This page intentionally left blank.

MALACOLOGIA, 1988, 28(1–2): 95–103

THE INITIAL STAGES OF RADULAR DEVELOPMENT IN CHITONS (MOLLUSCA: POLYPLACOPHORA)

D. J. Eernisse[1] & K. Kerth[2]

ABSTRACT

The initial stages of development of the chiton radula were examined in *Mopalia lignosa* (Gould, 1846), *M. muscosa* (Gould, 1846), *Lepidochitona fernaldi* Eernisse, 1986, and *L. caverna* Eernisse, 1986. It starts in postmetamorphic juveniles with the secretion of the 2nd, 5th and 8th pairs of laterals, which are the main functional teeth of adult chitons. Moreover, it appears that juveniles are equipped with an efficient feeding instrument nearly as soon as radula formation begins, and certainly before the chitons have their complete set of teeth. This is evident from the mineralization of the 2nd laterals ("magnetite" teeth) from the start, the indications of normal degradation of "used" radula teeth in young juveniles, and observations of feeding in juveniles. As juveniles mature, new laterals are added between existing ones. The 1st laterals and the central tooth originate by fragmentation of a medial "precursor" plate. The phylogenetic implications of the polyplacophoran mode of tooth pattern formation are discussed and related to inferences concerning a primitive ancestral molluscan radula.

Key words: radula; Polyplacophora; chiton; morphogenesis; ontogeny; phylogeny.

INTRODUCTION

Comparative ontogenetic investigations of the molluscan radula have potential to reveal shared patterns of radular formation or divergent patterns that distinguish between particular lineages of mollusks. For all mollusks, only polyplacophorans (Minichev and Sirenko, 1974; French translation by Sirenko & Minichev, 1975), Solenogastres ("aplacophorans") (Salvini-Plawen, 1972, 1978), and pulmonates (Kerth, 1979) have been thoroughly investigated. Minichev and Sirenko (1974) describe the radula in several genera of "larval" polyplacophorans as having a broad, monostichous form. They conclude from this observation that the radula of primitive mollusks is derived from a monostichous ancestral state. Salvini-Plawen (1981; 1985) has reached similar conclusions for two species of Solenogastres (or Neomeniomorpha), based on Pruvot's famous larva (Pruvot, 1890) and his own observations (Salvini-Plawen, 1972, 1978) of *Simrothiella*, although he shows only a slender connection between two already well shaped halves in *Simrothiella.* In contrast, Kerth (1979) showed that the radulae of embryos of several pulmonate families pass through a distichous stage.

If the general scheme proposed by Minichev and Sirenko (1974) and Salvini-Plawen (1985) is correct, then polyplacophorans (also referred to as chitons hereafter) and "aplacophorans" would appear to have a fundamentally different ontogenetic sequence of radular development from pulmonates, suggesting a possible phylogenetic discontinuity. This, and the availability of chiton larvae, led us to reexamine the process of radular formation in chitons. Here we reexamine the ontogeny of radular development in four chiton species: *Mopalia lignosa*, *M. muscosa*, *Lepidochitona fernaldi*, and *L. caverna*. The successful culturing of chitons through metamorphosis has been difficult for most workers, and often published descriptions have been based on cultures with a low percentage of metamorphosing juveniles. These four species were selected because of the fortuitous availability of healthy larvae and juveniles. In retrospect, this selection also permitted comparisons between two families, between closely related species of two genera, and between free spawners (both *Mopalia* spp.) and brooders (both *Lepidochitona* spp.). Finally, we infer a more general view of the basic polyplacophoran radula from our comparisons of these four species, and compare this view to the one proposed by Minichev & Sirenko (1974).

[1]Friday Harbor Laboratories, University of Washington, Friday Harbor, Washington 98250 USA. Current address: Museum of Zoology and Department of Biology, University of Michigan, Ann Arbor, Michigan 48109 USA.

[2]Zoologisches Institut, Universität Würzburg, Röntgenring 10, 8700 Würzburg, F.R. Germany.

MATERIALS AND METHODS

Larvae and juveniles of four chiton species were obtained from adult chitons spawning at Friday Harbor Laboratories. All adults except for *Lepidochitona caverna* were collected on San Juan Island, Washington U.S.A. Adults of *L. caverna* were descended from a breeding population first maintained at Santa Cruz, California U.S.A. (site of original collection, Eernisse, 1984; 1986) and later at Friday Harbor Laboratories on San Juan Island.

Mopalia lignosa and *M. muscosa* free spawned their gametes, and embryos hatched as swimming larvae in less than two days after fertilization for *M. lignosa*, and less than four days after fertilization for *M. muscosa*. These swimming larvae were maintained in beakers for approximately one week with daily changes of filtered sea water and kept at ambient sea water temperatures (12 to 14° C). For each of the following samples of known age, the radulae of 4 to 14 specimens were examined, all fixed in 70% ethanol.

The first series of larvae and juveniles was obtained from a single spawning *M. muscosa* female and several lightly spawning males, on June 10, 1985. Fixations were made at 7, 8, 9, 10, 11, 13, 15, 17, and 21 days after fertilization. Less than 10% of several hundred larvae had metamorphosed by 13 days, when a selection of representative larvae and all the benthic survivors of one of three cultures were fixed. At 17 days, about 40% of the remaining larvae in the cultures had metamorphosed and the benthic survivors of the better of the two remaining cultures were fixed. Finally, at 21 days, nine metamorphosed juveniles were fixed.

The best series of larvae and juveniles was obtained from two *M. lignosa* spawning within hours of collection on August 1, 1985. An isolated male spawned first, and his sperm were introduced to an isolated female, prompting her to spawn copiously. The resulting larvae were observed at least daily until they were near to metamorphosis. The first fixation was made at eight days, when about 40% of the larvae in all cultures (and in the fixed subsample) were metamorphosed. The next fixation was made at 12 days, approximately one day after more than 95% of the larvae had completed metamorphosis. Subsequent fixations for this study were made at 18, 22, 29, 36, 51, 66, and 105 days after fertilization (length of juveniles examined: 0.35 to 1.6 mm), and other animals from this cohort were kept alive including 19 that were still alive at 14 months (mean length ± st. dev. = 21.4 mm ± 3.26; max. length = 27.6 mm; min. length = 13.3 mm).

In contrast to the free spawners *M. muscosa* and *M. lignosa*, the brooders *L. fernaldi* and *L. caverna* care for their embryos until the emerging larvae are capable of crawling and are within one or two days of metamorphosis (Eernisse, 1984). A large selection of adult brooders of these species were kept in the lab, and juveniles were collected near adults shortly before or after they had metamorphosed. For *L. caverna*, these juveniles ranged from recently metamorphosed, about 0.5 mm length, to considerably older juveniles, to a maximum of 1.8 mm length. For *L. fernaldi*, we examined a series of juveniles ranging from 1.1 mm to 1.6 mm length. The exact age of juveniles collected in this way could not be determined. However, for *L. fernaldi*, additional broods were removed from three adults and cultured as for *M. lignosa* and *M. muscosa*. The age of each of these three broods (i.e. days since fertilization) was estimated with a high degree of confidence based on the appearance of previously timed developmental features in the embryos (Eernisse, 1984). Their age in relation to metamorphosis could be determined by direct observation. All 45 larvae and juveniles from one brooder were fixed on July 11, 1985, when about 70% of the larvae had metamorphosed (approx. 13 days after fertilization), including 1 of 45 metamorphosed on July 8 (at 10 days), and 15 of 45 on July 10 (at 12 days). Juveniles from two other brooders were fixed at about 19, 25, and 28 days after fertilization. The length of the 13 to 28 day old *L. fernaldi* juveniles ranged from 0.35 mm to 0.5 mm.

In addition to the above species, we examined premetamorphic larvae of *Lepidochitona cinerea* (Linnaeus, 1767) (a kind gift from Prof. Dr. W. Haas, Bonn, Fed. Rep. of Germany).

In preparation for phase contrast and Nomarski-interference contrast light microscopy, specimens were first rehydrated, then the calcareous dorsal plates and girdle spicules were dissolved with 1N HCl. Next, specimens were macerated in cold 5-10% KOH (1 to 2 h). Finally, the radulae were prepared by pressing the macerated tissue under a cover glass in hot glycerine gelatine.

For SEM observations, juveniles and adults were macerated in warm 5% KOH only until

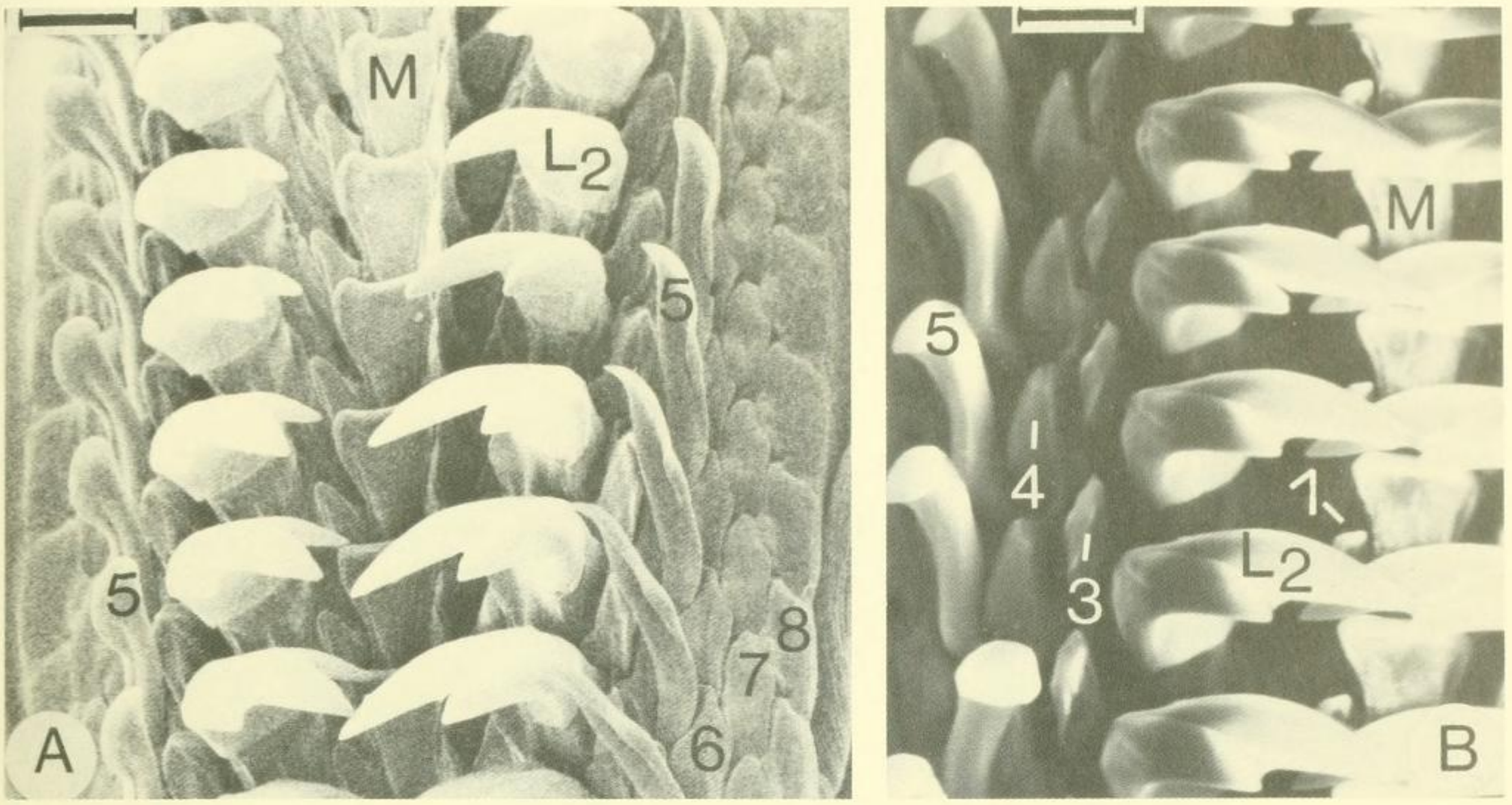


FIG. 1: Radulae of adult *Mopalia lignosa* in dorsal (slightly lateral) views with SEM. A. Adult (length 43 mm) from San Juan Is., Washington, USA; total radula length 8.6 mm with 33 transverse rows of mineralized teeth. Complete transverse rows 6-11, scale bar: 190 μm. B. Small adult (length 16 mm) from Año Nuevo Pt., California, USA. Left central portion of transverse rows (approx. ⅓ distance from first anterior row) with teeth spread in preparation, scale bar: 80 μm. L_1 to L_8 = laterals, M = medial (central) tooth.

the radulae were clean and could be teased away from other tissue. After a distilled water rinse, radulae were stored in 70% ethanol, then transferred to 100% ethanol before mounting on a specimen stub. The radulae were sputtercoated with gold for two to six minutes and scanned at 40 kV on a JEM 1200 EX™ STEM (in conjunction with energy dispersive Xray microanalysis of juvenile and adult radulae as reported in a subsequent study, Eernisse and Fontaine, in prep.) or at 15 kV on a JEOL SM-35 SEM.

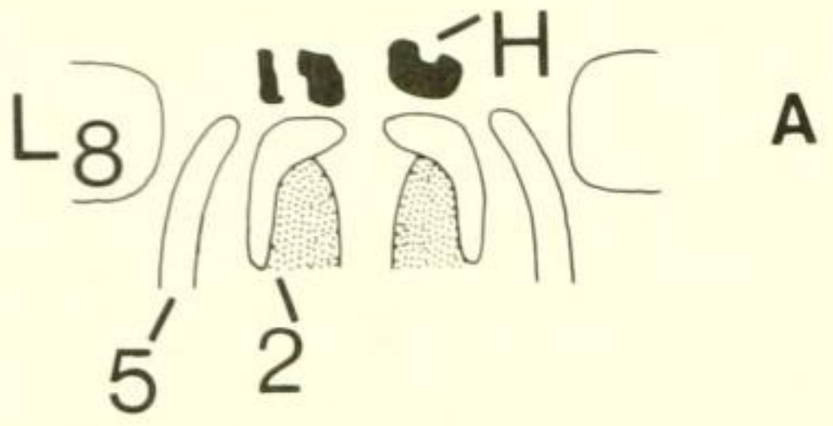
RESULTS

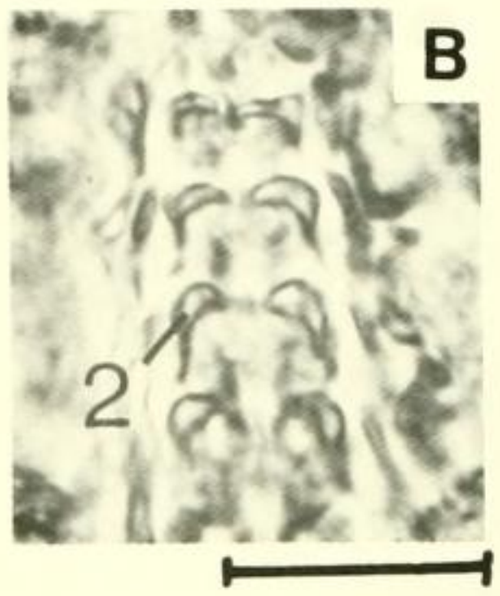
The chiton radula

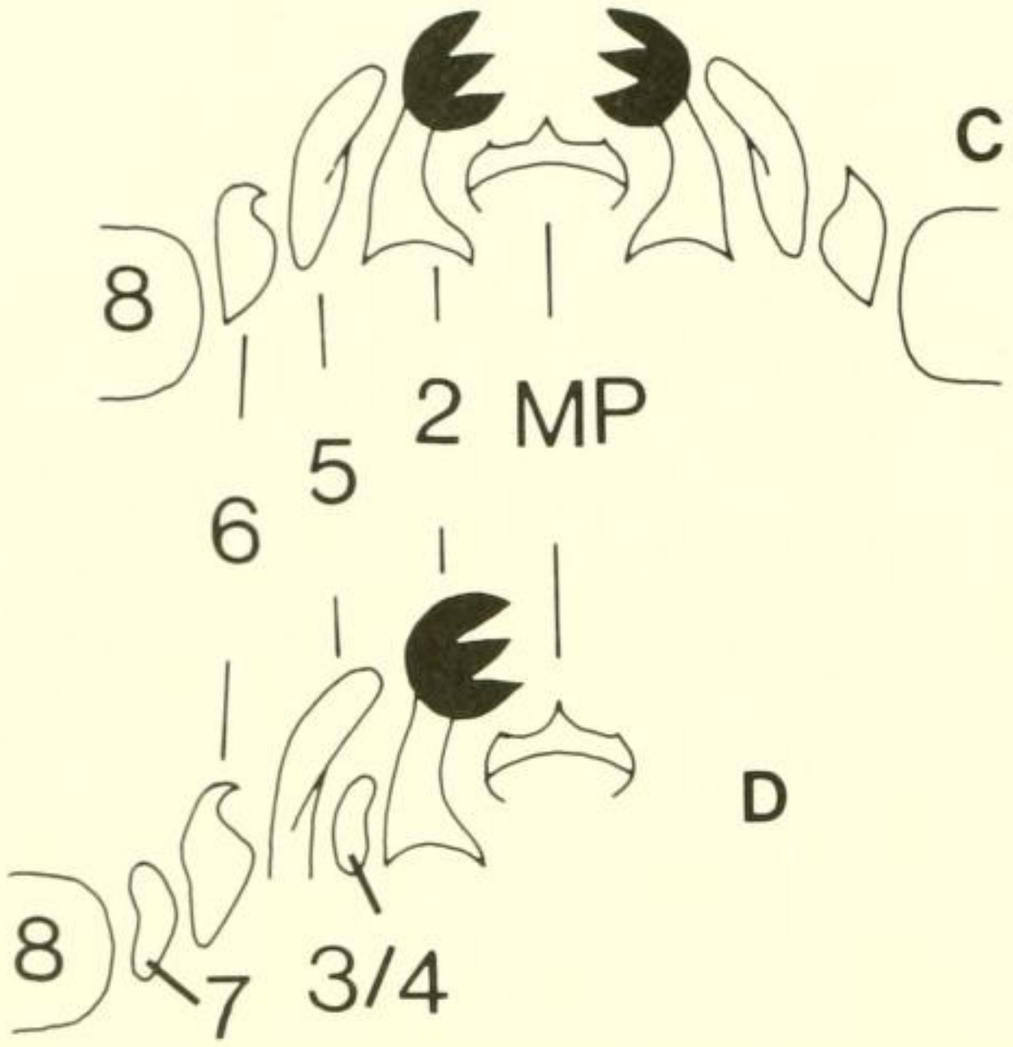
The chiton radula is remarkably uniform in tooth number and type, bearing transverse rows of 17 teeth of predictable shapes (Figs. 1A,B) except 11 or 13 teeth per row in *Juvenichiton* (Sirenko, 1975). Each row is "stepped," or v-shaped, with each tooth anterior (at its base) to the next most distal tooth. The eight lateral teeth (L_1 to L_8) on each side of the medial or "central" tooth ("M") are attached to the elastic radular membrane. The L_2 and L_5 pairs are the most elongate teeth. The L_2 pair are the main working teeth and bear highly magnetized dark caps (Lowenstam, 1962; Carefoot, 1965; Towe and Lowenstam, 1967), usually each with one to three sharp cusps. Each L_5 tooth has the general appearance of a sickle, usually with a flattened distal tip, and lies in close association over the mineralized portion of the L_2 tooth from one row posterior. The relationship of the L_5 and L_2 cusps suggests that they cooperate in scraping and collecting food or, alternatively, the L_5 cusps protect other soft parts from the highly mineralized L_2 cusps as these teeth roll back into their normal tube-like orientation. Finally, the margins of the radula are stabilized by the plate-like $L_{6,7,8}$.

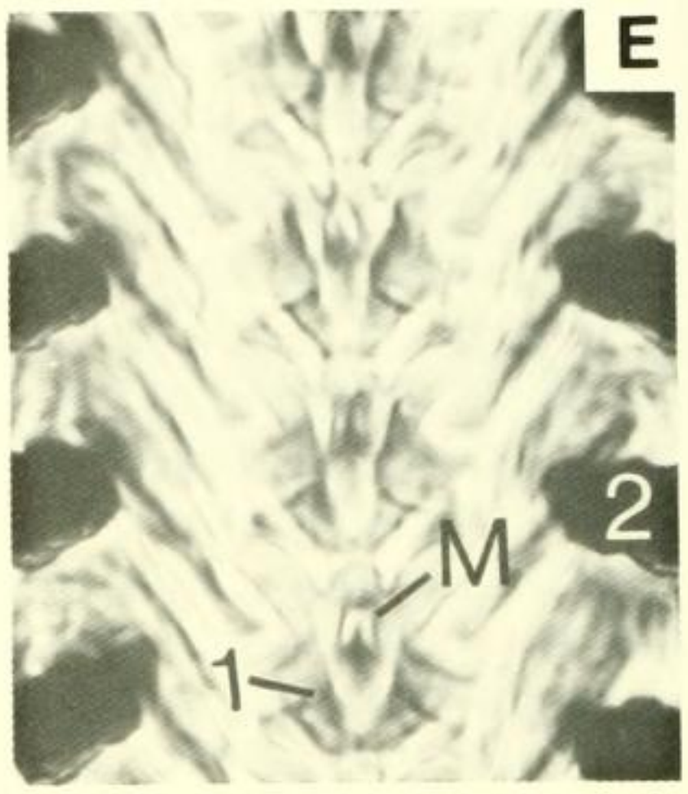
The development of the juvenile radula

We found no radular structure in "trochophore" larvae (those larvae that still had a prototroch); the radula first appears after metamorphosis. Even the specimens of *L. cinerea* with conspicuous valve rudiments (plate-anlagen) lacked radulae. The first radulae were recognized in *M. lignosa* 8 days after fertilization (3 to 6 longitudinally repeated, transverse rows of teeth); in *M. muscosa* in the course of the first week after metamorphosis (up to 10 transverse rows);









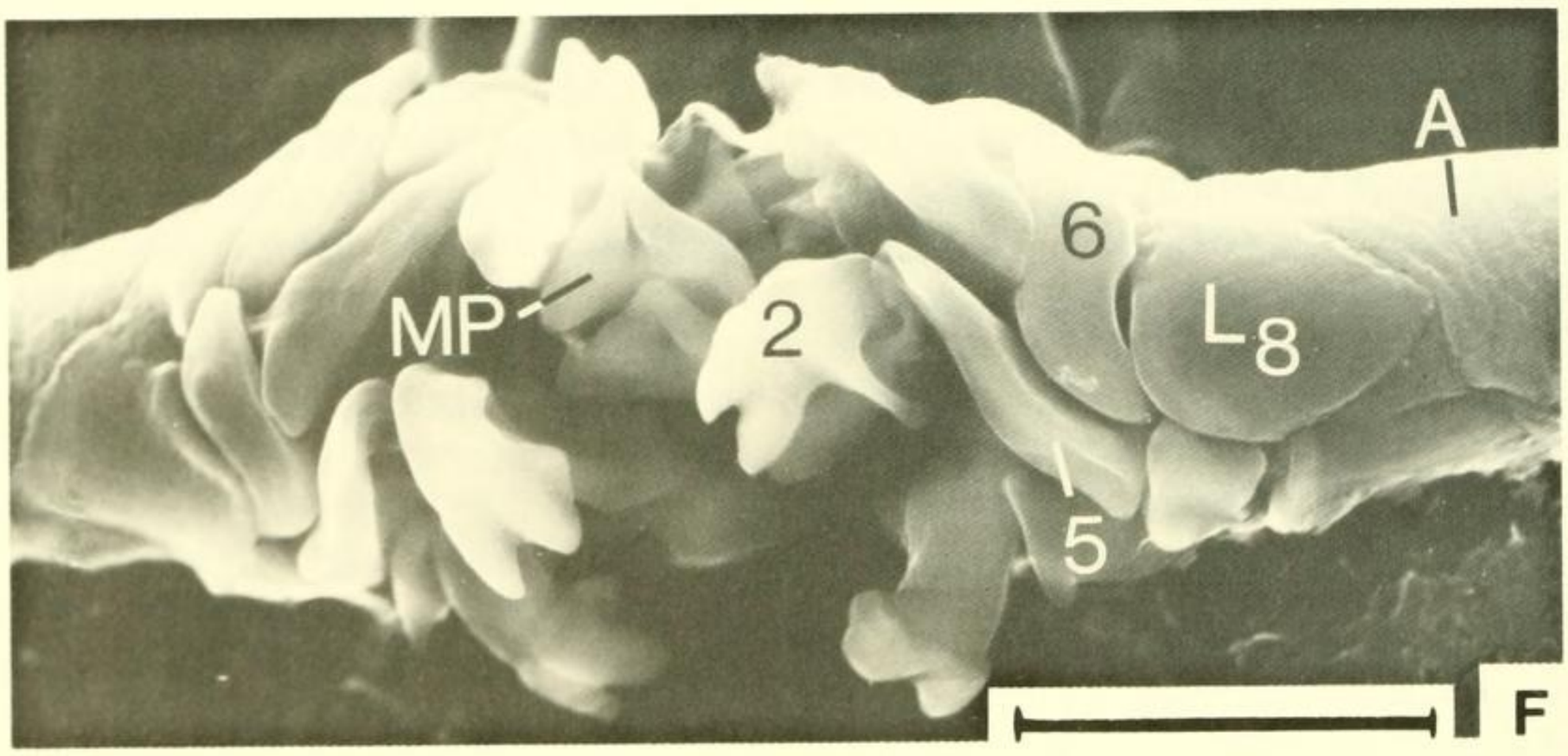
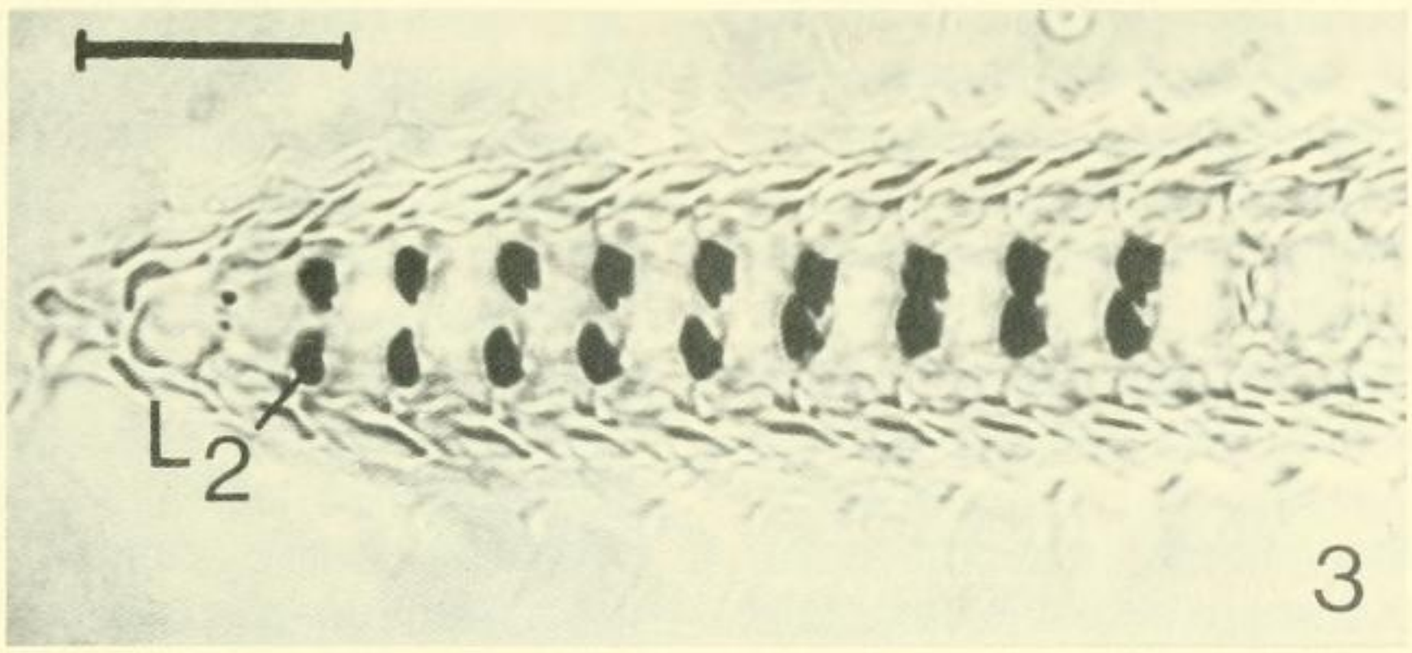


FIG. 2: Radula morphogenesis in juvenile chitons. A. Foremost transverse row of the larval radula with 3 pairs of teeth (composite reconstruction with teeth slightly separated from camera lucida drawings of *Mopalia lignosa, M. muscosa, Lepidochitona fernaldi*). H = hump. B. Earliest larval radula of *L. fernaldi* 13 days after fertilization, phase contrast, scale bar: 20 μm. C. Transverse row with 9 teeth (composite reconstruction as in Fig. 2A of *M. lignosa, M. muscosa, L. fernaldi*) corresponding with Fig. 2F. D. Transverse row with 13 teeth (camera lucida drawing as in Figs. 2A,C of *L. fernaldi*). E. L_1-pair and medial tooth (*L. fernaldi* oldest series). Compare with the medial "precursor" plate (MP) in younger juveniles (Figs. 2 C,F), phase contrast, scale bar: 20 μm. F. Bending plane of the radula, anteroventral SEM view (*M. lignosa*, 19 days after fertilization). Note the shape of the medial plate. Scale bar: 10 μm, A = alar membrane (subradular membrane) of the radula.



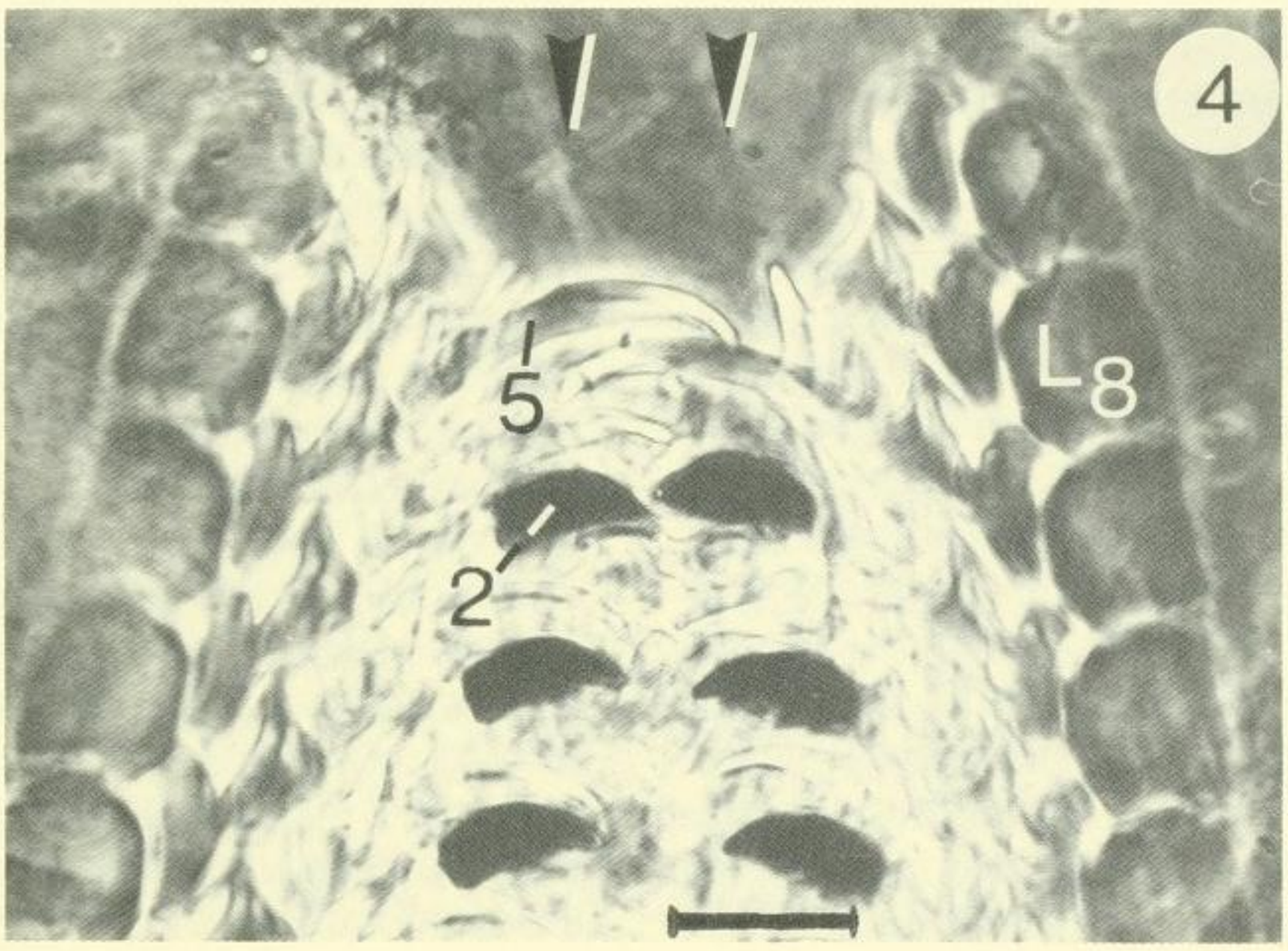


FIG. 3: Light micrograph dorsal view of radula (*L. fernaldi* 25 days after fertilization) with prominent dark-capped cusps ("magnetite teeth") of L_2-pairs. Left to right: anterior to posterior. Scale bar: 20 μm.
FIG. 4: Anterior end of a juvenile (1.1 to 1.6 mm length) radula with degradation. The foremost inner laterals and the medial tooth are shed (arrows). (*L. fernaldi*, phase contrast). Scale bar: 20 μm.

and in *L. fernaldi* 13 days after fertilization (4 to 7 transverse rows).

The tooth shape and pattern were identical in the youngest specimens of *M. lignosa*, *M. muscosa*, and *L. fernaldi*: Radular development consistently starts simultaneously with the paired formation of the "magnetite teeth" (L_2), the sickle-shaped L_5 teeth, and the outermost marginal plates (L_8). Therefore the first transverse row of the newly formed radula usually consists of 6 teeth (pairs of $L_{2,5,8}$). More rarely 4 teeth (pairs of $L_{2,5}$) or, much more rarely, a single pair (L_2) was noted. Each tooth was easily identified from the start by its characteristic shape (Figs. 2A,B,F). There is a bilaterally-symmetrical tooth pattern from the outset. The cusps of the anterior-most L_2 pair were dark-capped even in the earliest cases, suggesting mineralization of these cusps from the onset of radular formation. Moreover, juveniles of all species considered here began active foraging movements within a week of metamorphosis, moving from side to side and leaving a trail of corresponding rasp markings in the substrate covering of diatoms. A medial tooth could not be detected in early stages of radular development. This finding is contradictory to observations of *Schizoplax* by Sirenko & Minichev (1975: figs. 2b,c). In a few cases amorphous humps ("H" in Fig. 2A) were observed in front of the foremost plates.

Further radular development was documented in *M. lignosa*, *L. fernaldi* and *L. caverna*. The radula elongates and the number of transverse rows increases up to 30 to 40 in the oldest series. Several of the 18 to 28 day old juveniles showed radula degradation which is characteristic of all older animals. For juveniles of all ages as in adults, the medial part of the radula's anterior end was shed first (Fig. 4).

New longitudinal rows of teeth appear with the increasing age of the chitons. A large

medial plate ("MP," Figs. 2C,D) and the L_6 teeth are next to be added between the existing $L_{2,5,8}$ teeth. The radular development is identical in the three species until each has nine teeth within the transverse row, but differences were observed after this stage. In each transverse row, additional teeth form in the order L_7, L_4 and L_1 in *L. fernaldi* and *M. lignosa*, but L_4, L_7 and L_1 in *L. caverna*. Almost all of the oldest specimens of *Lepidochitona* appeared to exhibit a complete radula with 17 teeth in the transverse row, although the small L_3 could not be identified unequivocally. New teeth are added to the radula of *M. lignosa* very slowly by comparison. The oldest juveniles have at most 11 longitudinal rows of teeth in their radula.

Minichev & Sirenko (1974) state that nearly all new teeth in the transverse row originate from a fragmentation of "precursor"-plates. Such a process can be excluded at least for the $L_{2,4,5,6,8}$ because we never observed these tooth pairs in an intermediate stage of fragmentation. On the other hand the medial plate apparently splits up to form the L_1 pair and the definitive medial tooth (Fig. 2D,H). This process was evident by comparing juveniles that had only a broad medial plate with juveniles at a slightly more advanced stage that had a small medial tooth flanked by the L_1 pair. The medial tooth could be identified as a small medial ridge on the "precursor"-plate before its apparent separation.

DISCUSSION

In the three species examined at early stages, radula formation starts soon after metamorphosis. First a symmetrical tooth pattern arises, consisting normally of several transverse rows of "teeth," each with three "tooth" pairs. A medial plate for each transverse row is added later. This sequence is basically the same as has been observed in radulae of many gastropods (Kerth, 1979; 1983a, b) including seven families of pulmonates and in two genera of opisthobranchs, *Polycera* and *Adalaria*, which pass through a stage with one to three pairs of laterals in each transverse row before a central tooth is added.

The radulae of the chitons we examined, however, differ considerably from those of the gastropods examined in their later development. In gastropods, new longitudinal rows of laterals are added only on the outermost margins of the radula (Kerth and Hänsch, 1977). In chitons, new longitudinal rows of laterals are inserted (i.e. erupt) between existing laterals. We found that the first teeth or plates to appear in a chiton radula are, appropriately enough, the main adult working $L_{2,5}$ teeth and L_8 plates, the latter previously suggested to serve as margin stabilizers. Evidence presented here would indicate that particular radular teeth are formed with characteristic shapes making them functional almost from the start, and certainly before all 17 teeth per row are present. Judging from their dark color, we concluded that the cusps of the initial L_2 pairs were apparently mineralized from the start. This result has more recently been confirmed with energy dispersive Xray microanalysis of *M. lignosa* juveniles only 16 days post-fertilization (Eernisse and Fontaine, in prep.). Finally, our observations of feeding behavior in newly metamorphosed juveniles provide strong evidence of the functionality of the newly formed radula.

Minichev and Sirenko (1974) described the radular development in four chiton genera and in some unidentified chiton "trochophores." Our results differ from theirs in several ways: (1) We observed no radulae earlier than postmetamorphic stages. (2) These authors describe a primordial radula in the unidentified trochophores with only one longitudinal row of broad plates. We didn't observe any comparable structure, although there occasionally were a few amorphous humps in front of the foremost transverse row (Fig. 2A). (3) Minichev and Sirenko (1974) depicted primary central teeth in the foremost parts of the youngest radula, but secretion of these teeth stopped very early. We were not able to find any comparable structure even with phase contrast or Nomarski-interference optics. (4) According to these authors, almost all of the laterals originate by fragmentation of a pair of "precursor"-plates on either side of the L_2 pair. Although the order of fragmentation is never explicitly stated in Minichev and Sirenko (1974: 1136), Sirenko and Minichev (1975: fig. 2b,c,d) clearly indicate that they believe the first fragmentation of the "precursor"-plates will lead to the adult L_3 and $L_{4\text{-}8}$ pairs, the next fragmentation to the L_4 and $L_{5\text{-}8}$ pairs, and so on until finally the L_7 and L_8 fragment. We can rule out such a fragmentation process in the species we examined for all laterals with exception of the L_1-pair. These and the medial tooth originate by fragmentation of the medial plate (Fig. 2C,E,F). (5) We observed a different order that new

teeth are added in each transverse row. Sirenko and Minichev (1975: figs. 2b,c,d) depicted very exactly the shape of the laterals in the earliest radula and because their drawings are completely in accordance with the shape of laterals in our investigated species, it is clear they have misinterpreted several teeth or plates. For example, the teeth or plates Sirenko and Minichev (1975: fig. 2d) have labeled L_3, L_4, and L_{5-8} should instead be labeled L_5, L_7 and L_8, respectively. (6) Minichev and Sirenko (1974: 1136, fig. 1:4) argued that the dark portions of the L_2 pairs are a secondary feature, with the first few L_2 pairs lacking mineralization altogether. We observed mineralization concurrent with the start of radular formation.

There is a possibility that our results differ from those of Minichev and Sirenko (1974) because they studied different chiton species, or because some of their species differ because they are brooders (e.g. *Schizoplax brandtii* and *Hanleyella asiatica*). However, our consistent results for members of two chiton families, and for both free spawners and brooders, suggests to us that the patterns we have observed are general for chitons. If we are correct then our results are important not only in documenting a previously unknown pattern of tooth formation but are also important to recent discussions of molluscan evolution. This is true because the ontogeny of the chiton radula has been used as a prime case in favor of a bilateral yet monostichous ancestral condition. In order to appreciate both the underlying assumptions and previously stated support for this idea, some review is necessary.

The discovery of living monoplacophorans and descriptions of their anatomy (Lemche and Wingstrand, 1959; Wingstrand, 1985) has again brought to prominence the often suggested hypothesis that metamerism is a basic feature of mollusks, perhaps a primitive condition shared with other metameric protostomium ancestors. Organs are also repeated in polyplacophorans (chitons) and in the cephalopod genus *Nautilus* as was discussed in depth by Naef (1926) and previous authors (for review see Wingstrand, 1985). Particularly striking are the repetition of kidneys, atria and gills in monoplacophorans, polyplacophorans, and in *Nautilus*. Other authors regarded the metameric condition as a convergence (Hoffmann, 1937; Boettger, 1959; Yonge, 1960; Salvini-Plawen, 1985) and argued that single paired systems were present in a hypothetical molluscan ancestor.

Wingstrand (1985) supports grouping the sister groups Polyplacophora and Conchifera (the latter group including monoplacophorans) as a monophyletic unit, the "Testaria" (Salvini-Plawen, 1972; 1980; Lauterbach, 1983), itself a sister group to the either mono- or biphyletic aplacophoran mollusks (i.e. the Caudovoveata and the Solenogastres). In support of this view, Wingstrand describes many testarian synapomorphic features including the radula and radular apparatus, the velum, the subradular organ, the large pharyngeal diverticula, the large digestive gland, the coiled intestine, the eight pairs of pedal retractor groups, and the already mentioned similarities of the heart complex. As Wingstrand (1985) has noted, even if as he has concluded, metamerism is primitive for testarians, it is difficult to determine whether a basic metameric organization is a plesiomorphic condition for testarians, present also in a protostomian ancestor or, alternatively, if metamerism is a synapomorphy for testarians. Only the "Aplacophora" are available for outgroup comparison and their nonmetameric condition could either be a primitive molluscan feature or attributed to convergent evolution due to a vermiform habit or neotenic reductions resulting from small adult body size. The serial nature of all known molluscan radulae might provide insight on the issue of metamerism but, not surprisingly, there is little general agreement on the features that are primitive to a radula. First, there are obviously two issues concerning the presumed serial or nonserial nature of the primitive radula, differing in whether the "metamerism" is bilateral (left and right) or longitudinal (serially repeated rows). Nierstrasz (1905) and Boettger (1955, 1959) proposed that the basic ancestral radula was bipartite (i.e. in two parts, symmetrical left and right) and distichous (i.e. arranged with two matched teeth in each longitudinally repeated row), while Salvini-Plawen (1972, 1978, 1981, 1985) contended it had a broad monostichous form. Meanwhile, Minichev and Sirenko (1974) and Ivanov & Tzetlin (1981) attributed to the Aplacophora and Polyplacophora a primarily monstichous radula and to the Conchifera a polystichous (Minichev and Sirenko, 1974) or a distichous (Ivanov & Tzetlin, 1981) radula.

Because aplacophorans have been regarded as the one or two earliest diverging of extant molluscan lineage(s) (i.e. Wingstrand,

1985) and because they have the simplest adult radula, the aplacophoran radula might be especially appropriate to consider. However, the highly specialized and diverse modes of feeding of many aplacophorans, especially those that are interstitial, could confound this conclusion. For example, about 25% of known members of the Solenogastres (Neomeniomorpha) lack a radula, using enzymatic secretions of a protrusible foregut to dissolve cnidarian tissue (Salvini-Plawen, 1985). The Caudofoveata (Chaetodermomorpha or Chaetodermatida) include several genera with a distichous radula and several that display a specialized feeding apparatus of disputed construction, whereas the distichous tooth pattern prevails unequivocally in members of the Solenogastres that have a radula (Salvini-Plawen, 1978). Moreover the radula of both aplacophoran groups clearly shows features of a bipartite construction: The teeth attach to a radular membrane which is often split medially, perforated by a series of slits, or is fused together from two ribbons (Heath, 1905; Salvini-Plawen, 1978; Scheltema, 1981; pers. comm. 1984; contrast with Hyman, 1967).

We have presented evidence that from the start the juvenile chiton radula is in most cases polystichous, not monostichous as believed by Minichev and Sirenko (1974). However, we believe the issue is much more fundamental than this distinction. Even if it could be shown that certain mollusks (i.e. two species of Solenogastres as claimed by Salvini-Plawen, 1985) pass through a monostichous stage in their radular formation, this would not necessarily indicate the primitive radular condition of a presumed early molluscan ancestor. Comparative ontogenetic studies might reveal the initial ancestral state (i.e. "Von Baer's laws") but this assumes that early ontogenetic stages are less prone to modification than later stages or, stated differently, the initial expression of a morphological trait reflects more accurately than later expressions an ancestral condition (Kluge and Strauss, 1985). In practice, testing this assumption requires outgroup comparison (Kluge, 1985) which in the present case is difficult because it would require comparisons of radular ontogeny with the ontogeny of a structure presumed to be homologous to the molluscan radula in a non-molluscan outgroup. Moreover, it would be mistaken to assume that the initial state of a juvenile chiton radula must correspond to the adult radula of a hypothetical ancestral mollusk. Instead, the juvenile condition of chitons is better compared to the ancestral juvenile condition, and simplicity (i.e. few teeth or even a monostichous condition) attributed to the inherently small size of juveniles.

Thus, there is no longer any reason to postulate that the presumed ancestor of early mollusks was equipped with a monostichous radula as suggested by Salvini-Plawen (1985), Minichev and Sirenko (1974), and Ivanov and Tzetlin (1981). In addition to the uncertainties inherent in using early ontogenetic stages to infer a primitive condition, two facts are incompatible with the suggestion of an ancestral monostichous condition. First, the predominant radula type of the Aplacophora is distichous and basically bipartite, even if there is an initial connection in the juvenile radula as claimed by Salvini-Plawen (1985). Second, none of six genera of chitons hitherto examined (this paper and Minichev and Sirenko, 1974) reveal any sign of a monostichous stage in their radular development, except for the "monostichous" radula of the unidentified "trochophore" depicted in Minichev and Sirenko (1974). We would reinterpret this latter case as distichous, consisting of two longitudinal rows of incomplete L_2 teeth. Both the prevailing aplacophoran radula type and the ontogenetic sequence of the chiton radula lead us to propose a rather different basic feeding instrument in early mollusks. We conclude that it was bilateral or even bipartite with one or more pairs of longitudinal rows of teeth. It would be tempting to assume that such a radula represents the ancestral type for all mollusks, but this extrapolation needs to be tested with additional comparative studies.

ACKNOWLEDGEMENTS

DJE acknowledges support by NSF Grant OCE-8415258 to R.R. Strathmann and DJE, and thanks Dr. A.O.D. Willows, Director, Friday Harbor Laboratories, University of Washington, and Dr. A. Fontaine, Electron Microscope Facility, University of British Columbia, Victoria, B.C., for making those facilities available, and Dr. E.N. Kozloff for help with translations. KK thanks U. Holzöder (Würzburg) for excellent cooperation.

LITERATURE CITED

BOETTGER, C., 1955, Beiträge zur Systematik der Urmollusken (Amphineura). *Zoologischer Anzeiger, Supplement*, 19: 223-256.

BOETTGER, C., 1959, Discussion in: Protostomian interrelationships in the light of *Neopilina* by H. LEMCHE. *Proceedings XV International Congress of Zoology, London*, Section 4, 386-389.

CAREFOOT, T. H., 1965, Magnetite in the radula of the Polyplacophora. *Proceedings of the Malacological Society of London*, 36: 203-212.

EERNISSE, D. J., 1984, *Lepidochitona* Gray, 1821 (Mollusca: Polyplacophora) from the Pacific coast of the United States. Ph.D. Dissertation. Univ. of California, Santa Cruz, 1984: 1-358.

EERNISSE, D. J., 1986, The genus *Lepidochitona* Gray, 1821 (Mollusca: Polyplacophora) in the northeastern Pacific Ocean (Oregonian and Californian Provinces). *Zoologische Verhandelingen* (Leiden), 228: 3-52.

HEATH, H., 1905, The morphology of a Solenogastre. *Zoologische Jahrbücher, Abteilung Anatomie*, 21: 703-773.

HOFFMANN, H., 1937, Über die Stammesgeschichte der Weichtiere. *Zoologischer Anzeiger, Supplement*, 10: 33-69.

HYMAN, L. H., 1967, *The Invertebrates*, Vol. 6, Mollusca 1. McGraw Hill Book Co., N.Y., London, 792 pp.

IVANOV, D. L. & TZETLIN, A. B., 1981, On [illegible] and evolution of the cuticular pharyngeal armature in trochophore animals having the ventral pharynx. *Zoologicheskii Zhurnal*, 60: 1445-1454 [in Russian].

KERTH, K., 1979, Phylogenetische Aspekte der Radulamorphogenese von Gastropoden. *Malacologia*, 19: 103-108.

KERTH, K., 1983a, Radulaapparat und Radulabildung der Mollusken. I. Vergleichende Morphologie und Ultrastruktur. *Zoologische Jahrbücher, Abteilung Anatomie*, 110: 239-269.

KERTH, K. 1983b, Radulaapparat und Radulabildung der Mollusken. II. Zahnbildung, Abbau und Radulawachstum. *Zoologische Jahrbücher, Abteilung Anatomie*, 110: 239-269.

KERTH, K. & HÄNSCH, D., 1977, Zellmuster und Wachstum des Odontoblastengürtels der Weinbergschnecke *Helix pomatia*. *Zoologische Jahrbücher, Abteilung Anatomie*, 98: 14-28.

KLUGE, A. G., 1985, Ontogeny and phylogenetic systematics. *Cladistics*, 1:13-27.

KLUGE, A. G. & STRAUSS, R. E., 1985, Ontogeny and systematics. *Annual Review of Ecology and Systematics*, 16: 247-268.

LAUTERBACH, K.-E., 1983, Erörterungen zur Stammesgeschichte der Mollusca, insbesondere der Conchifera. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, 21: 201-216.

LEMCHE, H. & K. G. WINGSTRAND, 1959, The anatomy of *Neopilina galatheae* Lemche, 1957. *Galathea Report*, 3:9-71.

LOWENSTAM, H. A., 1962, Magnetite in denticle capping in recent chitons (Polyplacophora). *Bulletin of the Geological Society of America*, 73: 435-438.

MINICHEV, Y. S. & B. I. SIRENKO, B. I., 1974, Development and evolution of radula in Polyplacophora. *Zoologicheskii Zhurnal*, 53: 1133-1139 [in Russian].

NAEF, A., 1926, Studien zur generellen Morphologie der Mollusken. 3. Theil. *Ergebnisse und Fortschritte der Zoologie*, 6: 27-124.

NIERSTRASZ, H. F., 1905, *Kruppomenia minima* und die Radula der Solenogastren. *Zoologische Jahrbücher, Abteilung Anatomie*, 21: 655-702.

PRUVOT, G., 1890, Sur le développment d'un solenogastre. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences [Paris]*, 111: 689-692.

SALVINI-PLAWEN, L.v., 1972, Zur Morphologie und Phylogenie der Mollusken: Die Beziehungen der Caudofoveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia. *Zeitschrift für wissenschaftliche Zoologie*, 184: 205-394.

SALVINI-PLAWEN, L.v., 1978, Antarktische und subantarktische Solenogastres (Eine Monographie: 1898-1974). *Zoologica (Stuttgart)*, 44: 1-305.

SALVINI-PLAWEN, L.v., 1980, A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia*, 19: 249-278.

SALVINI-PLAWEN, L.v., 1981, The molluscan digestive system in evolution. *Malacologia*, 21: 371-401.

SALVINI-PLAWEN, L.v., 1985, Early evolution and the primitive groups. *In* TRUEMAN, E. R. & CLARKE, M. R., ed., *The Mollusca, "Evolution,"* 10: 59-150. Academic Press, London.

SCHELTEMA, A., 1981, Comparative morphology of the radulae and alimentary tract in the Aplacophora. *Malacologia*, 20: 361-383.

SIRENKO, B. I., 1975, A new subfamily of chitons Juvenichitoninae (Ischnochitonidae) from the north-west Pacific. *Zoologicheskii Zhurnal*, 54: 1442-1451 [in Russian].

SIRENKO, B., & MINICHEV, Y., 1975, Développement ontogénétique de la radula chez les Polyplacophores. *Cahiers de Biologie Marine*, 16: 425-433.

TOWE, K. M. & LOWENSTAM, H. A., 1967, Ultrastructure and development of iron mineralization in the radular teeth of *Cryptochiton stelleri* (Mollusca). *Journal of Ultrastructure Research*, 17: 1-13.

WINGSTRAND, K. G., 1985, On the anatomy and relationships of Recent Monoplacophora. *Galathea Report*, 16: 7-94, 12 pl.

YONGE, C. M., 1960, General characteristics of Mollusca. *In* MOORE, R. C., ed., *Treatise on Invertebrate Paleontology*, Part 1 (Mollusca 1): 3-36. Geological Society of America and University of Kansas, Lawrence, Kansas.

Revised Ms. accepted 17 March, 1987