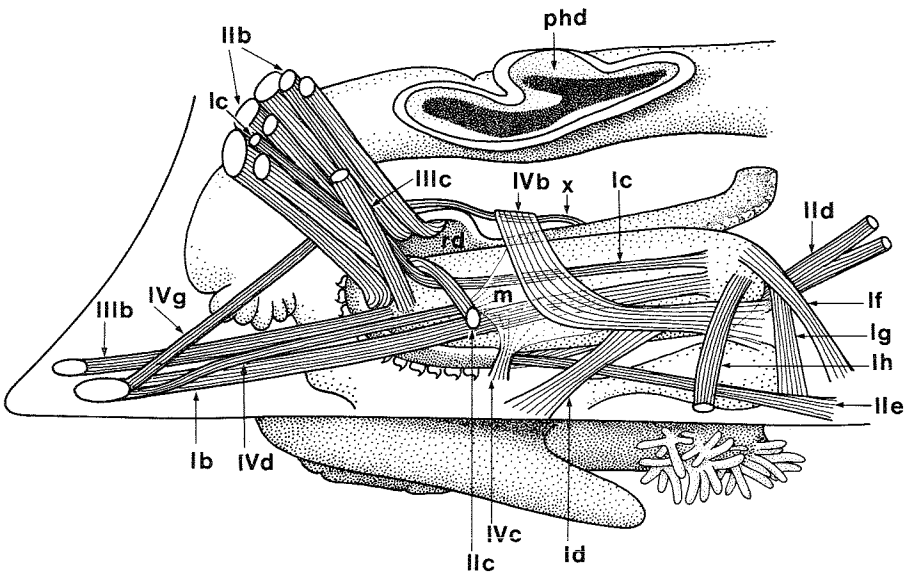

Fig. 18. *Vema ewingi,* specimen 2. As Fig. 17, but practically all radula muscles seen from the left side are included. m, membrana lateralis, a connective tissue membrane to which some muscles (IVc, IVd) attach; phd, opening of pharyngeal diverticula into the pharynx; rd, radula diverticulum of left side.

Muscles: Ib, m. protractor vesicae major; Ic, m. protractor vesicae minor; Id, m. vesicae anterolateralis; If, m. vesicae posterolateralis; Ig, m. vesicae posteromedialis; Ih, m. vesicae ventralis; IIb, "m. protractor radulae"; IId, m. radulae longus; IIc, m. tensor radulae; IIe, m. pharyngeus marginalis; IIIb, m. protractor cartilaginis profundus; IIIc, m. cartilaginis anterolateralis; IVb, m. transversalis anterior; IVc, m. tensor membranae lateralis; IVd, m. tensor membranae anterior; IVg, m. protractor diverticulorum; x, branches of IVg, on the dorsal side of the radula diverticula.

dorsalis, IId-d in the figures) is clearly a retractor of the radula ribbon, acting on the ventral side of the radula sheath just behind the radula diverticulum (Fig. 16, Pl. 5). The ventral portion (IId-v in the figures) passes down to the roof of the oral cavity and is clearly a protractor of the subradular membrane; some of its small branches may also retract the subradular sac (Fig. 16). Muscle IId is by far the longest of the radula muscles. The two heads extend caudally to a level far behind the radula vesicles and attach to the dorsal shell medial to pedal retractors B and C (Figs 10,11).

III. Muscles of the radula cartilages

IIIa) m. radulae impar (m. r. i.) — Figs 16, 15, Pl. 6

IIIb) m. protractor cartilaginis profundus (m. pr. ca. p.) — Fig. 18

IIIc) m. cartilaginis anterolateralis (m. ca. a-l.) — Fig. 18. Is perhaps a levator more than a retractor

IIId) m. protractor subradularis (m. pr. sr.) — Not found in *Vema.*
Only the small muscle IIId could not be identified in *Vema.* The other three muscles are easily reconstructed in both genera.

IV. Other muscles of the radula apparatus

IVa) m. radulae minor (m. ra. mi.). A small muscle, not clearly identified in *Vema*

IVb) m. transversalis anterior (m. tr. a.) — Fig. 18, Pl. 6

IVc) m. tensor membranae lateralis (m. te. m. l.) — Fig. 18

IVd) m. tensor membranae anterior (m. te. m. a.) — Fig. 18

IVe) m. transversalis posterior (m. tr. p.). Very small in *Vema,* not reconstructed.

IVf) m. pharyngei preorales (mm. pha.). Present as small strands from pharyngeal roof to anterior shell in *Vema.* Not shown in the figures.

IVg) m. protractor diverticulorum (m. pr. div.) - Fig. 17.

Muscles IVa-IVg are all small and seem to maintain the radula, the radula sheath, the larger muscle bundles, and pharynx in their proper positions. Muscle IVg is continuous dorsally with its contralateral partner, and with small longitudinal muscles on the dorsal side of the radula diverticula. These latter are marked × in Figs 16, 17 and 18 and correspond in part to Plate's muscle 4 (Plate 1897, p. 46, figs 20,25) in the Polyplacophora.

5. DISCUSSION

5.1. Morphological features of metamerism in recent Monoplacophora

The original description of metarism in recent Monoplacophora was founded on a very small material (L. & W. 1959a). Only one somewhat defective specimen (III), cut transversely, was available for graphic reconstructions, while another specimen (IV), cut horizontally, was used for wax-plate reconstruction as a control. Mistakes caused by deficient preservation and individual variation could therefore hardly be excluded, and it was thus natural that the results were reluctantly accepted. Moreover, the violent theoretical criticism in many subsequent papers cast doubts and uncertainty as to the presence of a metameric organization in these animals and the way it was described.

Now that more material has accumulated, a general review of the metameric structure of these animals seems useful. The new material leaves no doubt about the presence of metamerism in the sense that some organs are repeated following a common rhythm. This has to be accepted as a fact, and is essential for the characterization of recent Monoplacophora. Its theoretical interpretation — whether the metamerism here is related to the metamerism of articulates or not — is of course still open to discussion but, I hope, on a more stable basis.

5.1.1. Introductory remarks

The new material revealed some mistakes and misinterpretations in the first descriptions, which must be considered in a new discussion of metamerism.

1. The "dorsal coelomic sacs" of the original report turned out to be misinterpreted. They are large pharyngeal diverticula, and they do not show metameric subdivision. The latter question was left open in the original report (op. cit. pp 55-57). Whether or not metameric tendencies can be seen in the developing mesoderm of embryos and larvae is still unknown.

2. The "nephrostomes" described with some reservation in the original report are not present in the pre-pericardial region, but it is possible that there are connections between the nephridia and the pericardia in the sectors F and G (Chapter 4.7).

3. A coiled larval shell like that originally described in *Neopilina galatheae* (Lemche 1957, L. & W. 1959a) is not present. The true larval shell as described by Menzies (1968) is a bulbous, bilaterally symmetrical structure with some exogastric coiling. This statement removed one of the most intriguing obstacles for understanding monoplacophoran morphology, for a bilateral metameric structure would not be expected in animals which have an asymmetrically coiled shell.

In other respects, e.g., with regard to repetition and spatial relations between muscles, nerves, nephridiopores, gills, atria, gonoducts, and gonads, the originally described metameric pattern of *N. galatheae* is confirmed in the new material. The specimens of *Vema ewingi* show significant differences, however; the species has a more complete metameric repetition of organs, and therefore confirms the original views.

5.1.2. The case of *Neopilina galatheae*

The new specimen 1 is immature but in general confirms the original description. The metamerism of the musculature, nerve connectives, nephridiopores, nephridia, gills, gonads, and gonoducts is practically identical in the new specimen and in the old mature specimen III (compare Figs 3, 8, 10 of the present account with figs 121, 135, 145 and 146 in L. & W. 1959a).

Even certain irregularities have been refound in the new material. Pedal retractors A and B are closer together than the others, and the gill C appears anteriorly dislocated in relation to pedal retractor C in the same way as in the old material (Fig. 3).

Comparison of the old material with the new

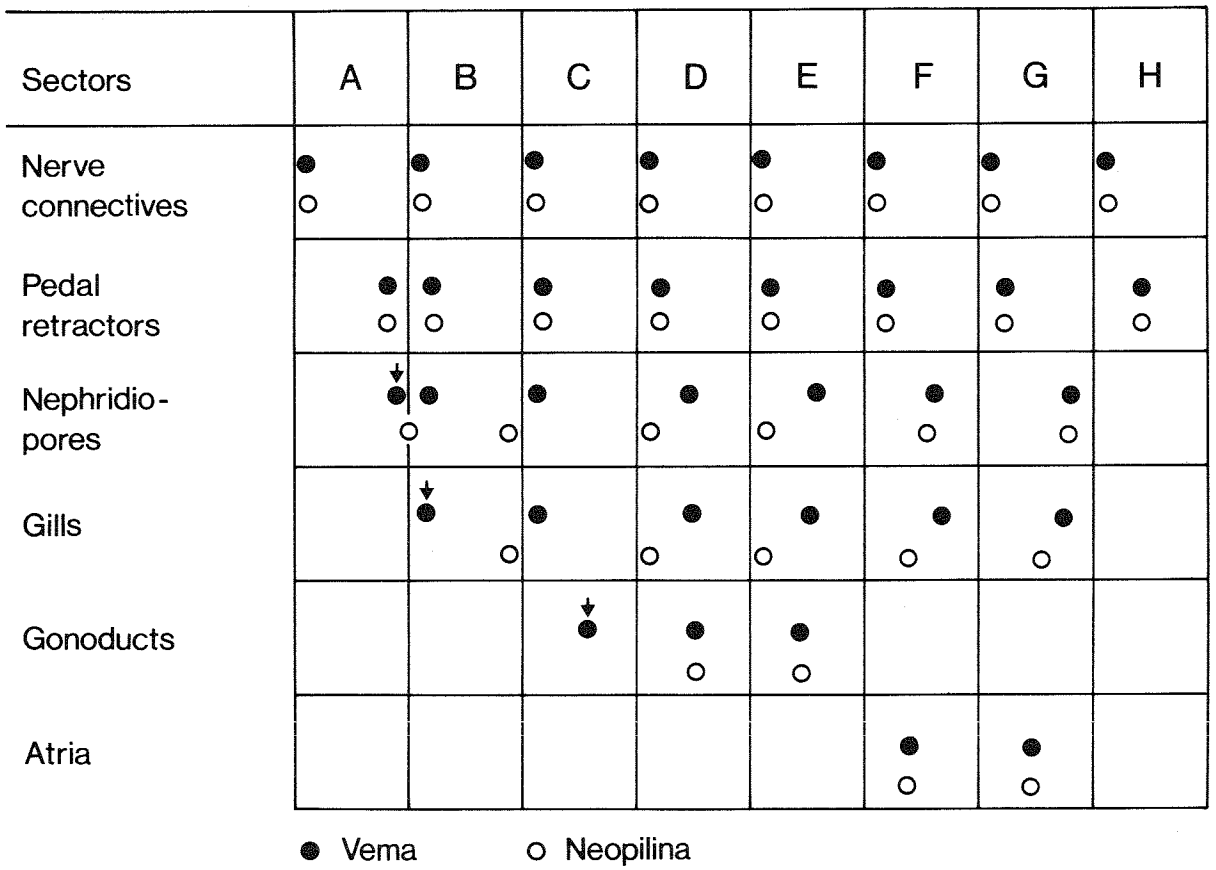

Table 1

The metameric repetition of organs in *Neopilina galatheae* (open circles) and *Vema ewingi* (filled circles) plotted into the system of sectors in both animals. The sector limits are arbitrarily chosen as the lateropedal nerve connectives (compare Figs 3, 4, and 8-11). Arrows indicate organs not present in *Neopilina*.

specimen 1 thus indicates that the picture originally given for *N. galatheae* is typical of the species. Individual variation seems to be restricted. In the case of specimen 1 the observed variations are: unilateal duplicity of the head of retractor C on the left side, where it consists of two unequal portions, and a strong asymmetry of the hindmost retractor (H); the left one is much smaller than the right one (Fig. 3).

I have summarized the metameric pattern of *N. galatheae* in Table 1, using the previously introduced sector system as an arbitrary, descriptive basis. Readers finding this too crude and subjective can compare with the actual reconstructions (Figs 3, 8, 10).

I also maintain that the often used diagram in fig. 165 of our original monograph (1959a) fits in principle with the new material and can be used for orientation, if it is remembered that the nephrostomes of kidneys C, D, and E are doubtful and should be removed. As indicated on p. 11 in the same monograph, diagrams like this are simplified to show as clearly as possible what is meant in the text, and readers must thus accept some loss of detail and accuracy of proportions. The legends of fig. 165 expressly state that the figure is a diagram, so we did not expect readers to use it as a piece of documentation for details. There are several figures in the same volume which show actual reconstructions for those readers who want precise information.

I was therefore astonished of the violence with which this diagram was criticized by Salvini-Plawen (1969b, p. 200). He calls it falsified ("verfälscht"), obviously meaning that the metamerism shown is a result of wishful thinking by the authors. He correctly remarks that the 1st gill is posterior to its proper place (which is immediately in front of the level of the muscle C, not immediately behind this level as in the diagram). This happened when the organs were spread to avoid their covering each other, whereas other correct spatial relations should be maintained. The 1st gill is, for instance, correctly placed in the diagram with regard to the interpedal commissure, and it is associated with the 2nd nephropore as in the animal.

Salvini-Plawen's "correction" of the same diagram (1969b, p. 200) shows some of the difficulties involved: The 1st gill has been "overcorrected" to a point as far in front of the true site as it was behind it in the original (it should be just in front of retractor C, not in front of B as in the "corrected" version). This disturbes the correspondance between gills and kidneys so that the 1st kidney seems to open at the base of the 1st instead of the 2nd gill, and the 2nd nephridium therefore erroneously appears to be lying in a hiatus of the gill series. In the animal each of the five gills has a nephridiopore at the base, and these nephridiopores belong to five consecutive kidneys. This as well as other spatial relations can be seen in the reconstructions of the original report (figs 121, 130, 135, 137, 145) which are accessible to all readers.

Salvini-Plawen's "correction" certainly annihilates the spatial correspondance between the gill series and the nephridiopore series, and produces other irregularities which interfere with the metarism. I do not know what to call this kind of "correction", but if Salvini-Plawen has used this "corrected" diagram I can see why he fails to discover the spatial correspondance between the repeated series of organs.

I hope that the present paper, in which unchanged reconstructions allow direct comparisons of the organ system in two different species, will eliminate the confusion that has arisen.

5.1.3. The case of *Vema ewingi*

V. ewingi (specimen 2) is especially important for discussions of the metamerism of Monoplacophora, since it has a more complete series of repeated units than *Neopilina.*

Its 8 pairs of pedal retractors look very similar to those of *Neopilina,* and although they appear to form a continuous series of metameric units, the individual retractors in the two species can be homologized because of characteristic positional relations to other organs (Figs 3-4. 8-11):

Muscle A attaches to the shell near m. oralis posterior.
Muscles A and B are closer together than the following ones.
Muscle C is attached anterolaterally to the heads of the long radula retractor.
Muscles D and E are in the sectors where the gonads are well developed.
Muscle F marks the anterior limit of the heart and pericardium.
Muscle G lies between the two pairs of atria.
Muscle H lies close to the rectum.

The use of the same lettering (A to H) for the single retractors and sectors in *Vema* and *Neopilina* is thus justified by well-established homologies. It is also used in Table 1, where the organ systems of *Vema* are compared with those of *Neopilina.*

The nervous systems of the two species are very

similiar. There are 8 pairs of lateropedal connectives, corresponding to the 8 pairs of pedal retractors. Each lateropedal connective passes immediately in front of the pedal muscle of the same sector, and it is obvious that the repetition of the connectives is dependent on that of the muscles. It has been suggested that this is a functional necessity, i.e., that the repetition of the connectives is not a separate metameric feature but a consequence of that of the muscles. But this argumentation is not completely convincing, for chitons have an 8-metameric repetition in the muscles, and yet their lateropedal connectives are considered to be irregular.

The two pairs of connectives in front of the foot region are small and difficult to follow in the new specimens. One of them could therefore not be completely reconstructed in specimen 1 *(Neopilina),* but specimen 2 *(Vema)* was better (Figs 3, 4). These connectives seem to innervate the statocyst and probably part of the postoral tentacle tufts, which appear to be unique, non metameric organs of the "head" region. Both have a spatial relation to musculus oralis posterior and probably innervate it, but this could not be stated with full certainty (see Figs 3, 4).

The situation of m. oralis posterior makes this muscle difficult to compare with the metameric pedal retractors, because it ramifies in the sides of the mouth, in the posterior lip, the velum, and other unique structures of the mouth region. M. oralis posterior is therefore more comparable to the other shell-attached retractors of the mouth region, such as m. preoralis, and m. oralis anterior, for which metameric features are absent or at least difficult to find.

For these reasons I regard the m. oralis posterior as a non metameric retractor of the mouth region, and the two prepedal nerve connectives are regarded as specialized nerves for the unique structures in the non metameric "head" region.

The nerves of the posterior body region (sectors A to H) are nearly identical in *Vema* and *Neopilina,* except for the small extra nerves in the sector H of *Vema.* This sector, which is the last in the series, only contains a pedal retractor, the two oblique muscles, and the lateropedal connective H, but no other clearly metameric structures. Such poor development and variability would be expected in the last member of a metameric series. This is seen in numerous annelids and arthropods, and in the Polyplacophora, where the anal region contains modified pedal retractors (Fig. 25). In the Polyplacophora this end section develops late, its muscles may be small and the shell plate (number 8) may occasionally be reduced in recent forms, whereas some fossil forms *(Septemchiton)* probably lacked this plate permanently (Bergenhayn 1955).

The heart region, including sectors F and G, is very similar in the two genera, well equipped with metameric structures: atria and pericardial diverticula, gills, nephridia, nephridiopores, nerve connectives, pedal retractor muscles, and oblique muscles (Table 1).

The most interesting differences between *Neopilina* and *Vema* are found in the prepericardial region, where *Vema* has a more complete metamerism than *Neopilina. Vema* has an extra pair of gills, nephridiopores, and gonoducts, all situated in such a way that they harmonize with the general metameric pattern of the animal (Table 1, Figs 8, 9).

When comparing *Vema* and *Neopilina* one is struck by the fact that the 8 pedal retractors and the lateropedal nerve connectives remain as a basic, 8-metameric pattern in both. When the number of gills, nephridiopores, and gonoducts is increased in *Vema,* these organ series are extended anteriorly with one unit, which seems to fit in the next anterior sector (Table 1, Figs 8, 9).

The 6 gills of *Vema* form a continuous series from sector B to sector G, and appear to correspond to the pedal retractor muscles B to G (Fig. 4). As in *Neopilina* the posterior gills are more posteriorly located within their sectors (D to G) than the anterior ones. In *Vema* the two anterior gills (B and C) are actually located on the sector limit, for their two gill nerves connect with the lateral nerve cord on each side of the lateropedal connective. That means that the two first gills have an innervation similar to that of the first gill in *Neopilina.*

The 7 nephridiopores of *Vema* appear to belong to nephridia in sectors A to G, and the 6 posterior ones are associated with the gill bases B to G. There is no gill corresponding to nephridiopores A, which open into the pallial groove independently, not far from pedal retractor A but in an aberrant location. However, its nephridium appears to correspond to the A sector (Fig. 9).

The extra gonoduct in sector C of *Vema* is also important, for although the gonad of this sector may be rudimentary it shows that also parts of the genital system can be multiplied in accordance with the general metameric rhythm. A simple duplication of gonads has sometimes been suggested for *Neopilina,* implying that duplication is a simpler process, different from metamerism. For *Vema* this is not a

satisfactory "explanation", for the genital apparatus of this species extends over 3 sectors and the gonoducts have the same positional relation to the pedal retractors in all these sectors (Fig. 9).

Some important observations can be derived from this comparison of the metameric repetition in the two genera.

1. The number of gills, nephridiopores and gonoducts is higher in *Vema* than in *Neopilina,* the extra units are situated in front of each series and are located so as to fit with the repetition of other organs.

2. The 8-metameric pattern of the pedal muscles, oblique anterior muscles and nerve connectives remains fixed, when the number of units in the other series varies.

There is thus some reason to believe that the muscles determine the metameric rhythm of the other organs, since their number and situation remains constant while there is some variation in the numbers of gills, nephridiopores and gonoducts.

5.1.4. General viewpoints

When describing *Neopilina* Dr. Lemche and I were struck by the metameric organization and suggested that this metamerism could be an ancestral feature in molluscs. We also suggested that it could have been inherited from some metameric ancestors common to annelids, arthropods and molluscs, as once maintained by Heider (1914), Söderström (1925), Naef (1926), and Johansson (1952). This would mean that the metamerism of molluscs is homologous with that of annelids-arthropods.

We realized, however, that terminal proliferation of segments of the type occurring during ontogeny in typical articulates was improbable in the case of *Neopilina,* in part because this animal ends with a well developed heart region with specialized segments, while the segments of typical arthropods become less specialized — "fade out" — posteriorly. Therefore we preferred to compare monoplacophoran metamerism, not with the metamerism of advanced articulates ("Tritometameren", Remane 1950), but with the more simultaneously occurring metameres in articulate larvae and embryos ("Deutometameren", Remane) or in oligomerous annelids. It was then presumed that the segmentation of the mesoderm seen in oligomerous and polymerous articulates is fundamentally the same (homologous), although the latter develop by a more complicated process, by terminal proliferation (L. & W. 1959a, pp 66, 67). Of course the discussion was hampered by the lack of knowledge of the ontogenetic development and by the erroneous description of a coiled larval shell.

Our suggestions obviously touched some very delicate general topics for they were followed by numerous articles pro et contra from different schools and individual scientists. The numerous papers cannot be reviewed extensively here, so the reader is referred to Marcus (1958), Boettger (1959), Beklemischev (1958, 1969), Yonge (1957a, b, 1960), Morton & Yonge (1964), Günther (1962), Purchon (1968), Ax (1960), Vagvolgyi (1967), Steinböck (1963), Hunter & Brown (1965), Salvini-Plawen (1968, 1969b, 1972), Stasek (1972), Götting (1980a), and Lauterbach (1983a). Most of these articles are sceptical or critical with regard to the significance of the metamerism of the Monoplacophora, but after seeing the new material, particularly the specimens of *Vema,* I think there is basis for some reconsideration.

First of all the new material shows once more that the recent Tryblidiacea are metameric in the sense that different organs are repeated along the body axis following a common rhythm. The reader can check this by studying the reconstructions of *Vema* and *Neopilina* in the present paper (Figs 8-9). It should be noticed that the reconstructions have not been changed to fit ideas of metamerism, but show the metameric structures as they came out of the graphical work.

A number of arguments have been used by authors who deny or doubt the presence of metameric repetition of organs in the tryblidians. Some of these arguments depend on different definitions of the concept of metamerism. Other arguments used by different authors restrict the concept so much that many annelids and arthropods, which are generally accepted as metameric, would fall outside the concept. This is clearly not satisfactory. A few such cases will be mentioned.

1. Many authors deny or doubt the presence of metamerism in *Neopilina* because there are no open, segmented coelomic cavities. But the mesoblast, particularly the musculature, the kidneys and the gonads, is clearly metameric in the adult specimens, and we do not know if there are open coelomic cavities in the embryo. If open coelomic cavities in the adult are required to recognize articulate metamerism, many arthropods and some annelids would be classified as non-metameric. Of course the presence of segmental coelomic cavities in Monoplacophora would facilitate the identification or

homologization with articulate metamerism, but rejection of the possibility that monoplacophoran metamerism is of the articulate type, is clearly not justified, as long as ontogeny is unknown.

2. Other authors do not accept the repetition in Monoplacophora as metamerism because the number of repeated units differs from one organ system to another (in *Neopilina:* 8 pedal retractors, 6 nephridiopores, 5 gills). Especially the presence of two pairs of units in some organ systems (2 pairs of atria and gonoducts in *Neopilina)* is often discarded as a metameric repetition and is sometimes directly used to deny a metameric pattern whatever.

But hardly any annelid or arthropod has a complete set of organs in all segments, and even reduction to one or two pairs is common (1 or 2 pairs of ostia in many arthropods, 2 pairs of gonads in many oligochaetes). The fact that the number of repeated units is different in the organ systems of *Neopilina* is therefore not a useful argument against a theory of metamerism. The presence of three pairs of gonoducts in *Vema,* whereas *Neopilina* has two, shows the weakness of this argument.

3. A non-metameric pattern is also believed to be indicated by the somewhat different situation of the organs in the "metameres" in different parts of the body (particularly gills and nephridiopores). But organs may have a variable situation in the segments of typically metameric animals: muscles, parapodia, etc., in different parts of annelids; limbs and limb muscles in the head region, thorax and abdomen of arthropods; ventral ganglia of the nerve cord in most articulates.

Clearly such arguments which will make a lot of typically metameric adult animals non-metameric cannot be used in the present discussion and at any rate cannot be used for the categoric conclusion that no metamerism is present. On the whole, I have not seen clear arguments which can prevent me from calling the repetition seen in the Monoplacophora for metamerism, in the sense that there is a correlated repetition of parts in the different organ systems. The determining factor could well be located in the mesoderm, particularly in the musculature, for it contains the maximum number of units (8) and it remains constant also in *Vema* when some other organs vary in number. That the metamerism seems to be induced from a segmented mesoblast is a point of similarity with articulate metamerism, but is perhaps a common feature of many metameric phenomena.

In itself this conclusion, that the Tryblidiida have a metameric structure, is of limited interest. The important question is whether the monoplacophoran metamerism is homologous with that of other animals, whether it is a feature restricted to and evolved in the Tryblidiida or if it is a common feature of the Mollusca in general, perhaps inherited from some articulate stem forms. It can be hoped that knowledge of the embryology can contribute to this question in the future, but at present it seems difficult to arrive at certain conclusions. The phylogenetic considerations in the following may contribute with some arguments.

5.2. Muscle metamerism in recent and fossil Conchifera

As the reconstructions of the present paper show, there are eight pairs of pedal retractors in *Neopilina* and *Vema.* As far as is known the attachments of these muscles cannot be clearly discerned on the inside of the thin and delicate shells of the recent forms. The number of retractors is therefore difficult to establish without sectioning and reconstructing the specimens, as shown by the following example.

Menzies (1968, pl. III) distinguished 6 pairs of scars on the inside of the shell of *Vema ewingi* after total staining of the shell. But in my specimens of the same species there are 8, and comparison with Fig. 4 of the present paper shows that Menzies has missed the posterior muscle (H) and that he has probably not been able to distinguish the two closely set anterior pairs (A and B).

The number of retractors is not established with certainty in the other recent species of Tryblidiacea. "At least six pairs" is mentioned for *Neopilina veleronis* (Menzies & Layton 1962, p. 404), and "tentatively seven pairs" for *Vema (Laevipilina) hyalina* (McLean 1979, p. 11). I would suppose that the true number is eight in these species, too, but this should of course be checked.

On the other hand, the present investigation has shown that the metameric repetition of some organs (gills, nephridiopores, gonoducts) is somewhat different in *Neopilina* and *Vema,* although the metamerism of the muscles remains constant in these genera. It is of course possible that the variation in the number of internal organs is still greater in other recent forms — also this should of course be investigated!

The typical fossil tryblidians have much thicker shells, and good specimens have distinct muscle scars on the inside so that the number of pedal

retractors is indicated. *Pilina unguis* (Lindström) from Gotlandian, *P. cheyennica* Peel from Lower Ordovician, *Tryblidium reticulatum* Lindstöm from Gotlandian, and *Archaeophiala antiquissima* (Hisinger) from U. Ordovician, all have a retractor pattern similar to that of recent *Neopilina* and *Vema.* On each side these fossils have a large complex scar, followed by 5 separate single scars. Comparison with the recent forms (Fig. 19) suggests that the complex anterior scar corresponds to the anterior group of muscles in *Vema* and *Neopilina,* which consists of the three formost pedal retractors (A to C), the heads of the long radula retractor, and the posterior oral muscle. These muscles are so closely set in the recent specimens, that one can hardly expect that fossils will show all of them as distinct units.

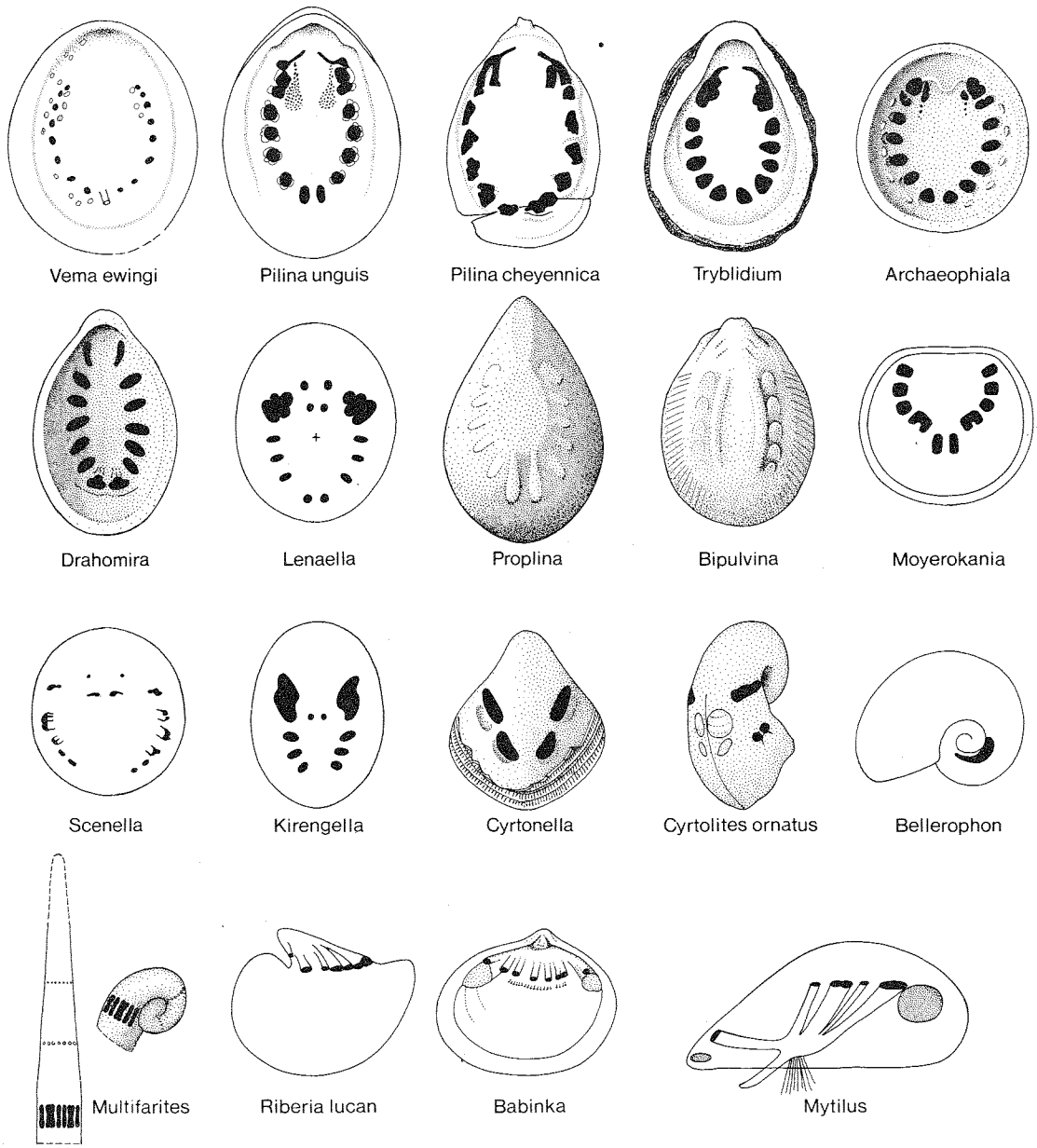

Fig. 19. Attachment of pedal retractor muscles (muscle scars) in some recent and fossil Conchifera mentioned in the text. All figures redrawn to fit a standard size. The state of the original specimens ("Steinkern", fossil shell or recent) not indicated.
The left figure of *Multifarites* shows diagramatically three sets of scars, two younger and one adult, on the peripheral-lateral wall of the shell, hypothetically uncoiled as in Bjaly (1973). The placing of the scars in intact *Multifarites* is roughly indicated in the right figure, which is a theoretical diagram based on Bjaly's text and figures.
The figures are based on illustrations and text in: Bjaly (1973), Knight & Yochelson (1960), L. & W. (1959b), McAlester (1965), Pojeta & Runnegar (1976), Rosov (1970), Peel (1977), Starobogatov (1970), Yochelson (1967), and Yonge (1953).

However, the presence of a separate muscle C is fairly obvious in the complex scar of *Pilina unguis* and *P. cheyennica,* whereas the retractor A and B cannot be clearly distinguished (Figs 130-134 in L. & W. 1959a). Thus, if this comparison is correct, there has been 8 pairs of retractors in *Pilina, Tryblidium* and *Archaeophiala,* and not only the 6 pairs which can be clearly seen as separate scars in the fossils (Fig. 19).

The interpretation of the complex anterior scar in the fossils depends in part on the homologization of the scar of the long radula retractor. In recent *Neopilina* and *Vema* this muscle attaches with two heads just medial to pedal retractors B and C (Figs 10, 11). In the fossil *Pilina unguis* there is a large scar a little in front of this position, medially located within the anterior complex, that is interpreted as the scar of the long radula retractor. This is of course important for the homologization of the patterns of the recent and fossil specimens. The homology of the long radula retractor is supported by the distinctly mottled appearance of this scar in *P. unguis,* indicating that this muscle — like the homologous radula retractor in the Polyplacophora — was subdivided into smaller units in a unique way (see Chapter 5.4.4; Pl. 10:44). The attachment area of the long radula retractor in the Polyplacophora is mottled in a way very similar to that of the radula retractor scar in *Pilina unguis.*

Other fossil Tryblidiacea deviate more from the retractor pattern seen in *Neopilina* and *Vema.* In *Drahomira* Perner from the Upper Silurian, *Lenaella,* Bjaly from the Lower Ordovician, and *Proplina* Kobayaschi from the Upper Cambrian and Lower Ordovician there may still be 7 or 8 muscles, but fusion has obviously taken place in different ways, so only 7 or 6 scars remain separate (Fig. 19). In other fossil tryblidians such as *Bipulvina* Yochelson from the Lower Ordovician, *Moyerokania* Rozov from the Lower Ordovician, and *Kirengella* Rozov from the Upper Cambrian, the reduction of scars to 4 or 5 pairs may partly depend on actual disappearance of muscles, but fusion of some scars can hardly be excluded.

The fossil molluscs mentioned up to now are of the same, cupshaped type as the recent tryblidians. Other fossil molluscs are more specialized and appear to belong to separate evolutionary lines. *Cyrtonella* Hall from the Silurian and Devonian, with 2 symmetrical pairs of scars on the high, probably exogastric shell is regarded as a "monoplacophoran" with symmetrical, untorted structure. Other forms with a high, planispiral shell have 1-3 pairs of muscle scars more laterally, sometimes at some distance from the aperture. Some of these forms are referred to the Bellerophontacea (Upper Cambrian to Trias), in which typically a single pair of muscle scars is preserved, as in *Bellerophon* Montfort (Fig. 19). There has been much discussion about the phylogenetical affinities and systematics of these planispiral forms, whether they were symmetrical and related to the Monoplacophora or have undergone torsion like gastropods (see Yochelson 1967, 1978, Rollins & Batten 1968, Starobogatov 1970, Runnegar & Pojeta 1974, Peel 1972, 1976, 1980, Runnegar & Jell 1976, Pojeta & Runnegar 1976, Berg-Madsen & Peel 1978, Salvini-Plawen 1980a, Runnegar 1981).

Multifarites Bjaly from the Lower Ordovician, is a remarkable, planispiral mollusc with a double row of 4 pairs of muscle scars near the aperture. Similar rows of smaller scars are repeated at two higher (more juvenile) levels on the spire (Bjaly 1973) (Fig. 19).

In the fossil Rostroconchia (Cambrian to Permian) the retractor scars seem to have partly fused and moved dorsally towards the apical region, where an irregular and confluent row of 5-7 scars can be seen in some specimens, e.g., *Riberia lucan* (Walcott) (Fig. 19). The rostroconchians are supposed to be related to recent Scaphopoda and Bivalvia, and a separate taxon Diasoma has been introduced by Pojeta & Runnegar (1976) for this supposedly monophyletic unit.

The Ordovician bivalve *Babinka* has 8 distinct pairs of muscle scars situated high up on the shell in the hinge region, very much as in rostroconchians (Fig. 19; McAlester 1965, 1966). Recent bivalves often have several pairs of retractor units in the same region *(Mytilus,* nuculids), but 7 pairs appear to be the maximum number, and the scars are usually more irregular (Yonge 1953).

The oldest mollusc with a recognizable tryblidian pattern of muscle scars is *Scenella* Billings from Middle Cambrian (Fig. 19). It has paired scars which indicate pedal retractors of the *Neopilina* type, but the scars are somewhat irregular and indistinct and the pattern appears to be somewhat different from that of the recent tryblidians. *Scenella* appears to have 6 or 7 pairs of scars, grouped into 3 large anterior and 3 or 4 smaller posterior on each side, but they seem to form a continuous series (Knight & Yochelson 1960, Runnegar & Pojeta 1974).

Muscle scars are not known from the numerous, usually small molluscs from the Lower Cambrian.

Some of them are classified as "Monoplacophora", because they are cup-shaped or exogastrically coiled like later forms with paired symmetrical scars (see e.g. Wen 1979). However, such classification must be very tentative when no scars show what kind of animal was inside. At any rate the lack of such information makes these Cambrian molluscs very difficult to use in a phylogenetical discussion.

It may be concluded:

1) Tryblidians with the *Neopilina* type of pedal retractor pattern and probably 8 pairs of muscles lived in the Ordovician and Silurian *(Pilina, Tryblidium* and *Archaeophiala)* and no considerable changes have occurred in the tryblidian line from Ordovician to recent *Neopilina* and *Vema.*

2) The *Neopilina* type of muscle scars is known from some upper Cambrian forms (e.g., *Proplina, Kirengella)* and from the Middle Cambrian *Scenella,* but these forms may have had fewer muscle scars, up to 7-8 in *Proplina* and 6-7 in *Scenella* as far as the fossils show. Tryblidians with a well documented 8-metamerism are not known from Cambrian times. Of course this does not show that such forms were absent, for molluscs with distinct muscle scars are rare in the Upper Cambrian, extremely rare in Middle Cambrian and absent in Lower Cambrian. If 8-metameric forms with well preserved, analyzable muscle scars were present, it would therefore be almost a miracle if one of them had been preserved. It should be recalled that *Neopilina,* as a Cambrian fossil, would certainly not show 8 pairs of distinct muscle scars. The accidental character of the fossil record is also shown by the absence of *Neopilina*-like animals in Post-Devonian deposits although they must have existed through Mesozoic and Cenozoic times.

   The fossils thus show that a tryblidian pattern of pedal retractors had developed in the Middle Cambrian, but no clear information is available about its evolution as regards the original numbers of scars.

3) Radiation of conchiferan molluscs resulted in a variety of scar patterns within the different Upper Cambrian to Silurian evolutional lines. The specialization was usually accompanied by reduction in numbers and fusion of scars *(Moyerocania, Multifarites, Cyrtonella, Bellerophon*-like molluscs, Rostrochonchia). Such reduction of numbers would be expected in Conchifera, for it is difficult to see a selective advantage of a metameric musculature in animals with a single (or paired) stiff shell covering the dorsal side.

Similarly, it is very difficult to find a selective advantage of a metameric structure in the recent tryblidians. It is therefore improbable that they should have developed a muscle metamerism progressively after the shell had evolved. It is simpler and more "parsimonious" to assume that early pre-tryblidians were 8-metameric and that this metamerism was preserved with very small changes within the tryblidian line. The almost identical appearance of the retractor pattern in Ordovician-Silurian forms and in recent *Neopilina* and *Vema* gives some support to this interpretation and, at least, does not contradict it.

A test of this theory that early pre-tryblidian ancestors had an 8-metameric musculature is obtained by cladistic reasoning. If, as will be shown later, the Tryblidiacea and the Polyplacophora appear homologous with regard to their 8-metameric musculature, it follows that such metamerism has been present in their common ancestors. These must have lived in the Cambrian (or earlier), for undoubted tryblidians and polyplacophorans were present in the Ordovician and the Upper Cambrian (Polyplacophora) and Middle Cambrian (Tryblidiacea) (for literature see Knight & Yochelson 1960, Smith 1960, Runnegar & Pojeta 1974, Bergenhayn 1960).

5.3. The Tryblidiacea (Monoplacophora) as Conchifera

It was pointed out by L. & W. (1959a, p. 68) that the subdivision of the Mollusca into the subphyla Amphineura and Conchifera could not be upheld after the discovery of *Neopilina,* which has a shell of conchiferan type and a nervous system like that of typical Amphineura. It was also soon accepted that the old system, or at least its definitions, had to be revised. Subsequent discussions, partly based on a phylogenetical approach, showed beyond doubt that the tryblidians could be included as primitive members of the classical Conchifera, since they share many advanced (apomorphic) features with Gastropoda, Cephalopoda, Bivalvia, and Scaphopoda (Boettger 1959, Ax 1960, Günther 1962, Götting 1968, 1974, 1980b, Kaestner 1969, Stasek 1972, Salvini-Plawen 1972, 1980a, Lauterbach 1983b).

Runnegar & Pojeta (1974) did not formally support this view. Like most authors mentioned they regarded the Monoplacophora as a primitive group from which the different conchiferan lines had sprung. But they gave up the old taxon Conchifera and divided it into two subclasses, the Diasoma (with classes Rostroconchia, Bivalvia and Scaphopoda) and the Cyrtosoma (with classes Monoplacophora, Gastropoda and Cephalopoda). But their system is in some conflict with their proposed phylogeny when they derive the Diasoma from the Monoplacophora (Cyrtosoma), and still more when they also regard the Monoplacophora (included in the Cyrtosoma) as the stem group of the Polyplacophora, which are not included in the Cyrtosoma. The proposed system thus makes the Monoplacophora paraphyletic in the sense of Hennig (1966) and appears unpractical, the more so as the derivation of the Polyplacophora from shelled Monoplacophora appears difficult to maintain (see below). With these exceptions Runnegar and Pojeta's opinions are not so far from the general tendencies in most papers. Boettger (1959) may be mentioned as an example. He stated that the tryblidians are conchiferans but are closely related also to the Polyplacophora (see also Pojeta 1980).

The classical "Amphineura", including the Polyplacophora and the Solenogastres (+ Caudofoveata) was maintained for some time as a counterpart of the Conchifera as in the old systems. But the term "Amphineura" was soon found misleading, because *Neopilina,* although not included in the "Amphineura", has a good amphineuran nervous system. Salvini-Plawen (1969b, p. 193, footnote) suggested that the name "Aculifera" (Hatschek 1891) should be revived for the Polyplacophora and Solenogastres + Caudofoveata. This term was regarded better, because it alludes to the calcareous spines characteristic of these animals.

However, a phylogenetic analysis soon indicated that the Aculifera (Amphineura) is doubtful as a taxonomical unit, for its two or three subgroups, Polyplacophora, Solenogastres, and Caudofoveata, are probably independent branches of the molluscan main stem. Salvini-Plawen (1969b, 1972, 1980a) therefore discarded the Aculifera (Amphineura) and proposed a new classification, partly based on cladistic phylogeny (1980a, p. 258). The cladogram shown in the present paper (Fig. 20) comes near that proposed by Salvini-Plawen, except for some details, and would probably satisfy the opinions of most neontologists.

5.3.1. The Conchifera as a monophyletic unit

The cardinal point of this cladogram is the monophyletic group Conchifera, in which the Tryblidiacea are included as a kind of primitive stem group. This arrangement is an unavoidable consequence of several synapomorphic characters which support a monophyletic origin of Tryblidiacea and other Conchifera, but are unknown in other molluscs (characters "a" in Fig. 20):

1) Presence of a single shell (divided in the Bivalvia).
2) Structure of the pallial margin (with three parallel folds, see L. & W. 1959a).
3) Characteristic location of the periostracum gland (L. & W. 1959b).
4) Structure of the shell (periostracum, prism layer and nacreous layer in primitive forms).
5) Presence of a typical shell gland and larval shell (the larval shell of tryblidians similar to that of *Patella,* see Chapter 4.1).
6) Presence of paired statocysts.
7) Presence of a well defined anterior jaw (Chapter 4.10.2).
8) Presence of a crystalline style (present though little differentiated in recent tryblidians, see Chapter 4.11.3).
9) Absence of calcareous spines (which are present as plesiomorphic features in the Polyplacophora and Solenogastres-Caudofoveata).
10) A subrectal commissure of the pedal nerve cords (instead of suprarectal in the Polyplacophora).
11) Presence of preoral antennae in tryblidians and gastropods (L. & W. 1959a).

A number of undoubted homologies, particularly in the radula dentition, the radula support, and the radula musculature, between recent Tryblidiacea and docoglossan gastropods, are not included in the list of conchiferan synapomorphies above, for they are present also in the Polyplacophora and thus clearly plesiomorphic at the conchiferan level. They were probably present already in the common ancestors of Conchifera and Polyplacophora, and thus do not show anything about the monophyletic origin of the Conchifera. Nor is the 8-metamerism of the tryblidian musculature mentioned, for I regard it as an ancient feature, present in polyplacophorans and probably at still earlier stages of molluscan evolution (see Chapter 5.6.1).

Some of the conchiferan apomorphies mentioned are reduced or lost in some recent Conchifera: shell

in some cephalopods and gastropods, larval shell in cephalopods and other forms with direct development, crystalline style in cephalopods, scaphopods and many others, anterior jaw in Bivalvia etc. But these features are unknown in non-conchiferan molluscs and are therefore classified as synapomorphic, i.e., are supposed to have first appeared in the common conchiferan ancestors (compare Fig. 20).

5.3.2. The Tryblidiacea as a "stem group" within the Conchifera

Within the Conchifera, practically all authors agree that the Tryblidiacea has been a kind of "stem group" from which Gastropoda, Cephalopoda, Scaphopoda, and Bivalvia have branched off, while the Tryblidiacea themselves survived to the present days as the Neopilinidae, with little or practically no change. The evidence used to support this belief is partly circumstantial and not clearly defined. Both neontologists and paleontologists have found that the other conchiferan classes can easily be derived from an animal similar to recent or fossil tryblidians. The tryblidians do not have the extreme specializations which justify the independent state of the other classes. A deriviation of all conchiferan subclasses from non-tryblidians, e.g., from Bivalvia, is out of the question, because that would require reduction of their specialized features and return to a standard type before the other classes, e.g., Cephalopoda can be derived.

Paleontologists have found forms which may well be intermediate stages in the development of the

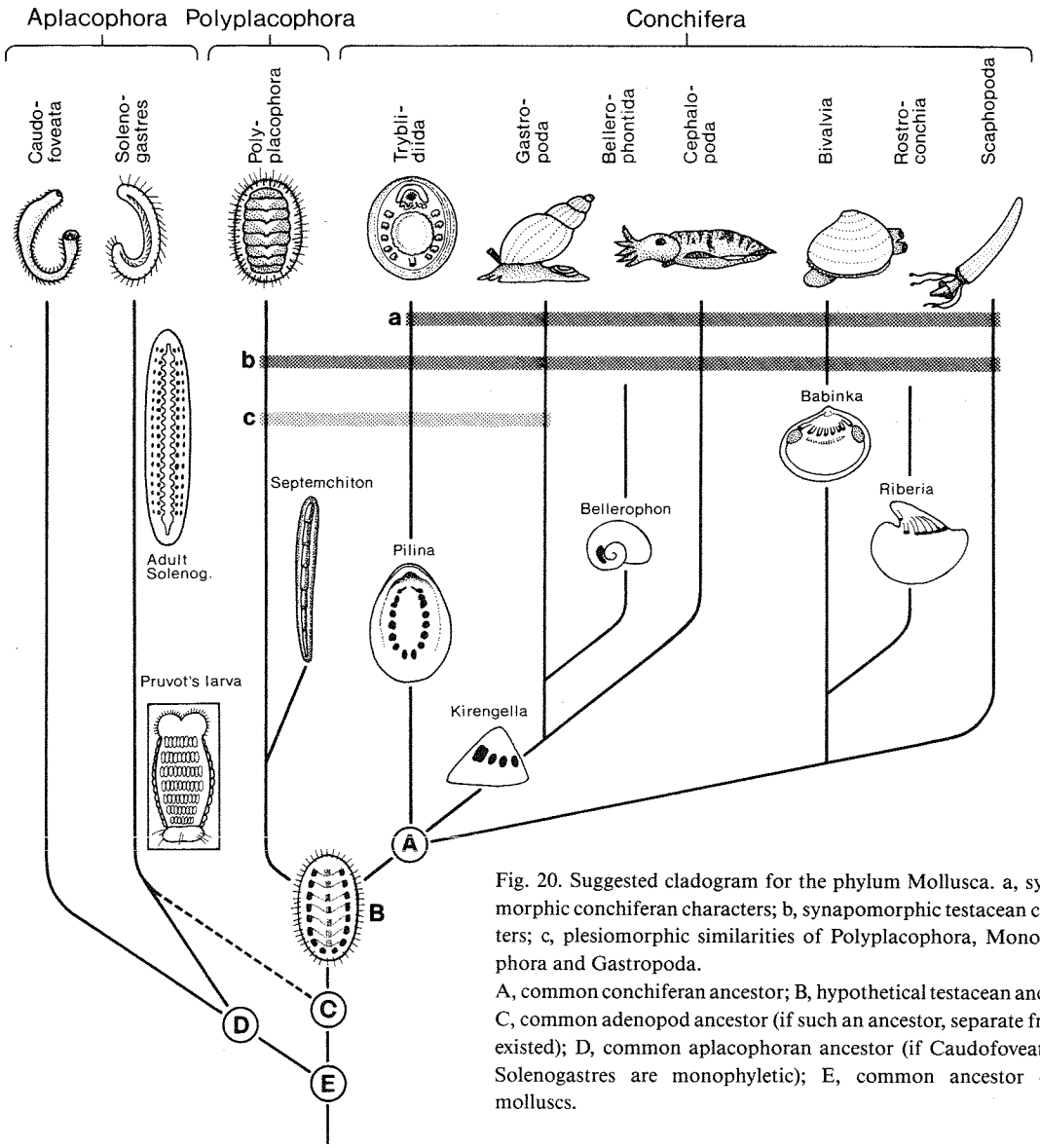

Fig. 20. Suggested cladogram for the phylum Mollusca. a, synapomorphic conchiferan characters; b, synapomorphic testacean characters; c, plesiomorphic similarities of Polyplacophora, Monoplacophora and Gastropoda.
A, common conchiferan ancestor; B, hypothetical testacean ancestor; C, common adenopod ancestor (if such an ancestor, separate from E, existed); D, common aplacophoran ancestor (if Caudofoveata and Solenogastres are monophyletic); E, common ancestor of all molluscs.

different classes from tryblidian-like forms (Runnegar & Pojeta 1974, Pojeta & Runnegar 1976, Pojeta 1980), but in many cases the incomplete preservation and lack of detail hampers the conclusions. For a critical review see, e.g., Yochelson 1978.

Probably the presence of "monoplacophores" of *Neopilina* type as early as the Upper or Middle Cambrian has also impressed many authors, but the geological age in itself does certainly not allow the conclusion that the Monoplacophora are ancestral to other Conchifera. All conchiferan classes, with the possible exception of Scaphopoda (Yochelson 1978), were present in the Lower Ordovician, and more or less reliable fossils indicate that most of them had their origin in Cambrian times (Runnegar & Pojeta 1974, Pojeta & Runnegar 1976). But we do not know precisely, when the different classes first appeared, or if typical Tryblidiacea were present at that time (see also Yochelson 1978).

These different arguments for the ancestral state of the Tryblidiacea within the Conchifera of course make the theory probable and certainly do not contradict it. But to neontologists like myself it is more conclusive that the tryblidians fit nearly perfectly with the morphotype (Nelson 1970) which can be reconstructed for the ancestral conchiferan, particularly if this reconstruction is supported by an outgroup comparison with the Polyplacophora.

This hypothetical conchiferan ancestor must have had all the characters which are classified as conchiferan synapomorphies above (Chapter 5.3.1.).

Moreover, it must have had a number of features, which are shared by the Polyplacophora and at least some of the Conchifera (although they may be lost in some). If these characters are homologous in the Polyplacophora and some Conchifera it is obvious that they must have been present in the conchiferan ancestor ("A" in the diagram, Fig. 20), and of course also in the common polyplacophoran-conchiferan ancestor ("B" in the diagram). For the present purpose it is unimportant whether these "b"-characters are synapomorphic in the Polyplacophora and Conchifera, i.e., evolved in the ancestor "B", or if they are symplesiomorphic at this level (sensu Hennig 1966), i.e., evolved in an earlier, placophoran ancestor.

The point is that both sets of characters, the conchiferan apomorphies ("a") and the common polyplacophoran-conchiferan homologies ("b") must have been present in the ancestor "A", for if not they would not be present in the recent Conchifera. This, however, gives two fairly detailed sets of characters, which inform us about the features which must be expected to have been present in the conchiferan ancestor.

Characters of the conchiferan ancestor:
("a" = conchiferan apomorphies, "b" = conchiferan-polyplacophoran homologies, apomorphic or plesiomorphic).

1) Body bilaterally symmetrical, flattened, with broad creeping sole, pallial groove surrounding foot and head, preoral unpaired fold ("velum") present, anus posteromedian in pallial groove ("b").
2) Heart posterior with two or more pairs of atria ("b").
3) Large pharyngeal diverticula and "liver" present, posterior part of intestine coiled ("b").
4) Gills of ctenidial type without cartilaginous skeleton ("b").
5) Mainly rasping type of radula, with little prominent or small rachidian, large hooked laterals, one or two combshaped inner marginals and one or more platelike outer marginals ("b").
6) Typical "amphineuran" type of nervous system ("b").
7) 8 pairs of pedal retractor muscles, maybe subdivided into mediopedal and lateropedal portions. A posterior oral muscle associated with the 1st pedal retractor on each side. Metameric oblique muscles probably present ("b").
8) Single shell, with periostracum, prismatic layer and nacreous layers; pallial margin with three folds; periostracum gland ventral to pallial margin; paired statocysts; preoral antennae, larval shell (protoconch), circumscript anterior jaw; crystalline style, nervous system with subrectal commissure; mantle without calcareous spicules ("a").

Taken together, this set of characters is a surprisingly complete description of a recent neopilinid, whereas other Conchifera deviate from this presumably ancestral morphology in different ways, particularly in the shape and structure of the shell, pallial groove, foot, metamerism of the musculature, radula dentition, and nervous system.

This clearly indicates that the recent tryblidians have maintained most features with very little or no change from the common conchiferan ancestor ("A") to recent forms, i.e., during the period when other more specialized conchiferan classes were branching off. It is also of interest for the paleontological as well as for the neontological discussion

that the ancestral conchiferan must have had an 8-metameric musculature. This point as well as the basis for other conchiferan-polyplacophoran homologies is discussed i Chapter 5.4.

The reconstructed conchiferan ancestor is deficient on some points where good arguments in the form of homologies between conchiferans and polyplacophorans are wanting. For this reason these points have been omitted in the list of ancestral features, e.g., the number of gonads, nephridia, gills and lateropedal connectives. There is perhaps a reasonable argument for the presence of more than one pair of gills in the ancestor, for it had probably more than one pair of atria (as *Nautilus,* Monoplacophora, ostia in many Polyplacophora), and the number of gills and atria may show some correlation (Chapter 5.6.2, Hunter & Brown 1965, see also Lauterbach 1953b).

5.3.3. Radiation within the Conchifera

Several ideas about the evolution of the conchiferan classes from tryblidian-like ancestors have been proposed, both by neontologists (e.g., Stasek 1972, Yonge 1960, Morton & Yonge 1964) and paleontologists (e.g. Runnegar & Pojeta 1974, Pojeta & Runnegar 1976, Pojeta 1980, Yochelson 1963, 1978, 1979, Yochelson et al. 1973). There are reasonable arguments for uniting the Scaphopoda, Bivalvia, and Rostroconchia into one monophyletic taxon, the Diasoma (Runnegar & Pojeta 1974), e.g., the laterally compressed form, the presence of a mantle cavity all around the animal, and the reduction of the head. Gastropods and cephalopods have similarly been regarded as being related (Cyrtosoma) because of their emphasis on the dorsoventral axis, the well developed head and restriction of the pallial groove to the (morphologically) posterior end around the anus. But in my opinion the tryblidians do not fit in any of these groups.

The real difficulties come when the pattern of side branches from a tryblidian-like stem is discussed. This difficulty can be expected, if the stem line has remained unchanged during the branching process, or if its changes are inconsiderable or unknown. If this is true, all conchiferan classes must have started as side branches from nearly identical stem tryblidians, and there is not even a theoretical possibility for establishing the sequence of side branches or the relative levels at which they parted from the main stem by using common comparative or cladistic methods. No wonder, then, that details are missing on this point in most phylogenetical diagrams.

What has been said up to now raises the question whether the recent Tryblidiacea are characterized by any clearly apomorphic features, i.e., characters not present in the common conchiferan ancestor. If not, the group is only characterized by plesiomorphies, and can, theoretically, be paraphyletic. As far as I see, the best potential synapomorphies are the almost circular foot, the thin shell, the radula formula 5 + 1 + 5, and perhaps the two pairs of gonads. But it is difficult to exclude that the first three of these characters could have been present also in the conchiferan ancestor, particularly if the variation in recent gastropods is considered. It is also possible that the ancestor had two pairs of gonads, particularly if it had a pronounced metamerism in the musculature (Chapter 5.6.).

The metamerism in several organ systems is clearly the most striking feature of recent tryblidians, but this could be a plesiomorphic feature inherited from the conchiferan ancestor. Since most recent conchiferans — with the exception of the tryblidians and *Nautilus* — lack metameric structure, this idea does not immediately appear to be "parsimonious". But if fossil forms are included in the discussion, it is fairly well documented that an ancestral metamerism, particularly in the musculature, has been reduced or lost in several conchiferan lines (see Chapter 5.6. for further discussion).

The lack of clear synapomorphic features in the recent tryblidians makes this group formally doubtful as a monophyletic unit, for all the ancestral traits make it look more like a "Primitivgruppe" or paraphyletic assembly in the sense of Hennig (1966). But I trust that more convincing synapomorphies will be found in the future, at least for recent tryblidians.

I have preferred the terms Tryblidiacea or "tryblidians" in all cases where a more narrow definition is necessary, and have avoided the old term "Monoplacophora", for I agree with Salvini-Plawen (1980a) and Lauterbach (1983b) that this term has become almost impossible to use in a critical discussion. The "Monoplacophora" has "hypertrophied" to include numerous fossil forms in which metameric muscle scars are unknown or even forms which seem to fit well in the basic lineage of other classes. This enlarged concept "Monoplacophora" is of course clearly paraphyletic.

Lauterbach (1983a, b) arrived at conclusions very similiar to those of the present paper. He is in doubt about the synapomorphies of the Neopilinida, but nevertheless deals with the neopilinids as a

monophyletic taxon with the other Conchifera as its sister group, which is called Ganglioneura (Hennig 1979). He divides the Ganglioneura into Rhacopoda (Hennig 1979), which includes Gastropoda and Cephalopoda, and Ancyropoda (Hennig 1979) with Scaphopoda and Bivalvia. This is almost completely in agreement with my diagram (Fig. 20), although I have hesitated to accept a clear sister-group relation between the Ganglioneura and the Neopilinida (Tryblidiida), mainly because the latter could be paraphyletic. It may be of some interest that Fig. 20 was drawn some years before I read Lauterbach's analysis, and I have therefore perhaps overemphasized the difficulties.

I think there are fairly good arguments for a monophyletic group Ancyropoda (Diasoma) and another monophyletic group Rhacopoda (Cyrtosoma minus tryblidians), but the critical argument for deriving these two groups together (as Ganglioneura) from the tryblidian-like ancestors requires some synapomorphies for the Ganglioneura. And I hesitate to accept concentration into ganglia as such a synapomorphy, when the result is so different in Ancyropoda and Rhacopoda, and the general pattern of the nervous system is similar to that of the tryblidians.

Salvini-Plawen (1980 p. 258) agrees on some points with the interpretations given here, but his class Galeroconcha is impossible for me to accept, although it may be practical for paleontological work. The Galeroconcha is defined as the Tryblidiida + the Bellerophontida, and it is true that these two groups are difficult to keep apart. But when Salvini-Plawen directly states that "the cap-shaped (limpet-shaped) Tryblidiina must be considered ancestral to the other conchiferans", the Galeroconcha becomes clearly paraphyletic. This result is also obtained when he admits that the Bellerophontida, the other subdivision of the Galeroconcha, is closely related to the Gastropoda. But neither of us hesitates about the ancestral state of the Tryblidiida or about their relations to the Bellerophontida.

In accordance with my general scepticism I have preferred to indicate the initial radiation of the Conchifera in a non-committal way in the diagram (Fig. 20).

Up to now the discussion has been focussed on the ancestral state of the Tryblidiida within the Conchifera, but a few remarks on selected features in other conchiferans are necessary to make the picture more complete.

5.3.4. Notes on the Gastropoda (and Bellerophontacea)

Recent gastropods are characterized by the torsion of the shell and visceral hump in relation to the head-foot axis, followed by asymmetry of many organs and more or less pronounced streptoneury of the nervous system. The high dorsoventrally elongated body, the well developed free head, and the restriction of the mantle cavity to the ad-anal parts can be apomorphic features shared by cephalopods, gastropods, and perhaps Bellerophontacea. Also the eyes of cephalopods and gastropods are said to show similarities (Salvini-Plawen & Mayr 1977), contributing as an argument for maintaining the gastropods, cephalopods and bellerophonts as a monophyletic superclass, called Cyrtosoma in this paper although not including the Monoplacophora which differ in all these respects.

No recent gastropods show distinct and typical metamerism in their retractor musculature, but 2 or 3 pairs of muscle scars are found in some bellerophont-like forms which may be torted or not but in either case are regarded as closely related to ancestral gastropods (see literature in Chapter 5.2.).

The gastropods of course share the common conchiferan apomorphies with the tryblidians (the character of the shell, mantle, statocyst, jaw, larval shell, subrectal commissure). The preoral antennae are homologous to those of *Neopilina.*

As mentioned by L. & W. (1959a), Golikov & Starobogatov (1975), MacLean (1979) and others, the Patellacea among the Gastropoda show a number of clearly homologous similarities with the Tryblidiacea and the Polyplacophora, particularly in the radula apparatus. The radula dentition is docoglossate with strong, hooklike laterals, more or less reduced rachidian, and small, platelike outer marginals. Two inner marginal teeth in the Lepetidae are characteristically comblike, quite as the inner marginal of the neopilinids (McLean 1979) and the polyplacophorans *Tonicella* and *Nutalochiton* (Pls 9, 10). Although the three radula types differ in the number of teeth in each row, it is likely that the pattern of tooth differentiation is homologous.

Also the radula support and the radula musculature of *Patella* show some characters which appear homologous with those of tryblidians and polyplacophorans, but there are no hollow radula vesicles in the Patellacea (Graham 1964, 1973, Chapter 5.4.3).

All these similarities between Patellacea and Tryblidiacea are clearly plesiomorphic, present also in the

Polyplacophora (see Fig. 20, "c"). They underline the primitive state of the tryblidians within the Conchifera and of the Patellacea within the Gastropoda. Non-patellacean gastropods are more specialized in these features. In my opinion this comparison allows the conclusion that the docoglossan radula is primitive (plesiomorphic) in comparison with the rhipicoglossan one. This was also the conclusion of Golikov & Starobogatov (1975), whereas Fretter & Graham (1962, p. 170) held the opposite view.

The subdivision of the U-shaped pedal retractor of Patellacea into a series of subequal portions looks superficially like a vestige of an original metamerism. Also the attachment of this U-shaped retractor in a zone parallel with and not far from the shell margin resembles conditions in the tryblidians, and at any rate is different from that in other gastropods (Golikov & Starobogatov 1975).

However, the patellaceans undergo extensive torsion and become secondarily symmetrical during and after metamorphosis, so the evidence for homology of the mentioned features is not strong. According to Fretter & Graham (1962, p. 442) and Crofts (1955, p. 748), the right and left larval retractors shift sides during metamorphosis, but both contribute to the adult U-shaped muscle. This makes homologization with the primarily symmetrical musculature in tryblidians and polyplacophorans fairly circumstantial and requires complicated supplementary assumptions (Golikov & Starobogatov 1975).

The direct connection of the gonad with the kidney in the Docoglossa (not with the nephridiopericardial duct as in other prosobranchs) can be of importance for comparisons with the Tryblidiacea, in which the gonoducts open directly into the nephridial sacs. This may be a case of true homology, and a similar case of possible homology can perhaps be assumed for the shape of the bulbous larval shell in patellaceans and tryblidians (Chapter 4.1.).

5.3.5. Notes on the Cephalopoda

Paleontologically the cephalopods are defined by the septa and the sipho in their high cyrtoconic shells. Recent cephalopods often reduce the shell, but numerous other characters make the group clearly monophyletic (arms, funnel, large coelomic cavity, etc.).

The well developed, free head, the restriction of the pallial cavity to the morphologically posterior end, and the well developed eyes and sense organs are additional features which are referred to when they are included in the "Cyrtosoma" of Runnegar & Pojeta (1974), together with gastropods and bellerophontaceans.

Remnants of tryblidian metamerism are not seen in recent cephalopods with the exception of the tetrabranchiate *Nautilus,* which has a heart complex with two pairs of gills, two pairs of nephridia and two pairs of atria and gill vessels. With regard to the metameric repetition of organs, this complex corresponds to the heart region (sectors F and G) in *Vema* and *Neopilina* in such a way that a homology has to be earnestly considered.

The repetition of kidneys, atria and gills in the heart region of *Nautilus* was regarded as a primitive feature, perhaps inherited from segmented ancestors by Pelseneer (1899, 1906), Söderström (1925) and Naef (1926), whereas other authors regarded it as the result of secondary duplication of organs (Hescheler 1900, Hoffmann 1937, Boettger 1959, Steinböck 1963, Yonge 1960, Morton & Yonge 1964, Salvini-Plawen 1968, 1969b, 1972). The presence in *Neopilina* of a probably homologous heart complex with similar duplication of course favoured the theory that it is an ancient (plesiomorphic) feature, for if not it has to be developed convergently two times.

Götting (1980a) also argued in favour of a primitive metamerism in the heart complex of *Nautilus.* He found it difficult to imagine a progressive development of metameric structures in animals like cephalopods, in which the space between mouth and anus is very restricted because of the narrow shell opening. One would expect an opposite effect of selection under these circumstances: a reduction of existing metameric structures, comparable with the reduction of myomeric metamerism seen in many cyrtoconic fossil forms.

The presence of two pairs of retractor muscles matching the two pairs of kidneys, gills and atria of *Nautilus* would certainly strengthen the homology with the heart complex of the Monoplacophora. The recent *Nautilus* has only a single paired retractor, but two pairs of retractor muscles were present in some fossil nautilomorphs (Lemche 1959c, Mutvei 1964b). This is quoted to support the possibility that some metamerism, including also the musculature, may have been preserved to fairly advanced levels of nautiloid development.

Mutvei (1964a, pp 90-93) also discusses the possibility that the numerous muscle portions which were situated close together as a more or less continuous muscle sheath in the wall of the domiciliar

cavity of Oncoceratomorphi were remnants of primitive metamerism. At least one oncoceratomorph species has 7 pairs of scars, which would fit well with the 8 pairs of muscles in recent Monoplacophora, but in other species the muscle sheath was divided into 15-25 more or less distinct paired portions. The significance of these oncoceratomorph muscle scars therefore appears questionable.

Several authors have derived the cephalopods hypothetically from cyrtoconic "Monoplacophora" of the *Cyrtonella* type, with metameric muscle scars. It is, however, difficult to reconstruct a believable morphoseries from such metameric forms to undoubted cephalopods. More or less typical septation of the apical region of the spire is seen in forms which could be ancestral cephalopods, gastropods or "monoplacophorans", so this characteristic is not enough for critical identification. Therefore the presence of a siphuncle in connection with septa is required for definite classification (Yochelson et al. 1973). Following these criteria, *Plectronoceras* from the Upper Cambrian would be the earliest cephalopod, but it has no muscle scars (Holland 1979).

Such fossils as *Knightoconus* from the Upper Cambrian has multiple septa and is thus a potential cephalopod ancestor, but no clear muscle scars are present in the moderately high, monoplacophoran-like shell. The fact that very similar fossils, e.g., *Kirengella* from Late Cambrian, have up to 5 pairs of muscle scars is of course suggestive, but the geological evidence for cephalopod origin from monoplacophorans with metameric muscles is incomplete (see Yochelson et el. 1973).

Cephalopods differ from other recent molluscs in having a very spacious body cavity which includes the pericardium, the gonadal cavities, the nephridiopericardial connections, the gonoducts, and various other lumina, all of which form a communicating system. This "coelom" is particularly spacious in *Nautilus* and decapods but is retricted to narrow channels in octopods. In *Octopus* the system of cavities arises as a schizocoel in a paired compact mesodermal rudiment (Marthy 1968).

The vascular system of cephalopods differs from that of other molluscs in a presumably advanced feature: some vessels have a continuous endothelial lining, whereas other molluscs (gastropods, bivalves, polyplacophorans) lack a true endothelium (see Rähr 1981, p. 70, Barber & Graziadei (1965-1967), like the majority of invertebrates.

5.3.6. Notes on the Diasoma (Bivalvia, Scaphopoda and Rostroconchia)

Neontologists have long discussed a possible phylogenetic relation between Bivalvia and Scaphopoda. Both groups have a poor development of the head and its sense organs, and the head is enclosed in the pallial groove which is continuous all around the body. This complete pallial groove is regarded as a plesiomorphic feature, present also in Monoplacophora and Polyplacophora, and contrasts with the reduction of the anterior part of the pallial groove in Gastropoda and Cephalopoda. The lateral mantle flaps, developing from the back of the scaphopod larva, grow down along the sides to enclose the body in a tube and look like right and left valves in a bivalve. In the nervous system there are some probably homologous similarities between the two groups, particularly the association or fusion of cerebral and pleural ganglia, the dislocation of the pedal ganglia into the base of the foot, and the situation of the "visceral ganglion" (parietal and visceral ganglia of gastropods) along the sides of the rectum.

The fossil rostroconchs were suggested as primitive relatives of the scaphopods and bivalves within a higher taxon, the Diasoma, because they are laterally compressed, with (bilobed) valves which tend to meet ventrally and (probably) with a poorly developed foot and head (Runnegar & Pojeta 1974, Pojeta & Runnegar 1976, Pojeta 1980). Development of scaphopod type of tubular shell seems to be nearly completed in some of them. Other rostroconchs seem to be more similar to the bivalve type, with only an unpaired protoconch uniting the two valves (Runnegar & Pojeta 1974, Pojeta & Runnegar 1976).

For comparison with tryblidians, the indications of muscular metamerism are of particular interest. In many recent bivalves, the pedal retractor is subdivided into several portions, which attach to the shell in a line between the adductor muscles (which are derived from the pallial musculature). The number of paired portions is up to 5 in some nuculids and *Mytilus,* and 7 in *Modiolus* (Yonge 1953), and they are more or less regularly attached in a straight line between the two adductors. This caused C. M. Yonge as early as in 1953 to derive recent bivalves from dorsoventrally flattened ancestral molluscs with 5 pairs of metameric pedal retractors. His reconstruction of the hypothetical ancestor fits very well with a tryblidian (op. cit., p. 444). But it should be noted that in 1953 *Neopilina* had not yet been discovered in the collections of the Galathea Expedition, and according to a footnote in the same paper (p. 444), the fossil

Monoplacophora were unknown to C. M. Yonge! Some scientists know too much!

For comparison with tryblidians, the fossil *Babinka* from the Ordovician is important, for it has 8 pairs of distinct and regular retractor scars between its adductor muscles (Vokes 1954, McAlester 1965, 1966). Below (lateral to) the pedal retractor scars there are triple groups of small scars (Fig. 19), interpreted by McAlester as gill retractors because of their position, which is similar to that of the gill retractors of *Neopilina.* Even if some of the small scars may be attributed to pallial muscles or oblique pedal muscles, McAlester's interpretation appears reasonable, for in *Neopilina* the pallial muscles are small and irregular, and there is one, or maximally two, oblique muscles outside each retractor. It is therefore indicated, with some degree of probability, that *Babinka* had metameric gills corresponding to the metameric retractors.

In rostroconchs the retractor muscles form a variable pattern around the apical region (Pojeta & Runnegar 1976). For the present discussion it is of interest that some riberiids, e.g. *Riberia lucan* (Walcott) had a fairly regular linear series of about 6 more or less confluent scars on each side, connected posteriorly by a larger scar (Fig. 19).

Metameric pedal retractors are not known in recent scaphopods with certainty.

5.4. Comparison with the Polyplacophora

Some comparisons between *Neopilina* and the Polyplacophora were made in the original monograph (L. & W. 1959a, pp 31, 45, 56-57, 61, and 65). Many subsequent authors have touched upon this subject, but I think the matter is so important for phylogenetical discussions on the tryblidians that some supplementary remarks should be made.

5.4.1. External features

Several external features appear similar in the Polyplacophora and Tryblidiacea, but it is often very difficult to say if they are synapomorphic or symplesiomorphic at this level, for only the rather specialized "Aplacophora" are available for outgroup comparison.

The flattened body shape, the broad and flat foot, and the continuous pallial groove, surrounding the foot and the head, are clearly homologous in chitons and tryblidians. The multiple gills look like a homologous feature, but numbers and situations as well as some structural details are different in conchiferans and chitons.

A preoral transverse fold with large lateral flaps in *Neopilina* was called a velum (L. & W. 1959a) and was compared hypothetically with a larval velum in conchiferans. In chitons the corners of the mouth disc are partly free, sometimes reaching far back into the pallial groove on each side of the foot as in *Cryptoplax* (Plate 1899, p. 392). These lateral flaps seem to correspond to the lateral flaps of the "velum" in *Neopilina,* but a clearcut homology can only be seen in *Lepidopleurus,* where the "velum" is delimited from the anterior lip by a distinct transverse furrow as in *Neopilina* (Pl. 8:29).

Other structures surrounding the mouth of tryblidians such as preoral tentacles, postoral tentacular tufts, and "feeding groove", are not known in Polyplacophora, but some homologies may be found with structures in non-tryblidian Conchifera (L. & W. 1959a, Salvini-Plawen 1980, p. 268).

5.4.2. The shell

It is difficult to find clear synapomorphic features in the shell structure of Polyplacophora and Conchifera. It is generally assumed that the shell field can be compared in the two groups, but there is some uncertainty about the delimitation of this shell field in the Polyplacophora, if comparison with the Conchifera is intended. Whether or not the mantle girdle should be included in this shell field has been debated (Beedham & Trueman 1967, Kniprath 1981, Haas et al. 1979).

It is usually agreed that shell secretion as such, i.e., the mineralization process, is homologous in Conchifera and Polyplacophora. Haas et al. (1979) have shown that the shell groove complexes in chiton larvae are roofed over by cell processes in such a way that the first mineralization can take place in a closed chamber similar to that of some conchiferan shell glands.

However, in many features polyplacophoran shells are completely different from conchiferan ones. The Conchifera have a small, well delimited shell gland, a larval shell, and a single or bivalved adult shell, whereas the Polyplacophora have an extended shell field with 7-8 shell-forming areas, no larval shell, 8 (rarely 7) adult shell plates, and a cuticularized mantle girdle with spicules.

A feature which seems to be unique in the Polyplacophora is the presence of aesthetes in the tegment layer of the shell (Plate 1897, 1899, von Knorre

1925). The presence of homologous structures in the Conchifera would of course greatly facilitate the comparison of the shells if they could be found. Lindström (1884) described some pores in the shell of *Tryblidium reticulatum* and believed they had been made by some boring organisms. However, these pores were reinterpreted as aesthete canals corresponding to those of the Polyplacophora by Knight & Yochelson (1960). If this interpretation could stand for critical analysis, it would greatly facilitate comparison between the shells of these forms, e.g., help to decide if the tryblidian shell has originated by fusion of several plates, similar to those of polyplacophorans. Mutvei (1964b, p. 234) was sceptical for the aesthete pores of Polyplacophora are restricted to the tegmental layer, whereas the canals seen in *Tryblidium* were said to penetrate all the calcified layers of the shell(?). Erben et al. (1968) studied thin ground sections of *Tryblidium* shells and found that the canals are restricted to the middle layer and that their inner ends are ramified. The latter seems to exclude the possibility that the canals of *Tryblidium* could have anything to do with aesthetes.

Comparison with the canals known in several bivalve shells also gave negative results. Bivalve canals penetrate all the shell layers except the periostracum (Odhner 1921, Omori et al. 1962, Omori & Kobayashi 1963, Schröder 1907, Soot-Ryen 1951, 1952). Waller (1980) has shown that in bivalves the canals are formed after the shell is deposited; long processes from the pallial epithelium etch their way through the calcified layers of the shell. A homology with the aesthete canals of the Polyplacophora is thus excluded, for the aesthetes are formed as tissue strings which are embedded in the shell substance along the marginal growth zones of the shells.

The phylogenetical history of the polyplacophoran and conchiferan shells has been extensively discussed, recently by Stasek (1972), Salvini-Plawen (1972, 1980a), Beedham & Trueman (1967), Haas et al. (1979), Kniprath (1981), and Pojeta (1980). In my opinion straight forward derivation of the single conchiferan shell and typical shell gland by fusion of the 8 polyplacophoran shell plates, formed by 8 formative areas on an extensive shell field, appears difficult and is not supported by ontogenetical or other morphological evidence (see Kniprath 1981). The opposite derivation, i.e., that the 8 polyplacophoran shell pieces arose by subdivision of a single conchiferan shell, appears still more improbable and is difficult to harmonize with the probable phylogeny of other organs, the shell gland, and the larval development.

Actually the conchiferan and polyplacophoran shells share only a few features, and only such features must be expected to have been present in the common ancestor: a periostracum or its equivalent, a more or less extensive shell field, and a capacity of the shell field to secrete mineralized layers under the periostracum. The conchiferan and polyplacophoran shells may then have evolved independently within the two evolutionary lines while preserving some basic features from the common ancestor (Stasek 1972, Beedham & Trueman 1967, Kniprath 1981). In conclusion, a direct derivation of the conchiferan shell from the polyplacophoran one or vice versa is not indicated by the structural patterns in these animals.

A more concrete theory, implying formation of the polyplacophoran (and conchiferan) shells by coalescence of calcareous spines of an aculiferan type in early ancestors, has recently been revived by Salvini-Plawen (1972, 1980a). The idea was expressed by Gegenbaur (1878) and Blumrich (1891, p. 457). Pruvot (1890) described a single larval specimen of the solenogaster *Nematomenia banyulensis* and found the back covered by 7 transverse bands of parallel spicules arranged as 7 composite plates. This looks very like the formation of the first 7 shell plates in chitons, particularly in *Middendorffia cuprearum* (see Kowalewsky 1883), where the initial calcifications are small "granulations" which later coalasce to form the shell plates (Fig. 21).

Pruvot did not show the larva of *N. banyulensis* in dorsal aspect, so Salvini-Plawen's figure (1972, p. 256) is a later reconstruction, based on Pruvot's lateral figure and a very clear description (Pruvot 1890, pp 691, 692). Pruvot's description had earlier been doubted by Heider (1936, p. 842) and Hyman (1967, p. 69), mainly because only a single larva of this metamorphic stage had been seen by Pruvot, and because a similar arrangement had not been seen in the other species of Solenogastres which had been embryologically investigated (Pruvot 1892, Heath 1918, Baba 1938, 1940, 1951, Thompson 1960). The weakness of Pruvot's evidence was partly amended by Salvini-Plawen (1972, 1980a), who referred to Thiele's (1913, p. 39) description of *Nematomenia protecta.* In this species Thiele found three large plates on the dorsal side of the head, each plate clearly having been formed by fusion of scale-like spicules. Thus, this shows that spicules in Solenogastres can fuse to form larger plates, but

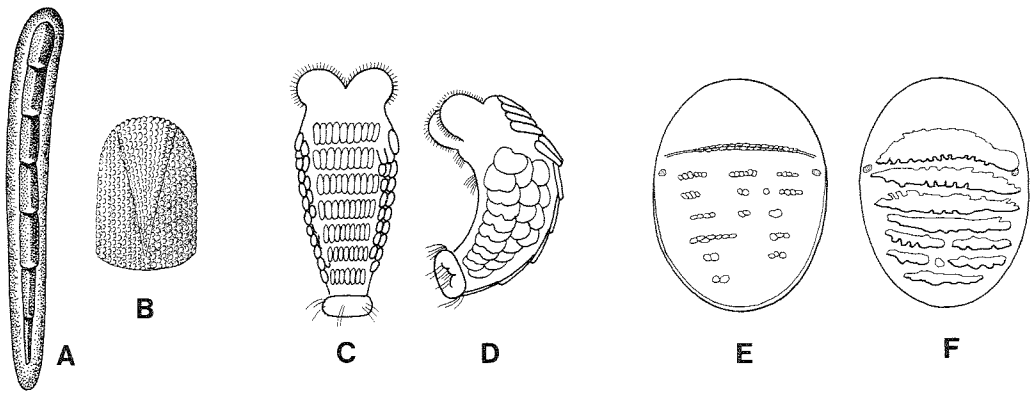

Fig. 21. Figures illustrating possible origin of the valves in the Polyplacophora. A, *Septemchiton vermiformis* Bergenhayn, 1955; B, anterior terminal valve of same, with tubercules ordered in longitudinal "laths"; C, supposed dorsal view of the larva of *Nematomenia banyulensis,* as drawn by Salvini-Plawen (1972); D, the same larva, in lateral view, as drawn by Pruvot (1890); E and F, *Chiton polii,* two developmental stages showing development of valves (after Kowalevsky 1883).

whether this actually occurred during the evolution of the chitonid shell is of course a different question.

It is certainly suggestive that chiton larvae usually develop 7 primary dorsal plates and that the 8th plate follows after some delay, although there is some variation between species with regard to the order of appearance of plates (Kowalewsky 1883, Christiansen 1954, Smith 1966). To Hyman (1967, p. 121) this common appearance of 7 primary plates indicated that the primitive Polyplacophora had been 7-shelled like the Ordovician genus *Septemchiton,* described by Bergenhayn (1955) and Sanders (1964). Salvini-Plawen (1972, 1980a) suggested that these 7 plates were homologous with the 7 fields on the back of *Nematomenia banyulensis,* and took the logical consequences following from this statement: 1) The common ancestor of the Solenogastres and the Placophora must have had 7 spicule fields on the back like *N. banyulensis.* 2) In most recent Solenogastres the spicule fields have re-disintegrated and scattered. 3) The 7-shelled Polyplacophora *(Septemchiton)* are separated as a primitive group, called Heptaplacota, derived by consolidation of the 7 shells from the spicule fields of the *Nematomenia*-like ancestor. 4) The modern chitons (Placophora) have evolved from the Heptaplacota by addition of an 8th shell piece. 5) The Conchifera have arisen from 8-shelled Placophora by fusion of the shell pieces.

This story is supported to some degree by the occurrence in some recent Polyplacophora of exceptional specimens with only 7 shell plates. Such 7-shelled individuals may make up 0.5% of the total population, but the significance of such variations is difficult to evaluate, as also 6, 5, 3 and even 9 plates are found, although more rarely (Hoffmann 1930, p. 173, Langer 1978).

I am inclined to regard the hypothesis of Salvini-Plawen as the most probable one as far as it concerns the derivation of the polyplacophoran shell through fusion of aplacophoran spicules or scales. It has been objected that aplacophoran spicules are unsuitable for such derivation, as they are formed by single cells. However, the formative cells of some polyplacophoran spicules can multiply to form larger shell-secreting complexes, so the difficulty does not seem to be insurmountable (Haas et al. 1979, Pojeta 1980). The pronounced metamerism of the spicule plates of Pruvot's larva, similar to the shell pieces of the Polyplacophora, supports such a derivation, even if the exact number of plates may be uncertain. The tubercles on the shell of some presumed chitons from Late Cambrian *(Preacanthochiton* Bergenhayn) have been interpreted as modified spicules (Pojeta 1980), but personally I think the structure of the shell pieces of *Septemchiton vermicularis,* described by Bergenhayn, is more convincing. The tegmentum of these shell pieces is said to consist of parallel laths, each lath being marked by a row of tubercles. This gives a picture very similar to that of the plates of larval *Nematomenia banyulensis,* which are said to consist of "spicules rectangularies simplement juxtaposées" (see Fig. 21).

A few comments are necessary on some points where I cannot follow Salvini-Plawen completely.

First of all, the number 7 for the spicule groups and the plates derived therefrom appears to be given too much weight as an argument, particularly when *N. banyulensis* is discussed. The 7 plates of spicules were found on a larva at the end of the metamorpho-

sis. It could therefore be compared with corresponding stages of young chitons, and these have usually 7 plates on the back, although they get an 8th plate later. Therefore the larva of Pruvot cannot be used to show that ancestral Polyplacophora had precisely 7 plates as adults, but it may indicate that a metameric dorsal skeleton with approximately 7 units was present.

Neither do I accept the idea that the Polyplacophora first developed 8 consolidated shell pieces which later in their evolution coalesced to form a single monoplacophoran shell. This makes the story much more complicated, and there is nothing in the development of the conchiferan shell indicating that 8 shell pieces have ever been present.

I prefer to assume that the common ancestor of the Polyplacophora and the Solenogastres had 8 spicule groups and the corresponding 8-metameric musculature. Development of the typical Solenogastres would then occur by dispersion of the spicules and multiplication of muscles as in Salvini-Plawen's original idea (Fig. 20). The next split of the cladogram would be between the Polyplacophora and the Conchifera. Within the polyplacophoran line the groups of spicules were consolidated to 8 shell plates. Within the conchiferan line a single shell must have developed, perhaps by fusion of spicules over a larger area of the back and progressive concentration of the shell field to a shell gland during further embryology in descendents. This is in accordance with the presence of spicules in the outer cuticle of many bivalves, as reported by Carter & Aller (1975) and Aller (1974).

There is no need to consolidate an 8-shelled polyplacophoran before deriving the Conchifera, for this complication is obviously introduced in order to account for the 8-metameric musculature of the neopilinids. But if an 8-metameric musculature is assumed to be present in the early adenoped ancestor, such an ancestor with nonconsolidated spicule plates can directly develop into a conchiferan without making the long way via advanced Polyplacophora. With regard to this point my theory is in agreement with the views of Pojeta (1980).

The degradation of the "Heptaplacota" to a side branch of one of the early polyplacophoran lines appears to me more acceptable. Basing a fairly fundamental dichotomy on the seven shell pieces appears too daring, when this feature is the only argument and occurs as a fairly frequent individual variation in the presumed sister group. Why not accept that the number of units (of shell pieces or muscles) was somewhat unstable, and still is, within the polyplacophoran line. The opposite view that the state of the "Heptaplacota" represents a plesiomorphic state appears less probable because of the complicated additional assumptions it requires[1].

5.4.3. The radula apparatus

The entire radula apparatus of the Polyplacophora shows so many features identical to those of the tryblidians that a derivation from a similarly shaped apparatus in a common ancestor appears unavoidable.

The radula ribbon itself is very similar to that of the tryblidians: The dentition is of the docoglossate type as in the patellacean gastropods. The rhachidian is small, the laterals are strong, hooked rods, the inner marginal (no. 5) is combshaped in *Tonicella* and *Nutalochiton* like the inner marginal (4th tooth) of *Neopilina,* and the outer marginals are small and platelike. Particularly the morphology of the unique combshaped tooth supports the homology (Pls 9, 10:40, Plate 1899). The numbers of teeth in a row are 8 + 1 + 8 in the Polyplacophora but only 5 + 1 + 5 in Tryblidiacea (McLean 1979). The docoglossan radula in the Patellacea has a similar tooth pattern *(Patella:* 6 + 1 + 6). Comblike teeth are absent in most species, but two of the inner marginals in Lepetidae have a similarly fringed margin, although the total number of teeth is reduced, probably in part by fusion (Golikov & Starobogatov 1975, p. 192).

The broad radula diverticula and the distinct subradular membrane in the Polyplacophora and Monoplacophora are similar. These features are found also in many gastropods and *Nautilus* (Griffin 1900) (Figs 18, 22).

The structure of the radula support is nearly identical in the Polyplacophora and the Tryblidiacea (Fig. 15, p. 37), and differs from that of other molluscs in several respects. The paired hollow radula vesicles which are kept rigid by internal fluid pressure are unique to Mono- and Polyplacophora. The accompanying cartilages are smaller and thinner in the tryblidians but are clearly homologous with those of the polyplacophorans (Fig. 15, Pls 6, 8). In both groups there is a lateral and a medial cartilage enwrapping the anterior tip of each radula vesicle.

1. Rolfe (1981) reports that the type material of *Septemchiton* has 8 valves, and the observation is supported by convincing illustrations. The "Heptaplacota" can therefore be discarded and the complications it has caused can be forgotten (added after completion of the manuscript).

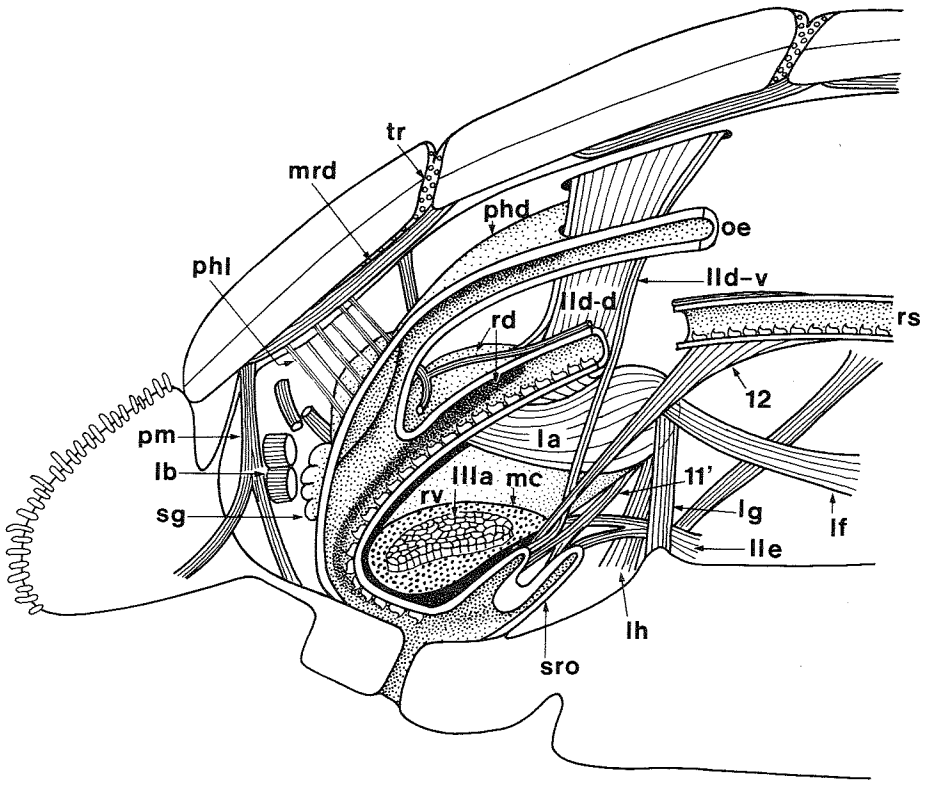

Fig. 22. *Acanthopleura spiniger.* Right half of anterior body region viewed from the median plane. Oral cavity, pharynx, radula apparatus, and some radula muscles are shown. Drawn from photograph of specimen, divided in the midline. Suggested homologies with monoplacophoran muscles indicated by equal lettering.

mc, medial cartilage; mrd, musculus rectus dorsalis; oe, oesophagus; phd, pharyngeal diverticula; phl, levator muscle strands of dorsal pharyngeal wall (diagrammatic = Muscles 18 and 19 of Plate); pm, preoral muscles, in part buccal dilators (Graham 1973), some strings pass to mantle; rd, radula diverticulum; rs, radula sheath; rv, radula vesicle; sg, salivary gland; sro, subradular organ; tr, musculus transversus.

Radula muscles: Ia, m. retractor radulae ("retr" of Plate); Ib, m. protractor vesicae ("protre" and "protri" of Plate); If, Ig, Ih, muscles radiating from posterior end of radula vesicle as in *Vema*, IId-d, m. radulae longus, pars dorsalis (retr' of Plate, "drr" of Graham); IId-v, m. radulae longus, pars ventralis (no 11 of Plate); IIe, m. pharyngeus marginalis ("31" of Plate, "opm" of Graham); IIIa, m. radulae impar ("m" of Plate, ventral approximator of Graham); 11', muscle 11' of Plate, retractor of subradular sac, coming from lateral wall, not seen in *Vema;* 12, muscle 12 of Plate, probable protractor of subradular membrane, attached to the radula sheath or wall of arteria visceralis.

The cartilages are restricted to the anterior third of the vesicle in the Tryblidiacea but extend further back in the Polyplacophora, the lateral one reaching the posterior tip of the vesicle where it forms a thin but distinct cartilaginous cap (Fig. 15). The homology of the medial cartilages is underlined by their connection with the unpaired median radula muscle (m.r.i.) in both tryblidians and polyplacophorans.

The hollow radula vesicles are clearly homologous in Tryblidiacea and the Polyplacophora but do not seem to be present in aplacophoran molluscs. They have probably evolved in the common ancestors of Conchifera and Polyplacophora (Testarian ancestor, "B" in the diagram, Fig. 20). One would therefore expect to find some homologous structures also in the radula support of non-tryblidian Conchifera, for they are descendants of the same ancestor. But hollow vesicles appear to be absent in all conchiferans other than the tryblidians.

In *Patella* the radula support has a certain general similarity with that of tryblidians and polyplacophorans (Pl.8). There are 3 major pairs of cartilages: The anteromedial, the posterior and the anterolateral cartilages (Graham 1964), called "Vorderknorpel", "Hinterknorpel" and "Seitenknorpel" by Nowikoff (1912). Pl. 8:33 shows a dissected specimen. Like Graham (1964) I had some difficulties in finding the two minor pairs of "untere Seitenknorpel" described by Nowikoff, for they are embedded in the musculature and poorly defined.

Comparisons with the Polyplacophora-Tryblidiacea show that the anteromedial cartilages of

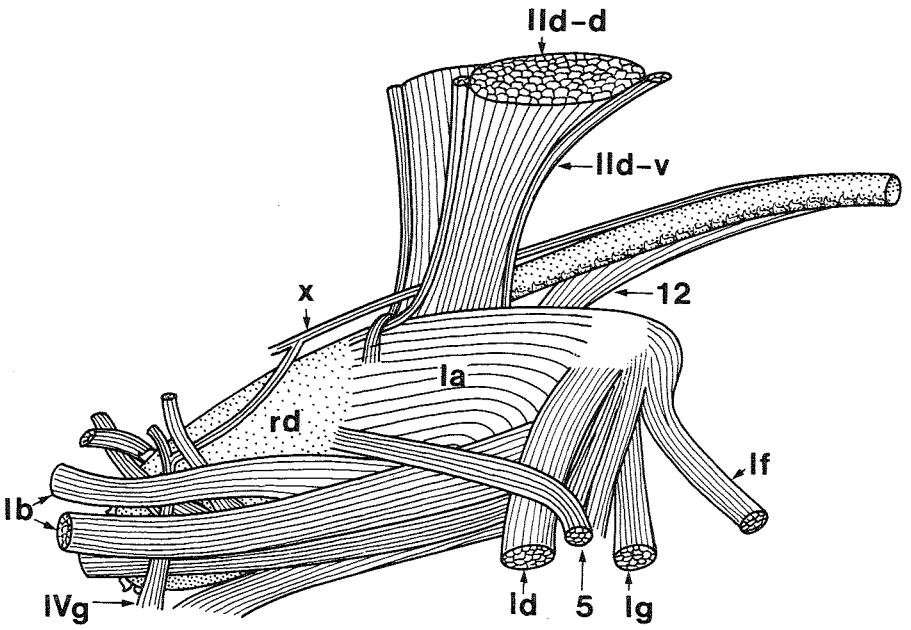

Fig. 23. *Acanthopleura spiniger.* Dissected radula apparatus with attached muscles seen from the left. Drawn after photograph. rd, radula diverticulum with plate of subradular membrane inside.

Muscles: Ia, m. retractor radulae ("retr" of Plate); Ib, m. protractor vesicae ("protre" and "protri" of Plate); Id, If, Ig, muscles radiating from posterior end of radula vesicles as in *Vema;* IId-d, m. radulae longus, pars dorsalis ("retf" of Plate, "drr" of Graham); IId-v, m. radulae longus, pars ventralis (muscle no. 11 of Plate); IVg, m. protractor diverticulorum (part of Plate's muscle 4); x, longitudinal muscle on dorsal side of radula diverticulum (Plate's muscle 4); 5, Plate's muscle 5, from radula diverticulum to lateral body wall; 12, Plate's muscle 12, protractor of the subradular membrane, attached to radula sheath.

Patella are the homologues of the medial cartilages and, perhaps, of the radula vesicles, for they are attached to the unpaired transverse radula muscle and are part of the "roll", over which the median part of the subradular membrane glides. The posterior cartilages of *Patella* must be the posterior end of the lateral cartilage of chitons, for it is the origin of several homologous muscles: the large retractors of the subradular membrane, the protractors of the radula vesicles and many others. To complete this homology, the posterior cartilages should be continous with the posterior ends of the lateral cartilages of *Patella.* There is in fact distinct solid connective tissue but little or no cartilage in the connecting bridges (Pl. 9:33). The sections show - as expected — that the anteromedial and posterior cartilages are clearly separated in *Patella,* forming what looks like a joint with an open cleft.

Nowikoff (1912) noticed that in *Patella* the anteromedial cartilage has distinctly smaller cells and other staining properties than the posterior and anterolateral cartilages. This was confirmed in my own sections of *Patella* (Pl. 12:47), and I think it indicates that the anteromedial cartilage has a different evolutionary background from that of the other cartilages. I am therefore inclined to accept Graham's hypothesis (1964) that the anteromedial cartilage of *Patella* contains the homologue of the radula vesicles, together with remnants of the medial cartilage. If this is accepted it means that the originally hollow vesicles have been filled up by invasion of small-celled tissue in *Patella.* Such a process is indicated in some Polyplacophora and is fairly far advanced in some of my sections of *Lepidopleurus* (Pl. 8:31).

Although Graham (1964) admitted that the anteromedial cartilages of *Patella* are the homologues of the radula vesicles, he concluded that, if so, the vesicles and the cartilages must have reversed their position. Pls 8:32 and 8:33 show that such a reversion is not necessary, for in chitons the vesicles reach into the anterior tip of the radula support; moreover, the posterior end of the lateral cartilage, which is the probable homologue of the patellid posterior cartilage, forms a posterior cap on the tip of the vesicle. This is particularly well chondrified and bulky in *Acanthochiton* (Pl. 8:32).

The finding of a probable homologue of radula vesicles in *Patella* is important, for it strengthens the previously obtained conclusion that ancestral conchiferans probably had hollow radula vesicles. At any rate it shows that the hollow vesicles cannot be used as a strong argument for a monophyletic deri-

vation of the Mono- and Polyplacophora, separate from the Conchifera, for the latter can also have shared such an ancestor.

5.4.4. The radula muscles of several species of Polyplacophora were described by Plate (1897). His results ae summarized and commented by Hoffmann (1930), Fischer-Piette & Franc (1960) and Hyman (1967). Comparisons with the radula musculature of gastropods and tryblidians were made by Graham (1973), who described the radula muscles of *"Lepidochitona cinereus"*.

In his general review, Graham (1973) found that comparable muscle groups corresponding to the elementary radula movements are present in prosobranch gastropods, polyplacophorans and tryblidians, whereas more or less different patterns were found in specialized snails. Polyplacophorans and tryblidians are similar in many details, so a considerable number of individual muscles can be homologized. The patterns of these two groups are also easier to compare, for many radula muscles are attached to the shell, giving an extra criterion for homologization. In gastropods the free muscular head is not covered by the shell, so few radula muscles are shell-attached. Only the median protractors of the subradular membrane retain an indirect or direct shell attachment in some gastropods: e.g., in *Monodonta, Littorina* and *Crepidula,* where the protractor joins the columellar muscle, and in *Patella, Cellana, Scutus* and *Diodora,* where the protractor joins the anterior part of the shell muscle (Graham 1973, p. 238).

To facilitate comparisons I present some drawings (Figs 16-18 and 22-24) showing the most prominent radula muscles of a tryblidian *(Vema)* and those of a polyplacophoran *(Acanthopleura spinifera).* The latter species was chosen because it is large and easy to dissect, and also because the genus was one of those used by Plate for his descriptions. I found the comparison with Plate's figures fairly difficult, and I noticed that other people have had the same difficulties.

In the following comparison the radula muscles of *Vema* (and *Neopilina)* are compared with those of *Acanthopleura,* using the functional subdivisions of the radula musculature introduced by Graham (1973). Reference is made to the terminology of Plate (1897), Graham (1973) and Hoffmann (1930) (for polyplacophorans) and L. & W. (1959a) (for tryblidians). For muscles which are homologous in Polyplacophora and Monoplacophora I have used the same (tryblidian) nomenclature in text and figures, in part in the abbreviated form.

Buccal dilator muscles. In *Vema* the following muscles probably act as oral dilators, for they converge from the shell to the wall around the mouth: m. oralis posterior, m. oralis anterior, m. praeoralis and the newly found dilator muscle (md), see Fig. 7. These muscles correspond in a general way to the polyplacophoran muscles called bd (= buccal dilators) by Graham and, probably, to muscles 2', 10, 17, 20, 21, and 23 of Plate (1897, pp 44, 45). Detailed identification is difficult, but the large m. oralis posterior of *Vema* (Fig. 7, "mop") seems to have a well defined homologue in *Acanthopleura* ("mop" in Fig. 24). In both species the origin of this muscle on the shell is associated with that of the first pedal retractor and it ramifies in the area around and behind the mouth, in the posterior lip and the velum. It may be identical with Plate's muscle 10 (Hofmann's muscle 24).

Buccal circular muscles. These are badly defined muscles in the ventral body wall of *Vema,* not studied in detail. Plate described a transverse muscle (nr. 2) which may act as a sphincter in *Acanthopleura.*

Protractors of the odontophore. In *Vema* undoubted protractors arise from the posterior tip of the radula vesicles and pass to the anterior shell wall (m. pro. ve. ma., m. pro. ve. mi., m. ve. a.-l.). They correspond very closely to the complex in Polyplacophora called "lpo" by Graham and the muscle complex called "protre" and "protri" by Plate (see Figs 18, 23, Ib-Ic).

In *Vema* the m. pro. ca. p., passing from the anterior end of the lateral cartilage to the anterior shell wall, is a typical protractor of the odontophore. A clear homologue seems to be lacking in *Acanthopleura* and other Polyplacophora (Fig. 18, IIIb)

Retractors of the odonthophore. The m. ve. posterolateralis of *Vema,* attached to the posterior end of the radula vesicle, seems to be homologous with the odontophoral retractor ("or") of *Lepidochitona* (Graham) and muscle 8 in *Acanthopleura* (Plate). In general, the muscles radiating from the posterior point of the radula vesicles show very similar pattern in *Vema* and the chitons (see Figs 16-18 and 22-23, Id-Ih).

Retractors of the subradular membrane. In *Vema* there are two regular retractors of the subradular membrane, m. re. ra. and the dorsal portion of m. ra. 1 (Figs 16-17, 22-23, Ia, IId-d).

1) M. re. ra., passing from the tip of the radula vesicles over their inner and outer surfaces to the posterior margin of the radula diverticulum on each side, is clearly homologous with the polyplacophoran muscle called "rsm" by Graham. It was designed "lat" by Plate in his Fig. 19, although its function was not realized by him. Hoffmann (1930), who gave portions of this muscle the numbers 2, 3, and 4, realized its function. The homologous muscle is clearly present in many gastropods and acts as the most important retractor of the subradular membrane. Its attachment on the posterior part of the odontophoral cartilages in prosobranchs is similar to that in tryblidians and polyplacophorans.

2) M. radulae longus (m. ra. 1.) of tryblidians was described as one muscle with two distinct portions, one dorsal and one ventral, with clearly different functions (L. & W. 1959a, p. 40, Figs 82, 128). This was obviously unfortunate and has caused some misunderstanding, which I hope will be eliminated by the present Fig. 16. The pars dorsalis of m. ra. l. is attached to the ventral side of the radula sheath immediately behind the radula diverticulum. It is therefore no doubt a retractor of the radula proper, i.e., the subradular membrane (Fig. 16, IId-d). The m. ra. l. originates high up on the shell, medial to pedal retractor C, the dorsal portion in front of the ventral portion (Fig. 11, mrl).

A homologous retractor of the subradular membrane is clearly the polyplacophoran "dorsal radula retractor" ("drr") described by Graham and the "retr" described by Plate. In the chitons it is a powerful muscle originating medially on the 2nd shell plate, just in front of and medial to the 2nd pedal retractor complex (Figs 22, 24, IId). It passes down to the basal end of the radula sheath, just behind the radula diverticula and attaches to the ventral side of the radula sheath. The homology of this muscle with the dorsal portion of the long radula muscle of *Vema* therefore seems to be beyond doubt. In a number of the polyplacophorans that I stained after the shells had been removed, this muscle head has shown a characteristic mottled appearance (divided into smaller portions, see Pl. 10:44). The same mottled appearance is characteristic of the muscle scar, interpreted as the scar of the long radula retractor in *Pilina unguis* (L. & W. 1959a, Fig. 42). This scar is situated medial to the anterior pedal retractors also in the fossil *Pilina* but is much larger than that of recent tryblidians, more like that of chitons. L. & W. (1959a, p. 44) therefore supposed that the mode of feeding of the fossil *Pilina* has been more like that of recent chitons, whereas the feeding of recent tryblidians is more problematic.

Protractors of the subradular membrane. The pars ventralis of the m. ra. l. of *Vema* and *Neopilina* is undoubtedly a protractor of the subradular membrane (Fig. 16, IId-v). It originates on the shell just behind the pars dorsalis, passes down under and between the radula vesicle and attaches to the oral margin of the subradular membrane in the roof of the oral cavity. Minute muscle flips are given off to the subradular sac on the way. A homologous muscle can be identified in the Polyplacophora. It is called median protractor muscle by Graham (1973, figs 4, 5, mpm). In *Acanthochiton* it attaches to the oral margin of the subradular membrane near the median line and joins the hind surface of the dorsal retractor before it attaches to the dorsal shell near the limit between plates 2 and 3 (Fig. 22, IId-v). The muscle is also described by Plate (1897, p. 44, muscle II). The combined attachment in chitons of a retractor and a smaller protractor of the subradular membrane is thus clearly homologous with the association of the two heads of the m. radulae longus in *Vema*, although the retractor part is more dominating in the Polyplacophora (Figs 16, 22, 23, IId-d and IId-v).

Graham (1973, p. 344) must have misunderstood our description and figures of *Neopilina,* for he thinks that the m. ra. 1. of this species is an exclusive protractor, corresponding to the mpm protractor in *Lepidochitona.* As seen in Figs 16 and 22, the muscle is actually double, one part being a protractor, the other a retractor.

M. pharyngeus marginalis is the 2nd clearly defined protractor muscle of the subradular membrane in *Vema,* attaching to the oral margin of this membrane and passing caudally along the lateral edge of the oral cavity and spreading in the muscular floor in front of the foot (Fig. 16, IIe). It clearly corresponds to the "opm" of *Lepidochitona* (Plate's muscle 31).

The muscle bundle called m. protractor radulae in *Neopilina* and *Vema* is problematic (Fig. 18, IIb). Its many portions attach under the lateral margin of the subradular membrane and pass forwards-upwards to the anterior shell where their attachments form a horseshoe-shaped area. Theoretically the muscle can work as a levator of the anterior end of the entire

odontophore, or its different portions may retract or protract the subradular membrane, depending on the more or less depressed state of the odontophore. Comparisons with chitons are not helpful in this case for chitons do not seem to have a clear homologue of this muscle.

Approximators of the radula vesicles. In *Vema* the muscle called m. radulae impar (m. ra. i.) is an unpaired, transverse muscle plate connecting the anterior ends of the medial cartilages of the radula vesicles. Its homologue in *Lepidochitona* was called "ventral approximator" ("va") by Graham (1973), and Plate designs it "m" in *Acanthochiton* (Figs 15, 16, 22, IIIa).

The m. protractor diverticulorum of *Neopilina* and *Vema* originates near the anterior shell margin together with the m. pro. ve. ma., but runs up into the angle between the radula sheath and the oesophagus (Fig. 17, IVg). It ramifies into thin bandlike muscles on the dorsal surface of the radula sheath, one following the anterior margin of the diverticule and the other the lateral margin. The latter ends in a short, unpaired band on the dorsal surface of the radula sheath behind the diverticulum. This framelike pattern of muscle bands is best seen in L. & W. (1959a, fig. 128), but see also Fig. 17. A clearly homologous muscle pattern is described for polyplacophorans (Figs 22, 23). Graham calls the longitudinal string on the upper side of the diverticulum "retractor muscle of the transverse fold" ("rtf") and Plate uses the number "4" (Figs 16-18, 22-23, IVg, X).

Comments: The Tryblidiacea and the Polyplacophora thus have a series of homologous features in the radula apparatus, but as far as is known up to now, these characters are never or rarely restricted to these two groups. Most are present in a more or less modified state also in conchiferans, particularly in patellaceans and other prosobranchs. The features are thus homologous to tryblidians and polyplacophorans but may have been present originally in the polyplacophoran-conchiferan ancestor ("B" in Fig. 20).

1. The dentition of the radula ribbon is of a docoglossan type, with poorly developed rachidian, hooked, rodlike laterals and few platelike outer marginals. The presence of combshaped inner marginals in some forms supports the homology between tryblidians and polyplacophorans. But combshaped marginals are also found in some patellacean gastropods.

2. The hollow radula vesicles are present in Tryblidiacea and Polyplacophora. A probable homologue is present in the anteromedial cartilage of *Patella* but is hardly recognizable in other gastropods or other conchiferans.

3. The lateral and medial cartilages of the odontophore are clearly homologous in tryblidians and polyplacophorans. Homologues can be found in *Patella* but are difficult to recognize in other conchiferans, although a general similarity of the odontophores is present.

4. The radula diverticula, flat lateral pouches from the distal part of the radula sheath, are clearly homologous in tryblidians and polyplacophorans but are present also in many gastropods and in *Nautilus* among the cephalopods (Griffin 1900, text-fig 8).

5. Many radula muscles are attached to the shell in polyplacophorans and tryblidians. In gastropods the radula muscles are not shell-attached, with the exception of the median protractor of the subradular membrane in some patellaceans and other prosobranchs.

6. Clearly defined homologies are present between many individual muscles and muscle groups in tryblidians and polyplacophorans, but the same muscles or muscle groups can often be identified in gastropods (Graham 1973), although often modified in different ways.

These radula characters can thus be used as synapomorphies to keep the Polyplacophora and Conchifera together, but do not support a monophyletic origin of the Tryblidiacea-Polyplacophora independent of the remaining Conchifera.

Functional aspects

The dorsal retractor of the subradular membrane (m. ra. l., pars dorsalis) of *Neopilina* and *Vema* is poorly developed as compared with that of chitons (Graham's muscle "drr" and Plate's "retr"), which indicates it has a different function. Lemche and Wingstrand suggested that the radula of *Neopilina* cannot be pressed down against the substrate for real rasping like that of chitons but is used as a transport ribbon for food which has been taken into the mouth cavity by other means, e.g., by way of the feeding grooves. The supposed protractor muscles of the subradular membrane (m. pro. r.) and the retractors of the same membrane (m. re. ra. and m. ra. l. pars dorsalis) would, then, pull the radula ribbon to and fro, and the required force would be very moderate.

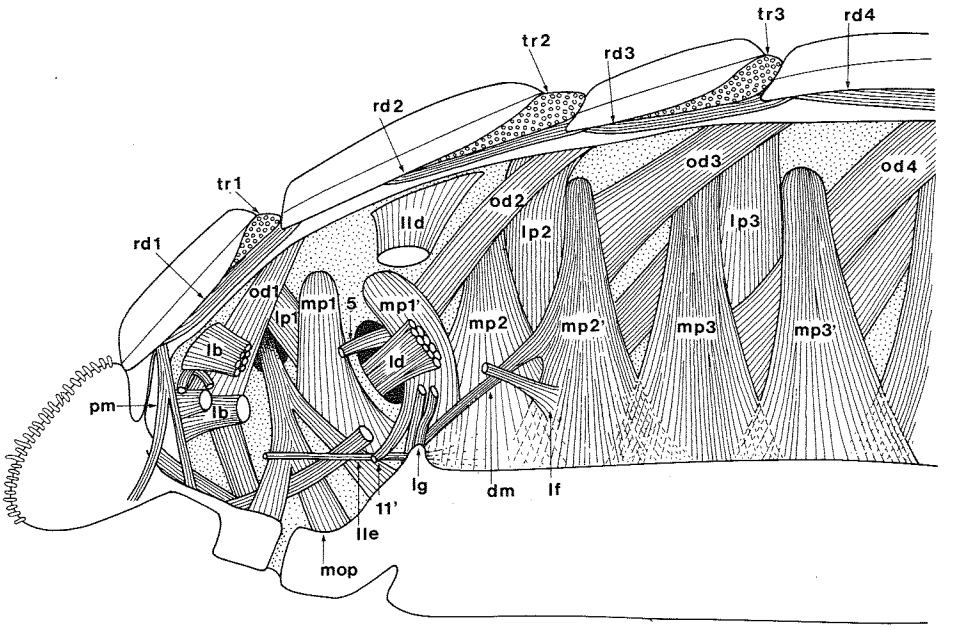

Fig. 24. *Acanthopleura spiniger.* Right anterior half of the body, drawn from the medial side, after removal of radula apparatus and digestive tract. Attachment of various muscles is shown.

Muscles: lp1-lp3, m. latero-pedalis 1-3, partly hidden in the lateral body wall (the corresponding post-apophysial latero-pedalis muscles are not visible at all); mp1-mp3, pre-apophysial medio-pedalis 1 to 3; mp1'-mp3', post-apophysial medio-pedalis 1 to 3. dm, muscle from mp2' to head diaphragm; mop, m. oralis posterior, the posterior branch may contain a branch of mp1; od1 to od4, m. obliquus dorsalis 1 to 4; pm, preoral muscle; rd1 to rd4, m. rectus dorsalis 1 to 4; tr1 to tr3, m. transversus 1 to 3. IId, m. radulae longus; for other radula muscles see Figs 22 and 23.

Graham discussed this possibility on the basis of his experience with gastropod radulas and was sceptical (Graham 1964, p. 328, and 1973, p. 344). He admits that the relatively weak muscles of *Neopilina* make real rasping as in chitons and *Patella* improbable, but he points out that much less force is necessary if the radula of *Neopilina* works partly by lateral brushing movements as in rhipidoglossan gastropods (cf. Ankel 1938). As pointed out earlier by L. & W. (1959a, p. 31), the combshaped inner marginal looks like a tooth with such a brushing function.

The remarkable "m protractor radulae" of *Vema* could be a specialization allowing the radula to be extended very far down to reach the substratum, for both foot and radula in *Neopilina* are attached high up on the shell and must be extended considerably to reach the level of the shell margin (L. & W. 1959a, Figs 8-10). That the foot of *Vema (Laevipilina) hyalina* can be extended to a level far below the shell margin and there be unfolded to a creeping sole was directly observed in living specimens by Lowenstam (1978). No observations were made on the radula, however.

The food of the species *Neopilina galatheae,* which lives on soft bottom, seems to consist mainly of disintegrated matter derived from the carpet of Xenophyophora. It has also been observed that xenophyophores *(Stannophyllum)* from the *Neopilina* locality (st. 716) show distinct lesions, probably made by a radula of a *Neopilina*-like animal (Tendal, 1985). This indicates that the radula can be pushed down to reach the substrate on which the animal creeps. The soft *Stannophyllum* carpets hardly require violent rasping, and lateral movements of the comb teeth may be important for collecting the food and bring it into the mouth.

With the exception of the comb teeth, the radula of tryblidians and polyplacophorans is of a rasping type like that of docoglossan gastropods. This certainly indicates that the ancestral radula of gastropods was very near the docoglossan type, as maintained earlier in this paper. Graham (1973, 1979) and Fretter & Graham (1962) are more inclined to regard the rhipidoglossan radula as the archaic type in gastropods, but this assumption forces us to admit that the docoglossan type has evolved independently (by convergence) in the Poly-

placophora, the Tryblidiacea and the Patellacea, which makes the theory less probable (see Fig. 20).

5.4.5. The body muscles

The body musculature of several species of Polyplacophora is well described by Sampson (1894, 1895), Plate (1897-1901) and Henrici (1913). The results are summarized by Hoffmann (1930), Fischer-Piette & Franc (1960) and Hyman (1967).

As a general rule, a standard set of muscles is repeated under each of the 8 shell pieces of the Polyplacophora. With the single exception of the m. transversus the muscles are paired, those under the right and left halves of each shell are strict antimeres and are also repeated under the preceding and following shells. However, the muscle sets under the foremost and hindmost shells are somewhat different, so comparison with the standard sets under the shells II and VII may cause some difficulties (Sampson 1895, Plate 1897, p. 87).

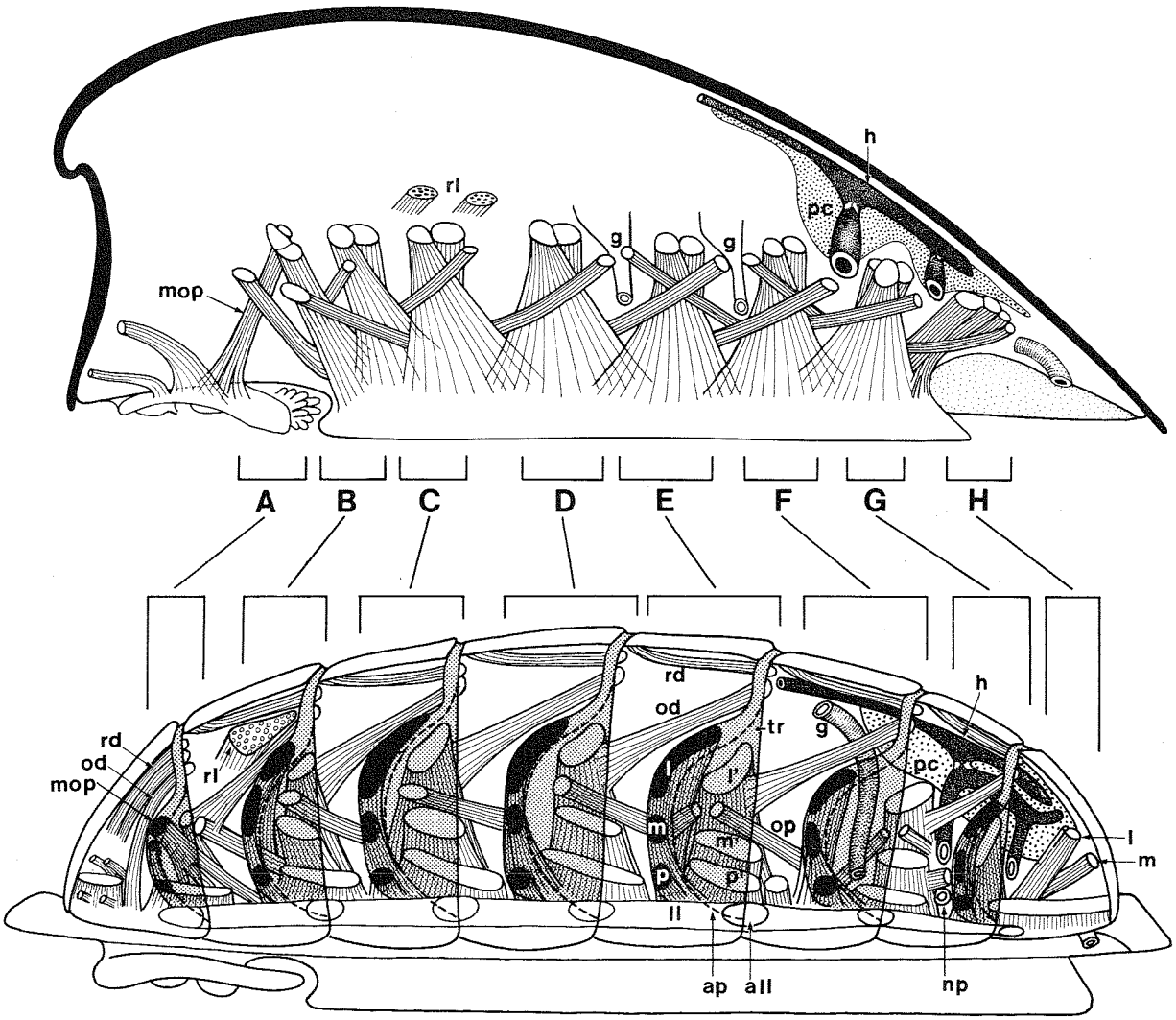

Fig. 25. Comparison between the pedal retractor groups (A-H) of Monoplacophora (top) and of a polyplacophoran (below). Both diagrams were supported by horizontal reconstructions of the muscle attachments. The dorso-ventral dimensions are strongly overemphasized. In the polyplacophoran (below) the attachment area of each transversus complex is marked by dark shadowing, and the pre-apophysial muscle heads which are confluent with the transversus, are black (l, m, p). The crossing of latero-pedalis and medio-pedalis muscles (see Fig. 26) could not be illustrated.

all, attachment areas of m. longitudinalis lateralis (see Henrici 1913); ap, anterior contour of apophysis (hatched); g, gonoducts; h, heart; l, latero-pedal muscle (pre-apophysial); l', latero-pedal muscle (post-apophysial), ll, m. longitudinalis lateralis; m, medio-pedal muscle (pre-apophysial); m', medio-pedalis muscle (post-apophysial); mop, m. oralis posterior; np, nephridiopores; od, m. obliquus dorsalis; op, m. obliquus posterior; p, pallial muscles (pre-apophysial); p', pallial muscles (post-apophysial); pc, pericard; rd, m. rectus dorsalis; rl, m. radulae longus; tr, m. transversus.

The standard sets under each polyplacophoran shell plate consists of the following components (some poorly defined mantle muscles are omitted):

1. Mm. recti dorsales, a pair of longitudinal muscles on each side of the dorsal midline, from the anterior margin of one shell to the anterior margin of preceding shell (Figs 24-26, 28, rd).

2. M. transversus, a transverse flat muscle band across the back, attached under the posterior margin of each shell, uniting the posterior margin with the anterior margin and apophyses of the following shell. The muscle plate is best developed laterally, over the apophyses (Figs 25-28, Pls 10, 11, tr).

3. Mm. obliquii dorsales, paired muscles, attached to the anterior margin of each shell between the apophyses and extending anterolaterally under the preceding shell (Figs 25-28, Pls 10, 11, od).

4. Mm. longitudinales laterales along the lateral margins of the shells, partly subdivided into segmental portions by insertions on the single shells (see Henrici 1913) (Figs 25, 26, 11).

5. Inner mantle muscle, attached from below to the lateral part of each shell and spreading into the mantle. In *Acanthopleura* (Plate 1897), *Chiton* (Sampson 1895) and *Lepidopleurus* (Figs 25, 26, 28, p), the muscle is divided into two or three for each shell piece. This subdivision corresponds partly to that of m. medio-pedalis; the larger portions of the muscle attach under the apophysis, the smaller one(s) in front of the apophysis under the preceding shell (Fig. 25, p and p').

6. The pedal retractors. As described by Sampson and Plate, there are four groups of pedal retractors under each shell, one anterior and one posterior group on each side. Each anterior group is attached to the ventral side of the apophysis and is usually just visible behind the posterior margin of the preceding shell when the apophysis is removed (Fig. 28, Pl. 11, mb) The posterior group of the same shell is attached further back, just in front of the free margin of the apophysis of the following shell. It should be noticed that "anterior" and "posterior" indicates the relative position of the two groups of one shell and may cause misunderstanding, for the muscle complexes to be compared with retractors of *Neopilina* appear to overlap the shell borders and include the "posterior" retractor group of one shell and the "anterior" group of the following shell (Fig. 25). Realizing the difficulty of the old nomenclature I have preferred to call the muscles pre-apophysial (formerly posterior) and post-apophysial (formerly anterior) and to use the letters A to H for the muscle groups, in accordance with the designations in the tryblidians. The l' E, m' E and p' E are the postapophysial muscles of the E group, l E, m E and p E are the pre-apophysial muscles of the same group. In the old nomenclature they would be called anterior

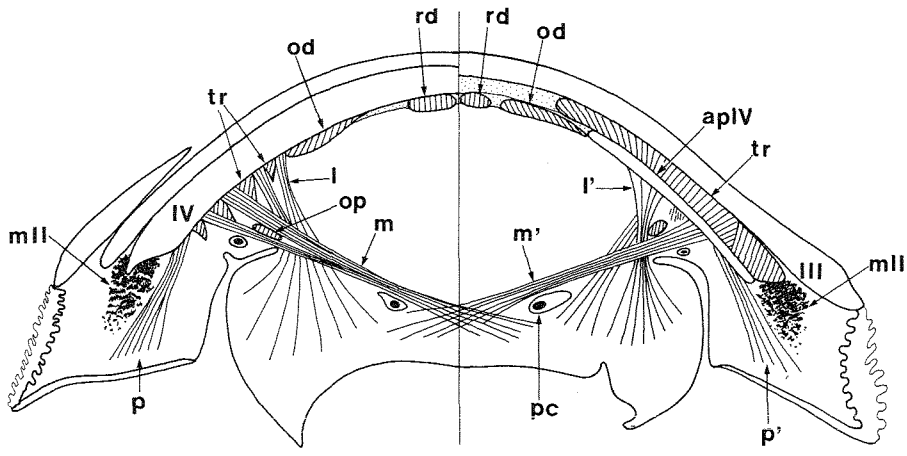

Fig. 26. *Lepidopleurus asellus.* Diagram based on two cross sections, showing the shell-attached muscles. Left side: level just in front of apophysis V (through valve IV), showing the m. transversus (tr) intermingling with the pre-apophysial m. medio-pedalis (m) and m. latero-pedalis (l). Right side: level of basal part of apophysis IV (through posterior part of valve III), showing m. transversus and the post-apophysial m. medio-pedalis (m') and latero-pedalis (l'). Compare Figs 25, 27, 28.

III and IV, valves III and IV; apIV, apophysis IV; l and l', latero-pedal muscles, pre-apophysial and post-apophysial, respectively; m and m', medio-pedal muscles, pre-apophysial and post-apophysial, respectively; mll, m. longitudinalis lateralis; od, m. obliquus dorsalis; op, m. obliquus posterior; p and p', pallial muscles, pre-apophysial and post-apophysial, resp.; rd, m. rectus dorsalis; tr, m. transversus.

muscles of shell VI (VI;1) and posterior muscles of shell V (V:2), respectively (see Fig. 25).

Within each retractor group the following muscles can be distinguished by the direction and course of their fibers:

7. M. latero-pedalis attaches high up on the shell, nearest the dorsal midline within the group, passes down in the body wall, crosses the m. medio-pedalis and ramifies in the foot margin lateral to the pedal nerve cord (Figs 25, 26, Pl. 6:16, 1 or lp).

8. M. medio-pedalis attaches lower down (more laterally) on the shell, passes down and crosses (interdigitates with) the latero-pedal muscle and ramifies in the foot center, medial to the pedal nerve cord. Some fibers cross the midline and interdigitate with fibers from the antimeric medio-pedalis. Note that the terms medio-pedalis as introduced by Sampson (1895) refer to the ramification in the foot (Figs 25, 26, Pl. 6:16, m or mp).

9. M. obliquus posterior, a smaller muscle, attaches at the level between the medio-pedalis and latero-pedalis in its group and passes posteriorly and obliquely downwards to the foot. Posterior obliquii were found under each shell in *Lepidopleurus* (Fig. 25, op).

10. M. obliquus anterior, a small muscle strip, attaches at the same level as and just in front of obliquus posterior. It passes forwards and down to the foot. This muscle is fairly variable in occurrence and was only distinct under two shells (V and VI) in *Lepidopleurus* but is more regularly present in *Chiton viridis* (Sampson 1895).

Comparisons with the body muscles of Tryblidiacea and Aplacophora

The Tryblidiacea completely lack a number of the dorsal muscles present in the Polyplacophora, such as mm. recti dorsales, mm. obliquii dorsales, mm. transversi, and mm. longitudinales laterales. This is to be expected, as in chitons the mentioned muscles serve to bend the body and move the shell pieces in relation to each other (Sampson 1895, Plate 1897, Henrici 1917), and such movements are of course completely blocked by the single shell in the Tryblidiacea (Fig. 25).

The mm. obliquii anteriores and posteriores in the Polyplacophora appear homologous with those of the Tryblidiacea, but the variations in their occurrence weaken the conclusion to some degree.

The mm. latero-pedales and medio-pedales appear directly homologous in Polyplacophora and Tryblidiacea. In both taxa these muscles cross on the way down the body sides. The m. latero-pedalis ramifies in the foot margin outside the pedal nerve, and the medio-pedalis ramifies in the center of the foot inside the pedal nerve. This was referred to by L. & W. (1959a, p. 45) as a similarity supporting the homology of the pedal retractors in the two groups (Fig. 26). But such pedal retractors, divided into lateropedal and mediopedal portions and ramifying in a similar way, seem to be present also in some Aplacophora (Thiele 1902, p. 310, Hoffmann 1930, p. 405, 407, Salvini-Plawen 1969b, p. 202-3, 1972, p. 232). In view of the fact that the foot is vestigial in the Aplacophora it is hardly astonishing that the

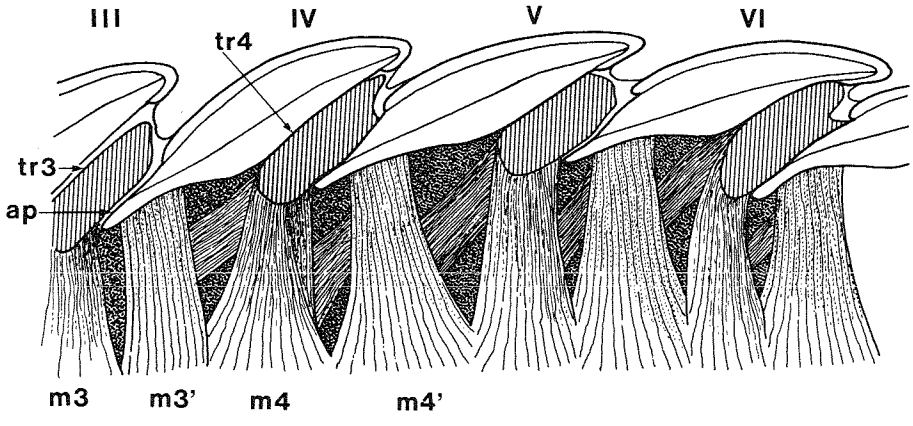

Fig. 27. *Acanthopleura spiniger.* Right body wall and sectioned valves III to VI seen from a medial direction. The para-sagittal section is located to the right of the midline, through the apophyses (ap). The medio-pedalis muscles are distinct, every second one (pre-apophysial, m3, m4 etc.) intermingles with and joins the transversus (tr3, tr4, etc.), whereas the post-apophysial ones (m3', m4', etc.) have independent heads attaching under the apophysis (ap). Camera lucida drawing of dissected specimen. Compare Fig. 28.

dorsoventral musculature is poorly developed and that the muscle strings pass more irregularly to each side of the pedal nerve in some species of Solenogastres.

There are thus convincing arguments for a homology of the pedal retractors, particularly the latero-pedalis and mediopedalis pattern, in Tryblidiacea, Polyplacophora and some Aplocophora. But when Tryblidiacea and Polyplacophora are compared, this similarity is clearly symplesiomorphic (archaic) and is no evidence for a strict monophyletic origin of these two groups. And although the homology is well established, it does not immediately follow that the repetition of the muscles (8-metamerism) is comparable in Tryblidiacea and Polyplacophora. This is of course an independent problem, for, in general, clearly homologous parts can be partly or completely independent with regard to metameric repetition in different evolutional lines (e.g. the number of nephridia or gonads in different annelids).

At first glance the 8 pairs of muscle groups in the Tryblidiacea would seem to fit well with the conditions in Polyplacophora, in which the 8 shell pieces seem to mark 8 pairs of muscle complexes. L. & W. (1959a, p. 45) made such a comparison and suggested that the muscle units to be compared with *Neopilina* retractors are complex groups, extending over the boundary of two consecutive shells in the Polyplacophora, and that the original 8 groups have

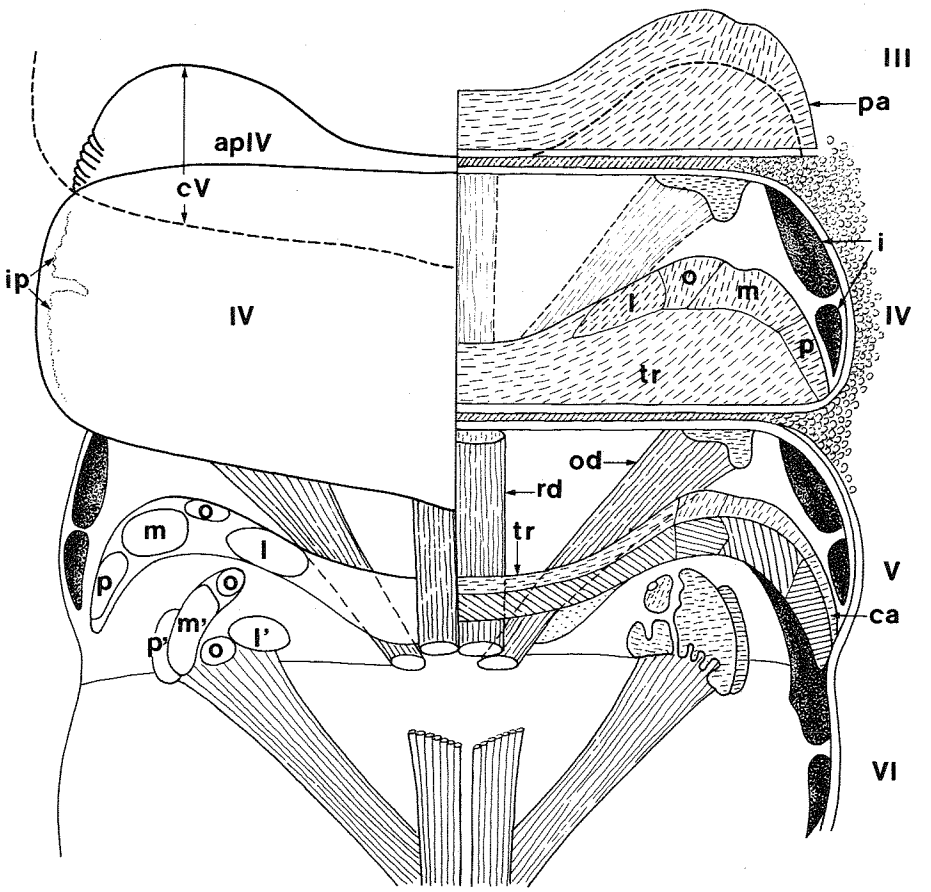

Fig. 28. *Acanthopleura spiniger.* Dorsal view of musculature below valves III to VI. The left half of valve IV and its apophysis is left intact, its right half removed like all other valves. The tegumental pouches containing the apophysis IV and V are shown on the right side, containing the transversus musculature in its dorsal wall. Under shell V the dorsal wall of apophysis pouch VI is cut open and partly removed, exposing the heads of the post-apophysial pedal retractors. A diagram of the approximate site of pedal retractors is shown to the left under shell V. Drawing of dissected specimen, compare photographs on Pls 10 and 11.

apIV, apophysis of valve IV; ca, cut surface through apophysial pouch VI; cV, area covered by posterior part of valve III; i, pouches for insertion plates; ip, insertion plates of valve IV; l and l', pre-apophysial and post-apophysial lateropedal muscles; m and m', mediopedal muscles, pre-apophysial and post-apophysial, respectively; o, obliquus muscles (anterior and posterior); od, m. obliquus dorsalis; p and p', pallial muscles, pre-apophysial and post-apophysial, respectively; pa, apophysial pouch, with transversus musculature on its dorsal wall; rd, m. rectus dorsalis; tr, m. transversus.

been partly subdivided into two by the development of the apophysis from the anterior margin of the following shell, as indicated in Fig. 27. The apophysis would, then, cut into each retractor group, dividing it into a post-apophysial group attached to the apophysis, a m. transversus between the apophysis and the next anterior shell, and a pre-apophysial group attached in front of the apophysis to the preceding shell (Figs 25, 27, 28, Pl. 11).

Some authors accepted in a general way this suggested homology between the 8-metamerism in the musculature of Tryblidiacea and chitons (Boettger 1959, Yonge 1960, p. 19, Ax 1960, Götting 1980a). But objections were raised particularly by Salvini-Plawen (1968, 1969b, 1972, 1980a), who proposed that polyplacophoran musculature is in fact 16-metameric. He regarded this as a step in a continuous process of reductions of the dorsoventral muscle strings, beginning with hypothetical turbellarian ancestors (numerous pairs), through the Solenogastres (numbers somewhat reduced) and the Polyplacophora (16? pairs) to the Monoplacophora (8 pairs) and ending with still stronger reduction in the Conchifera, e.g., in bivalves (7 pairs or less) and gastropods (one pair or even ½ pair). This series is of course beautiful and mentally satisfactory in a way but to me it does not seem to be convincingly supported by facts for the different steps. At any rate I doubt that the polyplacophoran musculature can be regarded as 16-metameric. The reasons for my opinion are:

1. In the Polyplacophora there are no indisputable series of 16 comparable muscle units along the axis of the animal. The main pedal retractors, m. mediopedalis and m. latero-pedalis, are divided into an anterior and a posterior portion under each shell border, giving a total of about 16 along the animal. But the anterior and posterior portions are different with regard to attachment, size, fiber direction and, in some species, with regard to fusion with the 7-metameric m. transversus (Figs 25, 27, 28). Every second component in the proposed "16-metameric" series is thus different from the other eight, and counting such a heterogeneous sequence to get the number 16 is hardly relevant.

The mm. obliquii posteriores may be repeated twice under some shells of *Chiton viridis* (Sampson 1895), but only 8 or 7 single pairs are present in *Lepidopleurus*. The inner mantle muscle may be divided into two or three very dissimilar portions under some shells of, e.g., *Lepidopleurus* (Fig. 25), but I do not think that the repetition is regular enough to be accepted as evidence for a 16-metamerism. To me these series — because of the deviating features of every second unit - look more like an 8-metamerism, where the original muscles have been separated into two unequal portions on each side of the joints between the shell plates.

It should be remarked that the theory of a 16-metameric pattern of muscles in the Polyplacophora stands or falls with the recognition of a convincing series of 16 comparable muscle units. No other structures in the animal itself support a 16-metameric pattern. The shell and the other muscles are clearly repeated 8 times and the many gills show nonstabilized repetition into many units. No support for a 16-metamerism can be obtained from outgroup comparison, for the tryblidiacean retractor muscles are clearly 8-metameric, and those of the Solenogastres appear nonstabilized, multiplied alternating with intestinal pouches.

2. Muscles of Polyplacophora other than those mentioned above are clearly 8- or 7-metameric, repeated one time for each shell piece: m. rectus, m. obliquus dorsalis, m. transversus, and m. longitudinalis lateralis. The muscle groups, of which the pedal retractors form an integral part, are also repeated 8 times. The attachment areas of these muscle groups are more or less completely covered by the broad and flat mm. transversi, present in a number of 7 (absent above the last group under the posterior margin of shell VIII). The heads of m. latero-pedalis and m. medio-pedalis of the posterior groups, although sometimes regarded as 16-metameric, usually fuse and intermingle with the m. transversus, which is a typical 8(7)-metameric muscle (Figs 25, 27, 28).

3. Comparison with the Monoplacophora indicates that the 8-metameric pattern of the pedal retractors is homologous in the two groups. The presence of the 8 paired muscle groups in both cannot be ignored as a numerical support for the idea that the muscle patterns are homologous also with regard to the number of units. An analysis of the relations to other organs gives some support to this homology:

In both taxa the muscle complex A is associated with the m. oralis posterior, which can be identified by its spreading in the ventral wall of the mouth region. The pericardium begins at the level of the muscle complex F. The atria of *Neopilina* are situated in the intervals between complexes F-G and G-H. Two pairs of ostia are present in Polyplacophora (most species), they have the same localiza-

tion (Fig. 25, see also Plate 1901, p. 480, and Hoffmann 1930, pp. 281-286). If only one pair of ostia is present it is located under shell VII (between muscle groups F and G) as in *Lepidopleurus* (Fig 25), and this is the location of the first ostium in the few forms which have more pairs of ostia. It should also be mentioned that muscle group H, in addition to its location on each side of the rectum, has a more specific similarity in the Tryblidiacea and the Polyplacophora. Its medio-pedalis crosses the midline ventral to the rectum and ramifies in the opposite side of the foot. This group (H) is not subdivided in the polyplacophorans, and there is no m. transversus, obviously because there is no apophysis (Fig. 25, Pl. 10:41, 43).

I consider the evidence for a 16-metamerism of the musculature in the Polyplacophora very doubtful, for it relies exclusively on the supposed 16- repetition of pedal retractors. Such results can be obtained only if one ignores the fact that every second muscle is different and forgets that 16 non-comparable units are counted.

No such objections can be raised against the presence of an 8-metamerism, for this interpretation is supported by several sets of 8-metameric structures (retractor muscles, muscle groups, shell pieces of the animal). Only this interpretation is supported by outgroup comparison, for the series of 8 muscle groups is clearly homologous with the 8 retractor groups in tryblidiaceans, in which even some of the single units of the series can be individually homologized because of comparable relation to other structures. Also the comparison of the 7 spicule plates of *Nematomenia* with the 7 or 8 plates of the Polyplacophora supports an 8- or 7-metamerism in the latter rather than a 16-metamerism.

Salvini-Plawen (1968, p. 193) pointed out that the situation of the nephridioduct between muscles VII_1 and VII_2 in Polyplacophora is imcompatible with our hypothesis that the 8 pedal retractors in Tryblidiacea have been divided to form two units each in Polyplacophora. But this is a mistake probably caused by the (confusing) classical numbering of the pre-apophysial and post-apophysial muscle portions in Polyplacophora, for the original idea (L. & W. 1959a, p. 45) is in good agreement with the facts Salvini-Plawen uses for his criticism.

To avoid further misunderstanding I have introduced the previously used letters A to H for the 8 muscle groups on each side in Tryblidiacea, and also for the muscle groups which are believed to be derived from them in Polyplacophora (Fig. 25). The nephridioduct of the Polyplacophora is situated between muscle complexes F and G, which means, between VII_1 and VII_2 in the classical annotation. In Tryblidiacea this corresponds to the interval between muscles F and G, where nephridium F is situated, so there is no trouble. Both in tryblidians and polyplacophorans nephridium F corresponds to the level of the foremost atrium (or ostium), so the identification is quite convincing (Figs 8, 9, 25).

The gonoduct of the Polyplacophora, which lies between VI_2 and VII_1 (classical annotation), causes some difficulties, but this problem is not mentioned by Salvini-Plawen. A comparison between Monoplacophora and Tryblidiacea (Fig. 25) makes it necessary to assume that the posterior gonoduct has changed its position when the monoplacophoran muscles divided to form the pattern of the polyplacophorans. If not, the posterior gonoduct would be expected to penetrate muscle F in the Monoplacophora, which is not the case. In view of the variability of the gonoducts in molluscs, such a redisposition does not seem improbable. It is recalled that the connections of the gonoducts are variable between different Aplacophora (Salvini-Plawen 1972, p. 250) and that the gonoduct in the Chitonida runs dorsal to the lateral nerve in most species but ventral to it in *Ischnochiton ruber, Tonicella marmorea* and *Katharina tunicata* (Plate 1901, p. 467).

It should be noticed that Salvini-Plawen's derivation of 8 pairs of pedal retractors in Monoplacophora from the hypothetical 16 pairs in the Polyplacophora leads to similar unpleasant results, if the two muscles under each shell in the Polyplacophora are supposed to fuse to form single muscles in the Monoplacophora. Then the polyplacophoran nephridium, lying between the two muscles under shell VII, would be expected to penetrate the muscle VII (G) in tryblidians, and it does not. This was referred to as a serious obstacle of our original theory, but on false premises (Salvini-Plawen 1968, p. 193).

5.5 Cladistic relations between Conchifera, Polyplacophora and Aplacophora

The situation of the Conchifera and Polyplacophora was, in a more general way, discussed in Chapter 5.3. It was concluded that the Conchifera, including the Tryblidiacea, are a good monophyletic unit, and the main synapomorphic features supporting this conclusion were mentioned.

It is also obvious and generally accepted that the Conchifera and Polyplacophora are closely related, forming a monophyletic unit of higher order, sometimes called "Testaria" (Salvini-Plawen 1972, 1980a, Lauterbach 1983b). The testarian synapomorphies supporting this relationship are:

1. Many features in the radula apparatus, e.g., radula dentition of docoglossan rasping type with characteristic differentiation, hollow radula vesicles, homologous lateral and medial cartilages of the odontophore, homologous radula diverticula, many homologous radula muscles (pp 66-67).

2. The "velum", the subradular organ, the large pharyngeal diverticula ("Zuckerdrüsen"), the large digestive gland ("liver"), and the coiled intestine.

3. The 8 pairs of pedal retractor groups, the anterior pair associated with a posterior oral muscle (pp 70-73).

4. Heart with 2 pairs of atria, situated between retractors F-G and G-H. Polyplacophorans have only two pairs of ostia in corresponding sites, and the number of ostia is somewhat variable. Among Conchifera only Tryblidiacea and *Nautilus* have 2 pairs of atria, so this apomorphy is somewhat uncertain.

Some of the mentioned synapomorphic features are reduced in the advanced conchiferan classes and are typically developed only in the Polyplacophora and Tryblidiacea. But in view of the fact that the Conchifera, including the Tryblidiacea, is a well established monophyletic unit, there can be no doubt about the phylogenetical consequences (see diagram, Fig. 20). Theoretically some of these features could be plesiomorphic, i.e., could have been present already in some Aplacophoran ancestors (e.g., point 3), but other characters, particularly those of the radula apparatus, appear sufficient to show that the Conchifera and Polyplacophora are strictly monophyletic.

Most autapomorphic characters for the Polyplacophora are restricted to shell morphology: the 8 (or 7) shell plates, the articulamentum, the aesthetes, and the apophyses (in recent forms). The many gills could be an autapomorphy, but this is true only if the multiplication of gills has been independent in Polyplacophora on one side and in neopilinids and *Nautilus* on the other. The characteristic girdle with cuticle and spicules is a polyplacophoran apomorphy, but not the presence of spicules as such, for spicules are a plesiomorphic feature present also in the Aplacophora. Only the restriction of the cuticle and spicules to the mantle margin is significant as an autapomorphic character of the Polyplacophora, and this character is obviously correlated with appearance of the middorsal shell plates.

The common testarian ancestor "B" in the diagram (Fig. 20) must have had the testarian apomorphies, also the 8 pairs of pedal retractor groups. I do not think that it had consolidated shell plates on the back, for nothing in the development of the conchiferan shell supports the theory that it has arisen by fusion of separate consolidated shell plates in an ancestor. But it is very probable that the back was covered by a cuticle and separate spicules, the latter perhaps even arranged into 8 transverse fields corresponding to the 8 retractors. By fusion of the spicules this ancestor may have evolved into a polyplacophoran with 8 shell plates or a conchiferan with a single shell (p. 61). The 8 pairs of retractors are supposed to be preserved in both sister groups.

In my diagram (Fig. 20) the Ordovician genus *Septemchiton* (Bergenhayn 1955) with 7 shell plates is placed as a side branch from the main stem of 8-shelled Polyplacophora, developed by the loss of one plate. Salvini-Plawen (1980a) proposed a new subclass, Heptaplacota, for *Septemchiton* and regarded it as ancestral to other Polyplacophora, obviously because a similar 7-metamerism seems to be present in Pruvot's famous larva of the solenogaster *Nematomenia* (cf. pp 59-61). The Heptaplacota are then supposed to have given rise to the 8-shelled Polyplacophora, from which the Conchifera are believed to have evolved by fusion of the shells. I hesitate to give the 7-shelled condition of the Heptaplacota so much weight as an argument in the phylogenetical discussion (see p. 61) for 7 or 8 shells may be an unstable character, as indicated by the intraspecific variation in recent chitonids. It is admitted that the plesiomorphic state of 7 shells gets some support by ontogeny, for recent Polyplacophora seem to form the 8th shell after some delay and thus exist as 7-shelled larvae for some time, although there is some variation (Smith 1966). And only a distinct interruption of shell formation at the 7-shell stage can be interpreted as a kind of ontogenetic repitulation, for it is hardly remarkable that the most posterior shell plate is the last to be formed.

The geological age of *Septemchiton* is a poor argument for its ancestral state in relation to other Polyplacophora. Is was found in the Lower Ordovician (Bergenhayn 1955) and Upper Ordovician (Sanders 1964), and we do not know the number of valves in the oldest, Upper Cambrian, Polyplacophora (Bergenhayn 1960).

The evidence for a primary 7-metamerism derived from Pruvot's description of *Nematomenia* is certainly circumstantial, for the 7 fields of spicules were found in a post-metamorphosis specimen. Chitons at a corresponding stage may also have 7 plates, although they have 8 as adults.

Although it is possible that the Heptaplacota can have had the ancestral relation to Polyplacophora suggested by Salvini-Plawen, I regard this idea as an unnecessary complication. The Heptaplacota have consolidated shell pieces; Salvini-Plawen's theory and the said idea, in itself uncertain, thus forces us to accept a formation of the conchiferan shell from separate consolidated shell plates, a hypothesis which lacks real support.

Down to the level of the "Testarian ancestor" ("B" in Fig. 20) the phylogeny can be reconstructed with reasonable probability because of evidence from anatomy, embryology and paleontology. The real difficulties come when the relations of the Aplacophora to the Testaria are considered. No modern zoologists will deny that the Aplacophora are good molluscs and share many homologous features with the Testaria, e.g., presence of a radula, dorsal cuticular cover with spicules, a ventral creeping sole (reduced in some Aplacophora) and a pedal gland (in some). No doubt, therefore, there has been a common ancestor of all the molluscs, an "Urmollusk" as indicated by "E" in Fig. 20. The morphological features of this ancestor can, of course, only be theoretically deduced, and this is difficult, because two of the earliest derived lines, the Solenogastres and the Caudofoveata, are admitted to be strongly specialized.

The simplest interpretation would be to regard the Testaria and the Aplacophora as sister groups, derived from the "Urmollusk" as indicated by the solid lines in the cladogram (Fig. 20). This would be the best alternative if it can be shown that the Caudofoveata and the Solenogastres are monophyletic, i.e., share some good synapomorphic features showing that all Aplacophora had a common ancestor ("D" in the cladogram) different from the testarian ancestor "B".

Potential apomorphic similarities between the Caudofoveata and the Solenogastres are the worm-like, almost cylindrical shape, and the extension of the dorsal cuticle down the sides towards the ventral midline, with total or partial reduction of the creeping sole as a consequence. This is usually accepted as a synapomorphic feature, for practically all zoologists suppose that the ancestral mollusc had a well developed creeping sole. But is has been stressed, particularly by Salvini-Plawen (1972) that the final reduction of the foot and pallial groove has taken place in different ways in Caudoveata and Solenogastres, and that the mentioned similarity therefore may be convergent. On the other hand, the initial stages of this development can have taken place in a common ancestor ("D" in Fig. 20) and the differences evolved after the Caudofoveata and the Solenogastres s. str. parted from each other. As long as this possibility is open, the cylindrical shape, the downward extension of the mantle and part of the reduction of the foot can still be a synapomorphic feature, supporting a monophyletic group Aplacophora.

That there are profound differences between the Caudofoveata (Chaetodermatoida) and the Solenogastres s. str. (Ventroplicata) has been known for a long time (Wirén 1892, Odhner 1919, Hoffmann 1949, Boettger 1955, 1959), but only Salvini-Plawen (1969a, b, 1972, 1980a) went so far as to suggest that the Aplacophora are directly paraphyletic and to propose an alternative cladogram. According to his hypothesis, the Caudofoveata and Solenogastres are completely independent branches of the molluscan main stem. The Caudofoveata are regarded as the first branch, and are regarded as a sister group of all non-caudofoveate molluscs. These are regarded as the other monophyletic sister group called Adenopoda. The adenopod ancestor ("C") has, in a dichotomous fashion, evolved into Solenogastres and the Testaria (dotted line in Fig. 20).

This alternative possibility can be made probable if Solenogastres and Testaria share synapomorphic features, showing that they are more closely related to each other than either of them is to Caudofoveata. Salvini-Plawen emphasizes the preoral extension of the pallial groove and the presence of a pedal gland. But these are good pieces of evidence only, if it can be presumed that they were absent in the molluscan ancestor ("E") and there is in fact no possibility to show with certainty that this condition is satisfied. Caudofoveata certainly lack the preoral pallial groove and the pedal gland, but both can have been reduced during specialization within the Caudofoveate line and may have been preserved in the Solenogastres and Polyplacophora as a plesiomorphic feature (the pedal gland is absent in adult Polyplacophora but is present in early ontogenetic stages).

Analogously, it is very difficult to get a strong case for synapomorphy in other features of Sole-

nogastres and Caudofoveata, or for Solenogastres and Testaria, the result being so dependent on the structure of the molluscan ancestor. And since this ancestor is really unknown and dependent on each author's private views on relationships and origin of molluscs, the conclusions must be fairly uncertain. I have therefore left open both alternative ideas about the Aplacophora in the diagram, but can admit that I think there is somewhat stronger support for a monophyly of the Aplacophora, mainly because some characters (extension of mantle, reduction of foot), although possibly convergent, are at least clearly apomorphic.

In either case the significance of the *Nematomenia* larva for the early phylogeny of molluscs is interesting. If the 7-metameric structure, as expressed in the spicules on the back, is homologous with the 7- or 8-metamerism of polyplacophorans, such metameric structure must have been present in the common ancestor. This means that a metameric structure of this kind must have been present in ancestor "C" or ancestor "E" depending on which phylogenetic interpretation is preferred. In both cases the metamerism is brought down to very near the origin of molluscs. Salvini-Plawen (1980a), supporting the diphyletic origin of Aplacophora, logically concludes that the adenopod ancestor ("C") had such metamerism similar to that of *Nematomenia.* It also follows that the spicule fields on the back must have scattered again during further development of the Solenogastres. If 7 pairs of retractor muscles, matching the structure of the back, have been present in the ancestor "C" they must have multiplied in recent Solenogastres, for these usually have many muscle strings, which alternate with intestinal pouches (Fig. 20). It is even questionable if the metamerism of Solenogastres is homologous with that of other molluscs. Such alternation of intestional pouches and retractor muscles is not seen in other molluscs but looks more like the typical "pseudometamerism" seen in several non-molluscan groups like Nemertini and Turbellaria. The multiplication in the Solenogastres could therefore be comparable to that in other animals with elongated body shape.

5.6. General discussion of metamerism in molluscs

The repetition of organs in *Vema* and *Neopilina* is reviewed and compared in Chapter 5.1. It is concluded that the repetition in different organ systems shows reasonable spatial correlation in the two species, although the absolute number of repeated units is greater in *Vema.* The latter has the most synorganized metameric pattern seen in a mollusc. The term "metamerism" is then used in a descriptive way to denote repetition of organs or units along the longitudinal axis of the animal.

The significance of this metamerism remains to be discussed: whether there is reason to assume that it is a fundamental feature in molluscs, and, if so, whether it is related to other kinds of metamerism seen in other protostomians, e.g., in turbellarians and articulates.

5.6.1. The metamerism of the musculature

The low, flattened Tryblidiacea have clearly had a distinctly metameric musculature in the early Paleozoic time, and the recent *Neopilina* and *Vema* have preserved the 8 pairs of pedal retractors. The number of muscle pairs was probably 8 also in some Ordovician and Silurian forms such as *Tryblidium, Pilina* and *Araeophiala,* although the number is obscured by partial fusion in the fossils. Even the Upper Cambrian and Lower Ordovician *Proplina* seems to have had 7 or 8 pairs, whereas the Middle Cambrian *Scenella* may have had 6 or 7 (Fig. 19, Chapter 5.2.).

Those "monoplacophorans" which have a high cyrtoconic shell and therefore are perhaps related to the Cyrtosoma (Rhacopoda) have fewer muscle pairs: *Kirengella* has 4 or 5 pairs. *Cyrtonella* 2 pairs, and *Moyerokania* 5 pairs. Such reduction would be expected if the animal is higher than long, with a dorsoventral axis much longer than the anteroposterior one. This tendency is more pronounced in the high, plainispiral forms like *Cyrtolithes* (2 pairs) or more typical bellerophontids, in which only one pair of scars is preserved (Chapter 5.2., Fig. 19). No recent gastropods or cephalopods have preserved multiple pedal retractors but more than one pair of retractors were present in some fossil nautiloids (Mutvei 1964a, Chapter 5.3.5.).

That some fossil Diasoma had about 8 pairs of pedal retractors can hardly be doubted (Rostroconchs, 6-7 pairs, *Babinka,* 8 pairs) and recent bivalves have preserved 1-7 pairs (Chapter 5.3.6.). In the Diasoma it is characteristic that the retractor scars on each side move up to form a line on each side of the dorsal midline and the reduction of the number of muscles seems to have been slow in some cases. No metameric retractors are known from recent scaphopods, but the situation in some proposed ancestral rostroconchs is uncertain (Pojeta & Runnegar 1976).

When these facts are considered in the light of the probable phylogeny of the Conchifera (Fig. 20), it may be stated that multiple retractor muscles or muscle scars (8 or less pairs) are known from all three evolutional lines, and were most common in older Paleozoic times. Reduction of the metameric musculature is obvious in the Cyrtosoma and the Bivalvia, and only Tryblidiacea and Bivalvia have preserved a metameric musculature to recent times. The idea accepted by most recent zoologists, that the metameric musculature is an ancient feature, retained from ancestral conchiferans, is therefore well established.

This conclusion is also acceptable if functional aspects are considered. It is certainly difficult to imagine a functional advantage of a metameric retractor system in the Conchifera, which have a rigid, inflexible shell. As maintained by Götting (1980a) for *Nautilus,* a progressive development of muscle metamerism under such circumstances appears improbable. On the contrary, such animals would be expected to reduce whatever metamerism present, and that is actually what was stated above in most conchiferan lines. It can also be expected that animals with a long dorsal attachment zone such as rostroconchs, bivalves and tryblidiaceans should preserve the metameric musculature better than the high cyrtosomic gastropods, bellerophonts and cephalopods, in which the space for muscle attachments becomes more restricted. These functional considerations, although not directly conclusive, support the idea that the metameric retractors must have been present in the conchiferan ancestors, and that later changes only have been in the direction of reduction.

The musculature of the Polyplacophora is of decisive interest for this discussion. In Chapter 5.3.5. it was concluded that the series of 8 paired retractors in Tryblidiida is homologous with the series of 8 paired groups of muscles in the Polyplacophora. In the Polyplacophora each of the first 7 muscle groups corresponds to and overlaps the 7 limits between the shell plates, whereas an eighth group extends along the posterior border of the last shell plate. Salvini-Plawen's (1969, 1972, 1980a) interpretation of polyplacophoran musculature as 16-metameric is difficult to accept, for all the shell-attached body muscles are parts of the 8 well-defined muscle groups. Some of these muscles are present as 8 units along the side of the animal, and one of them, the m. transversus, covers the heads of the other muscles of the group and is confluent with some of them. This makes the definition of the 7 anterior groups particularly clear (Figs 25, 28, Pl. 10) — the 8th group lacks a transversus.

The m. medio-pedalis and m. latero-pedalis are duplicated within each group except the 8th one, so that a pre-apophysial and a post-apophysial portion has been formed within each group. This appears to be a secondary subdivision, caused when the apophyses evolved in recent Polyplacophora. A count along the side of the animal will thus give 16 units of these subdivided muscles, but regarding this as a 16- (or 15-) metamerism is justified only if the units counted are comparable. And in this case every second unit differs from the others (pre-apophysial and post-apophysial portions are different). Moreover, the heads of the post-apophysial components are fused and sometimes indistinguishable from the clearly 7-metameric m. tranversus (Fig. 28, Pls 10, 11). I therefore maintain that 8-metamerism rather than 16-metamerism is by far the most probable interpretation (pp 72-73).

Presence of 8 homologous pairs of muscle groups in Tryblidiacea and Polyplacophora leads to the conclusion that such 8-metameric muscle groups must have been present in the commmon ancestor of Tryblidiacea and Polyplacophora (Testarian ancestor, "B" in Fig. 20). This hypothetical animal must have lived already in Middle Cambrian, for tryblidians with metameric muscles were present in Middle and Upper Cambrian (Chapter 5.2.) and isolated polyplacophoran shells are known from Upper Cambrian (Bergenhayn 1960). The presence of a metameric musculature can thus be followed down to the level of the testarian ancestor with reasonable certainty.

There is even some evidence of a 7- or 8-metamerism earlier in molluscan development, in the adenopod ancestor ("C") or in the ancestor of all molluscs ("E"). But this hypothesis depends on acceptance of Pruvot's old description of the larval *Nematomenia banyulensis* (Chapter 5.4.2.), in which 7 transverse fields of spicules were present on the back. I find it very probable that a corresponding metamerism was present in the musculature of this larva, inducing the metameric pattern on the back. If comparable with the retractor metamerism of the Polyplacophora and Monoplacophora, such metamerism of the retractor musculature would be expected to have been present also in the common adenopod ancestor, or in the "Urmollusk" if the Aplacophora is regarded as monophyletic (Fig. 20). This theory that the metamerism of the dorsal shell

plates in the Polyplacophora and the spicule groups of the *Nematomenia* larva are induced by the underlying musculature will probably meet with objections, for many scientists have more or less clearly expressed the opposite opinion, viz., that the 8 shell plates of chitons are the primary feature, and that the musculature adjusts to this by developing an 8-metamerism. But I consider the arguments for a primary metamerism in the musculature stronger or at least equally good: 1) It has been shown that the main musculature appears in larval chitons before the shell plates or even the shell fields are formed (Heath 1899, Hammarsten & Runnström 1925, p. 276). Although not strong, this argument speaks in favour of a muscular metamerism as the primary factor. 2) The opposite possibility, that the metamerism of the musculature is dependent on the dorsal shell plates is contradicted by the Tryblidiacea, in which the musculature is clearly metameric although the shell is undivided.

It is admitted that conditions in adult Aplacophora complicate the theoretical interpretation, for many Solenogastres s. str. have numerous strings of pedal retractors, alternating with a corresponding series of gastric pouches (Fig. 20). Their spicules do not show the 7-metameric pattern reported for Pruvot's larva but are more irregularly scattered. It is therefore understandable and logical that Salvini-Plawen (1980a), while admitting that the 7-metameric dorsal spiculation must have been present in the adenopod ancestor, suggests that the Solenogastres early lost these spicule fields by disintegration and scattering of the spicules.

The history of the pedal retractor musculature on the Aplacophoran level is thus highly hypothetical and is open to numerous theories, for example:

1) The multiplication of musculature into numerous strings in the Solenogastres can be an autapomorphic feature in this group, for a similar muscular metamerism, synorganized with repetition of intestinal pouches, is not known in other molluscs.

2) The repetition of muscles in Solenogastres can also be an ancient feature, inherited from premolluscan ancestors with typical pseudometamerism, where numerous retractor strands and intestinal pouches alternate. This was the alternative preferred by Salvini-Plawen (1972, 1980a). However, this implies that the adenopod ancestor, with 7 spicule fields on the back, should lack synorganization between these plates and the numerous retractor strand inside, and this does not appear immediately probable.

3) It is also possible that the adenopod ancestor with 7 or 8 spicule fields had 7 or 8 pairs of retractor muscles. This could be an ancient feature, eventually inherited from non-molluscan ancestors with 7 or 8 pairs of intestinal pouches, perhaps also with a repetition in other organs. This 7-8 pattern could have passed further directly to Polyplacophora and Monoplacophora without changes, whereas derivation of the Solenogastres would require secondary multiplication of muscles and pouches, and, of course, disintegration of the spicule fields.

The choice between these three alternatives could be favoured by outgroup comparison with the Caudofoveata if these are an independent line separate from the Adenopoda, but the information obtained in this way is doubtful in part because the embryology is unknown. According to Salvini-Plawen (1975) there are 3 to 6 pairs of muscle bundles near the anterior end of some species, but they pass down and attach to the cerebrally innervated "oral shield", called "pedal shield" by Salvini-Plawen (1972). It is uncertain whether the muscles in the Caudofoveata are homologous with true pedal retractors, for the "oral shield" is at any rate not identical with the ciliated, ventrally innervated foot of other molluscs (see Salvini-Plawen 1972). The "oral shield" and the foot proper are regarded as derivatives of a hypothetical common locomotory surface of molluscan ancestors, but nevertheless the two parts are regarded separate enough to be used as major arguments when the phylogenetic independence of the Caudofoveata is discussed. The homology of the retractorlike muscles is therefore uncertain, but this does not change much, for the numbers of these muscles in Caudofoveata do not indicate a clear choice between the alternatives mentioned above.

It may be concluded:

1) that an 8-metameric pattern of pedal retractors is an original feature in conchiferan molluscs, present already in the conchiferan ancestor, although the number of muscle pairs has been reduced in most recent forms.

2) that a homologous 8-metamerism is present in the Polyplacophora, in which the muscle groups overlap the limits between the shell plates and some component muscles of the groups are subdivided. It is concluded that the 8-metamerism is a synapomorphic

feature in Conchifera and Polyplacophora and must have been present in the testarian ancestor.

3) the 7-metameric pattern of spiculation on the back of the Solenogaster *Nematomenia banyulensis* might indicate that this animal had a homologous 7- or 8-metamerism in the musculature. If so, the origin of the metameric pattern must be moved further back in the molluscan history, to the adenopod ancestor or to the common ancestor of all molluscs (the latter if the Aplacophora are monophyletic). The strength of the conclusion under this point is, unfortunately, dependent on acceptance of Pruvot's description of the larval *Nematomenia.*

5.6.2. The metamerism in other systems

The multiplication of soft organs other than muscles, so striking in the recent Tryblidiacea, is difficult to evaluate with regard to its general significance in the phylogeny of molluscs. First of all, few other recent molluscs show signs of a similar metamerism; secondly, fossil molluscs usually show nothing, and, finally, the embryology of recent Tryblidiacea is unknown.

Chapter 5.1. summarizes the new results relating to the metameric repetition of organs in *Neopilina* and *Vema,* particularly how the repetition of other organ systems matches that of the musculature. It is hoped that the new reconstructions and descriptions eliminate some of the doubts and misunderstandings which hampered previous discussions.

The most important new result is that the metamerism of the 8 pairs of pedal retractors remains unchanged in the two species, although the number of gills, nephridiopores, and gonoducts is greater in *Vema.*

For the theoretical discussion it is important that *Vema* has 3 pairs of gonoducts, and probably also 3 pairs of gonads, although only 2 pairs of gonads could be clearly seen in the immature specimen. The presence of only 2 pairs of gonads in the originally examined *N. galatheae* was sometimes quoted as a negative argument in discussions on metamerism. It was interpreted as a case of simple duplication which, for some reason, was regarded as a simpler process than metameric repetition. The three gonoducts have a corresponding situation within each of the three sectors C, D, and E in *Vema,* and although no distinct gonad could be found in sector C, there is no doubt about the identification of the gonoduct (Fig. 9).

V. ewingi has the most extensive repetition of organs, including pedal retractors (8 pairs), posterior oblique muscles (8 pairs), lateropedal connectives (8 pairs), nephridiopores (and ?nephridia, 7 pairs), gills (6 pairs), gonoducts (3 pairs) and atria (2 pairs). For documentation see Chapter 5.1.

This repetition in several organ systems, together with the fact that the units in the different systems are disposed so as to conform with a common metameric pattern, is characteristic of both Tryblidiacea examined. In my opinion the irregularities observed with regard to number and precise location of units in the different series are not larger than those seen in numerous articulates, which are accepted as metameric animals. I therefore object strongly to the numerous authors who *a priori* reject the term metamerism for the Tryblidiacea using arguments which would make many typical articulates non-metameric. The presence of only two pairs of atria or two or three pairs of gonads in Tryblidiacea is thus no argument against metamerism, for the same is found in many arthropods and annelids (see also Chapter 5.1.4.).

The structures of *Vema* would not be in conflict with a hypothesis that its ancestors had developed from larvae with a paired, serially divided mesoderm, perhaps even with open coelomic sacs. This would be in agreement with the fact that many of the metameric organs in *Vema* are mesodermal, e.g., muscles, kidneys, nephridiopores, gonads, gonoducts, and heart atria.

This hypothesis, which is like the one originally suggested by L. & W. (1959a, pp 66, 67), receives doubtful support from a cladistic-type comparison with other molluscs. Actually most recent molluscs show no or only few features which can be regarded as remnants of tryblidiacean-type metamerism. If we except the pedal retractors, which have been 8-metameric during a considerable part of the molluscan history, only the atria of the heart, the gills, and with some reservation the nephridia show any trace of multiplication in other molluscs.

The atria. Two pairs of skematical atria and pericardial sacs are present in Tryblidiacea and *Nautilus.* In chitons the atria are fused on each side and the two atria thus formed unite to an unpaired sac behind the unpaired ventricle (Plate 1901, Hoffmann 1930, p. 281ff). In the majority of polyplacophorans there are two pairs of ostia, located at the same levels as the atria in Tryblidiacea (between retractors F-G and G-H). Those chitons in which the ostia are reduced to one pair have this single pair lo-

cated at the level where the anterior atrium is found in *Neopilina* (between F and G).

Two possibilities are clearly present (cf. Fig. 20):

1) The two pairs of atria (or ostia) have developed independently by convergence in tryblidiaceans, polyplacophorans and *Nautilus,* or

2) the two pairs are a strict homology, present already in ancestral molluscs or at any rate not later than in the common testarian ancestor. In the latter case the two pairs must have been reduced by convergence to one pair at least 3-4 times.

It is not immediately obvious which of these alternatives is the simplest one.

The gills. Two pairs of gills are present in *Nautilus,* and a functional connection with the 2 pairs of atria is obvious. Tryblidiacea have 5-6 pairs of gills and 2 pairs of atria, with the anterior atrium on each side being fed by the foremost 4 (or 5) gills. The multiple gills of the Polyplacophora are usually regarded as a secondary multiplication within this group, and this is certainly probable. However, Hunter & Brown (1965) suggest that the original number of gills has been 4 (2 pairs), based on the 2 pairs of ostia. That ancestral molluscs may have had 2 pairs of gills and atria was also mentioned as a possibility by Pantin in a discussion with Yonge.

It should also be mentioned that small indistinct scars located outside the retractor scars in such a way as to suggest attachment of gill muscles are present in the tryblidiacean *Pilina unguis* and some other fossil forms. But in *Neopilina* some other muscles, mm. obliquii and pallial muscles, attach in the same region so the small muscle scars are not absolute evidence for the presence of gills in the fossil. Rows of 4-5 small scars were also seen outside the pedal scars C to G in the fossil bivalve *Babinka.* As suggested by McAlester (1965, 1966) some of them may be marks of gill muscles, but again it is uncertain if they can be regarded as convincing evidence for multiple gills in this species.

The nephridia. Six or seven pairs of nephridia appear to be present in *Neopilina* and *Vema,* respectively, as judged from the number of nephridiopores opening into the pallial cavity. The lobulated nephridia are difficult to count for they interdigitate in such a way as to make delimitation between different kidneys difficult in some cases. The number of pores, however, is definitely established in both species. It is also quite definitely established that the nephridia D and E receive the gonoducts in the D and E sectors and thus serve as terminal parts of the functional gonoducts. The examined specimen of *Vema* also has a smaller gonoduct in sector C, connected with the nephridium C, i.e., 3 pairs in all, but the gonad C is perhaps vestigial.

Among other recent molluscs only *Nautilus* has more than one pair of nephridia. In front of the 2 kidneys on each side there is a gonoduct with its own opening to the pallial cavity (Griffin 1900, Hoffmann 1937). The two pairs of nephridia, two pairs of gills, and two pairs of atria seen in *Nautilus* appear to form a complex very similar to the heart region of Tryblidiacea.

The gonad. The two pairs of gonads present in the examined recent Tryblidiacea must be mentioned once more, partly because there is some uncertainty and misunderstanding in the literature. *Neopilina galatheae* was described by L. & W. (1959a, pp 59-61) as having two pairs of gonads and gonoducts. No doubt was possible on this point as far as the horizontally sectioned male (spec. IV) was concerned, for an open cleft between the two testes on each side could be followed all the way through the animal (op. cit., fig. 123). In the transversely sectioned female (spec. III) the separation of the two ovaries was more difficult, because of extensive intermingling of lobules from the two ovaries and because of the plane of the sections, but there was no reason to doubt that two separate ovaries were present on each side. Two pairs of nephridia served as gonoducts (D and E), as shown by the presence of mature eggs or sperm in the duct systems (op. cit., figs 123, 157).

In the new material the two gonads on each side are difficult to delimit clearly in the immature specimen of *N. galatheae* (specimen 1), but the two pairs of gonoducts and their connections with the proper nephridia are distinct (Fig. 8). In the immature specimen (2) of *Vema ewingi* (specimen 2) the two gonodal rudiments on each side are well separated, but a third gonad, expected to be present in sector C, could not be clearly seen in the thick sections, although a small gonoduct is present in this sector (Fig. 9).

5.6.3. Comments

The simple accumulation of facts above, where multiplication of organs contra non-multiplication is recorded, gives the result that the majority of recent molluscs are non-metameric. Reconstruction of the phylogeny of the organ systems in the usual way, using this material and the cladogram in Fig. 20, will

therefore give ample evidence for a non-metameric structure of most organs in the ancestral molluscs. The appearance of the supposed ancestors is then deduced from the homologous features of the offspring. Such methods have clearly been used by many authors and have resulted in a categorical statement that the molluscs are non-metameric.

I doubt that such a procedure, which works approximately like a majority vote, leads to reasonable results in a case like this, for there are important complications:

1) The metameric repetition in different organ systems is rarely independent. On the contrary, a metameric repetition in one organ system is usually correlated — spatially and numerically — with metameric repetition in other organs. This is a general rule in annelids and also in "pseudometameric" animals like many turbellarians.

2) The pedal retractor muscles are the best known metameric structures of molluscs, in part because they can be seen (as scars) also in many fossil forms. The available evidence strongly indicates that an 8-metamerism was present in the retractors of ancestral Testaria and was progressively reduced in many lines, leading to absence of metamerism in most recent forms (see p. 105).

3) The metamerism of non-muscular organs relies on much less convincing evidence. With the exception of some probable gill muscle scars in *Pilina* and *Babinka,* no information about the non-muscular organs can be derived from the fossils. The state of metamerism can therefore only be deduced from recent anatomy. This is clearly unsatisfactory, for we know that the metamerism of the pedal retractors has been reduced within several lines. A correlated reduction can therefore be expected to have occurred in other organ systems, which were metameric in the ancestors.

Absence of metamerism in the nephridia of gastropods is, for example, not a good argument for non-metamerism of nephridia in conchiferan ancestors, for we know that the multiple retractors have been reduced to one pair within this line, and the fate of the nephridia can have been the same. Massing such negative arguments from recent Conchifera as proof for a non-metameric structure of conchiferan ancestors is thus a doubtful method.

Conversely, the presence of metameric repetition of pedal retractors and the observed reduction of the metamerism within different lines support the idea that metamerism was an original feature in the Conchifera. It is even probable that other soft parts such as gills, atria, nephridia, gonads, etc. had a more complete metamerism in the ancestral Conchifera, and that this metameric pattern has been preserved in recent *Neopilina* and *Vema.* This seems to be a more reasonable hypothesis than assuming that the metamerism of tryblidians developed progressively within this very line, an idea which is in conflict with the general trend for reduction of metameric structures, which would be expected in univalved animals.

The 8-metameric Polyplacophora and the testarian ancestor may originally have had a more complete metamerism, but recent chitons show a metamerism only in the shell plates and the muscles. The history of the metamerism at the aplacophoran level can only be guessed by extrapolation and the result is dependent on the weight given to arguments coming from the uncertain 7-metamerism of Pruvot's larva and from the multiple muscle strings of the Solenogastres. The muscle strings of the latter alternate with intestinal pouches in a way which makes comparison with other molluscs difficult.

The comparative data from recent and fossil molluscs are thus still insufficient for a well-supported theory about the history of molluscan metamerism. But it can be concluded with considerable certainty that a muscular metamerism is an original feature in the Conchifera and Polyplacophora and must have been present in the testarian ancestors. It is even possible that this metamerism of early testarians was correlated with repetitions in other organs as it is in recent Tryblidiacea. I maintain this possibility, for which there are some good arguments, as a contrast to the often repeated categorical statement that "the molluscs are non-metameric". Without further specification the latter statement is clearly unjustified and, in the case of testarians, grossly misleading. It is misleading also at the aplacophoran level, for metameric tendencies are shown by the Solenogastres, particularly by the larval *Nematomenia* described by Pruvot, but there is some uncertainty about the presence of metamerism in the ancestral aplacophorans and about the kind of metamerism originally present in ancestral Mollusca.

5.7. The ancestry of the molluscs

It was concluded above that a 7- or 8-metameric structure was probably an ancestral feature of the shell-bearing molluscs, Testacea. Metameric features of another type are present also in many recent Solenogastres, but the material of recent molluscs does not clearly show whether the common ancestor

of all molluscs was metameric or what kind of metameric structures it had.

To get further with these questions it is necessary to consider the phylogenetic origin of molluscs, i.e., to find a probable sister group of molluscs among non-molluscan invertebrates. This has been dealt with by numerous authors during the last 100 years and a review covering all conflicting ideas cannot be given here. Vagvolgyi's well-written paper from 1967 may be used as an introduction.

Although different in many details, the many theories can be roughly grouped as follows:

1. Turbellarian theory. Molluscs are said to have evolved from turbellarians or plathelminth ancestors as a separate line, independent of annelids or more advanced spiralian groups: Lang (1894, p. 858), Nierstrasz (1922), Steinböck (1963), Salvini-Plawen (1969b, 1972), Morton & Yonge (1964), Fretter & Graham (1962).

2. Modified turbellarian theory. The molluscs are said to be derived, together with annelids, from a common stem with its root in Turbellaria or turbellarian ancestors. The state of the coelom and metamerism within the common stem is usually not precisely commented: Hammarsten & Runnström (1925), Boettger (1959), Beklemishev (1958, 1969), Vagvolgyi (1967), Stazek (1972).

3. Coelomate theory. The molluscs are clearly a sister group of annelids. The common annelid-mollusc is equipped with some kind of coelom, usually also with some metamerism: L. & W. (1959a), Ax (1960), Reisinger (1970), Siewing (1976), Götting (1980b).

4. The original annelid theory. The molluscs evolved from the annelid stem after development of eumetamerism (typical annelid metamerism): Pelseneer (1899), Heider (1914), Söderström (1925), Naef (1926), Johansson (1952). This theory in its original form is now largely abandoned.

The molluscs clearly belong to the complex called Spiralia, which is characterized mainly by some ontogenetical features supposed to be apomorphic: spiral 4d cleavage, trochophore-like larvae, and an orthogonal nervous system. The typical Spiralia are the Plathelminthes s. str., Nemertini, Gnathostomulida, Entoprocta, Mollusca, Sipuncoloida, Echiuroida, and Annelida. The Arthropoda, although not typical Spiralia with regard to ontogenesis, are usually regarded as related to the Annelida. The relation to the typical Spiralia of the different "Scolecid" groups such as Rotatoria, Nematoda, Gastrotricha, Kinorhyncha, and Priapulida is uncertain, but this problem is left open here and may be irrelevant to the present discussion.

That the Mollusca belong to the spiralian complex is generally accepted today. The critical question is whether they are an independent spiralian lineage, i.e., a sister group of all other recent Spiralia, or whether they are specifically related to one or a few other spiralian groups.

The Mollusca of course share with Turbellaria some general spiralian features such as spiral 4d cleavage (Reisinger 1970), trochophore-like larvae (Salvini-Plawen 1972) and an orthogonal nervous system (Reisinger 1970), but such characters certainly give no or little information on relations within the Spiralia. The flattened shape and the development of a ventral, postoral creeping sole, often with a ciliated surface, have often been referred to as specific characters common to Turbellaria and Mollusca, but they are clearly plesiomorphic spiralian features preserved extensively in Turbellaria and most Mollusca. The plesiomorphic state of the foot is shown by the presence of a ciliated ventral locomotory organ in some adult annelids (*Dinophilus, Protodrilus, Diurodrilus*) and in many larval Spiralia, where it is sometimes called neurotroch (see Jägersten 1972). Many entoproct larvae have such a ventral ciliated field developed as an elongate flattened foot similiar to that of molluscs (Nielsen 1971). It is obvious that the ventral ciliated organs are homologous in larval and adult Spiralia and are homologous with the molluscan foot. This character is therefore no good argument for a specific sister group relationship between molluscs and turbellarians. But of course, if no other clear synapomorphic features can be found between molluscs and other specified spiralian groups, the conclusion will be that molluscs are an independent line from turbellarian-like spiralian ancestors.

But Mollusca have a series of supposedly advanced characters lacking in recent Turbellaria: presence of an anus, a heart with a pericardium, metanephridia, gono-pericardial connections, metamerism and some larval features. The general organization of Mollusca thus seems to be more advanced than that of the Plathelminthes. Most authors therefore derive the molluscs from the common spiralian stem above the Plathelminthes, at a level where an anus, a gono-pericardial complex, metanephridia, and a typical trochophore larva are supposed to be present. Some authors even suppose that the spiralians developed a more elaborate coelom and some kind of metamerism before the mol-

luscs branched off. A few of these features will be discussed briefly below.

Ontogeny. The spiral-4d cleavage of the molluscs in general conforms with that of the other Spiralia, both with regard to morphological patterns and prospective potencies of the blastomeres. That the cell configurations at the animal pole of the blastula, once called "molluscan cross" and "annelid cross", are not comparable has long been known (Korschelt & Heider 1936, p. 866). The cleavage pattern and the potencies of the blastomeres are largely the same in the two groups, but small differences in relative size and positions of the blastomeres caused the old embryologists to include non-homologous cells in the two crosses. If we forget the man-made crosses and redefine annelid and molluscan crosses with the cell lineage in mind the real differences turn out to be moderate (Siewing 1969, pp 65-67). Salvini-Plawen appears to have overemphasized these differences (1969b, p. 207): "der tiefgreifende Unterschied in den sogenannten Kreuz-Bildungen ... welcher nur über so neutrale und nicht-determinierte Zustände wie bei der Turbellaria erklärbar ist". It is enough to suppose that the last common ancestor of annelids and molluscs had these "neutral conditions".

For many years the trochophore theory of Hatschek (1878, p. 80) gave a kind of system in the jungle of larval forms in spiralian invertebrates. Features satisfying a more or less defined trochophore concept were found in larvae of Annelida, Echiuroida, Sipunculoida, Mollusca, Entoprocta, and perhaps Myzostomida. Other larvae of the same groups were regarded as specialized from a primary trochophore type, e.g., the veliger larva of many molluscs (with enlarged ciliary tracts) and the strongly deviating types called pericalymma larvae (Salvini-Plawen 1973, 1980b), in which the prototroch and epispheral epithelium grows down and covers hypospheral larval parts.

The ciliary tracts of the trochophore were regarded as the most characteristic common feature: the prototroch (often double) and the metatroch both consist of compound cilia and are separated by an adoral zone of smaller, simple cilia and a neurotroch (or gastrotroch) passing posteriorly from the oral ciliation in the ventral midline. This ciliary apparatus was regarded as an advanced feature in comparisons with the larvae of polyclad Turbellaria (Müller's and Goette's larvae) and Nemertini (Pilidum and Desor's larva) in which the ciliation is almost homogeneous. For this reason a phylogetic relation between these plathelminth larvae and the trochophore was only supported by some general features and was accepted with great hesitation (compare Salvini-Plawen 1980b).

The many structural details appear to make homology of the ciliary apparatus well founded in the typical trochophore, and the absence of these features in plathelminth larvae makes it look like a good synapomorphy of the "higher Spiralia". This indicates that Annelida, Echiuroida, Sipunculoida, Mollusca, Entoprocta and Myzostomida form a monophyletic unit, derived from a common stem separate from that of Plathelminthes and Nemertini.

It has been maintained that molluscs never or rarely have a metatroch and that the evidence of the ciliary apparatus should be weakened in this group (Hatschek 1878, p. 84, Salvini-Plawen 1980b, pp 393, 403). The trochophore-like larva of *Teredo* (Korschelt & Heider 1936, p. 937) is sometimes mentioned as the only mollusc larva with a metatroch, but several veliger larvae could be added. Waller (1981) has published SEM figures of *Ostrea,* showing a distinct postoral metatroch with compound cilia, and a similar structure is said to be common in other veliger larvae (Strathmann et al. 1972). C. Nielsen (personal communication) has shown me SEM figures of several prosobranch veligers showing both prototroch and metatroch with typical compound cilia. That many molluscan larvae lack the metatroch is certainly no argument against the homology of the trochophore ciliary apparatus in cases where it is complete.

Salvini-Plawen (1969b, 1972, 1980b) has criticized the trochophore theory and advanced as an alternative the "pericalymma" larva as the primary larva of Annelida, Echiuroida, Sipunculoida, and Mollusca. Larvae of this type are the "Hüllglocken" larvae of Solenogastres, scaphopods and some bivalves among molluscs, the "endolarva" of *Polygordius* and some annelids, and the "serosa larva" of *Echiurus* (Salvini-Plawen 1980b). The "calymma" is a cap of tissue, growing down from the episphere and the trochoblasts and covering parts of the hypospheral parts of the larva. To me it seems doubtful whether these very different pericalymma types are homologous throughout the system. The different relations of the calymma to the mouth opening clearly speaks against a homology in annelids, where the mouth opens through the calymma, and in molluscs, where the mouth remains in a normal position under the calymma. This rather indicates that the calymma

has arisen by convergence — independently in these two groups, as has sometimes been suggested.

According to Salvini-Plawen (1980b, p. 403) the pericalymma is not "gleichartig" in the recent representatives, and its primary morphological appearance in ancestral forms is therefore not apparent. Under such circumstances I feel it is difficult to argue for the homology of this larval type or for its presumed role as an original larva in the groups concerned. Further, when so little can be said about the ancestral state of the pericalymma larva, it is difficult to see how it can be said that the trochophore type has evolved by convergence from this type in Annelida, Sipunculoida and Mollusca. This, I think, is the main weakness of the pericalymma theory as now formulated, and that it fails to explain the obvious similarities of the trochophores, which hardly can be explained as a case of wholesale convergence.

Under these circumstances I am reluctant to accept the pericalymma and prefer a trochophore theory, because the homologies are better supported for the trochophore than for the pericalymma. This means that there is some fairly good evidence in the trochophore structure for a monophyletic origin of the "higher" Spiralia, including Annelida, Echiuroida, Sipunculoida, Mollusca, Entoprocta, and perhaps Myzostomida.

The anus. The evidence of the anus is controversial because of the conflicting ideas about the phylogenetical evolution of the spiralian ancestor. Many authors believe that the presumed turbellarian-like ancestral Spiralia lacked an anus ("planula theories"). The anus must then be evolved as an apomorphic achievement during further specialization of the spiralian line. If so, the anus is an argument for the derivation of molluscs together with some advanced Spiralia. But this conclusion is somewhat confused by the statement by Karling (1965, 1966) that one or several "anal" openings are present and seem to have evolved convergently in different Turbellaria, mainly in polyclads.

If an anus was present already in ancestral Bilateria, as supposed in the different variations of the enterocoel theory (Remane 1950, 1958, 1963, 1967, Jägersten 1955, 1959), it follows that there has been convergent reduction of this structure in Plathelminthes, and the presence of an anus in Mollusca becomes a more circumstantial argument. Of course the absence of an anus in the Plathelminthes s. str. makes them poorly suited as ancestors for derivation of molluscs. But according to the enterocoel theory this character is an advanced feature in recent turbellarians, which are excluded as direct ancestors of molluscs also because of other specializations, mainly in the genital system. A derivation of molluscs from a generalized plathelminth ancestor with anus is thus possible, also in this case, but not probable for other reasons.

The Gono-pericardial complex. The arguments derived from the heart, the pericardial sacs, the metanephridia and the gono-pericardial connections of molluscs are briefly summarized by Götting (1980a). It is tempting to compare the molluscs with echiuroids and annelids, which have a comparable dorsal vessel (heart) and a paired coelom, connected with metanephridia and gonads. A central — and much discussed — point is the significance of the heart and the pericardium, and the following discussion of this problem is strongly influenced by discussions with Nørrevang, Rähr and other colleagues at this institute (see Rähr 1981, pp 69-71).

The blood spaces of invertebrate vessels are generally derived from the embryonic blastocoel, a fact known for 100 years: Bütschli (1883, "blastocoel theory"), and Lang (1903, "haemocoel theory"). Some blastocoelic channels remain as open, non-delimited clefts, communicating with other similar spaces in the mesenchyme which fills the blastocoel in adult animals. Defined vessels are formed when blastocoelic channels are surrounded or closed up between epithelial organs such as intestine, coelomic sacs, ectoderm, etc. Epithelial walls when present in such defined vessels are obviously derived by apposition of the epithelial walls of the surrounding organs. It is consequently the basal side of the epithelium, more precisely the basal lamina, which is the innermost layer in contact with the blood in such vessels.

Hearts and contractile vessels are surrounded by contractile coelomic epithelium with the myofilaments localized in the epithelial cells of coelomic origin outside the basal lamina. For illustrations of the principle see Rähr (1981, *Branchiostoma*), Lang (1903, Taf. 3) and Anderson (1966, pp 27-30, annelids).

It may thus be summarized that a basal lamina is the innermost component of the wall of invertebrate vessels, and the epithelium is located outside this lamella. Hearts are usually contractile because of contractility of surrounding coelomic (or pericardial) epithelium. An endothelium in the vertebrate

meaning, situated inside the basal lamina, is not present, and does not form a morphological and functional closed barrier as in vertebrates. Actually the blood vessels of invertebrates have no epithelial walls of their own; as it was expressed by Lang (1903, p. 194), the walls are supplied from surrounding organs.

Ultrastructural investigations have confirmed this for a number of invertebrate groups: Acrania, tunicates, echinoderms, enteropneusts, annelids, molluscs (see Rähr 1981, p. 70). The hirundineans, in which the original vascular system is partly or completely replaced by coelomic channels, are of course specialized. The arthropod heart and pericardium seem to develop in early stages following the general model. A basal lamina followed by a pericardium-derived muscular epithelium forms the wall of the heart, but great changes, perhaps including formation of a "mixocoel", occur later. Some scattered cells (blood cells, often vagile) occur inside the basal lamina in *Branchiostoma* and some annelids (Hanson 1949, p. 152 ff, Nakao 1974, Rähr 1981) and may form a non-continuous layer. A completely unique "vascular system" is present in the Nemertini (see Hyman 1951, p. 486 ff). It is said to be closed by walls consisting of an inner endothelium-like layer, a thick intermediate "basal lamella" and an outer muscular epithelium. It does not look like anything in other invertebrates, so like Lang (1903, p. 355) I have to give it up. Maybe it should be regarded as a coelom (Ruppert & Carle 1963).

Among molluscs the hearts of the Polyplacophora, Gastropoda and Bivalvia have been shown ultrastructurally to conform the principles outlined above (see literature in Rähr 1981, p. 70, Økland 1980). The heart is surrounded by a pericardial epithelium, which has its basal lamina on the luminal (blood) side (Pl. 12). The musculature is partly detached as free trabecules in the heart lumen below the pericardial epithelium, but contact between these trabecules and the basal lamina seems to indicate that the origin of the musculature is basiepithelial (compare Økland 1980).

The cephalopods are so far different in that there is an endothelium-like layer of cells on the inner side of the basal lamina in some vessels (Barber & Graziadei 1965-1967, Gray 1969). But this "endothelium" is discontinuous in some places and is not a barrier to solutes in the same way as vertebrate endothelia (Abott et al. 1981, 1982). It is, functionally at least, more comparable to the scattered and often clearly vagile cells attached to the inner side of the basal lamina of *Brachiostoma* (Rähr 1981) and some annelids (Nakao 1974, see also Ruppert & Carie 1983). The location of the musculature in cephalopod blood vessels appears typical: In the basal part of the presumed coelomic cells (pericytes) next to the basal lamina (Barber et al. 1965).

These considerations hardly lead directly to a definite homologization of molluscan pericardial sacs with the paired body coelom of echiuroids and annelids, for vessels with contractile walls have obviously been formed several times by similiar inclusion of blastocoelic channels between coelomic walls in invertebrates, for instance in *Branchiostoma* (Rähr 1981).

But it is certainly tempting to compare the molluscan heart complex with the dorsal contractile vessel present in many annelids and echiuroids. In annelids the walls of this vessel are formed by the contractile epithelia of the paired coelomic sacs around a longitudinal vascular lumen formed by incomplete fusion of the coelomic walls dorsally of the intestine (see Anderson 1966, p. 27). The blood space is directly lined by a basal lamina. A homologization along these lines would, of course, involve that the pericardial sacs of molluscs are homologous with the much larger coelomic cavities of echiuroids and most annelids. That both types of cavities are connected with metanephridia and are invaded by germinal cells to form localized gonads must be quoted as a similarity and is certainly no argument against a homology. This is also true of the embryonic development, for the material in which the pericardial and coelomic cavities are formed is in both cases the progeny of the 4d cell. A basic condition for this comparison is that the pericardial sacs of molluscs are originally paired. This is obvious in *Neopilina* (L. & W. 1959a), and in embryos of cephalopods (Marthy 1968), some gastropods (Raven 1958) and polyplacophorans (Hammarsten & Runnström 1925, p. 278).

Objections to the homology of the pericardia of molluscs with paired annelid coeloms are of various kinds, although hardly conclusive. The 4d cell gives rise to a large number of organs and structures in annelids, so the gono-pericardial apparatus of molluscs can be homologous only with part of these, and the evidence provided by development can only be general and unprecise (see Vagvolgyi 1967, Salvini-Plawen 1968, 1972).

It has also been stressed that the theory involves a hypothesis that the molluscan coelom, if originally of an annelid or prot-annelid type, must have been

reduced to a small pericardium during the evolution of most molluscs. It has been regarded as a weakness of the theory that no such reduction is evidenced during the ontogeny of molluscs or by comparative evidence (Vagvolgyi 1967, Salvini-Plawen 1968, 1972, Clark 1964, p. 253). But the weight of such negative arguments can be doubted, and the large gono-pericardial cavities of cephalopods, for which a good alternative explanation is lacking, may be a potential argument for a larger coelom in ancestral molluscs (Naef 1926).

Clark (1964, 1980) has repeatedly correlated the development of the coelom with locomotary specializations of different animals. He has shown that the extensive development (and metamerism) of the coelom in annelids has been strongly favoured by its involvement as a hydroskeleton in peristaltic burrowing. This functional role is lacking in molluscs, where no peristaltic movement is present, and it is therefore understandable that the coelom remains small. Clark doubts the homology of the pericardial sac of molluscs with the coelom of annelids for his definition of the annelid coelom is strongly influenced by its function as a hydroskeleton.

Salvini-Plawen rejects the homology more categorically and maintains that the annelid coelom and the molluscan gono-pericardium have arisen independently, the annelid coelom favoured by its function as hydrostatic skeleton, the molluscan pericardium favoured by its functional importance for the heart activity. The main argument is thus the different functions (see Salvini-Plawen 1968, p. 205). But this argument is deficient, for the heart function of the coelom in molluscs is matched by a closely corresponding function in the annelids, where the contraction of the dorsal vessel depends on the apposed muscular walls of the coelom. I agree that this significance for blood circulation must be important as a selective advantage (see Salvini-Plawen 1968). As it is a feature shared by the coelom of annelids, echiuroids and the pericardium of molluscs it speaks in favour of a homology of the two cavities rather than against it.

Salvini-Plawen is convinced that the pericardium of molluscs is a structure sui generis, developed within the early molluscs, more or less as a result of a functional "need" for free mobility and protection of the heart (1968, p. 201). But it seems unnecessary to assume an independent origin of this apparatus in molluscs when a very similar propulsory apparatus has been formed from parts of the coelomic wall in annelids and echiuroids.

In a kind of model Salvini-Plawen (1968, p. 195) has tried to show how a continuous development of the pericardium can have taken place in acoelic, turbellarian-like molluscs: The compact molluscan ancestor with open blood spaces in the mesenchyme is supposed to have evolved a pulsating heart out of one of these channels. The subsequent evolution of a pericardium as an open space around this heart is then thought to have been induced (or favoured) under the influence of a functional need for free mobility and protection of the heart.

I find this model little probable, for the initial contractile heart is an open mesenchymal space without tight walls and will probably be inefficient as a pump. It should be stressed that no heart or heart function will remain in a form like *Lepidochiton* (Pl. 12:48), if the pericardium is removed. Only a space, perhaps with some muscle fibers, remains in the mesenchymatic tissue, with free communications to surrounding mesenchymal spaces. Pumping of blood and pressure filtration of urine would, under these circumstances, be impossible. Even the contractility of the presumed heart primordium is questionable, for in other animals the heart musculature lies in the pericardial epithelium.

I find it difficult to accept this model as a start for a progressive development of the molluscan heart, and regard the alternative model — that a blood space is locked up between preexisting contractile epithelia - for much simpler and in reasonable agreement with observed facts.

Altogether I still maintain that the evidence is good for a homology of the heart-gono-pericardial complex of molluscs with the dorsal vessel-coelomic complex of the annelids and echiuroids. The structure and the situation of heart and pericardium is the same, although in molluscs the entire complex is short and restricted to the hind part of the body. The connection with the metanephridia and the gonads is an additional support to the homology, and the functional significance of this apparatus for blood circulation, excretion and gonad function is partly identical in both groups.

This piece of evidence therefore indicates a derivation of molluscs from some prot-annelid level of the spiralian stem. The common ancestors of molluscs and annelids-echiuroids must have had some kind of body cavity with muscular walls which could be specialized as walls of the contractile vessels when a blood circulation evolved. It is not necessary for this interpretation that the body cavity was very large or metamerically divided, only that it extended on both

sides of the intestine. Once formed, the selective advantage of a regular blood circulation can be expected to have made this mechanism relatively stable from a phylogenetical point of view. It has been preserved in molluscs and also been maintained in annelids, in spite of the fact that the latter have been specialized for peristaltic movement by excess development of coelom and metameric organization.

It is very possible that the body cavity (coelom) of the common ancestor of annelids and molluscs had established contact with metanephridia and gonads before the stage when a heart was developed. This would represent a condition similiar to that found in myzostomids and sipunculoids, in which no organized blood pump is developed.

Metameric structure. The phylogenetical significance of the metamerism has been dealt with by several recent authors, with particular reference to Spiralia: Beklemischev (1958, 1969), Ax (1960), Clark (1963, 1964, 1980), Schmidt (1966), Salvini-Plawen (1968, 1972, 1980a), Vagvolgyi (1967), Stasek (1972), and Götting (1980a). Again, the excellent review of Vagvolgyi (1967) is recommended as introductory reading.

Serial repetition of organs is a common feature in most spiralians: different turbellarian groups, Cestoda, Nemertini, Myzostomida, Annelida, Arthropoda, and Mollusca, but there are great differences with regard to numbers of repeated units and the degree of synorganization between the repeated organs.

It is therefore hardly astonishing that the molluscs, if being a branch of the spiralian stem, show metameric repetition. But this general statement is hardly informative in a phylogenetical sense.

Vagvolgyi, Stasek, and Beklemischev suggest that the common ancestors of Annelida, Arthropoda and Mollusca, being Spiralia of a "super-turbellarian" level, developed repetition of different organ systems, and that the repeated series of organs were primarily unorganized. In articulates, including annelids and arthropods, a synorganized metamerism including most organ systems developed, greatly favoured by selectional forces because of the function of the segmented coelom as a fluid skeleton in peristaltic movements (Clark 1964, 1980). This ultimately lead to teloblastic production of a long segmented body in some not precisely defined way.

The molluscs were also supposed to have inherited an uncoordinated repetition of some organs. The serial organs are then supposed to have become synorganized, reduced or stabilized within the different molluscan lines. The obvious independent multiplication of gills in the Polyplacophora is quoted as a kind of proof, showing that such a story can be true. Of course this theory gives a kind of phylogenetical background for the presence of metameric recapitulation of molluscs but hardly says more than that such repitition is common within the Spiralia. The critical question, whether molluscan metamerism has any features in common with that of other defined Spiralia, for instance turbellarians or annelids, is thus avoided.

The original "annelid theory" compared molluscan metamerism directly with the metamerism of advanced annelids (or was said to do so by opponents). This idea, originally proposed by Pelseneer (1899), Heider (1914), Söderström (1925), and Johansson (1952) was subjected to crushing attacks by many opponents and can actually not be upheld in the original formulation. It should be remarked that Naef (1926, p. 41) was one of the first to realize that segmentation in molluscs is different from that in annelids; the molluscs lack the teloblastic production of segments so typical of the annelids.

L. & W. (1959a, pp 66, 67) also made some reservations with regard to the metamerism of *Neopilina*. We noted that the posterior position of the heart complex, particularly the complete development of metameric structures in the "telson", is incompatible with teloblastic production of segments. We therefore preferred a comparison with the larval segments of annelids, which tend to be produced simultaneously (op. cit., p. 67). Unfortunately our more categorical statement, made as an introductory remark, was the one most quoted (op. cit., p. 66). I agree completely with the majority of recent authors, that molluscan metamerism cannot be compared with the teloblastically produced "eumetamerism" of advanced annelids.

Steinböck (1963), like Boettger (1959) and Beklemischev (1958), classifies the repetition of organs in molluscs as "pseudometamerism" of a similar type as that seen in turbellarians and nemerteans. This is contrasted to the "eumetamerism" of annelids and arthropods, characterized by more strict and orderly recapitulation of organs, teloblastic formation of segments and metameric subdivision of the coelom. If the two concepts "pseudometamerism" and "eumetamerism" are regarded as mutually exclusive, it is hardly astonishing that the said authors could find no (eu-)metamerism in *Neopilina* and other molluscs.

Clark (1964, 1980) for practical reasons suggests that the terms "pseudometamerism" and "eumetamerism" be maintained, but admits that transitional forms may occur. He also warns against the use of "metamerism" in the undefined form as a separate argument in phylogenetical discussion. He did not find that the multiplication of organs in molluscs satisfies the concept of "eumetamerism" and is inclined to regard it as a specialization of its own, independent of that of annelids. The "eumetamerism" of annelids, including the large metameric coelom, is regarded as a unique specialization for peristaltic movement and appears to have been favoured phylogenetically by the selective advantage given by this mechanism.

Salvini-Plawen (1969b, 1972) supports the view that molluscan metamerism is of the "pseudometameric" kind and has formulated a coherent theory. Deriving the molluscs directly from turbellarians he considers the regular alternation of numerous retractor muscles and gastric pouches in many Solenogastres as a turbellarian feature, well known for 100 years, particularly in the Turbellaria Seriata (Lang 1881, *"Gunda"* theory). Such "pseudometamerism" is usually believed to have arisen convergently several times in different lines of plathelminths and nemertians, usually in larger forms with an elongate shape. The primary metameric structure in such "pseudometameric" turbellarians is usually believed to be the gastric pouches, which facilitate the distribution of nutrients.

This theory is supported by some morphological evidence, particularly by the similar alternation of retractor muscles and gastric pouches in some turbellarians and Solenogastres. But this "pseudometamerism" in the more or less wormlike Solenogastres could also have arisen as a convergent specialization within this group in the same way as it obviously has in some Turbellaria. It is therefore not necessary to regard the muscle metamerism of Solenogastres as homologous with that of other molluscs (Testaria), which appears to be different. The metamerism of the retractors of the Polyplacophora and Monoplacophora is not correlated with a repetition of gastric pouches, and the number of metameres is stabilized, and is usually 8 (Chapter 5.6.1.). Positive arguments for comparing testarian metamerism with the "pseudometamerism" of Solenogastres and turbellarians are thus lacking. On the contrary, the correlation of the muscle metamerism in Tryblidiacea with repetitions in other mesodermal organs indicates that this is a more fundamental rhythmicity in the mesoderm and may be completely different, also with regard to the origin.

Salvini-Plawen's (1969b, 1980a) theory that the metamerism of the retractor muscles has been reduced stepwise through the molluscs, was mentioned on pp 72 and 73. He suggested that numerous pseudometameric muscle pairs, derived from supposed turbellarian ancestors, were preserved in the Solenogastres, and had been reduced to 16 pairs in the Polyplacophora, to 8 pairs in the Monoplacophora and to 8 or less than 8 pairs (8, 7, 5, 1 or ½) in different Conchifera. I certainly agree that reductions have taken place in the Conchifera, but I maintain that the musculature of chitons is 8-metameric; 16 muscle pairs can only be obtained by very optimistic counting (pp 72-73). In general I hesitate to homologize the metamerism in Solenogastres with that of other molluscs in the way necessary for the theory (see above), but admit that the idea is beautiful and theoretically possible. One complication should be mentioned, however. Salvini-Plawen (1980) supposed that the adenopod ancestor ("C" in Fig. 20) had been an animal with a 7-metameric spicule pattern on the back, similiar to that of Pruvot's famous larva. This pattern was supposed to be a kind of "preadaptation" for the development of the Polyplacophora. But if the Solenogastres have taken over the "pseudometamerism" from turbellarians it follows that the adenopod ancestor must have had multiple pairs of retractors inside, at least if the story has been as suggested by Salvini-Plawen, and there would be no synorganization with the 7 plates in the dorsal skeleton. This does not appear immediately probable.

It was concluded above that the presence of a gono-pericardial complex is an argument for derivation of molluscs together with the annelids from the spiralian stem (pp 84-86), i.e., that the Annelida and Mollusca are sister groups. The common ancestor must have been a kind of prot-annelid before appearance of peristaltic burrowing and evolution of teloblastic metamerism, probably with paired coelom, heart and gono-pericardial complex. It is difficult to find a recent animal clearly related to such a prot-annelid, but I feel sure that it has existed, because I do not believe that annelid eumetamerism, with all locomotory specializations in different organ systems, was introduced as a single phylogenetical event, a macromutation as suggested by Vagvolgyi (1967, p. 166).

In this connection it is a highly relevant question whether the molluscan segmentation was originally

coelomic or not. Götting (1980a) summarized the arguments indicating that the metamerism was originally coelomic: the two pairs of gonads, atria and pericardial diverticula of *Neopilina,* the 2 pairs of atria (ostia) of chitons, the 2 pairs of gonoducts and the 6 pairs of nephridia in *Neopilina* support an origin from coelomates. The relations of the nephridia to the coelom are uncertain in *Neopilina,* but they are clearly homologous with typical, coelom-connected nephridia in other molluscs. Metameric metanephridia are admittedly connected with metameric coelomic sacs in other invertebrates, so this can be taken as an argument for a metameric structure of the coelom in ancestral molluscs. The number of gonoducts (3 pairs) and nephridia (7 pairs) of *Vema* gives some additional support to these arguments (see also Lauterbach 1983a, b).

Negative arguments can easily be obtained from recent molluscs. But as discussed on pp 80-81 the recent Conchifera are poor witnesses when the state of metamerism in ancestors is discussed, for if originally present, it can hardly by expected to have been preserved when the metamerism of the retractors can be shown to have been reduced during phylogenetical development.

Conclusions

As expected, the review of theories in this chapter can hardly result in definite conclusions about molluscan ancestry or about the prehistory of molluscan metamerism. But in my opinion some arguments are strong enough to favour the probability of some of the numerous ideas proposed.

1. The molluscs belong to the Spiralia. This can hardly be doubted.

2. The trochophore larva, particularly its ciliary apparatus, favours a derivation of molluscs from the spiralian stem above the level of Plathelminthes and Nemertini, for these groups have not developed a clear trochophore ciliation.

3. The presence in molluscs of a gono-pericardial complex with heart, pericardium, metanephridia and pericardium-connected gonads indicates a derivation from Spiralia with a dorsal contractile vessel formed by paired coelomic cavities functioning as a pericardium with metanephridia, and with gonads lying in coelomic (pericardial) diverticula. The gono-pericardial complex is thus a potential synapomorphy supporting a sister group relation between molluscs and articulates (Annelida, Arthropoda).

4. Absence of teloblastic production of segments and of typical coelomic metamerism in recent molluscs makes it difficult to argue for a direct articulate origin. The common ancestor of molluscs and articulates is therefore supposed to have been a prot-annelid with heart and gono-pericardial complex, but still lacking the advanced coelomic metamerism characteristic of the annelids. The coelom (pericardium) of this ancestor can perhaps have been oligomerically subdivided as indicated by the multiple nephridia of some recent molluscs. Such prot-annelids are hypothetical, but if they did not exist we are forced to assume that annelid evolution of a syn-organized metameric coelom, teloblastic production of segments, and full specialization of peristaltic creeping was a single unique evolutional event (macromutation). In my opinion this is hardly probable.

5. The metamerism of molluscs is in itself hardly unexpected, for many features support their incorporation within the Spiralia, a group in which different kinds of metameric repetition are common. But this statement is not very informative from a phylogenetical point of view. Metamerism in recent molluscs, when present, is of two fairly different types:

A. An oligomeric repetition, probably 7- or 8-metamerism, is present in Polyplacophora and some recent and fossil Conchifera but is obviously reduced in many recent forms. This type of metamerism seems to be the original type in the Testaria. More uncertain arguments indicate that it was present also in the common molluscan ancestors. Multiplied gastric pouches are not involved in this type of metamerism.

B. A typical pseudometamerism, including multiple pedal retractors alternating with gastric pouches, is present in some Solenogastres, but such metamerism is unknown in other molluscs.

6. Other features, independent of metamerism, were used when the origin of molluscs from a prot-annelid level of the spiralian stem was discussed above. Such prot-annelids may well have had an oligomeric type of organization, with few segments and a subdivided coelom (pericardium); from these elements oligomeric body muscles, nephridia, gonads, and gonoducts were formed. They would therefore fit with the theoretical ancestors of molluscs, and make an original presence of oligomeric repetition of organs clearly possible. They would also satisfy the somewhat uncertain indications that the molluscan metamerism was originally associated with some subdivision of the coelom.

7. Derivation of molluscs from prot-annelids does not favour the idea that pseudometamerism of the Solenogastres type was present in ancestral molluscs. The fact that this type of repetition is correlated with multiplication of gastric pouches rather indicates that it is an independently developed feature (sui generis) within the Solenogastres.

I thus return to an idea similar to that expressed by L. & W. (1959a), i.e., that molluscs can have been originally oligomeric and in this respect comparable to larval articulates. While these considerations are certainly not conclusive in a strict sense, they show that presence of oligomerism in ancestral molluscs is a possibility, the categorical denial of which cannot be justified by any presented facts.

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