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On the Ontogeny, Anatomy, and Ecology of the Tropical Freshwater Gastropod *Stenomelania* (Cerithioidea, Thiaridae)

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With 8 Figures and 1 Table

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Abstract

Ecological, ontogenetical and anatomical features of two sympatric and syntopic species of the tropical freshwater gastropod *Stenomelania* are presented in direct comparison with *Melanoides tuberculata*.

Stenomelania was collected from a Nipa mangrove on Cebu Island (Philippines), and in the field differentiation of species was not possible. The release of free-swimming veligers from the brood pouch and differences in ecological demands between early ontogenetic and late ontogenetic individuals could be observed. Juveniles lived under brackish-water influence and adults inhabited freshwater.

Analysis of shell characters revealed that two different modes of development – planktotrophy and lecithotrophy – occur in *Stenomelania*. Analysis of teleoconch characters, features of the operculum and differences in radular teeth demonstrate that actually two species can be distinguished, of which the slender and lecithotrophic one is considered to represent *Stenomelania plicaria* and the planktotrophic species is distinguished as *S. punctata*. Each of both species shares several characters with *Melanoides tuberculata* and thus close relation between *Stenomelania* and *Melanoides* is evident.

As in *Stenomelania*, two modes of development were also found in *Thiara*, which sheds new light on the phylogeny of Thiaridae and demonstrates that future research in this gastropod group may greatly contribute to unravel general aspects of evolutionary ecology, in particular the colonization of freshwater habitats.

Introduction

The Thiaridae TROSCHEL, 1857 are a widely distributed group of cerithioidean gastropods, which inhabit limnic environments in the tropics of the world. Since the Thiaridae were suspected to represent a polyphyletic group

[compare HOUBRICK (1988) and GLAUBRECHT (1996)], and systematics are currently under revision, we tentatively confine Thiaridae to those freshwater cerithioideans, which have a specialized incubatory pouch in the head-foot. *Stenomelania* FISCHER, 1885 is generally considered to comprise *Melanoides*-like Thiaridae with elongate, pointed shells, which are found near and sometimes in the brackish environment of estuaries. The distribution of *Stenomelania* includes the Oriental region from India to the islands of the western Pacific (STARMÜHLNER 1976, 1984, 1993).

Limnic organisms usually exhibit a series of adaptive characters. The reduction of a free-swimming larva as well as acquisition of viviparity in most Thiaridae have been considered a key innovation for entering the freshwater biotopes (e.g. FRETTER & GRAHAM 1962; CALOW 1978). Brooding strategy and viviparity of Thiaridae, however, is also found in Planaxidae (HOUBRICK 1987). Thus it was concluded that a specialized brood pouch, in concert with corresponding ontogenetic mode, must have evolved already in the marine, cerithioidean stem lineage of Thiaridae and Planaxidae (GLAUBRECHT 1996).

The thiarid *Stenomelania* was reported to produce veliger larvae and therefore believed to represent a somewhat transitional stage in the invasion of freshwater by cerithioideans (SESHAIYA 1940; STARMÜHLNER 1984; HOUBRICK 1987). Free-swimming veligers have been observed in *Stenomelania* sp. from India (SESHAIYA 1940), in *Stenomelania aspirans* from the Philippines (MORRISON 1954) and STARMÜHLNER (1979) observed the release of veligers in *Stenomelania* from Sri Lanka, which he assigned to *S. torulosa* (BRUGUIERE, 1789).

We observed free-swimming veligers in *Stenomelania* during our stay on Cebu Island (Philippines). In the field a large assemblage of individuals seemed to represent a single species of which the teleoconch characters called for attribution to the very variable *Stenomelania plicaria* (BORN, 1780) (see below). When back at our institutes, the documentation of protoconchs as was expected revealed a larval shell, however, a second type of protoconch was also found, which is very similar to that of the lecithotrophic *Melanooides tuberculata* (MÜLLER, 1774) (see e.g. RIEDEL 1993). This knowledge triggered off further research and thus gave rise to this paper. Did we have a case of poecilogony, or two or more sympatric and syntopic populations?

Materials and Methods

Material was collected in February/March 1994 on Cebu Island, Philippines, and for the most part originates from a Nipa mangrove south of Argao (Fig. 1). Living *Stenomelania* were examined in the field and with the aid of a binocular microscope at the University of San Carlos, Cebu City, by K.B. and F.R. Part of the samples (n = 47) were fixed in ethanol (70%) for anatomical investigation by M.G.

From the shells of n = 67 adult specimens of *Stenomelania* sp. conchological characters were extracted in respect to morphometric analysis (Fig. 4). Maximum height and diameter, total number of whorls, height of aperture, each height of last seven whorls (7 to 1), diameters of whorl 8 and 2 were measured and ontogenetic development of axial ribs was noted. The apex of the *Stenomelania* teleoconch is usually corroded or decollated to very different degrees. In some specimens only 4 or 5 apical whorls are missing, in others more than 10. Thus the ratio of maximum

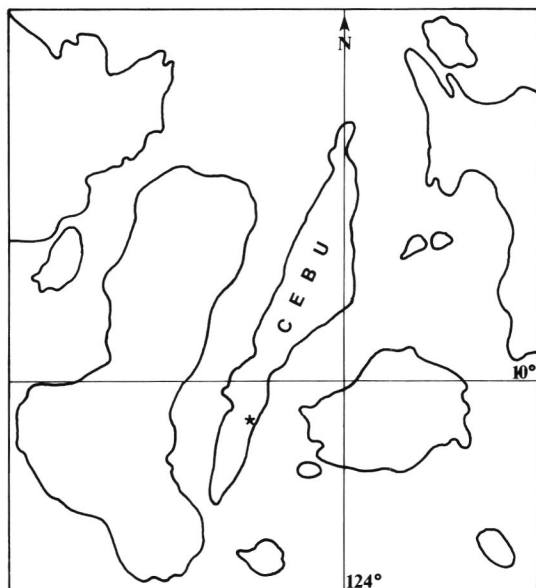


Fig. 1. Central Philippines with Cebu Island and indication of area of investigation at Argao (asterisk). Not to scale.

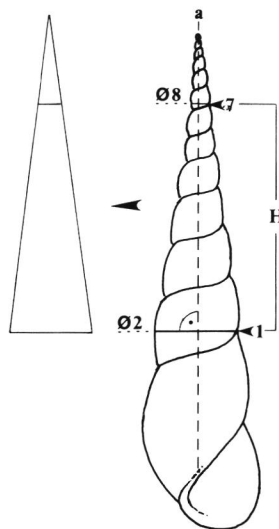


Fig. 2. Sketch on shell geometry in *Stenomelania* sp. to show determination of the apical angle. For details see text. **H** = height, **a** = axis of shell, **1** = end of first whorl, **7** = end of seventh whorl, **Ø2** = diameter of second whorl, **Ø8** = diameter of eighth whorl (numbering of whorls in reverse to ontogenetic formation). Not to scale.

height and diameter is insufficient to describe proportions of shells. In consequence, the apical angle of teleoconchs was calculated with the aid of a triangle, which was constructed using the diameter of the "second" and "eighth" whorl and the height between "first" and "seventh" whorl (Fig. 2). Due to decollation of apical shell, numbering of whorls is here in reverse order to ontogenetic formation, which means that the last, most voluminous body whorl represents number 1.

The selection of n = 15 alcohol fixed specimens for anatomical examination, was based upon characteristic ("extreme") shell morphology and the animals have been studied in particular with regard to the brood pouch and radular teeth. Radulae were extracted during dissection and buccal tissue dissolved using 5% KOH solution. The anatomy of brood pouches was studied using a Wild binocular microscope and documented by camera lucida drawings. Radulae as well as juvenile shells with preserved protoconchs were sputtercoated with gold and examined with the aid of a SEM.

Voucher material is deposited in the Zoological Institute and Museum of the University of Hamburg.

Results

Systematic remarks

Stenomelania FISCHER, 1885 (synonym, *Radina* PRESTON, 1915) has usually been considered to represent a subgenus of the polymorphic and widely distributed freshwater genus *Melanooides* OLIVIER, 1804 (STARMÜHLNER 1976, 1984, 1993). The type species of *Stenomelania* is *S. aspirans* (HINDS, 1847). Based upon conchological and anatomical

examination, STARMÜHLNER (1976, 1984, 1993) considered at least six more species belonging to the genus *Stenomelania*. Species-specific characters, however, are difficult to recognize, in particular a re-evaluation of described anatomical features (STARMÜHLNER 1976, 1984, 1993) of the pallial oviduct as well as radula characters of these taxa revealed no clear evidence for species diagnoses (GLAUBRECHT 1996).

As an example, in most *Stenomelania* species the oviduct enters the glandular uterus at the posterior third, but in *S. aspirans* a median position has been figured by PACE (1973) and STARMÜHLNER (1976, 1993). Drawings of the anatomy of *S. plicaria* from Taiwan (PACE 1973), from Vanuatu (STARMÜHLNER 1976) and from Samoa (STARMÜHLNER 1993), however, indicate that the different positions of the entering oviduct may occur within a single species. The anatomical examinations presented below seem to confirm a considerable intraspecific variation in *Stenomelania* spp. A full revision of the group is needed to resolve systematic problems and thus we refrain from producing a new concept. We follow here the conservative path, attributing our specimens of *Stenomelania* to two widely distributed nominal species, which have been reported from the area of the Phillipines. The taxonomic attribution is based upon conchological characters, which have been depicted in the literature, especially in STARMÜHLNER (1976, 1984, 1993).

Environmental setting

Coastal swamps created by the mangrove palm *Nypa fruticans* (Arecales; see Fig. 3) contain a fair amount of gastropod taxa belonging to the families Neritidae, Littorinidae, Ellobiidae, Potamididae and Thiaridae. The main factor controlling the extension of a *Nypa* mangrove is salinity. High tide must reach the bases of the palms petioles. Salinity appears to be a daily demand and thus spring tides or occasional storm events do not have any effect on the vertical ("inland") expansion of *Nypa fruticans*. Maximal vertical distribution of *Nypa* reflects the high stand of "normal" tides. Freshwater influx represents another necessity and creates the brackish-water environment, which characterizes a mangrove, and thus quantity of inflow is a major factor controlling the horizontal expansion of the *Nypa* palm. It is evident that the environment must differ significantly between sections of the mangrove, from nearly marine to almost continuous freshwater conditions, and these differences are actually clearly reflected by gastropod zonation.

The *Nypa* mangrove we have examined on Cebu (near Argao) in respect of its gastropod fauna is supplied with freshwater by a narrow creek mainly originating from a spring. This creek is not much broader than one meter at its mouth to the sandy beach. At the study site near Argao the horizontal extension of the mangrove has its



Fig. 3. *Nypa fruticans*. The mangrove created by this palm represents the favoured settlement area of *Stenomelania punctata* pediveligers. Not to scale.

maximum (80 m) at the transition to the sea, but is separated from it to a large extent by a road dam. The mangrove expands about 250 m in vertical direction, following the creek and narrowing to a width of about 20 m when terminating. This upper portion of mangrove is characterized by low salinity even during high tides. Here adults of *Stenomelania* sp. commonly occur, while in the middle and lower portion only juveniles could be found. The smallest juveniles occurred close to the sea, living in and on muddy layers, which cover the sandy bottom and from which they start their upstream migration.

Maximum population density of the *Stenomelania* species has been noted beyond the mangrove in freshwater environment where penetration of salt water occurs only occasionally during extremely high tides. This freshwater section of the creek ("Charly's Place") was manured intensively with human and animal (pigs and goats) excrements. Several hundred specimens of *Stenomelania* to the square meter could be counted, associated with *Clithon* sp. and *Neritilia* sp. (both Neritimorpha, Neritoidae). *Thiara* cf. *scabra* (MÜLLER, 1774) (Cerithioidea, Thiariidae) remained further downstream, on muddy ground near roots in the shallow creek effected by each high tide. This snail, however, like *Stenomelania* sp. is mainly active in freshwater and more-or-less rests when the water salinity rises. Adult individuals of *Stenomelania* sp. were tested in this respect. They retracted into their

shell when placed in seawater and immediately regained activity when transferred to freshwater.

Stenomelania sp. was also observed in the large Argao River and Matutinao River, where they had migrated upstream for several hundred meters and exhibited the same behaviour as in the mangrove creek.

Shell characters

General remarks

In the field, we considered the teleoconchs of *Stenomelania* (compare Fig. 5G) to represent one single, but highly variable species. We placed a larger number of fully grown individuals for comparison and all transitions were present. The teleoconchs ranged from being almost smooth to prominently ribbed, the shapes varying from more-or-less short to tall and from relatively broad to slender. The colour of the shells ranged from light to dark brown. From comparison with material, which has been described and figured extensively in the literature (e.g. BROT 1874; VON MARTENS 1897; SARASIN & SARASIN 1898; STARMÜHLNER 1970, 1976, 1984, 1993), and from comparison with museum collections, it is evident that all specimens from the Argao sample fall within the conchological variability known for *S. plicaria*.

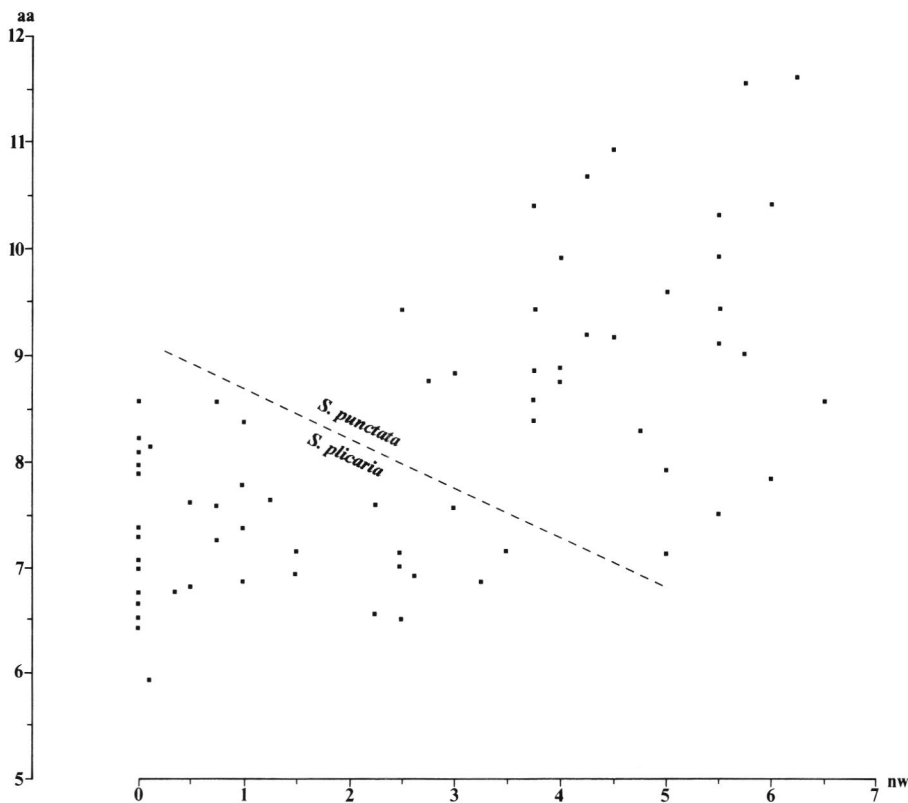


Fig. 4. Morphometric analysis of *Stenomelania punctata* and *S. plicaria* teleoconchs. The y-axis indicates the axis angle (**aa** correspond with half apical angle) of the shells, the x-axis indicates on which whorl (**nw** = number of whorls) axial ribs appear latest in ontogeny. The broken line is not based upon the small, insignificant gap between two clouds of dots, but on correlation with differences in anatomy. For more details see text.

Examination of juvenile shells revealed two different types of protoconchs and subsequently teleoconchs, anatomy and radulae were analyzed in detail to resolve the problem. Morphometric analysis of adult shell parameters were plotted and actually, the relation between the apical angle and the development of axial ribs (Fig. 4) implied that two distinct taxa can be differentiated within the Argao sample (see chapter "Comparative remarks"). Further investigations (see below) showed that differences in radula characters correspond with the morphometric analyses: Thus, the obviously statistically insignificant separation of two clouds (Fig. 4) represents an actual dividing line. In the following, the name *S. plicaria* is provisionally retained for one species while the second one is determined as *S. punctata* (LAMARCK, 1822).

Stenomelania punctata

The general appearance is that of a large, elongate thiarid, exhibiting an outline similar to *Melanooides* species, but is usually less sculptured.

The protoconch (Figs. 5C and D) shows almost one embryonic whorl with a maximum diameter of 0.15 mm and one and a quarter larval whorls, which measure 0.23 mm across. The protoconch is about 0.28 mm high. While the embryonic shell is smooth except for terminal growth lines, the larval shell is sculptured by 7–9 spiral lirae. The larval aperture is of the sinusigera type, the beak projecting for about 0.12 mm. This protoconch type is characteristic of planktotrophic cerithioideans (BANDEL 1975, 1982, 1993; HOUBRICK 1987, 1991).

The juvenile shell is set with two spiral ridges, which are crossed by 26–27 axial ribs per whorl, producing a reticulated pattern, but only on the ontogenetically earliest whorls (Fig. 5B). The initial three or four whorls are shouldered while later whorls are more-or-less regularly rounded. Secondary keels are intercalated beginning on the fourth whorl and become increasingly indistinct on the following whorls. The orthocline (with opisthocline trend) ribs become dominant and decrease in number to about 15 per whorl (Fig. 5A). About 18 teleoconch whorls are formed during ontogeny of which at least the final 2.5 whorls are smooth (aside from growth increments), which, however, contribute almost 2/3 to the total height of specimens. On the other hand axial ribs terminate earliest in ontogeny before the last six whorls are formed (compare Fig. 4).

In most adult specimens 9–11 teleoconch whorls are preserved (maximally 15). The largest shell that could be attributed to *S. punctata* is 51.5 mm high. The apical angle (see Fig. 2) of the shells varies between 14.5° and 23.5°, with most specimens ranging within 17° to 21°. The maximum diameter of adult shells equals approximately the apertural height, both measurements ranging around 12 mm (maximum: 15 mm). The aperture exhibits a regu-

lar concave outer lip and base, and a straight to slightly convex inner lip (see Fig. 5G). The teleoconch of *S. punctata* has usually a uniform dark brown colour, however, some specimens show rudiments of a colour pattern, either yellowish broad striae or brown spots on brighter shell portions.

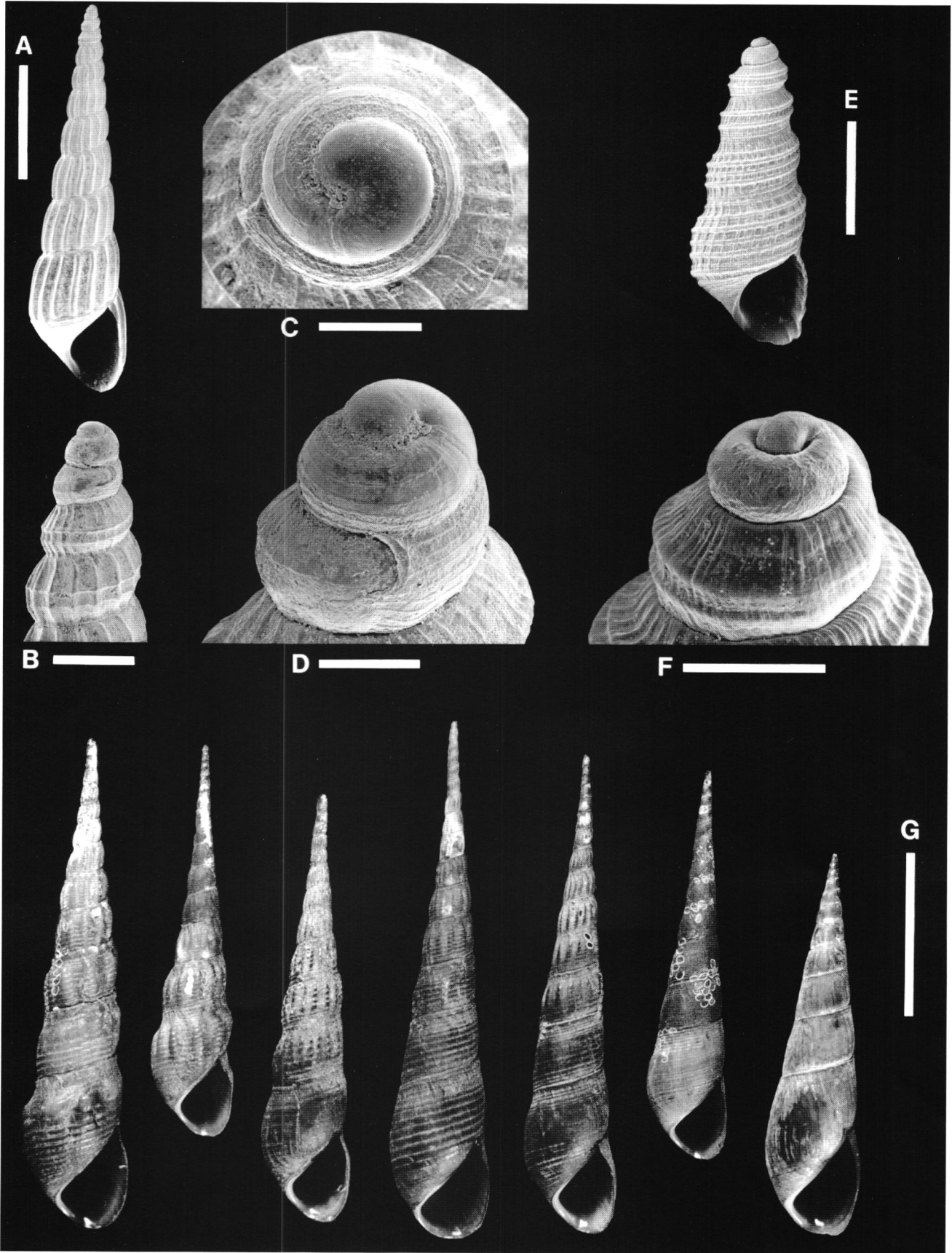
Stenomelania plicaria

The general appearance is that of a large, pointed and slender thiarid, phenotypically resembling the polymorphic *Melanooides tuberculata*.

The protoconch of *S. plicaria* (Fig. 5F) is very similar to that of *Melanooides tuberculata* (see RIEDEL 1993; GLAUBRECHT 1996). The initial 1.5 to 1.7 whorls have a diameter of 0.3 to 0.35 mm and show an irregularly wrinkled shell, a sculptural pattern, which is known to be caused by retarded calcification during early ontogeny (RIEDEL 1993). The wrinkled shell does not demarcate the actual protoconch as the embryonic shell (formed until the embryo hatches) is confined to the initial 2/3 to 3/4 whorls, measuring about 0.15 mm across. A larval shell cannot be recognized. Thus one whorl of the wrinkled portion represents already the teleoconch.

S. plicaria may form about 18 teleoconch whorls during ontogeny. Beginning with the second whorl, two spiral keels and about 45 axial riblets create a pattern of rectangles (Fig. 5E). On the following whorls the number of keels increases (4–7 on the fifth whorl) while the number of (prominent) axial riblets decreases (25–15 on the fifth whorl). The pattern of rectangles is distinct on five to six juvenile whorls. In most specimens the spiral keels are the dominant feature and only in few specimens the axial riblets are equally pronounced. On the remaining 12 to 13 teleoconch whorls, which are formed, the development of sculpture is very variable (see Fig. 5G). Spiral ridges as well as axial ribs may become the prominent ornamentation. Axial ribs terminate earliest before the last three whorls are formed and more than half of the specimens still show axial ornamentation on the body whorl (compare Fig. 4). Early juvenile whorls are always shouldered whereas late ontogenetic whorls may be slightly shouldered or not.

Some adult shells are preserved with 15 whorls, representing the lowest degree of apical decollation. Shell height may reach 69.5 mm at maximum. The apical angle of the shell varies between 12° and 17.5° with most specimens ranging within 13° to 16°. The aperture is only slightly higher (highest value: 15.5 mm) than the shell measures across at maximum (highest value: 13.5 mm) and shows the same features as described above for *S. punctata*. The conchs show the same dark brown colour as in the other species and in case that brighter shell portions occur they are usually spotted.



Comparative remarks

The two species can easily be differentiated with the aid of the protoconch, which, however, is always corroded in adult shells. Attribution of juvenile shells with preserved protoconch to corresponding adult shells is directly possible in specimens where only few apical whorls are decollated. Early teleoconch whorls of *S. plicaria* show prominent, characteristic spiral lirae. On the other hand juvenile whorls of *S. punctata* are ornamented with dominant axial ribs. In specimens without the juvenile whorls preserved, a morphometric analysis of teleoconch characters allows to differentiate the two species (Fig. 4).

In the field, most specimens can be attributed correctly when considering that the apical angle of *S. punctata* is usually larger than in *S. plicaria*, the teleoconch of the former is smooth at least for 2/3 of its height and the latter shows distinct spiral lirae on all whorls. *S. plicaria* may show axial ribs on late ontogenetic whorls, which may be more or less shouldered. Both specimens form about 18 teleoconch whorls, however, comparing equal numbers, the shell of *S. plicaria* is always higher, which means that increase in height per whorl is larger.

S. plicaria shows a protoconch and juvenile whorls, which can be distinguished from those of *Melanoides tuberculata* only in detail. Moreover, teleoconch characters show the same unusual variability, however, shells of *S. plicaria* are significantly slenderer. From shell characters alone, it could be considered that *Stenomelania plicaria* represents a slender species of *Melanoides*.

Anatomy

The gross anatomy of *Stenomelania* species and/or radulae respectively, have been described in SARASIN & SARASIN (1898), BOLLINGER (1914) SESHAIYA (1936), ABBOTT (1948), PACE (1973) and especially STARMÜHLNER (1976, 1984, 1993).

Radula characters confirm the differentiation of two species based upon conchological features. The radulae are taenioglossate and, compared with *Melanoides tuberculata*, are larger in both *Stenomelania* species. Overall pattern of the shape of the individual teeth, however, is very similar in the two genera. Rachidians are three times

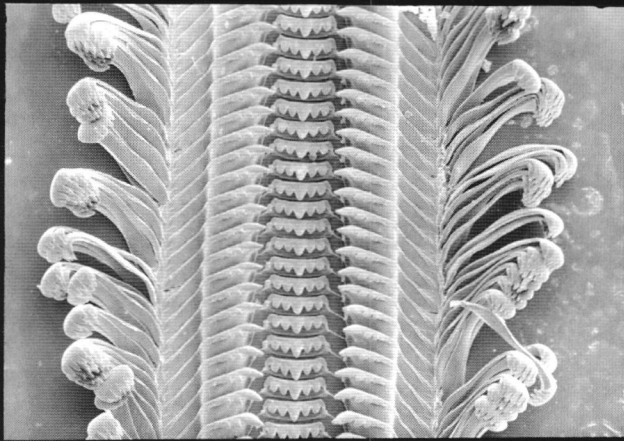
wider than high and lack basal extensions. Lateral teeth are largely extended in width and show a single strong median cusp. The spoon-like marginals exhibit numerous finger-shaped cusps (Fig. 6). All *Stenomelania* radulae studied here show a distinct character, which has not been described from other Thiaridae. The rachidian teeth feature hook-shaped lateral protrusions, extending from each of the peripheral cusps (Fig. 6C and E). Protrusions are recurved and each seems to articulate with the lateral rim of the inner denticle of the corresponding lateral teeth, thus forming a kind of "hook and eye system" (Fig. 6E).

Specimens, which are assigned to *Stenomelania punctata* revealed a relatively long radula ribbon of about 130–150 rows of teeth, compared to the lower number of 80–100 in *S. plicaria* (70–100 rows in *Melanoides tuberculata*). In *S. punctata* as well as in *S. plicaria* the rachidians exhibit a 2–3/1/2–3 pattern, with the median cusp most pronounced (Fig. 6). While most rachidian teeth show two cusps on each side of the median cusp, some carry three on one side (Fig. 6C), others three on both sides. The lateralia show usually a 1/1/3 pattern in *S. punctata* and a 1/1/2 pattern in *S. plicaria*. Some variation, however, was found in the latter, where a third denticle may also be pronounced, but only indistinctly (Fig. 6D). One specimen of *S. plicaria* was found to have formed three inner cusps (3/1/2), the pattern, however, confined to one column of lateral teeth. The marginalia exhibit additional interspecific differences (Fig. 6F). The number of cusps of the inner and outer marginalia is either 6 + 8 or 8 + 8 in *S. plicaria*, and either 8 + 8, 8 + 10 or even 10 + 10 cusps in *S. punctata*, which thus in average shows higher numbers and also a greater variation.

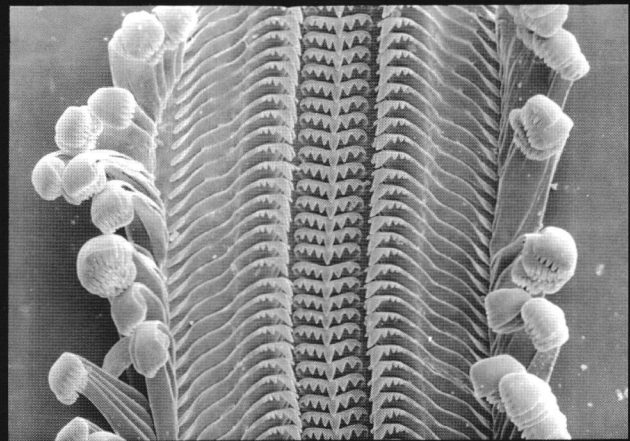
The radula patterns noted here for *Stenomelania* can be compared only to a certain extent with those described for species of this genus in the literature. Even were the number of cusps has been noted thoroughly, it remains uncertain to which phenotype or shell form the authors referred. However, the dentition pattern revealed in SARASIN & SARASIN (1898) and described and figured by STARMÜHLNER (1976, 1984, 1993) support our observation that in general the marginalia of *S. plicaria* exhibit fewer cusps than those of *S. punctata*.

Operculum features seem also to confirm a differentiation of two species. The operculum of both species is paucispiral with excentric nucleus near the base. The

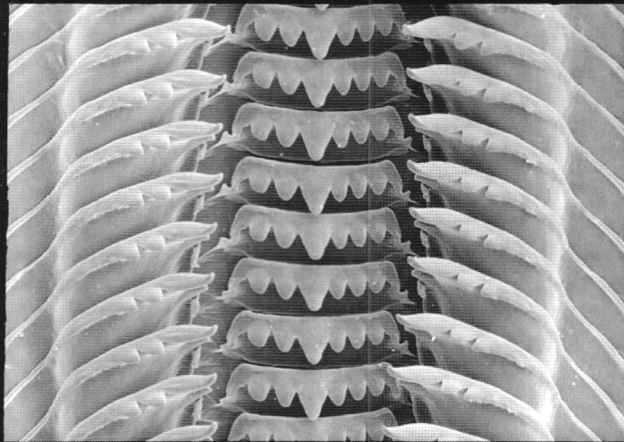
Fig. 5. Shells of *Stenomelania*: **A:** Juvenile *S. punctata*. Scale bar = 2 mm. **B:** Apical whorls of *S. punctata* showing transition of protoconch to early teleoconch with reticulated sculpture. Scale bar = 0.25 mm. **C:** Same specimen as in B, apical view of initial whorls. Scale bar = 0.1 mm. **D:** Same protoconch as in C but in lateral view, showing spiral ridges of larval shell and larval hook of the sinusigera type. Scale bar = 0.1 mm. **E:** Juvenile *S. plicaria*. Scale bar = 1 mm. **F:** Same specimen as in E. Magnification of apical whorls demonstrates the lack of a larval hook. The shell of the initial whorl is wrinkled. Both features indicate lecithotrophic development. Scale bar = 0.25 mm. **G:** Conchological variation of teleoconchs. The right specimen represents *S. punctata*, the others can be attributed to *S. plicaria*. Scale bar = 2 cm.



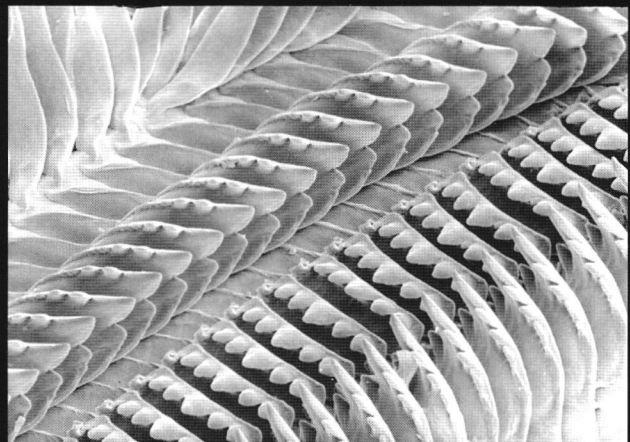
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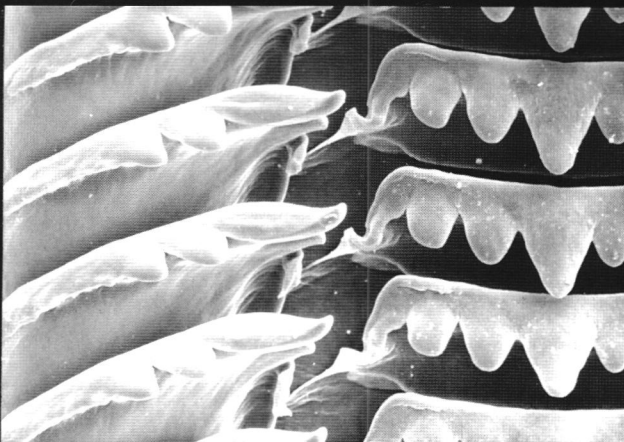
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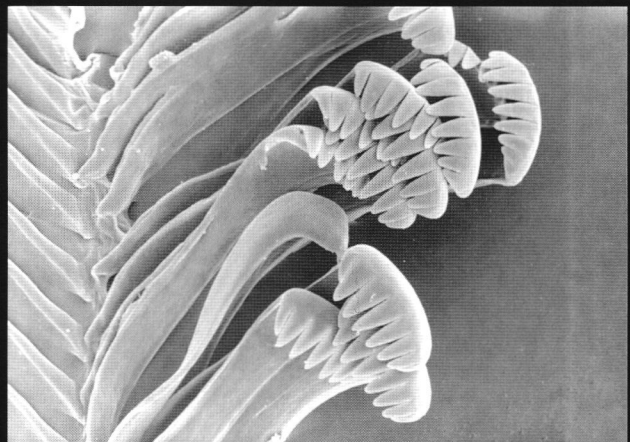
C



D



E



F

nucleus, however, was found to be positioned on the left (columellar) side of the operculum in *S. punctata* (n = 5) and on the right (outer) side in *S. plicaria* (n = 10). The attachment area of the operculum is reinforced by a ridge, which is most pronounced near the base.

The **head-foot** is commonly black with pale sole. The snout is about as broad as long, with vertical mouth opening. The head tentacles show bulgy bases which carry the eyes (Figs. 7 and 8A). A pair of anterior elongate salivary glands interconnect to the buccal mass (Fig. 7). The nerve system is dialyneurous with the cerebral ganglia close together and the subesophageal ganglion at short distance to the left pleural ganglion.

The **mantle edge**, as typical for Thiaridae and also for many other cerithioidean taxa (HOUBRICK 1988), is papillated in the two *Stenomelania* species (Fig. 8B). The ventral side of the mantle rim exhibits up to 15 more-or-less retractile papillae. There is one larger rectal papilla near the anus, at a short distance to it about 9–10 additional papillae of more-or-less equal size, and in front of the osphradium 3–4 more prominent papillae (Fig. 8B). Position and shape of pallial organs are also typical for Thiaridae (GLAUBRECHT 1996). Females reveal completely closed pallial gonoducts (Fig. 8B). The oviduct in the two *Stenomelania* species enters the glandular, sac-like pallial section of the gonoduct near the base, which is a posterior position. In the literature (see above) different positions have been described, but for other species assigned to *Stenomelania*. A slit-like vagina is formed by the opening of the otherwise fused lateral and median lamellae near the distal end of the gonoduct. A ciliated groove at the base of the pallium leads to the opening of the brood pouch (Fig. 7).

A **brood pouch** is located in the neck region of the female, extending from below the right tentacle in the head-foot, far back to the first body whorl (Figs. 7 and 8). Each brood pouch contained a large number of eggs in cleavage (yellow yolk), which were not housed in capsules. The eggs revealed no obvious differences, which could be correlated with lecithotrophic development in *S. plicaria* and planktotrophic development in *S. punctata*, respectively. The brood pouch of the two *Stenomelania* species show neither compartments formed by layers of tissue as in *Melanoides tuberculata* and *Tarebia granifera* (LAMARCK, 1816), nor seems the pouch epithelium to be transformed into a nutritive phase as it has been described for these latter Thiaridae (GLAUBRECHT 1996).

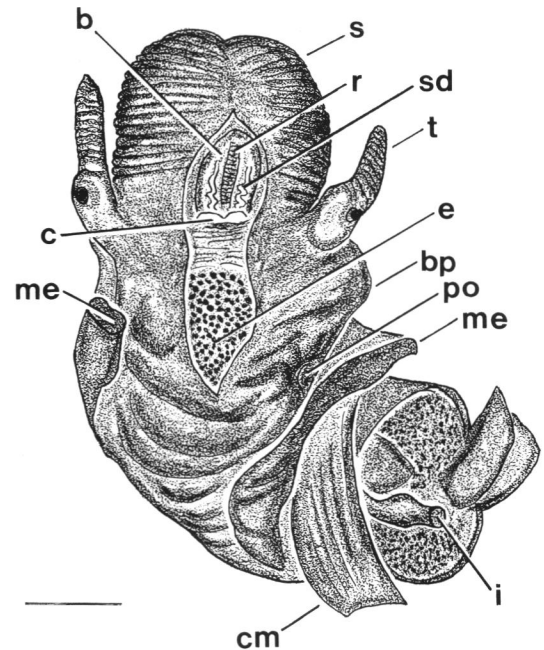


Fig. 7. Gross anatomy of *Stenomelania plicaria*. Dorsal view of female showing location of opened incubatory pouch (**bp**), embryos (**e**) therein and brood pouch porus (**po**); dorsal part of mantle (**me**) removed and dorsal part of snout (**s**) opened to show buccal apparatus (**b**) with radula (**r**), salivary ducts (**sd**) and glands respectively, and cerebral ganglia (**c**); **cm** = columellar muscle, **i** = intestine, **t** = tentacle. Scale line = 2 mm.

Observation in living *Stenomelania*: Individuals, which were collected also in Argao but several days later than the dissected animals, were examined in Cebu City using a microscope. Some brood pouches revealed shelled embryos ($\varnothing \approx 0.15$ mm) that were all at the same stage of development, almost ready to hatch as free-swimming veligers. The operculum appeared to be functional, but the embryos did not retract into their shell when disturbed. Some of them were taken from the brood pouch and kept in freshwater for more than a day. They did not only stay alive, but also had continued their development. The larvae then swam with the aid of two small ciliated velar lobes and the operculum was now used to close the aperture. Eyes had not yet been developed, the pallial cavity not formed but the mantle margin had been further differentiated. The advanced organisation of the digestive system indicated that the veligers were ready to feed on microplankton and thus ready to take off for larval life in the open sea. Adult females held overnight and dissected the next day had similarly advanced veligers in their brood pouches, which apparently were ready to hatch.

Fig. 6. Scanning electron micrographs of *Stenomelania plicaria* (A, C, D, E, F) and *S. punctata* (B) radulae. A and B: mid-section of radula ribbon; C: detail of lateral and rachidian teeth; D: oblique view; E: close-up of C, revealing hook-shaped protrusion of rachidians; F: close-up of marginal teeth. Scales as indicated.

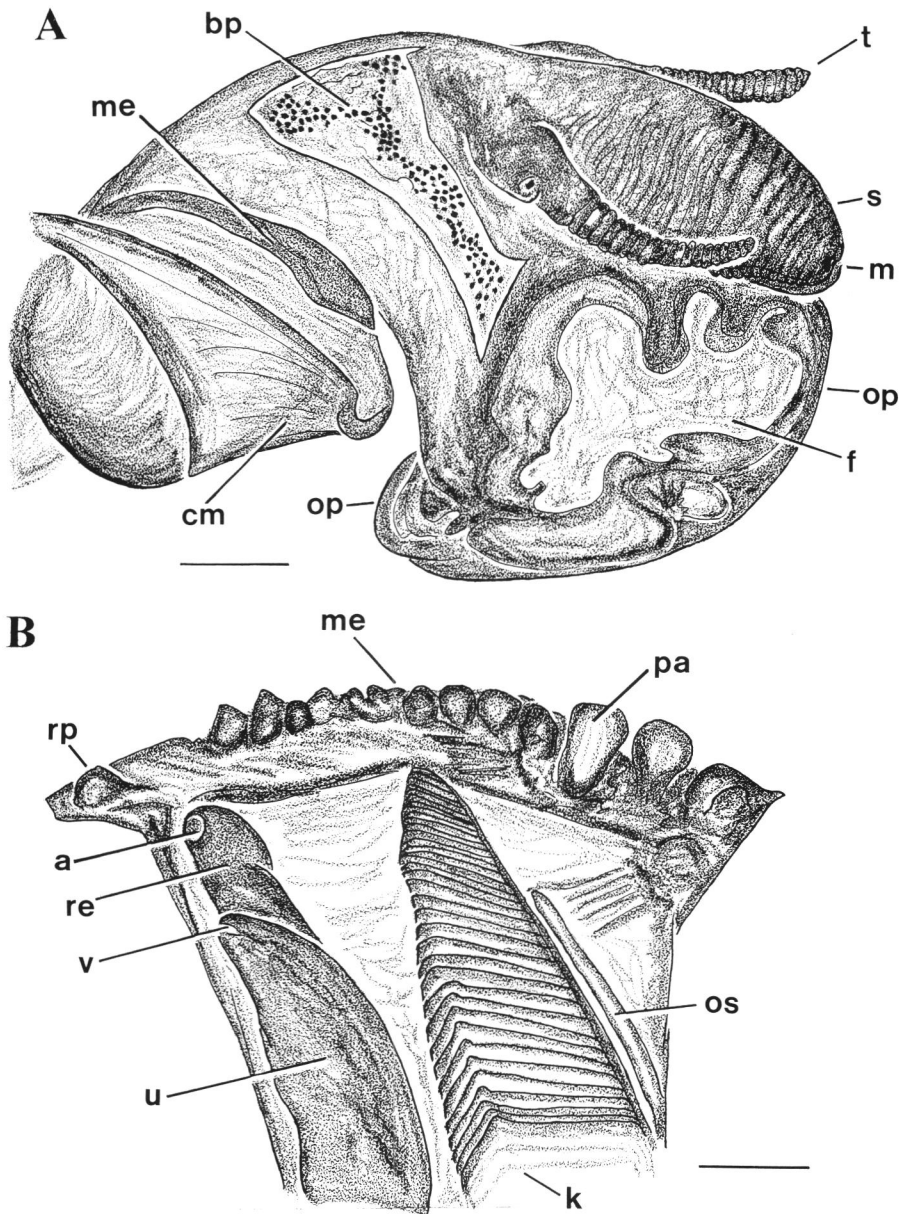


Fig. 8. Gross anatomy of *Stenomelania punctata*. **A:** Right side of female showing elongate snout (s) with mouth opening (m), tentacles (t), large foot (f) with operculum (op) and location of the opened brood pouch (bp) (with embryos) at the right side of the head-foot (propodium); cm = columellar muscle, me = mantle edge, **B:** Ventral mantle with pallial organs; a = anus, k = ctenidium, me = mantle edge, os = osphradium, pa = mantle edge papillae, re = rectum; rp = rectal papilla, u = uterus (pallial oviduct), v = vaginal opening. Scale lines = 1 mm.

Brood pouches filled with very similar embryos almost ready to hatch, were found also in *Thiara* cf. *scabra*, of which individuals were collected from the same Nipa swamp (see above).

Discussion and Summary

Table 1 compiles the data, which are presented in this paper.

The compilation of essential characters or traits supports the common view that *Stenomelania* and *Melanoides* are closely related. The taxonomic status, however, remains uncertain. *S. plicaria* shares with *M. tuberculata* (but not with *S. punctata*) the lecithotrophic development, sculptural elements of early ontogenetic as well as of late

ontogenetic shell, and a comparable number of rows of radular teeth. *S. punctata* shares with *M. tuberculata* (but not with *S. plicaria*) the maximum shell size and a comparable apical angle, and maybe also a higher number of cusps in marginal radular teeth. *S. plicaria* shares with *S. punctata* (but not with *M. tuberculata*) the kind of environment in early ontogeny, the simple brood pouch and the hook-like protrusions of the central radular teeth.

We refrain from evaluation of character states in respect of plesiomorphies and apomorphies within a three-taxa-relation. The marine Planaxidae share with Thiariidae the character complex of a brood pouch (GLAUBRECHT 1996) and presumably both are adelphotaxa (HOUBRICK 1988). It seems to be obvious that the colonization of freshwater represents an apomorphic trait. However, it is not clear

Table 1. Compilation of data from *Stenomelania* and *Melanooides* species.

Character	<i>S. punctata</i>	<i>S. plicaria</i>	<i>M. tuberculata</i>
Environment			
juvenile	brackish water	brackish water	freshwater
adult	freshwater	freshwater	freshwater
Development	planktotrophic	lecithotrophic	lecithotrophic
Prominent sculpture			
early teleoconch	axial ribs	reticulation	reticulation
late teleoconch	almost smooth	axial and spiral ribs	axial and spiral ribs
Shell parameter			
maximum height	about 5 cm	about 7 cm	about 5 cm
apical angle	mostly 17–21°	mostly 13–16°	mostly 17–25°
Operculum			
position of nucleus	basal-left	basal-right	basal-left
Brood pouch	no compartments	no compartments	compartments
Gonoduct	closed	closed	closed
Radula			
rows of teeth	130–150	80–100	70–100
rachidian teeth	hook-like protrusions	hook-like protrusions	protrusions lacking
marginal teeth	8–10 cusps each	6–8 cusps each	7–10 (up to 13)

if this represents a synapomorphy of Thiaridae or independent autapomorphies of different genera. This may be implied by the fact that planktotrophic as well as lecithotrophic development occurs not only in *Stenomelania* but also in *Thiara*. The estuarine environment with connection to the open sea is a necessity for species of both genera. For conchological as well as anatomical characters (excluding radular teeth), however, we consider *Melanooides* to be more closely related to *Stenomelania* than is *Thiara*. Does that mean that colonization of freshwater occurred at least twice in the Thiaridae and are there species – although there is no indication – of *Melanooides*, *Tarebia* H. & A. ADAMS, 1854 or further thiarid genera (see e.g. GLAUBRECHT 1996), in which planktotrophy has not yet been detected? Is secondary acquisition of planktotrophy possible? The loss of planktotrophy is considered by the great majority of malacologists to be irreversible (in phylogenetic terms), which means that lecithotrophic species are presumed to produce only lecithotrophic offshoots.

It is not yet possible to open Pandora's box because too many gaps of knowledge have to be filled. However, we hopefully have demonstrated that thiarids represent a group of gastropods, which has the potential to unravel general aspects of evolutionary ecology.

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