

## A SYSTEMATIC REVISION OF THE SOUTHEAST ASIAN FRESHWATER GASTROPOD *Brotia* (CERITHIOIDEA: PACHYCHILIDAE)

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### ABSTRACT

We here present morphological and molecular genetic data on species of the Southeast Asian freshwater pachychilid *Brotia*, based on examination of material originating from various museum collections world wide, including type material, as well as material from field collections in Thailand and Indonesia. We show that a number of previous systematic assumptions about *Brotia* are in need of correction. Based on our analyses, we suggest a revised and more specific characterisation of this genus and outline the taxonomic and systematic implications of our findings. Accordingly, *Brotia* is restricted herein to viviparous pachychilids possessing as morphological characteristics a subhaemocoelic brood pouch, a pallial oviduct with only a simple, deep, and papillated spermatophore bursa, as well as embryonic shells with a wrinkled apical whorl. This typical embryonic shell structure results from a peculiar mode of ontogeny that includes a yolk sac protruding from the apical whorl during most stages of embryonic development, which are retained in the maternal brood pouch. A molecular phylogeny based on two mitochondrial gene fragments (646 bp of COI and 826 bp of 16S) shows that *Brotia* as encompassed here forms a monophyletic group. The application of the revised concept results in a significantly reduced number of species assigned to *Brotia* with implications also for a considerable reduction of the distributional area covered by members of the genus. In total, 35 species are recognized; the systematic affinities of eight of them remain unclear, however. Data on the morphology, distribution and if known on the biology of these species is presented.

Key words: taxonomy, systematics, Cerithioidea, Pachychilidae, *Brotia*, *Melania*, morphology, viviparity.

### INTRODUCTION

It is a major challenge of modern biosystematic research to provide classifications that correctly reflect phylogenetic relationships among organisms. The complexity of work required to achieve this goal has inspired the allegory of an Herculean task, as so aptly formulated by Graf (2001) for his catalogue of North American Pleuroceridae. However, while in the Greek myth the job was finished by unusual ways and means, in systematics accuracy is needed. In addition to a well-founded hypothesis on the natural relationships between taxa, a sound systematics also necessitates thorough revision of the taxonomy, which alone is a challenge as exemplified for various freshwater gastropods, such as Pleuroceridae (Graf, 2001), Pachychilidae

(Köhler & Glaubrecht, 2002a), or Neotropic Ampullariidae (Cowie & Thiengo, 2003). In the current work, we attempt to combine both a taxonomic revision and a phylogenetic study, in order to improve our understanding of Asian freshwater snails of the genus *Brotia* H. Adams, 1866, which still are poorly known.

*Brotia* is a member of the Pachychilidae, a family that was earlier incorporated within the so-called “melanians” or “Melaniidae”, which represent a polyphyletic assemblage of freshwater Cerithioidea (reviewed by Glaubrecht, 1996, 1999; molecular phylogeny in Lydeard et al., 2002). Views on the correct familiar assignment of *Brotia* have changed in recent decades due to our steadily improving knowledge. According to earlier systematic opinions, the genus was affiliated either with Thiaridae (e.g., Morrison, 1954; Brandt, 1968, 1974;

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Davis, 1971) or Pleuroceridae (e.g., Vaught, 1989); this was reviewed by Köhler & Glaubrecht (2002a). Molecular phylogenetic studies, however, show that *Brotia* is a pachychilid (Köhler et al., 2004), which in turn represent one of six cerithioidean freshwater clades next to, for example, the Thiaridae, Pleuroceridae, Melanopsidae, to name a few only here (for a molecular phylogeny of the Cerithioidea, see Lydeard et al., 2002).

Freed from systematic misconceptions, Pachychilidae were recently highlighted as an ideal focal group to address biological aspects of more general importance connected, for example, to processes of speciation and morphological adaptation (Rintelen et al., 2004), the evolution of different modes of reproduction (Köhler et al., 2004), as well as biogeographical problems (Glaubrecht, 2000; Glaubrecht & Rintelen, 2003).

Taxonomy and systematics especially of the Asian Pachychilidae have remained confusing for a long time, as outlined by Köhler & Glaubrecht (2001, 2002a). Most Asian pachychilid species sooner or later were attributed to *Brotia* by one or the other author (e.g., Martens, 1900; Thiele, 1928, 1929; Rensch, 1934; Abbott, 1948; Solem, 1966; Brandt, 1968, 1974), which rendered *Brotia* a taxon frequently referred to in systematic literature but in turn most vaguely defined by means of its morphology, distribution, and species composition.

In an initial study, it was shown that *Brotia* as perceived up to then was an assemblage composed of four species groups characterized by the possession of different reproductive and embryonic shell morphologies (Köhler & Glaubrecht, 2001). In the meantime, it has been substantiated that each of these groups indeed represents a distinct evolutionary lineage. The degree of morphological distinctiveness of these lineages has been considered large enough to justify the treatment as separate genera. Accordingly, in addition to *Brotia*, the following Asian pachychilid genera are currently recognized: *Sulcospira* Troschel, 1858 (Köhler & Glaubrecht, 2005), *Pseudopotamis* Martens, 1900 (Glaubrecht & Rintelen, 2003), *Tylomelania* S. Sarasin & F. Sarasin, 1897 (Rintelen et al., 2004; Rintelen & Glaubrecht, 2005), *Adamietta* Brandt, 1974, *Paracrostoma* Cossmann, 1900, and *Jagora* Köhler & Glaubrecht, 2003. Therefore, the status of various supraspecific pachychilid taxa was clarified in the last few years. Although we now know much better which species do not belong to *Brotia*, this has not necessarily improved our knowledge of *Brotia* itself.

For this reason, the current work aims at a taxonomic and systematic revision of the genus by comparative analysis of morphological and mitochondrial sequence data. This shall contribute to a stable and unequivocal taxonomy and systematics of *Brotia* as a group frequently referred to in accounts on Asian freshwater gastropods and at the same time provide the fundament for future studies on the phylogeny, evolution, and biogeography of these promising model organisms.

## MATERIAL AND METHODS

### Nomenclatural Remarks

The treatment of some species group names introduced by Troschel (1857) is subject to dispute. Bouchet & Rocroi (2005) argue that the non-hierarchical usage of the names "Thiarae", "Pachychili", as well as "Bithyniae", "Lithoglyphi", "Hydrobiae", and "Ancyloti" by Troschel (1857) stands in contrast with the procedure in the rest of his work, in which the ranks assigned to the formed names are indicated by formal endings, such as "-idea", "-ina", or "-acea". In case of the above-cited group names, Troschel (1857) explicitly refrained from such an assignment of family ranks for the somewhat ambiguous data he was faced with. For this reason, it was suggested by Bouchet & Rocroi (2005) to ignore these names. However, it has also been pointed out that some of these names, such as Bithyniidae, Thiaridae, or Hydrobiidae, are commonly published with Troschel as author. In contrast to the suggestion of Bouchet & Rocroi (2005) and unless it might otherwise be stipulated by an official decision of the ICZN, we prefer to further employ the names introduced by Troschel (1857), not only because we regard them as available and valid irrespective of the circumstance that the author refrained from the assignment of a specific rank, but also in order to keep continuity in the use of zoological names.

### Material Examined

This study is based on examination of material from various museum collections world wide (see under repositories). Most samples investigated comprise dry shells only; some others were fixed in 70–96% ethanol or in formalin. In many cases, preserved museum material was not suitable for a more detailed



examination of gross anatomy, for example, by histology, because the bodies were in a bad condition due to partial decay. It has furthermore proven impossible to extract DNA from museum material. In order to achieve a broader basis for our examinations, new collections were undertaken in Thailand and Indonesia. This voucher material is preserved in 75–96% ethanol, and is deposited with the Malacological Collection of the ZMB. To allow proper and quick fixation of the soft bodies, some shells were cracked prior to ethanol preservation. Consequently, the basis of available samples varies considerably between the different species in respect both to quality and quantity of available material. From some species hardly more than some dry shells were accessible, rendering it impossible to sufficiently assess the morphological and geographical range, whereas from others material was available suitable for various kinds of examinations.

#### Morphological Examination

Dimensions of adult and embryonic shells were measured with callipers to 0.1 mm using standard parameters (Figs. 1, 2). These parameters were analysed using statistic software SPSS (vs 9.0). Anatomy was studied using a stereo microscope. Extracted radulae were cleaned as described by Holznagel (1998) and mounted on stubs and coated with Gold-Palladium for SEM examination with a Jeol FSM 6300 scanning electron microscope. Embryonic shells extracted from ethanol preserved specimens or from dried shells were cleaned

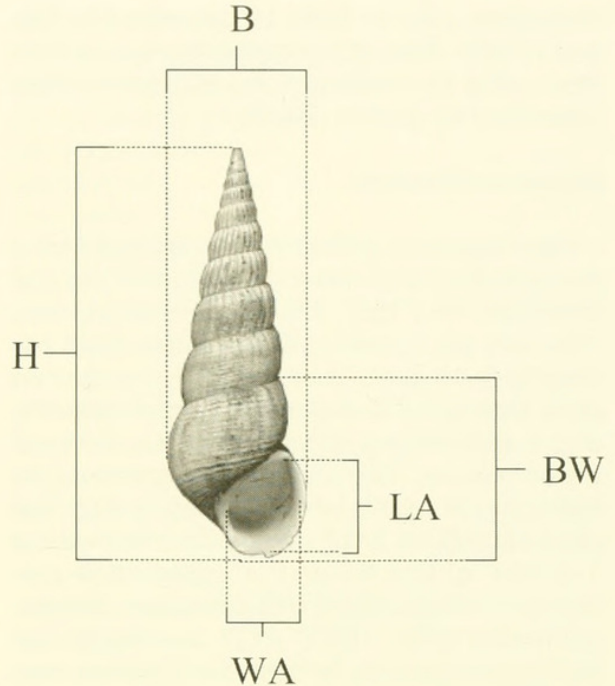


FIG. 1. Shell parameters used for morphometrical analyses.

mechanically and by sonication and prepared for SEM as given for the radulae. Since in viviparous freshwater Cerithioidea a distinct transition from the larval or primary shell (= protoconch) to the adult or secondary shell (= teleoconch) is lacking for the loss of free larval stages, we apply the more general term "embryonic shell" for all shelled stages retained in the brood pouch. Embryonic shell parameters were measured as shown in Figure 2. Soft tissues were treated with hexamethyl-

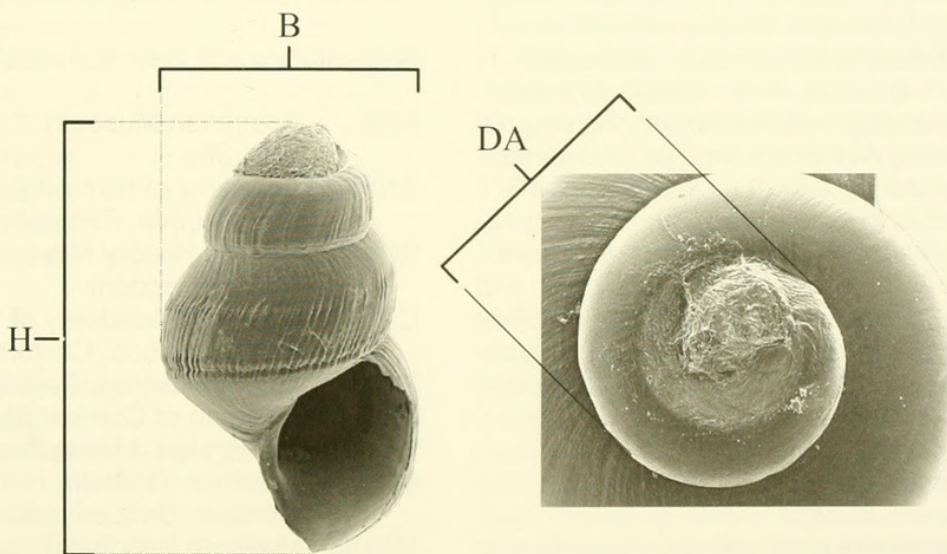


FIG. 2. Embryonic shell parameters used for morphometrical analyses.



disilazane prior to SEM as described by Nation (1983). Stomach morphology was examined using the methodology and terminology described by Strong (2003).

### Molecular Genetics

Two fragments of the mitochondrial genes of the Cytochrome Oxidase I ("COI", 646 bp) and the 16S rRNA ("16S", 826 bp) were sequenced. The data set contains 40 sequence pairs belonging to 16 species of *Brotia*, five sequence pairs belonging to four species of *Adamietta*, and a sequence pair each of two species of *Paracrostoma*. Two additional sequence pairs belonging to *Jagora* were included as outgroup representatives. DNA was purified from about 1–2 mm<sup>3</sup> of foot tissue from specimens preserved in ethanol by CTAB extraction (Winne-penninckx et al., 1993). PCR amplification of the fragments were performed in 25 µl volumes containing 1x Taq buffer, 1.5 mM MgCl<sub>2</sub>, 200 µM each dNTP, 1 U Taq polymerase, approximately 100 nM DNA and ddH<sub>2</sub>O up to volume on a Perkin Elmer GeneAmp 9600 or 2400 thermocycler. After an initial denaturation step of 3 min at 95°C, cycling conditions were 35 cycles of 1 min each at 95°C, 45–53°C, and 72°C, with a final elongation step of 5 min. Primers used were LCO 1490 5'-GCTCAA CAAATCATAAAGATATT-3' and HCO2198 var. 5'-TAWACTTCTGGGTGKCCAAARAAAT-3' (Folmer et al., 1994, modification of HCO2198 by A. B. Wilson) for COI, and 16SF 5'-CCGCACTTAGTGATAGCTAGTTTC-3' (Wilson et al., 2004) and H3059-Inv 5'-CGGTYTG AACTCAGATCATGT-3' (Palumbi et al., 1991) for 16S, respectively. PCR products were purified with QiaQuick PCR purification kits (Qiagen) following the standard QiaQuick PCR purification protocol. Both strands of the two genes were cycle sequenced with the original primers using ABI Prism BigDye™ terminator chemistry and visualized on an ABI Prism 377 automated DNA sequencer. The resulting sequence electropherograms of both strands were corrected manually for misreads and merged into one sequence file using BioEdit Version 5.0.1 (Hall, 1999). Sequences are accessible via GenBank (accession numbers in Table 6).

### Sequence Analysis

COI sequences were aligned manually and checked by translating the DNA sequences into amino acids in DAMBE 4.1.19 (Xia & Xie,

2001) using the genetic code for invertebrate mitochondrial DNA. 16S sequences were aligned using the online version of ClustalW provided by the homepage of the European Bioinformatics Institute ([www.ebi.ac.uk/clustalw/](http://www.ebi.ac.uk/clustalw/)) (Thompson et al., 1994) using default settings. A combined data set was constructed by concatenating the sequences. Pair-wise genetic distances were calculated with PAUP\* (Swofford, 1999). Phylogenetic trees were reconstructed using Neighbor Joining (NJ) (Saitou & Nei, 1987) and Maximum Parsimony (MP) as implemented in PAUP\*. In addition, a Bayesian method of inference (BI) was employed to estimate phylogenetic relationships (e.g., Huelsenbeck et al., 2002; Holder & Lewis, 2003) using MrBayes 3.0 (Huelsenbeck & Ronquist, 2001). NJ analyses were conducted using the random initial seed option to break ties and under a general time reversible model of sequence evolution (GTR+I+Γ; Gu et al., 1995) to correct for multiple substitutions. In the MP analyses, the heuristic search algorithm was employed with ten random additions of taxa and tree bisection-reconstruction (TBR) branch swapping. Gaps were treated as fifth base. Other settings were left on default. Prior to BI analyses, it was explored which substitution model fits best the sequence data set by running a hierarchical likelihood ratio test implemented in MrModeltest (Nylander, 2002). For BI analysis a Metropolis-coupled Markov chain Monte Carlo (4 chains, chain temperature = 0.2) was run for 750,000 generations. A 50% majority-rule consensus tree was constructed for the last 2,500 trees in order to assess the posterior clade probabilities for each node (bpp).

### Repositories and their Abbreviations

AMS	Australian Museum, Sydney, Australia
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.
BMNH	Natural History Museum, London, United Kingdom
CAS	California Academy of Sciences, San Francisco, California, U.S.A.
IMC	Indian Museum, Calcutta, India
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
MHNG	Muséum d'Histoire Naturelle, Genève, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MZB	Zoological Museum, Bogor, Indonesia



NMB	Naturhistorisches Museum, Basel, Switzerland
RMNH	Natural History Museum Naturalis, Leiden, The Netherlands
SMF	Senckenbergmuseum, Frankfurt/Main, Germany
ÜMB	Überseemuseum, Bremen, Germany
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.
ZMA	Zoölogisch Museum, Amsterdam, The Netherlands
ZMB	Museum für Naturkunde, Humboldt-Universität Berlin [formerly Zoologisches Museum], Germany
ZMH	Zoologisches Museum und Institut, Universität Hamburg, Germany
ZSI	Zoological Survey of India, Calcutta, India
ZSM	Zoologische Staatssammlung, München, Germany
ZMZ	Zoologisches Museum, Zürich, Switzerland

## Abbreviations

B	breadth of shell
BW	height of the body whorl
bp	brood pouch
bpp	brood pouch pore
c	cerebral ganglion
cg	capsule gland
cr	crescent fold
crt	septate crescent thickening
ct	ctenidium
DA	diameter of apical whorl of embryonic shell
dg	digestive gland
dgd	digestive gland duct
eg	egg capsule
ey	eye
ft	foot
gg	genital groove
gp	gastric pad
gs	gastric shield
H	height of shell
hd	head
int	intestine
kd	kidney
LA	length of aperture
lf	lateral fold
ll	lateral lamina
m	median
mc	mantle cavity
me	mantle edge
mf	marginal fold
ml	medial lamina

mr	mantle roof
N	number of whorls
oes	oesophagus
og	oviductal groove
op	operculum
ovd	oviduct
ovr	ovary
p	pedal ganglion
pl	pleural ganglion
rad	radula
s	statocyst
sa	sorting area
sb	spermatophore bursa
sbg	sub-oesophageal ganglion
sd	standard deviation
sg	sperm gutter
sn	snout
snn	snout nerve
spg	supra-oesophageal ganglion
ss	style sac
st	stomach
t <sub>1</sub>	major typhlosole
t <sub>2</sub>	minor typhlosole
tn	tentacle
tnn	tentacular nerve
ts	testis
WA	width of aperture

## SYSTEMATIC ACCOUNT

## Pachychilidae Troschel, 1857

*Brotia* H. Adams, 1866

*Brotia* H. Adams, 1866. Type species, by monotypy: *Melania pagodula* Gould, 1847.  
*Antimelania* Fischer & Crosse, 1892. Type species, by subsequent designation in Pilsbry & Bequaert (1927): *Melania variabilis* Benson, 1836.  
*Wanga* Chen, 1943. Type species, by original designation: *Melania henriettae* Griffith & Pidgeon, 1834.

## Taxonomy and Systematics

*Brotia* was originally established for the round and multispiral operculum of the type species, which however is a characteristic exhibited by a number of pachychilid taxa and not peculiar for *Brotia* (Köhler & Glaubrecht, 2001, 2002a, 2003). In the 19<sup>th</sup> and 20<sup>th</sup> century, a vast number of species were affiliated with *Brotia* by a number of authors without sufficient knowledge of their gross morphology (e.g., Brot, 1874–1879; Martens, 1897,



1900; Martens & Thiele, 1908; Abbott, 1948). This procedure has caused considerable systematic confusion as to the taxonomy of *Brotia* and other described supraspecific taxa from Asia (see overview in Davis, 1971: 68, 69; Köhler & Glaubrecht, 2002a). A first, more comprehensive treatment of *Brotia* species based also on features of the soft body was presented by Brandt (1974). This author also suggested a subdivision of *Brotia* into three subgenera: (1) *Brotia* s. str., (2) *Senckenbergia* Yen, 1939, and (3) *Paracrostoma* Cossmann, 1900. This suggestion was refuted, however, by Köhler & Glaubrecht (2001), who argued that radular and opercular features alone are insufficient to differentiate supraspecific taxa among the Pachychilidae. Instead, it was shown that characters of the reproductive tract and embryonic shells are more informative at this level. Using these morphological structures, a preliminary subdivision of *Brotia* into four species groups was suggested by Köhler & Glaubrecht (2001). Two of these groupings have since been established as genera independent of *Brotia*: *Tylomelania* endemic to Sulawesi (Rintelen et al., 2004; Rintelen & Glaubrecht, 2005) and *Jagora* endemic to the Philippines (Köhler & Glaubrecht, 2003). The status of the two remaining groupings, so-called "*Brotia pagodula* group" and "*Brotia testudinaria* group", have remained unresolved thus far. Only recently it has been suggested on basis of molecular genetic data that both species groups indeed form distinct monophyletic lineages (Köhler et al., 2004). According to this mitochondrial phylogeny, it was suggested to transfer all species of the "*Brotia testudinaria* group" designated by Köhler & Glaubrecht (2001) to *Adamietta* Brandt, 1974 (Köhler et al., 2004: 2221). In regard to this suggestion, in the current study *Brotia* is restricted to the members of the "*Brotia pagodula* group" as delineated by Köhler & Glaubrecht (2001). Accordingly, morphological features characteristic for *Brotia* are (1) an irregularly wrinkled apical whorl of the embryonic shell and (2) a pallial oviduct possessing a simple, deep, and ciliated spermatophore bursa.

#### Morphology and Differential Diagnosis

**Shell:** Relatively large, often up to 4 or 5 cm. Moderately thick, broadly to elongate conical, turreted spire, apex eroded or truncated. Sculpture variable comprising axial ribs, sometimes with nodules, and spiral ridges or lines. Body whorl comparatively large;

aperture ovate, well rounded or angled below, pointed above. No features peculiar to *Brotia*.

**Embryonic Shell:** Relatively large among viviparous pachychilids; average height 1 to 6 mm, up to four whorls. Apical whorl asymmetrical, irregularly wrinkled; initial shell sharply delimited from subsequent whorls with more or less smooth sculpture (for peculiar ontogeny of *Brotia* causing wrinkles see below).

**Operculum** (Fig. 3C): Either round, up to eight whorls, central nucleus or slightly oval for last whorl increasing in diameter with up to six whorls.

**External morphology and mantle cavity** (Figs. 3A, B): Animals light to dark brown, dark grey or black, often with light patches; broad, furrowed snout. Cephalic tentacles moderately long, each with tiny eye on side of base. Females with subhaemocoelic brood pouch; "egg transfer" or "genital groove" on right side of head connects pallial oviduct with brood pouch pore near base of right tentacle; present also in males. Mantle margin smooth; mantle cavity occupying approximately two thirds of first whorl. Osphradium delicate, slightly undulating, forming narrow ridge embedded in shallow trench, lying adjacent to anterior part of ctenidium. Ctenidium large, broad tapering posteriorly; beginning shortly behind mantle edge, extending posteriorly almost to end of cavity, on average twice as long as osphradium. Hypobranchial gland inconspicuous, adjacent to rectum.

**Radula:** Taenioglossate, relatively large, robust. Up to 30 mm long corresponding to half of shell height. Posteriorly embedded in connective tissue, coiled behind buccal mass in radular sac. Rachidian squarish, with one pronounced, more or less pointed central cusp flanked by up to three accessory denticles that taper in size; glabella well developed. Anterior margin of rachidian concave or straight, lower rim concave by posteriorly extending glabella. Lateral teeth with rounded glabella; major cusp flanked by up to three smaller denticles on each side. Inner marginal teeth with two, outer marginal with up to three denticles; hooked; simple flange or ledge at outer margin; more pronounced in outer marginal teeth.

**Nervous System** (Fig. 3E): Cerebral commissure long, cerebro-pleural connectives short. Sub-oesophageal ganglion fused with left pleural ganglion. Pedal ganglia deeply embedded in propodium, connected to pleural



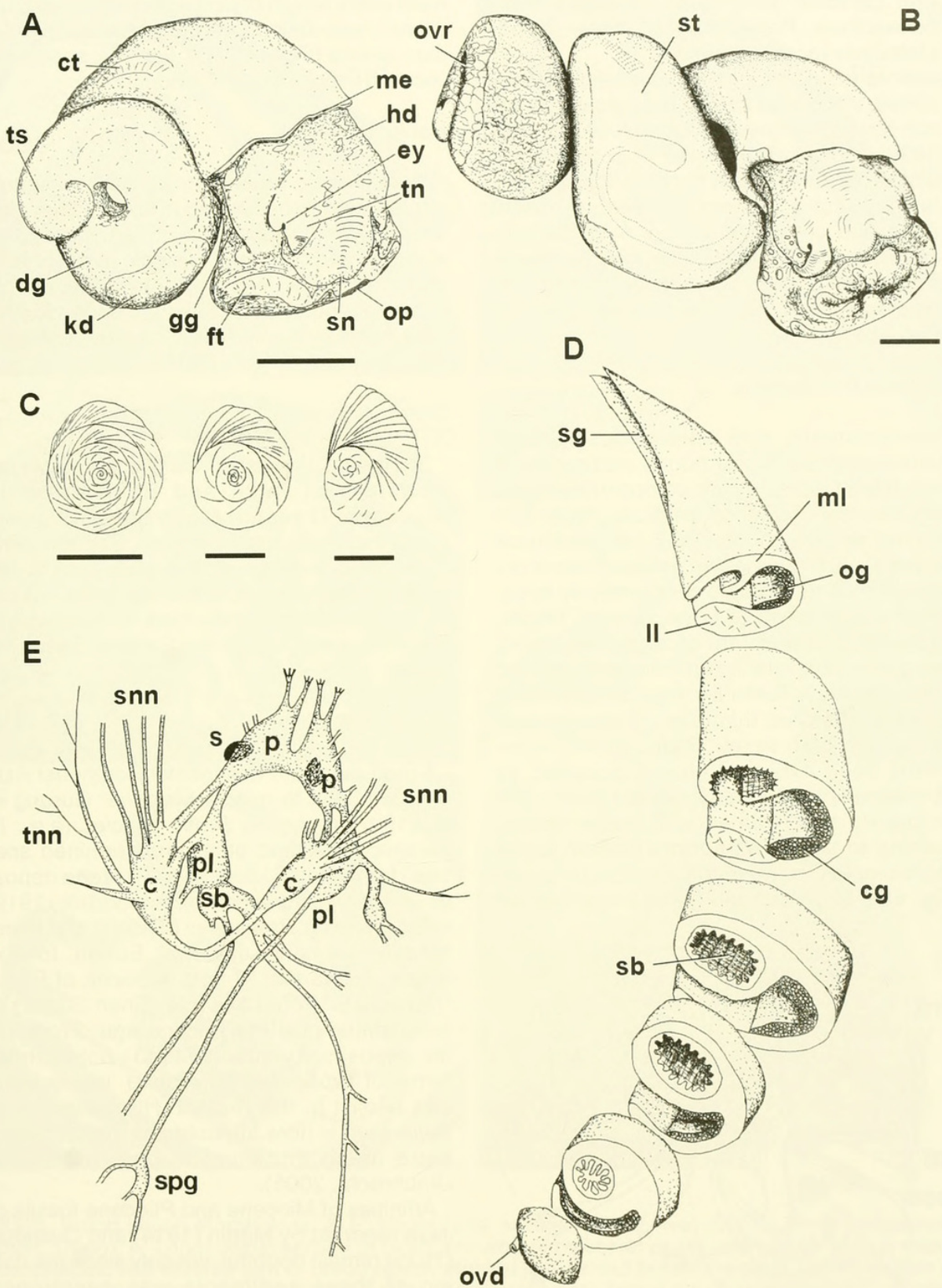


FIG. 3. Soft anatomy of *Brotia*. A: External anatomy of *B. pagodula* (Thailand, male); B: External anatomy of *B. episcopalis* (Sumatra, female); C: Opercula (from left to right: *B. pagodula*, *B. episcopalis*, *B. costula*); D: Pallial oviduct of *B. pagodula*; schematic reconstruction showing various cross-sections from anterior to posterior; E: Schematic reconstruction of nervous system of *B. pagodula*. Scale bars = 10 mm.



and cerebral ganglia by relatively long connectives. Pedal ganglia closely joined, statocysts located basally.

**Alimentary System:** Oesophagus longitudinally folded, transverse septae not present. Stomach typical pachychilid (Strong & Glaubrecht, 1999), including presence of sorting area, single digestive gland duct, narrow glandular pad, cuticular gastric shield, crescent ridge and groove (e.g., Fig. 4, *B. citrina*). Major and minor typhlosole may be fused. Epithelium of style sac heavily ciliated with golden gloss. Crystalline style cylindrical or club-like.

### Reproductive System

Gonochoristic with balanced sex ratio. Subhaemocoelic brood pouch occupying almost entire visceral cavity, compartmentalized with lamellae of thin adventitious tissue embedding embryos (Figs. 5A–E for histological sections). Juveniles within pouch of same ontogenetic stage. Gonads comparatively large, comprising last two to three visceral whorls, adjacent to and dorsal of digestive gland. Ovary orange to light brown consisting of broad lobes (Fig. 6E). Testis light yellow consisting of highly branched thin tubes. Pallial gonoduct open in both sexes. Pallial oviduct comprising deep oviductal groove bounded by parallel laminae (Fig. 6A); ciliated sperm gutter forming along free edge of medial lamina, opening to papillated spermatophore bursa approximately at two thirds of oviductal length (Fig. 6B); large capsule gland comprises al-

most entire length of pallial oviduct; capacious, ciliated spermatophore bursa formed by median lamina (Figs. 6C, D); Fig. 3D, schematic reconstruction of pallial oviduct).

### Habitat

Most species inhabit small, clear mountain streams; some occur also in lakes. Often confined to specific habitats, such as upper course of rivers, and restricted to single rivers or river systems. Rarely more than two species co-occur with notable exception of endemic species flock in Kaek River, central Thailand (Glaubrecht & Köhler, 2004).

### Distribution

Southeast Asia, from foot hills of Himalayas in northeast India and Bangladesh to Myanmar, Thailand, Malaysian Peninsula, Sumatra, Java, and Borneo. Reports from Java and Borneo are scarce, date back to 19<sup>th</sup> century. *Brotia* as here defined does not occur in most parts of Indochina, in Sulawesi, in the Philippines, or on the Smaller Sunda Islands.

### Fossil Record

Fossil record in continental Southeast Asia extends back to middle Miocene. Gurung et al. (1997) report on *Brotia* species (e.g., *B. palaeocostula* and other undetermined species) from middle Miocene to Pliocene deposits of Nepal (Churia group). Annandale (1919) mentions fossil *Brotia* from Miocene and Pleistocene sediments of Lower Burma, for example, "*B. variabilis*" from Miocene of Pegu, "*B. baccata*" from Lake Inlé (Shan States) of presumably post-Pleistocene age. From latter deposits, Bequaert (1943) noted three forms of *Brotia* and *Sulcospira*, respectively that persist to the Recent. His reference to *Sulcospira* is here attributed to *Brotia*, *Sulcospira* being endemic to Java (Köhler & Glaubrecht, 2005).

Affinities of Miocene and Pliocene fossils of Java reported by Martin (1914) and Oostingh (1935) remain doubtful, not only since the dating of these sediments was questioned (Oostingh, 1935: 2). Judging from figures in both publications, we consider the species in question, for example, "*Brotia oppenoorthi*", not congeneric with Recent *Brotia*. Instead, at least some species represent thiarids.

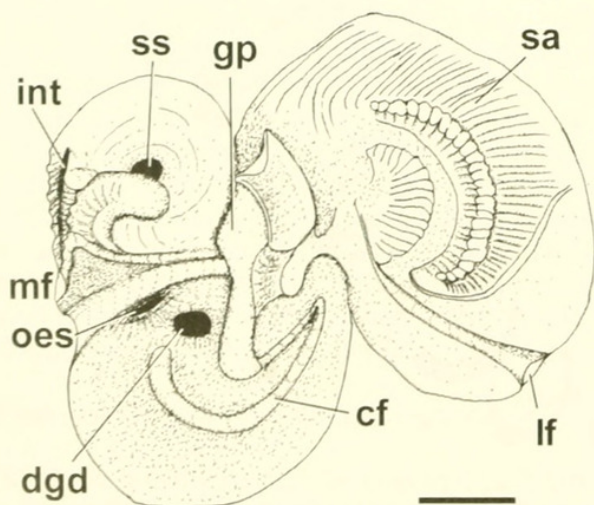


FIG. 4. Stomach anatomy of *B. citrina* (Thailand, Mae Sot; ZMB 200.212). Scale bar = 5 mm.



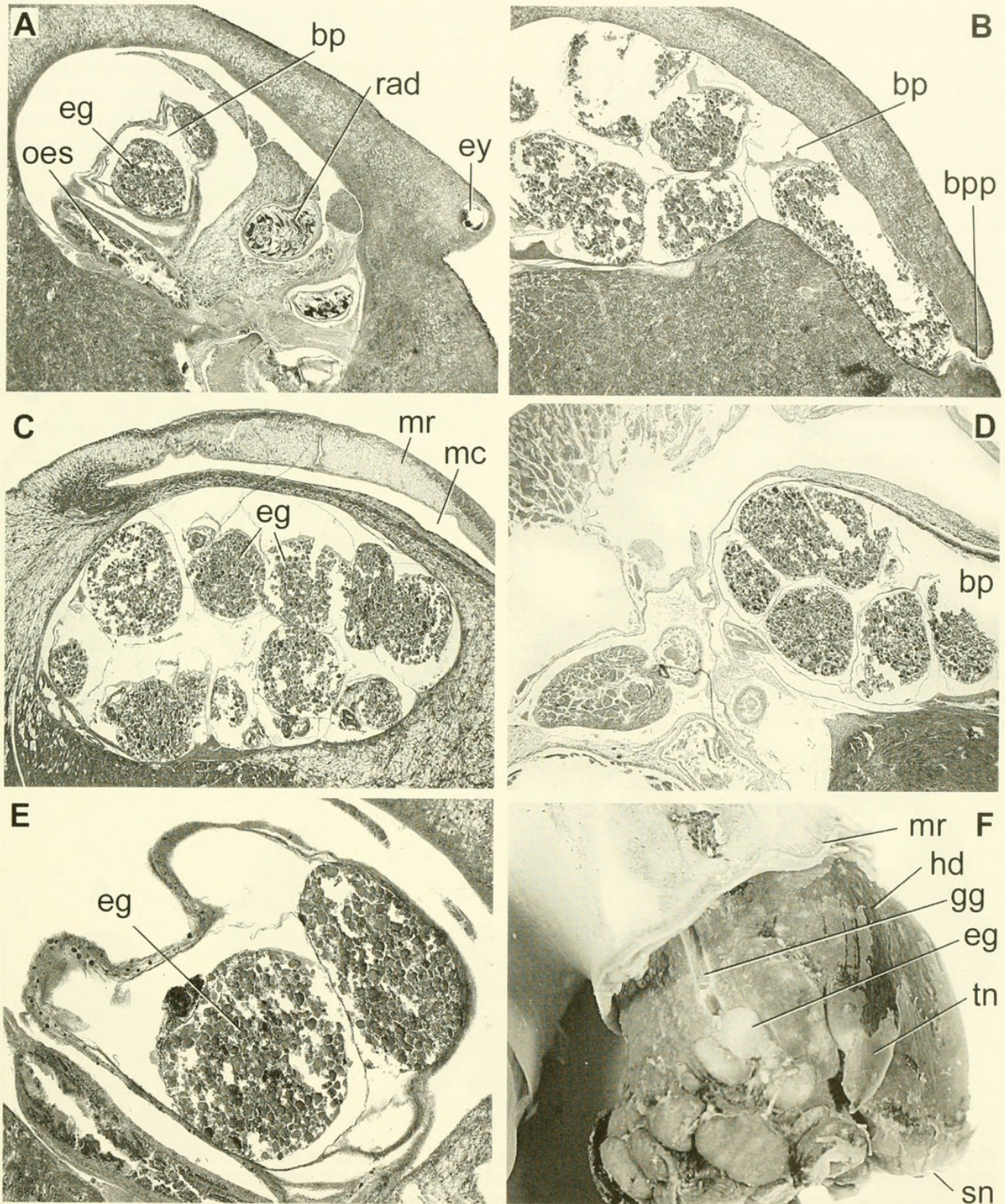


FIG. 5. Brood pouch morphology. A-E: Histological sections of the head-foot of *Brotia episcopalis* (ZMH, Trang); A: Longitudinal section of head, showing the visceral cavity with radula, buccal mass, oesophagus, and anterior part of brood pouch situated just behind buccal mass; B: Cross-section at about mid head; brood pouch occupies most of visceral cavity, brood pouch pore visible; C: Cross-section some mm posterior to B; brood pouch filled with numerous egg capsules each embedded in thin membrane; D: Cross-section at posterior end of brood pouch; E: Detail of A; egg capsules in higher magnification; F: Macro-anatomical photograph of *B. pseudosulcospira* (ZMB 200.196); head of female with egg capsule sitting in genital groove just in front of brood pouch pore.



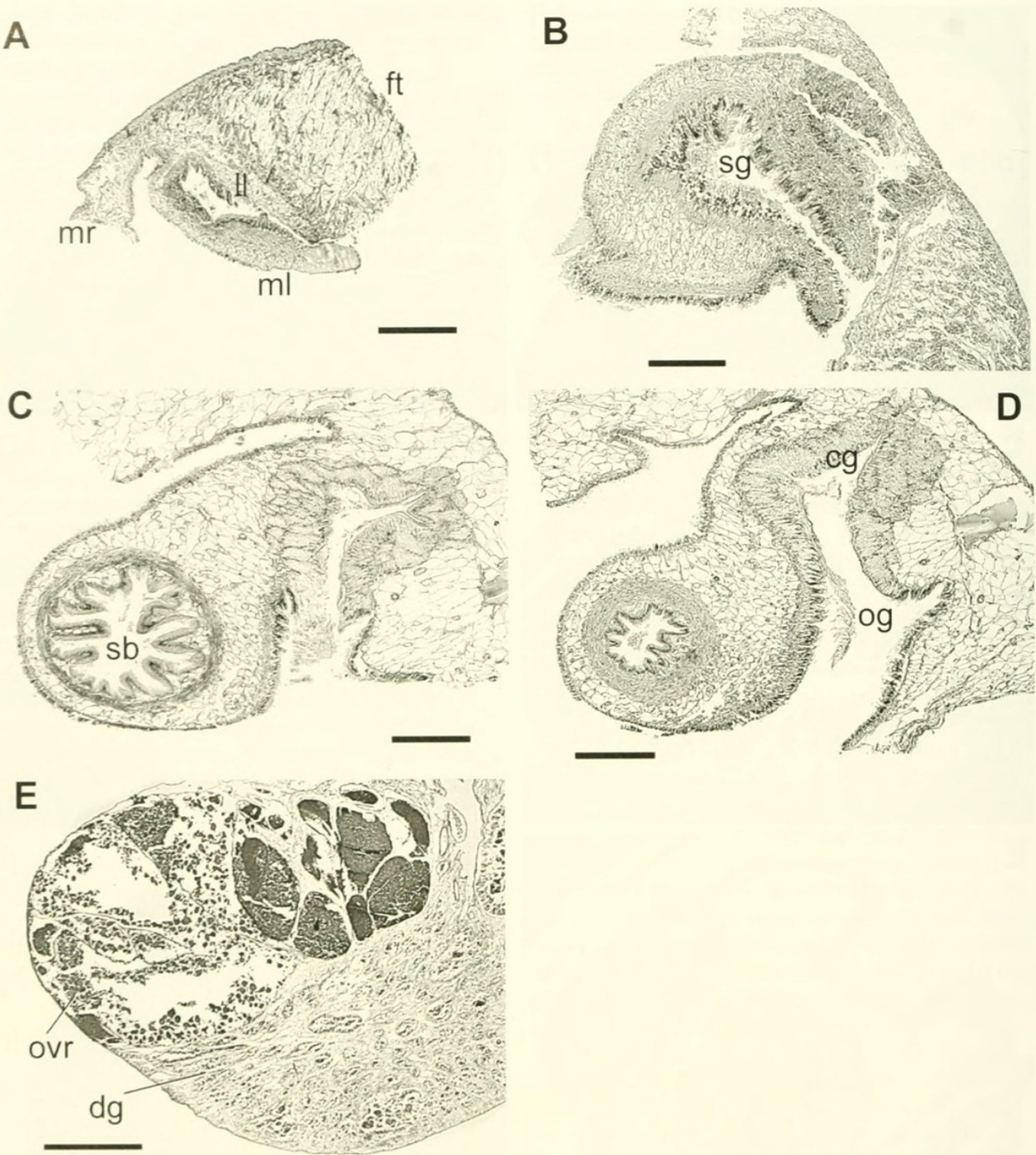


FIG. 6. Female reproductive anatomy. A–D: Histological sections of pallial oviduct of *B. pagodula* (ZMH; Myanmar); A: Cross-section at anterior end of pallial gonoduct; lateral lamina fused with mantle, simple medial lamina free; B: Cross-section at about one third of oviduct length; heavily ciliated sperm gutter formed by medial lamina; C: Cross-section at about half of oviduct length; spermatophore bursa formed by medial lamina, capsule gland comprising base of oviductal groove; D: Cross-section at about two thirds of oviduct length; ciliated spermatophore bursa; E: Cross-section of visceral whorl of *B. episcopalis* (ZMH, Trang); ovary filled with egg capsules, adjacent and posterior to digestive gland. Scale bars = 1 mm.

Also fossil shells from Europe were attributed to *Brotia* (Papp, 1953). The fossil taxon *Tinnyea* was treated as a subgenus of *Brotia* (Papp, 1953) and various species have been affiliated with this Southeast Asian taxon, such

as “*Brotia escheri*” (Brongniart, 1822) and “*B. vasarhelyii*” (Hantken, 1887) from Pannonian deposits near Budapest, Hungary – Upper Miocene (Lörenthey, 1902), Burgenland, Austria – Upper Miocene (Fischer, 1994), and



Mainz Basin, Germany – Upper Oligocene to Lower Miocene (Kadolsky, 1995). Placement of these and other fossil species in *Brotia* does refer only to (rather superficial) shell similarity and ignores the uncertain freshwater origin of the deposits. Assignment of European fossils to *Brotia* is rejected here; whether some fossils might be included in the Pachychilidae awaits critical evaluation of the fossil material, which we have not examined yet.

#### ACCOUNT OF RECENT SPECIES IN ALPHABETICAL ORDER

*Brotia armata* (Brandt, 1968)  
(Figs. 7, 8, 12A, B)

*Brotia* (*Paracrostoma*) *pseudosulcospira armata* Brandt, 1968: 275, pl. 10, fig. 62 (“Maenam Kaek in Phitsanulok Prov. at Gaeng Song rapids, 45 km E Pitsanulok” = Thailand, Prov. Phitsanulok, Kaek River at Kaeng Song rapids, approximately 60 km E of Phitsanulok), holotype SMF 197380, 35 paratypes ZMH; types seen.

*Paracrostoma pseudosulcospira armata* – Brandt, 1974: 186, pl. 13, fig. 43; Köhler & Glaubrecht, 2002a: 144.

*Brotia armata* – Glaubrecht & Köhler, 2004: 283–287.

*Paracrostoma morrisoni* Brandt, 1974: 188, 189, pl. 14, fig. 47 (“Maenam Kaek at Sopa Falls, 71 km E of Pitsanulok” = Thailand, Prov. Phitsanulok, Kaek River at Sopa Falls, 71 km E of Phitsanulok), holotype SMF 215966, six paratypes SMF 215967, 12 paratypes SMF 271191, 38 paratypes SMF 193587, 11 paratypes BMNH 1976119, 14 paratypes RMNH 55135/14; types seen; Köhler & Glaubrecht, 2002a: 141, 142.

*Paracrostoma paludiformis dubiosa* Brandt, 1974: 188, pl. 14, fig. 46 (“Kaek River, 80 km E of Pitsanulok” = Thailand, Prov. Phitsanulok, Kaek River, 80 km E of Phitsanulok), holotype SMF 215964, six paratypes SMF 215964, five paratypes RMNH 55284/5; types seen; Köhler & Glaubrecht, 2002a: 142.

#### Taxonomy and Systematics

Originally described as subspecies of *B. pseudosulcospira*, it was transferred to *Brotia* and is treated as distinct species in the Kaek River species flock by Glaubrecht & Köhler (2004). According to these authors, *P. morrisoni* and *P. paludiformis dubiosa* are considered as synonyms.

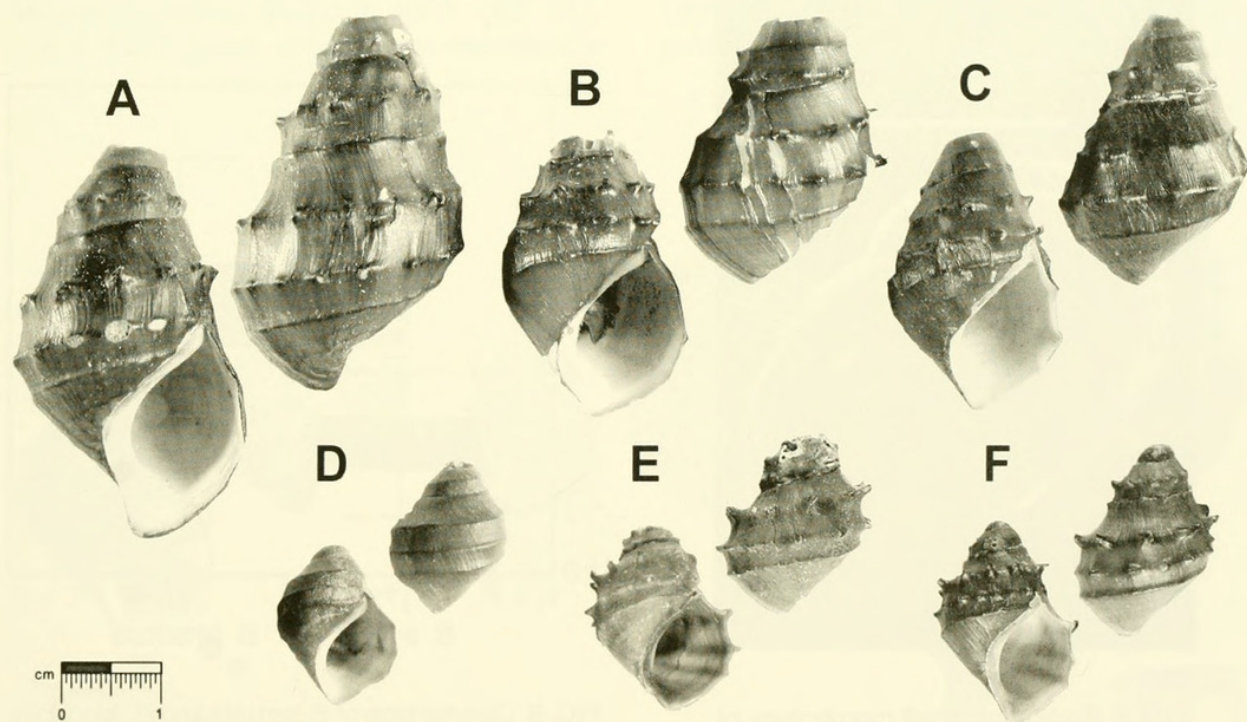


FIG. 7. Shell morphology of *B. armata*. A–D: Paratypes of *P. pseudosulcospira armata* SMF 193587; E–F: Paratypes of *P. morrisoni* SMF 215967. Scale bar = 10 mm.



## Material Examined

Thailand: Prov. Phitsanulok, Kaek River: Sakunothayan Falls, 33 km E of Phitsanulok (ZMB 200.265; ZMH); Kaeng Song rapids, 45 km E of Phitsanulok (SMF 193587; ZMB 200.193); resort, 53 km E of Phitsanulok (ZMB 200.254); Poi Falls, 60 km E of Phitsanulok, 16°50.75'N, 100°45.06'E (ZMB 200.268); Thung Salaeng Luang National Park, 90 km E of Phitsanulok, 16°52'N, 100°38'E (USNM 794081; ZMB 200.252, 200.265).

## Differential Diagnosis

Shell relatively small, conical to oval, not more than three rather flattened whorls; one to three spiral cords supporting a spiral row of sometimes spiny nodules.

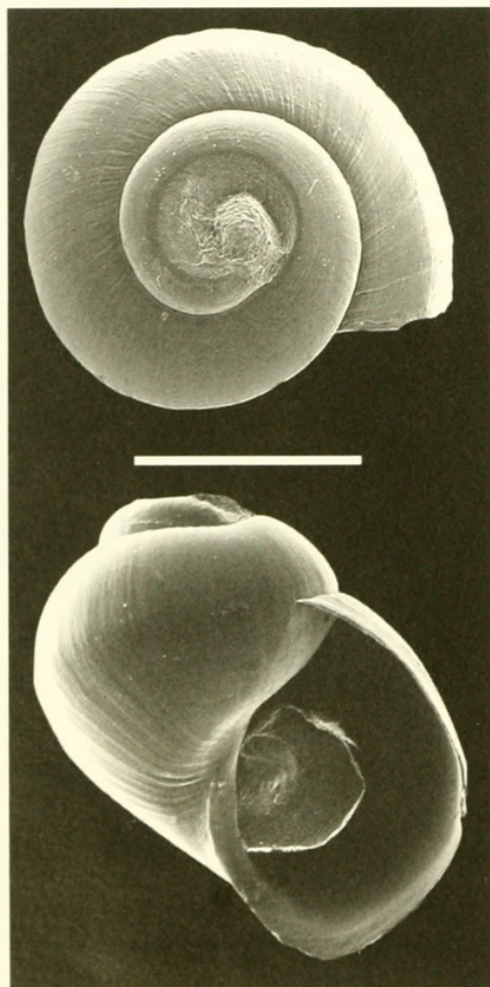


FIG. 8. Embryonic shell morphology of *B. armata*. SEM images of embryonic shell removed from brood pouch (paratype BMNH 1976111); apical and front view. Scale bar = 1 mm.

## Description

**Shell** (Fig. 7): Relatively small, oval to conical, up to three flattened to slightly convex whorls, tip eroded. One to three spiral cords, especially upper ones supporting spiral rows of spiny nodules; on body whorl often additional cord visible. Some shells almost smooth. Aperture broadly ovate, large compared to shell, basal margin produced. Size:  $H = 26\text{--}38\text{ mm}$ ,  $B = 18\text{--}24\text{ mm}$ .

**Embryonic Shell** (Fig. 8): Smooth except for axial growth lines, sharp transition between apical area and penultimate whorl after about half of first whorl. Size of juveniles kept in brood pouch: 2.0–2.5 mm, 2.5 whorls.

**Operculum**: Oval, up to four whorls that increase in diameter, sub-central nucleus.

**Radula** (Figs. 12A, B): Length of ribbon:  $m = 18.4\text{ mm}$  ( $sd = 4.4\text{ mm}$ ;  $n = 15$ ), up to 180 rows of teeth. Central tooth with elongated main cusp and two or three much smaller accessory denticles on each side that taper in size; glabella narrow with straight lateral margins, rounded posterior rim that does not reach the basal rim of central tooth. Laterals with broad main cusp flanked by one to two accessory denticles on each side. Inner and outer marginals with large, broad outer cusp and spiny inner denticle.

**Stomach**: Typical, as in *B. binodosa* (Fig. 13).

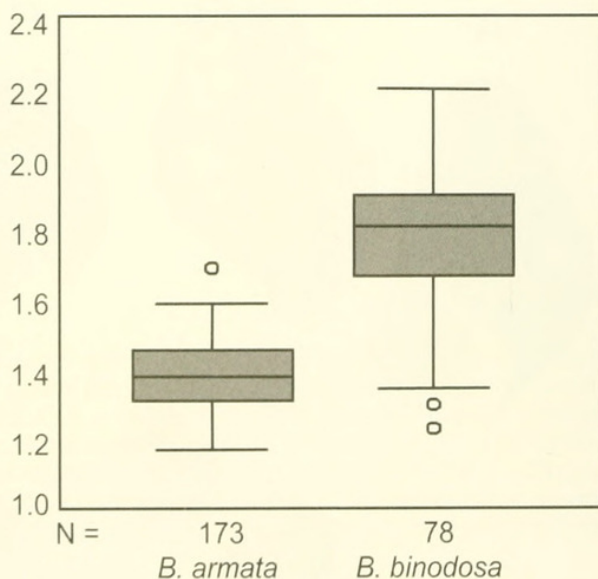


FIG. 9. Comparison of *B. armata* and *B. binodosa* by means of shell parameter  $H/B$ . Box plot diagram showing median, the 25%- and 75%-percentile and largest non-extremes (less than 1.5 times of box height).



TABLE 1. Result of discriminant analysis of shell parameters of *B. armata* and *B. binodosa*.

	Predicted group membership	
	<i>B. armata</i>	<i>B. binodosa</i>
<i>B. armata</i>	134 (97.8%)	3 (2.2%)
<i>B. binodosa</i>	11 (14.1%)	67 (85.9%)

#### Distribution

Thailand: Prov. Phitsanulok: Endemic to Kaek River; only in middle course between Sakunothayan Falls (33 km E Phitsanulok) and Thung Salaeng Luang NP (90 km E Phitsanulok).

#### Remarks

*Brotia binodosa* with similar sculpture is more turreted and slender possessing more whorls. Both species deviate mainly in proportion of shell height to width (H/B, Fig. 9), although not statistically significant (Table 1). *Brotia pseudosulcospira* lacks spines, is larger with a darker, thicker, smoother shell.

*Brotia binodosa* (Blanford, 1903)  
(Figs. 10, 11, 12C, 13)

*Melania binodosa* Blanford, 1903: 282, 283, pl. 8, fig. 2 ("Siam, in fluminibus majoribus" =

in large rivers, Thailand; restricted to Sopha Falls, at the Kaek River near Phitsanulok by Brandt 1974: 175), holotype BMNH 1903.2.28.2, paratype BMNH 1903.2.28.3 (Figs. 8A, B); types seen.

*Brotia binodosa* – Solem, 1966: 15, figs. 1a, b; Glaubrecht & Köhler, 2004: 287–289.

*Brotia (Brotia) binodosa binodosa* – Brandt, 1974: 174, 175, pl. 12, fig. 26.

*Brotia spinata* – Köhler & Glaubrecht, 2002a: 148 [partim].

*Brotia (Brotia) binodosa spiralis* Brandt, 1974: 176, pl. 12, fig. 27 ("Thailand: Kaek River, 38.5 km E Phitsanulok" = Thailand, Prov. Phitsanulok, Kaek River 38.5 km E of Phitsanulok), holotype SMF 220340; type seen.

*Brotia spinata spiralis* – Köhler & Glaubrecht, 2002a: 130.

#### Taxonomy and Systematics

Revised by Glaubrecht & Köhler (2004), who suggested *B. binodosa spiralis* to represent a junior synonym. Member of the Kaek River species flock in Central Thailand.

#### Material Examined

Thailand: Prov. Phitsanulok: Chattrakan Fall, Kwae Noi River in the Chattrakan NP, N of Nakhon Thai (ZMB 200.202); Kaek River (SMF 193577; RMNH 55288); Kaeng Song Falls (SMF 193874); resort, 53 km E of Phitsanulok

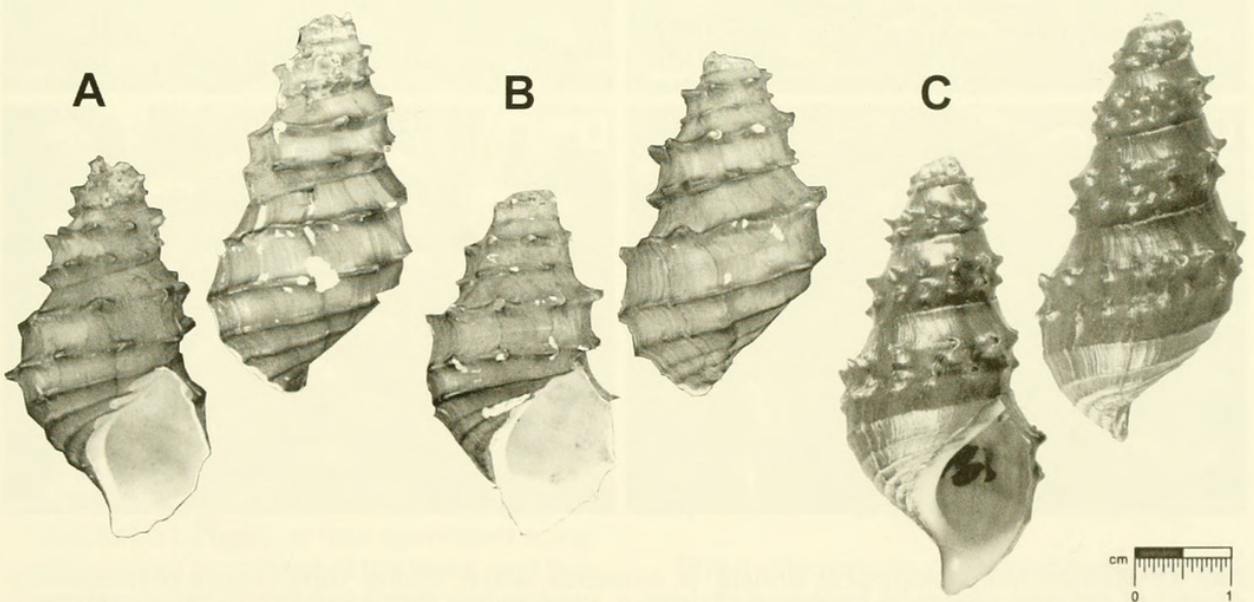


FIG. 10. Shell morphology of *B. binodosa*. A: Holotype of *M. binodosa* BMNH 1903.2.28.2; B: Paratype BMNH 1903.2.28.3; C: Thailand, Kaek River, Sopha Falls (ZSM 19983219). Scale bar = 10 mm.



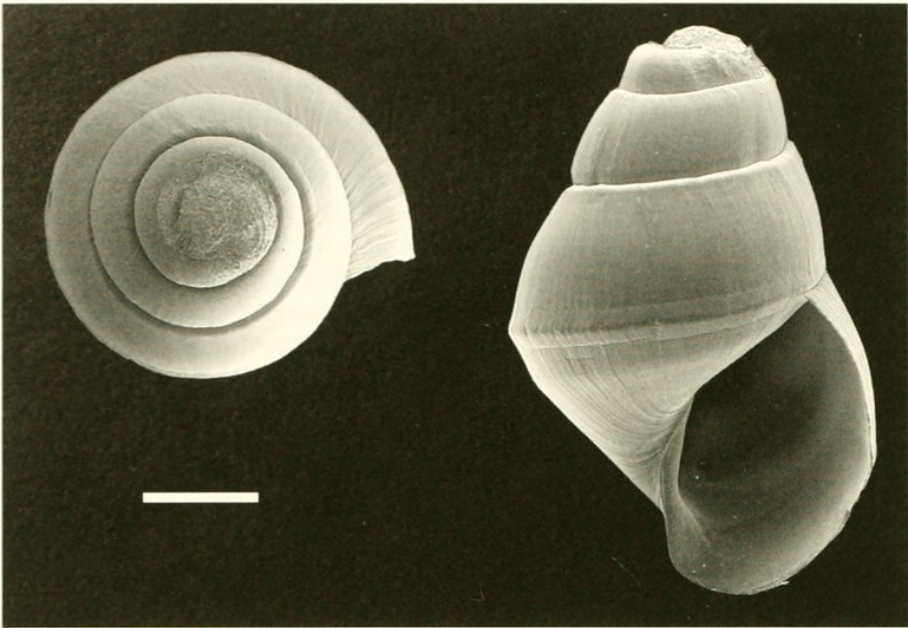


FIG. 11. Embryonic shell morphology of *B. binodosa*. SEM images of embryonic shell removed from brood pouch (Thailand, Kaek River; ZSM 19983219); apical and front view. Scale bar = 0.3 mm.

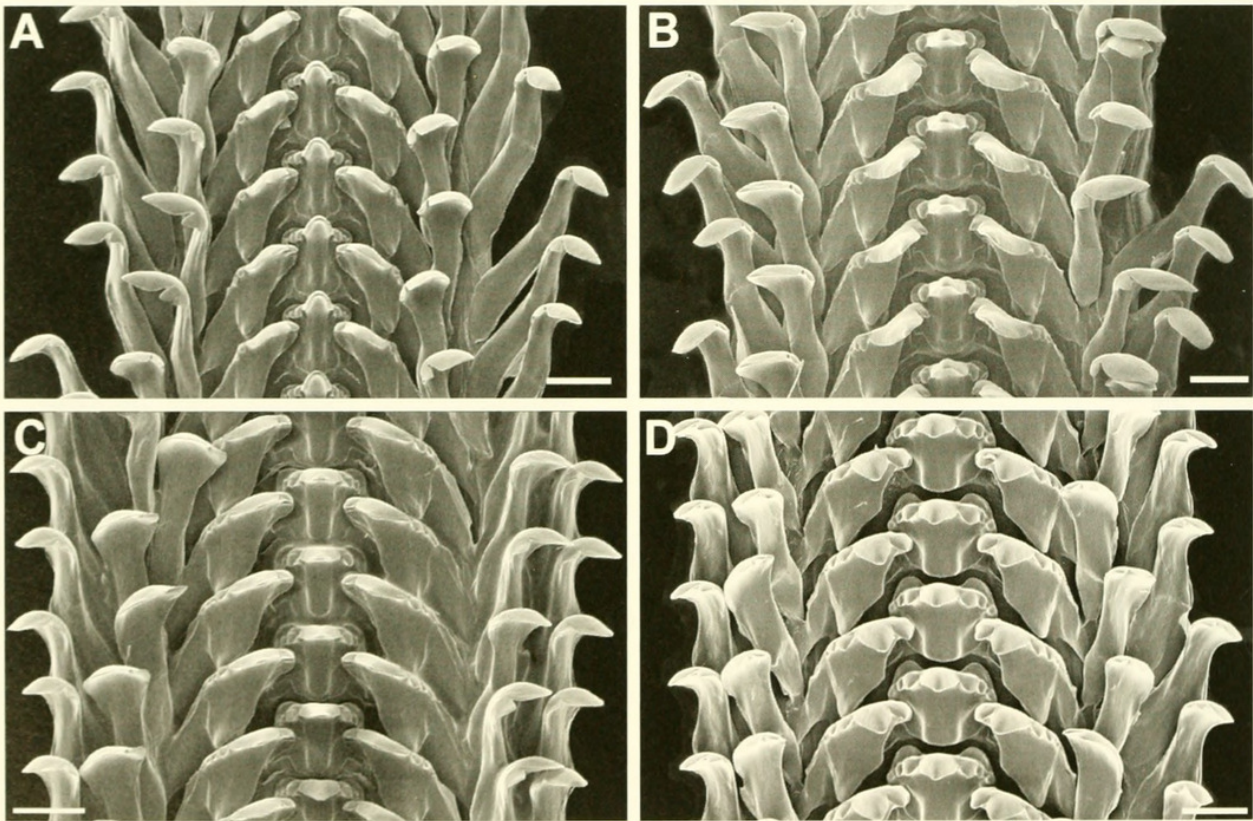


FIG. 12. Radular morphology of *B. armata*, *B. binodosa*, and *B. citrina*. SEM images of radula segments viewed from above. A: *B. armata* (Thailand, Kaek River; ZMB 200.252); B: *B. armata* (Thailand, Kaek River; ZMB 200.254); C: *B. binodosa* (Thailand, Kaek River; ZMB 200.192); D: *B. citrina* (Thailand, Pa Charoen; ZMB 200.207). Scale bars = 100  $\mu$ m.



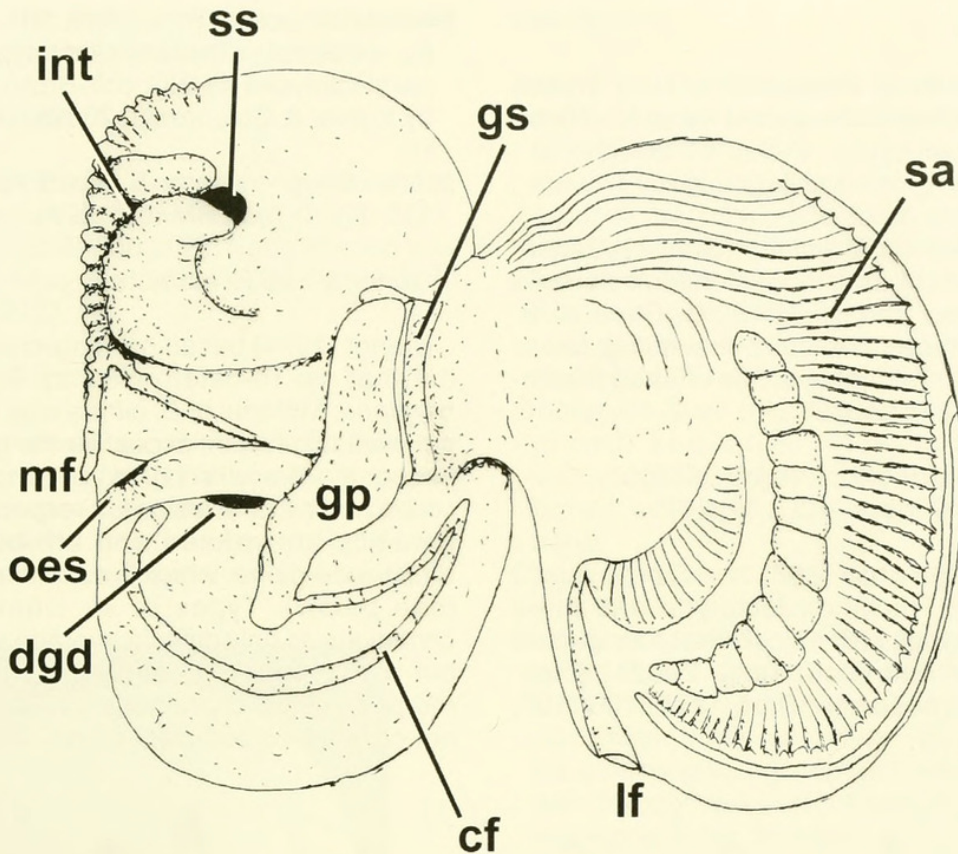


FIG. 13. Stomach anatomy of *B. binodosa* (ZMB 200.269; Thailand, Kaek River).

(ZMB 200.267); Poi Falls (ZMB 200.269; SMF 205137); Sopha Falls (ZSM 19983214, 6, 8; RMNH 55288/6; SMF 193575, 220339; AMS 146761); Thung Salaeng Luang NP (ZMB 200.192; ZSM 19983217; SMF 193578; BMNH; AMS 146760); Tap Tami Falls (ZSM 19983215; SMF 193576; ZHM).

#### Differential Diagnosis

Shell elongately turreted, sculptured by two spiral rows of pointed nodules or tiny spines, each supported by a spiral cord.

#### Description

**Shell** (Fig. 10): Medium sized, spire elongately turreted with three to four whorls, eroded tip. Whorls convex with subsutural depression, separated by narrow, inconspicuous suture. Sculptured by more or less developed spiral ridges, most prominent at the base, and two spiral rows of pointed nodules or tiny spines, each supported by a spiral cord. Shell thin but solid; colour brown to red-brown, glossy

surface. Basal whorl relatively large. Aperture oval, angled, produced below, inside white. Shell size: H = 25–35 mm. B = 14–18 mm.

**Embryonic Shell** (Fig. 11): Conical, comprising up to  $3\frac{1}{2}$  whorls. Sculpture smooth, faint growth lines. Spiral keel at about the centre of the whorl from third whorl on. In some specimens, this keel supports two spiral rows of smooth knobs.

**Operculum**: Oval, with up to five whorls gradually increasing in diameter; nearly central nucleus.

**Radula** (Fig. 12C): Length of ribbon:  $m = 20$  mm ( $sd = 1$ ;  $n = 3$ ), up to 190 rows of teeth. Very similar to *B. armata*, rachis tends to be more squarish in size.

**Stomach** (Fig. 13): Typical, as in *B. citrina* (Fig. 4).

#### Reproductive System

Three dried shells contained between 131 and 145 shelled juveniles varying in height between 1 and 3 mm, respectively (ZSM 19983217).



Distribution

Thailand: Prov. Phitsanulok: Only known from Kaek River and adjacent Kwae Noi River.

Remarks

Very similar to *B. spinata* (Godwin-Austen, 1872). *B. binodosa* is more slender, columella more curved (Blanford, 1903). Shell of *B. armata* is more conical possessing fewer whorls. Discriminant analysis of shell parameters: Figure 9, Table 1.

*Brotia citrina* (Brot, 1868)  
(Figs. 4, 12D, 14, 15)

*Melania citrina* Brot, 1868: 11, 12, pl. 3, fig. 13 ("Siam" = Thailand), lectotype and three paralectotypes MHNG, coll. Brot (designated by Köhler and Glaubrecht, 2002a) (Figs. 14A–C); types seen; Brot, 1875: 106, 107, pl. 13, fig. 5.

*Melania citrinoides* Brot, 1886: 101, 102, pl. 5, fig. 4 ("Siam" = Thailand), lectotype and four paralectotypes MHNG, coll. Brot (designated by Köhler & Glaubrecht, 2002a) (Figs. 14D–H).

*Brotia citrina* – Köhler & Glaubrecht, 2002a: 131, fig. 1I (non Brandt, 1974).

Taxonomy and Systematics

Brandt (1974) based his diagnosis on material that we re-determined as *B. dautzenbergiana*. Material of *B. citrina* was apparently not available to him, except for the types. Consequently, Brandt's (1974) description of *B. citrina* and his conclusions in respect to its systematics are refuted and attributed to *B. dautzenbergiana*, which is considered distinct (see below). Types of *M. citrina* and *M. citrinoides* do only differ in average shell height but not in respect to other morphological or morphometrical characteristics. This feature is not considered sufficient to indicate separate

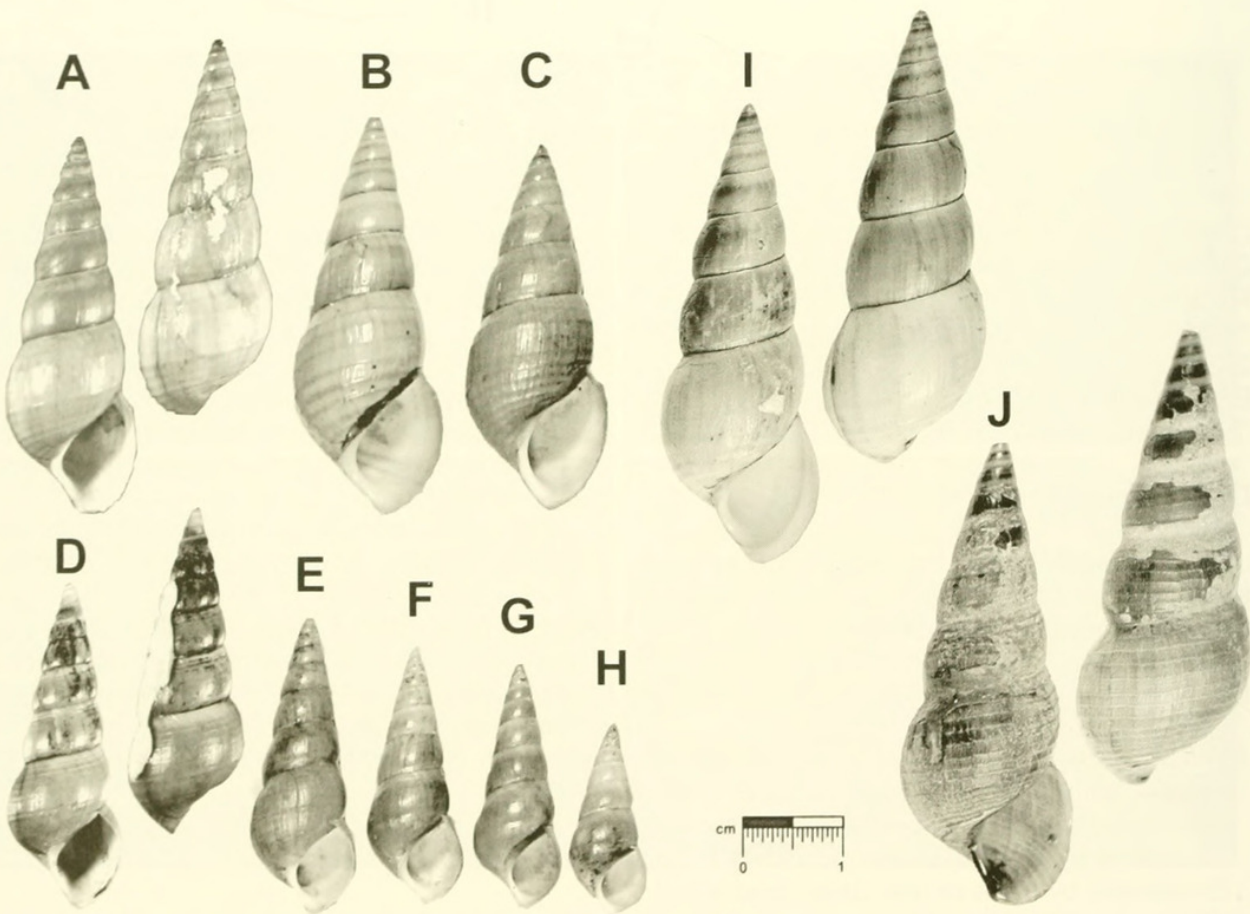


FIG. 14. Shell morphology of *B. citrina*. A: Lectotype of *M. citrina* MHNG, front and rear; B–C: Paralectotypes MHNG; D: Lectotype of *M. citrinoides* MHNG, front and rear; E–H: Paralectotypes MHNG; I: Thailand (ZMB 26.874); J: Thailand, Pa Charoen (ZMB 200.207). Scale bar = 10 mm.



status. For this reason, we agree with Brandt (1974) treating both taxa as synonyms.

#### Material Examined

Thailand: Prov. Kamphaeng Phet: Pa Charoen waterfall, S of Mae Sot, 16°30.51'N, 98°44.89'E (ZMB 200.207); Nang Khruan waterfall near Mae Sot, 16°24.59'N, 98°39.27'E (ZMB 200.212).

#### Differential Diagnosis

Highly turreted shell, thin but solid, smooth except for growth lines and fine, closely spaced spiral lirae; aperture wide, produced below; colour yellowish to olive-brown. Rachidian cusp relatively broad, upper rim well rounded.

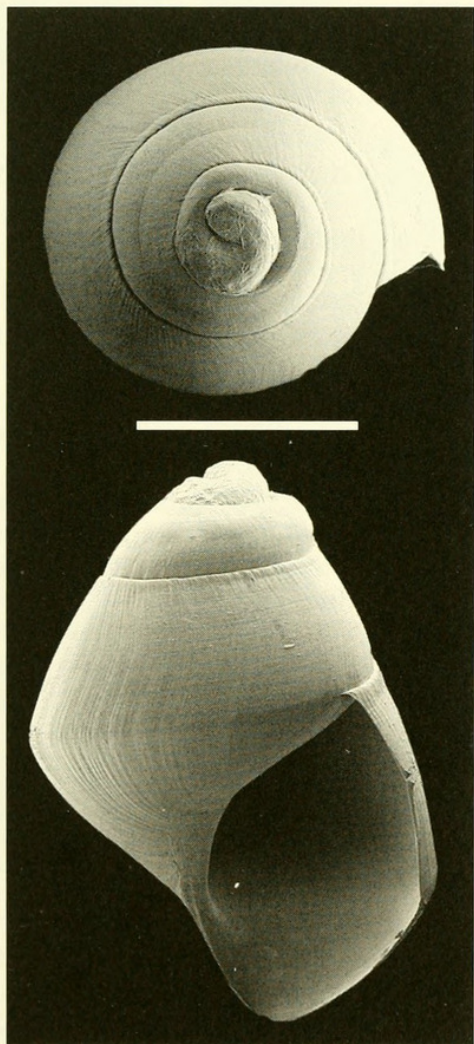


FIG. 15. Embryonic shell morphology of *B. citrina*. SEM images of embryonic shell removed from brood pouch (Thailand, Pa Charoen; ZMB 200.207); apical and front view. Scale bar = 1 mm.

#### Description

**Shell** (Fig. 14): Elongately turreted, thin but solid, six to ten convex and regularly rounded whorls; narrow suture. Sculpture of regularly spaced spiral ridges becoming more prominent at the base, fine axial growth lines; some shells completely smooth. Colour yellowish to light olive brown, glossy surface. Aperture wide, oval, angled, produced below, pointed above, sharp to thin margin. Shell size: H = 21–63 mm, B = 9–22 mm.

**Embryonic Shell** (Fig. 15): Smooth with faint growth and spiral lines; conspicuous subsutural depression; colour light greenish brown with broad chestnut brown spiral band.

**Operculum**: Round, up to eight regular whorls, almost central nucleus.

**Radula** (Fig. 12D): Central tooth relatively broad, basal margin well rounded. Central cusp flanked by three smaller denticles on each side. Inner marginals with two cusps, the outer one being broader. Outer marginals with mostly two, sometimes three cusps, outer one being broader.

**External Anatomy**: Animal dark grey with light grey patches. Columellar muscle well developed, relatively short and broad.

**Stomach** (Fig. 4): Inner septate crescent pad of the sorting area weakly developed, outer one well developed, laminated part of sorting area with fine, densely arranged laminae; typhlosoles fused at  $\frac{4}{5}$  of style sac length.

#### Reproductive System

Females contained between 18 and 56 juveniles that varied in height between 2.2 and 5.5 mm, up to 3.5 whorls ( $n = 3$ ; ZMB 200.207). Large embryos lay anteriorly in the pouch.

#### Distribution (Fig. 36)

Thailand: Prov. Kamphaeng Phet: Two localities in vicinity of Mae Sot as only known records. Not recorded by Brandt (1974) otherwise giving an excellent overview of the gastropod fauna of Thailand.

#### Habitat

Relatively cold, fast flowing, clear streams, well oxygenated, on limestone substratum. Buried in sand or mud, under rotten leaves or sunken wood presumably feeding on detritus.



TABLE 2. Result of disriminant analysis of shell parameters of *B. citrina* and *B. dautzenbergiana*.

	Predicted group membership	
	<i>B. citrina</i>	<i>B. dautzenbergiana</i>
<i>B. citrina</i>	19 (95.0%)	1 (5.0%)
<i>B. dautzenbergiana</i>	2 (4.7%)	41 (95.3%)

Remarks

From *B. dautzenbergiana* to be distinguished by its more conical shell, uneroded spire, in average fewer whorls, and lack of dark brown spiral band; or by statistical analysis of shell parameters (Table 2, Fig. 16).

*Brotia costula* (Rafinesque, 1833)  
(Figs. 17–19)

*Melania costula* Rafinesque, 1833: 166 ("Ganges"); types not traced.  
*Antimelania costula* – Morrison, 1954: 15 [partim].  
*Brotia costula* – Benthem Jutting, 1956: 374–378, fig. 76 [partim]; 1959: 92–95 [partim]; Brandt, 1974: 175, pl. 13, figs. 37–39 [partim]; Köhler & Glaubrecht, 2001: 295–299 [partim]; Köhler & Glaubrecht, 2002a: 132 [partim].  
*Brotia costula episcopalis* – Subba Rao & Dey, 1986: 26 [partim].  
*Brotia (Antimelania) costula* – Subba Rao, 1989: 108, 109 [partim].  
*Melania carolinae* Griffith & Pidgeon, 1834: 598, pl. 13, fig. 3 ("India"), ex Gray ms, lectotype and paralectotype BMNH 1874.10.12.11 (designated by Köhler & Glaubrecht, 2002a) (Figs. 17B, C); types seen.  
*Melania plicata* I. Lea, 1835: 20, pl. 23, fig. 95 (*non M. plicata* Menke, 1830) ("Bengal, Calcutta").  
*Melania variabilis* Benson, 1836: 746, 747 (*non M. variabilis* DeFrance, 1823) ("The river Gumti at Jonpur, and tolly's nullah near Calcutta" = Gomati River, Jaunpur, Uttar Pradesh, 25°44'N, 82°41'E), lectotype BMNH 1872.12.2.2 (designated by Köhler & Glaubrecht, 2002a) (Fig. 17A); types seen; Souleyet, 1852: 545; Reeve, 1860: species 204; Brot, 1870: 281 [partim]; Brot, 1875: 85–87, pl. 10, figs. 1, 1a–d [partim].  
*Melania (Melanoides) variabilis* – Nevill, 1885: 251, 252 [partim].

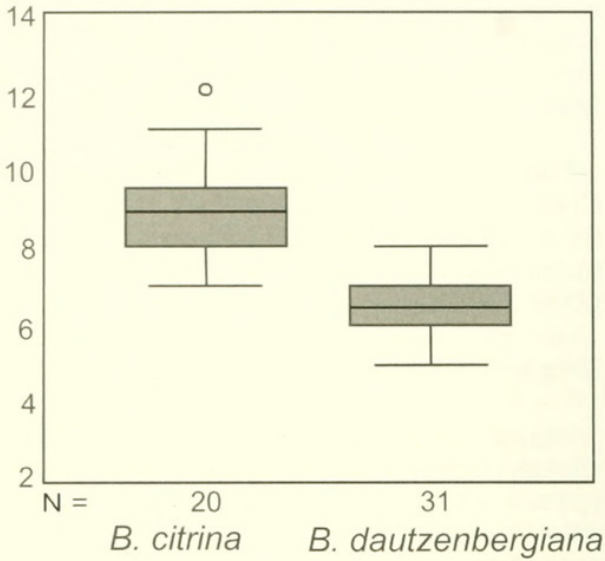


FIG. 16. Comparison of *B. citrina* and *B. dautzenbergiana* by means of number of whorls (N). Box plot diagram showing median, the 25%- and 75%-percentile and largest non-extremes (less than 1.5 times of box height).

*Melanoides (Tiara) variabilis* – Preston, 1915: 23, 24.  
*Acrostoma variabilis* – Annandale, 1920: 110; Annandale et al., 1921: 560–562, pl. 6, figs. 3–6; Prashad, 1921: 485–488 [partim].  
*Brotia variabilis* – Rensch, 1934: 239 [partim]; Bequaert, 1943: 433, 434, pl. 33, figs. 11–16; Solem, 1966: 15 [partim].  
*Brotia (Antimelania) variabilis* – Adam & Leloup, 1938: 85, 86 [partim].  
*Melania varicosa* Troschel, 1837: 174 ("Bengalien, Ganges" = Bengal, Ganges), lectotype ZMB 2.226a (here designated for the stabilisation of the name) (Fig. 17F) and 13 paralectotypes ZMB 2.226b; types seen; Philippi, 1844: 15, 16, pl. 3, fig. 2.  
*Melanoides varicosa* – H. Adams & A. Adams, 1854: 297.  
*Melania indica* Souleyet, 1842: pl. 31, figs. 12–15 ("India, Ganges"), five syntypes MNHN; types seen; Souleyet, 1852: 545.  
*Melanoides indica* – H. Adams & A. Adams, 1853: pl. 31, figs. 5, 5a, b.  
*Melania menkiana* [sic !] I. Lea, 1842: 242 (replacement name for *M. plicata* I. Lea, 1835, *non M. plicata* Menke, 1830; misspelled for intended "*M. menkeana*"); Brot, 1860: 280; Hanley & Theobald, 1874: 110.  
*Melania menkeana* Brot, 1875: 91, 92, pl. 11, fig. 1, 1a, b (replacement name for *M. menkiana* Lea, 1842).  
*Melania (Melanoides) variabilis menkeana* – Nevill, 1885: 260.



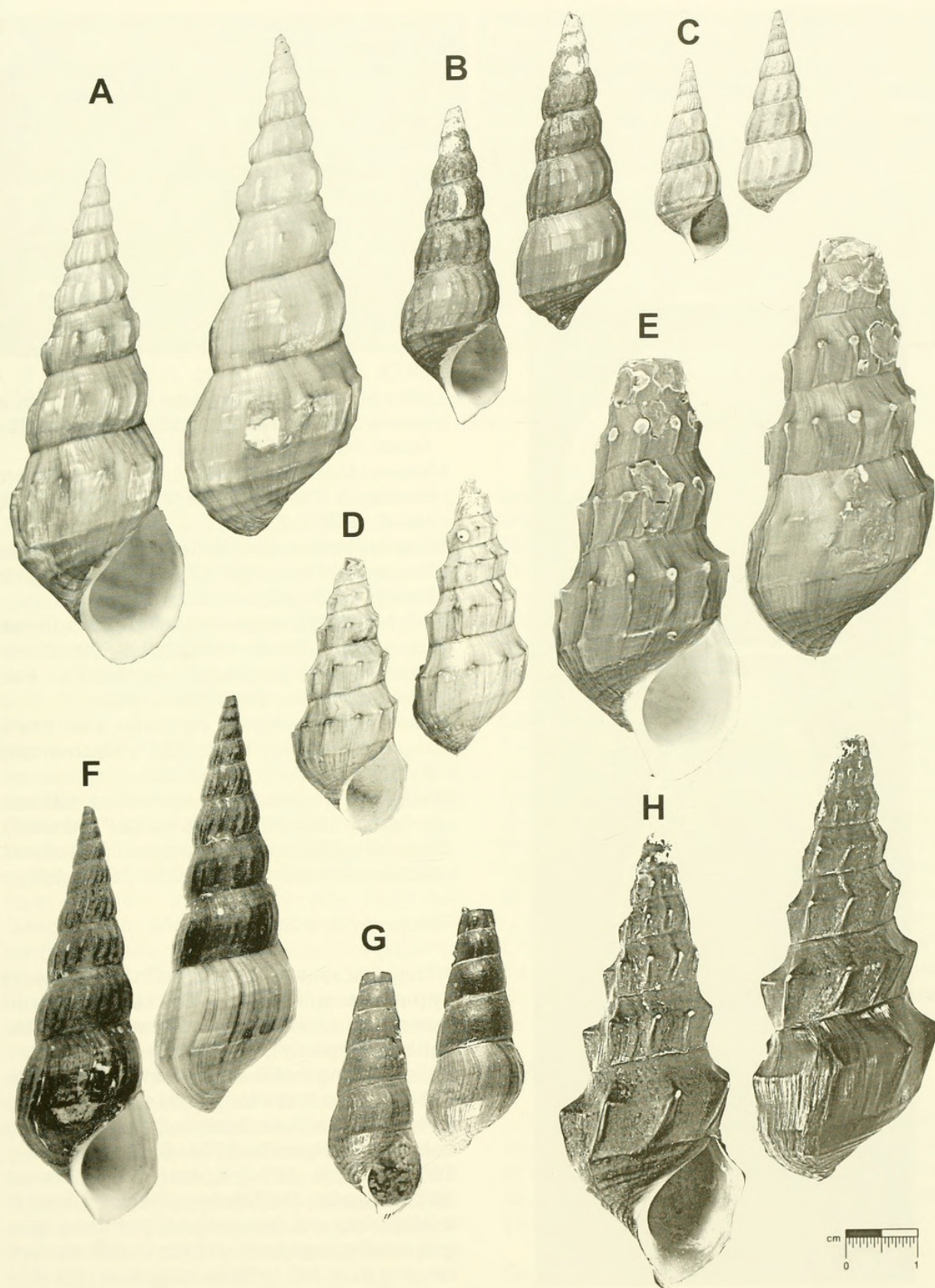


FIG. 17. Shell morphology of *B. costula*. A: Lectotype of *M. variabilis* BMNH 1872.12.2.2; B: Lectotype of *M. carolinae* BMNH 1874.10.12.11/A; C: Paralectotype BMNH 1874.10.12.11/B; D: Lectotype of *M. spinosa* BMNH 1907.10.28.79; E: Paralectotype BMNH 1907.10.28.80; F: Lectotype of *M. varicosa* (ZMB 2.226a); G: Syntype of *M. hainesiana* USNM 119741; H: Bangladesh, Chittagong (RMNH 76332). Scale bar = 10 mm.



*Brotia menkeana* – Yen, 1939: 59, pl. 5, fig. 13.  
*Melania spinosa* Hanley, 1854: pl. 1, fig. 7  
 ("River Jumna, Sylhet, British India" = River  
 Jamuna, Sylhet, Prov. Chittagong, Bangla-  
 desh, 24°53'N, 91°52'E) (*non M. spinosa*  
 Gray, 1824), lectotype BMNH 1907.10.28.79  
 and paralectotype BMNH 1907.10.28.80  
 (Figs. 17D, E) (designated by Köhler &  
 Glaubrecht, 2002a); types seen; Brot, 1875:  
 92, 93, pl. 12, fig. 2.

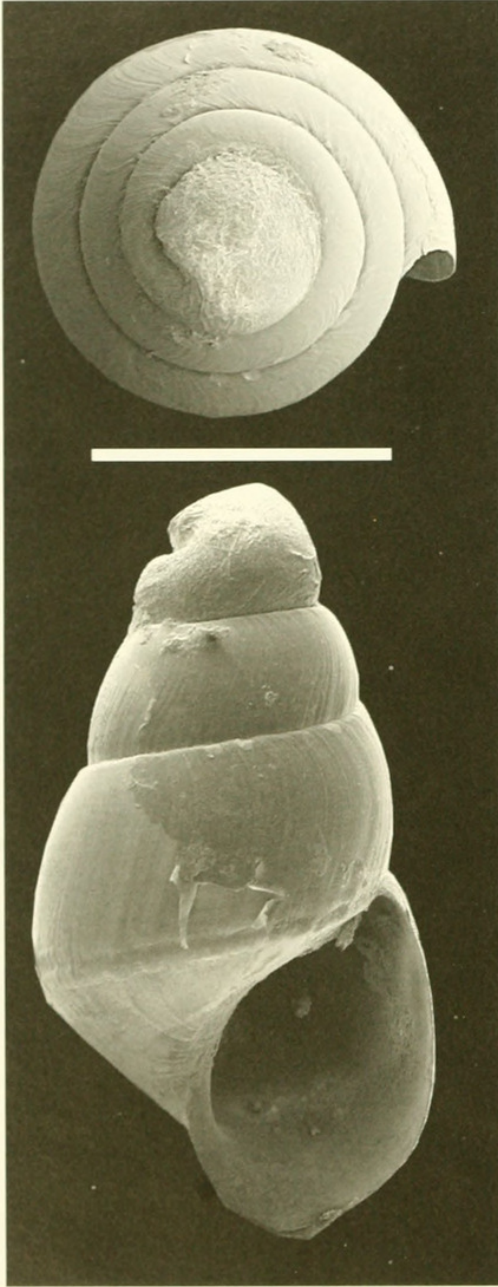


FIG. 18. Embryonic shell morphology of *B. costula*. SEM images of embryonic shell removed from dried material (ZMB 35.811); apical and front view. Scale bar = 1 mm.

*Melania variabilis* var. *spinosa* – Hanley &  
 Theobald, 1873: pl. 75, fig. 6.  
*Melania hainesiana* I. Lea, 1856: 144 ("India"),  
 nine syntypes USNM 119741 (Fig. 17G); types  
 seen; I. Lea, 1864: 78, pl. 22, fig. 18; Brot,  
 1875: 109, 110, pl. 14, fig. 4.  
*Melania (Melanoides) variabilis* var. *hainesiana*  
 – Nevill, 1885: 255.  
*Melania corrugata* Reeve, 1859: pl. 3, fig. 10  
 ("India, Java") (*non M. corrugata* Lamarck,  
 1822).  
*Melania spinata* – Brot, 1875: 89, 90, pl. 10,  
 fig. 2a (*non M. spinata* Godwin-Austen, 1872).  
*Melania episcopalis* – Hanley & Theobald,  
 1873: 31, 32, pl. 72, fig. 7, pl. 75, figs. 5, 7  
 (*non M. episcopalis* H. Lea & I. Lea, 1850).  
*Melania (Melanoides) variabilis episcopalis* –  
 Nevill, 1885: 256 [partim].  
*Melania (Melanoides) variabilis* subvar. *aspera*  
 Hanley & Theobald, 1874: pl. 109, fig. 6;  
 Nevill, 1885: 252.  
*Melania (Melanoides) variabilis* subvar. *cincta*  
 Hanley & Theobald, 1874: pl. 109, fig. 5;  
 Nevill, 1885: 252.  
*Melania (Melanoides) variabilis* subvar.  
*microstoma* Nevill, 1885: 261 ("Sylhet").  
*Melania (Melanoides) variabilis* var.  
*pseudospinosa* Nevill, 1885: 258.  
*Melania (Melanoides) variabilis* var. *semi-*  
*laevigata* Nevill, 1885: 254 ("Cachar and  
 Sylhet").  
*Melania (Melanoides) variabilis* subvar.  
*subtuberculata* Nevill, 1885: 252 ("Calcutta").  
*Melania (Melanoides) variabilis* subvar.  
*subspinosa* Nevill, 1885: 252 ("Calcutta").

#### Taxonomy and Systematics

This species was delineated in various ways by previous authors, the plethora of synonyms witnessing serious difficulties in species recognition especially by 19<sup>th</sup> century authors. Presupposing that *B. costula* is highly variable, 20<sup>th</sup> century authors frequently subsumed similar taxa from across Southeast Asia under this name (e.g., Rensch, 1934; Benthem Jutting, 1956; Brandt, 1974; Köhler & Glaubrecht, 2001). Brandt (1974) hypothesised that *B. costula* forms a "rassenkreis" of three geographical subspecies: (1) the nominate form ranging from NE India to Indochina, (2) *B. c. varicosa* (Troschel, 1837), with suggested occurrence on Sumatra, Java and Borneo, and (3) *B. c. peninsularis* Brandt, 1974, restricted to the Malay Peninsula. This suggestion was refuted using comparative morphological and



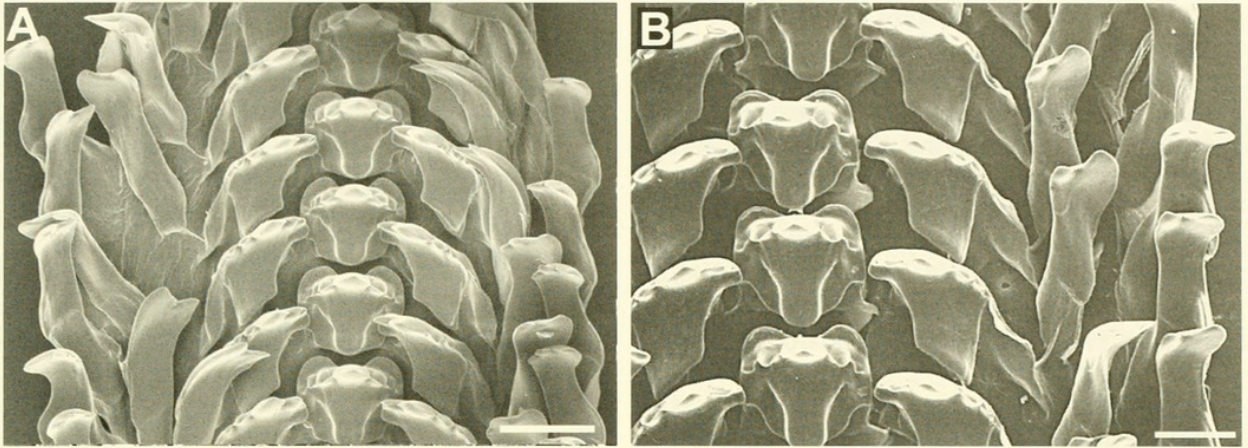


FIG. 19. Radula morphology of *B. costula*. Radula segments viewed from above. A: India, Sikkim (ZMB 2.227); B: India, Manipur (BMNH). Scale bars = 100  $\mu$ m.

molecular genetic data (Köhler & Glaubrecht, 2001). Köhler & Glaubrecht (2001) demonstrate that taxa from Borneo and Java, which were assumed to constitute the *varicosa* subspecies, among other features possess a different embryonic shell morphology and, thus, are clearly distinct from *B. costula*. In addition, the molecular phylogeny shows that taxa from Sumatra, such as *B. torquata*, Malay Peninsula, such as *B. episcopalis* and *B. peninsularis*, and Myanmar, such as *B. herculea*, are also distinct (Figs. 78, 79). *Brotia costula* is encompassed here in a much more restricted way by means both of its distribution and its morphology. Accordingly, under *B. costula* we subsume only those taxa described from northern India, especially from the Ganges plain and Bengal, that exhibit corresponding shells, opercula and radular patterns (if available). Forms possessing spiny axial ribs, such as *M. menkiana*, are tentatively considered conspecific unless data on soft body morphology or molecular genetics may show otherwise. Here we follow Benson (1936: 747) who stated for *M. variabilis* that "... several of these varieties [i.e., with or without spiny nodules] would, if viewed apart, be easily mistaken for distinct species, but they melt into each other so gradually, occasionally showing characters of more than one variety combined in the same shell, that no doubt remains of their blending in one species".

#### Material Examined

India (ZMB 200.044, 200.061, 200.064; CAS 6199): Ganges (ZMB 200.058, 200.062); Sikkim (ZMB 2.227, 200.078); Assam (ZMB

200.042, 200.052; BMNH 1935.10.9.5-17, 1888.12.4.1492-3), Guwahati (ZMZ 522377); Brahmaputra (ZMB 200.302-3); Durang (BMNH); Himalayas (BMNH 1841.7.23.9); Meghalaya: Jaintia-Khâsi hills (BMNH); Manipur (BMNH); Keladyne River (BMNH 1899.12.4.1761-2); Kolkata (ZMB 20.738; 200.063; BMNH; CAS 25326); Bengal (ZMB 45.849; BMNH 1888.12.4.1480-2; ZMZ 522371); Bengal, River Toolsi Ganga (BMNH); Bengal, River Atrai (BMNH); Settlepore (ZMZ 522372); Madhya Pradesh: Jonapura (ZMZ 522370); Bhutan: Duars, West Bhutan (BMNH); Bangladesh: Chittagong (BMNH; RMNH 71332; ZMB 35.811); Rajshahi: Basudebpur (BMNH); Malaudi (BMNH); River Jamuna (BMNH 1907.12.30.207); Sylhet (ZMB 200.071); Nepal: Prov. Narayani, Chitwan Distr., Bis Hajaar Lakes, 27°36.44'N, 84°26.34'E (ZMB 112.783), Prov. Koshi, Sunsari Distr., Haripur, tributary of the Sapta Koshi, 26°33.28'N, 86°59.6'E (ZMB 112.660).

#### Differential Diganosis

Shell highly turreted, large, up to 12 whorls, sculptured by regularly spaced axial ribs throughout, only exceptionally these ribs may lack completely; in some specimens, ribs support a spiral row of spiny nodules.

#### Description

*Shell* (Fig. 17): Medium sized to large, solid but not very thick, 6 to 12 whorls, pyramidal spire, frequently eroded tip; colour uniform light to olive-brown; whorls well rounded in diameter, separated by well-defined, thin



suture; sculpture of basal spiral ridges and regularly spaced axial ribs that occasionally support small, spiny nodules arranged in a spiral band at centre of whorl; some specimens smooth; aperture wide, well rounded at base, comprising about  $\frac{1}{5}$  of shell height. Size: H = 20–87 mm, B = 8–36 mm.

*Embryonic Shell* (Fig. 18): Smooth except for fine growth lines. Maximum height 4 mm, 3.5 whorls. Average proportions: H = 2.3 mm, B = 1.1 mm, HA = 0.27 mm, BA = 0.48 mm, DA = 0.63 mm (for n = 6).

*Operculum*: Slightly oval, four to six whorls, central nucleus; almost fits aperture.

*External Morphology*: Uniformly coloured, dark grey to black; grey foot sole with scattered light spots.

*Radula* (Fig. 19): Ribbon length of up to 30 mm, corresponding to about half of the shell height, about 180 rows of teeth. Rachidian with single main cusp, three smaller denticles on each side tapering in size; upper margin concave by inflated, rounded corners; lower rim rounded; glabella narrow, well rounded at its base, lateral margins slightly concave. Laterals with main cusp flanked by three smaller denticles. Inner and outer marginals with two to three denticles, somewhat pointed, of about same size and shape.

#### Distribution (Fig. 20)

Northeast India (Bihar, Uttar Pradesh, Madhya Pradesh, Manipur, Meghalaya, Mizoram, Sikkim, Assam, West-Bengal), Bangladesh, Bhutan, and Nepal. Namely, Ganges-Meghna-Brahmaputra River system with affluent rivers.

#### Habitats

Clear creeks with sandy bottoms, large rivers, and even ponds (Subba Rao, 1989).

#### Remarks

Reports from Sri Lanka (Annandale, 1920), Hainan and China (Yen, 1939), Sumatra and Java (Rensch, 1934; Benthem Jutting, 1956), Thailand, the Mekong, Borneo (Brandt, 1974), Melanesia (Abbott, 1948), and the Philippines (Bandel & Riedel, 1998) refer to other species.

Conchologically similar are *B. episcopalis* from the Malay Peninsula, *B. sumatrensis* from Sumatra, *B. herculea* from Myanmar, and *B. jullieni* from Cambodia; all were repeatedly synonymized with *B. costula*. *Brotia episcopalis* and *B. sumatrensis* tend to be smaller and more conical in shape. In *B. episcopalis*, the upper whorls are smooth and

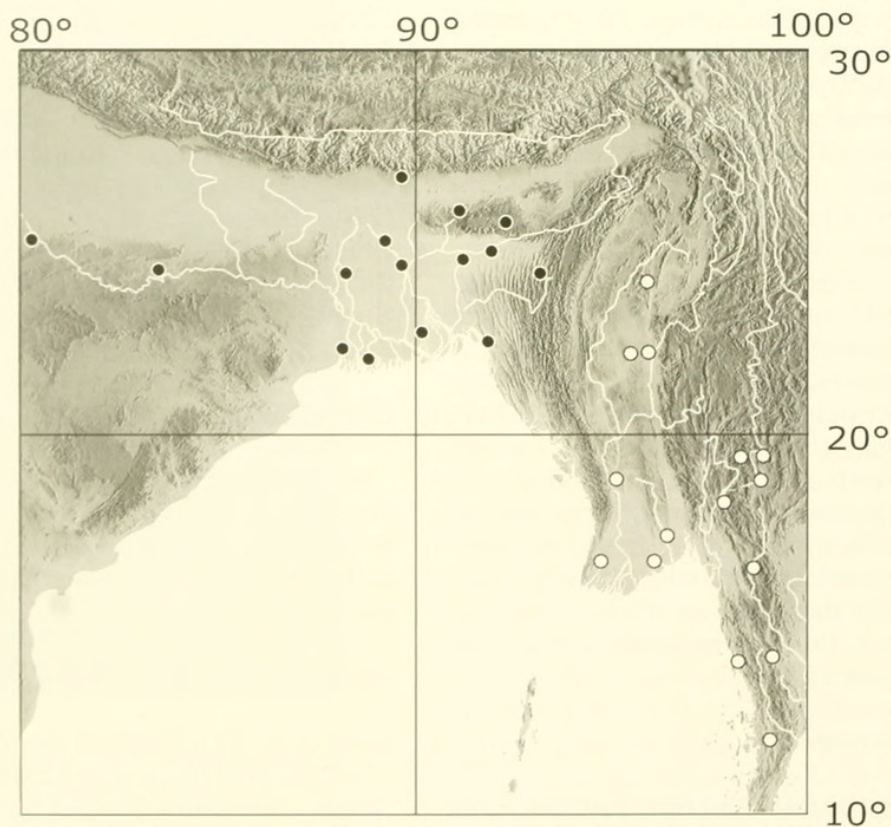


FIG. 20. Distribution of *B. costula* (closed circles) and *B. herculea* (open circles).



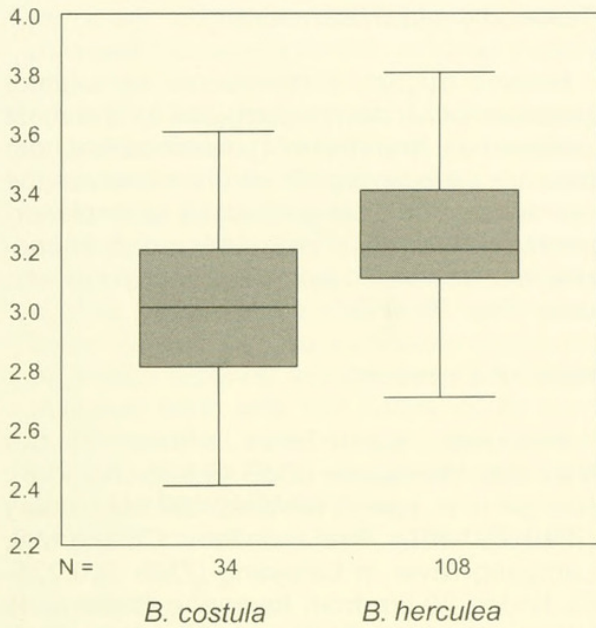


FIG. 21. Comparison of *B. costula* and *B. herculea* by means of shell parameter H/LA. Box plot diagram showing median, the 25%- and 75%-percentile and largest non-extremes (less than 1.5 times of box height).

axial ribs are more conspicuous and not as regularly spaced as in *B. costula*, in which closely spaced axial ribs are always present. *B. jullieni* exhibits a larger, broader, and more conical shell, with a more pronounced spiral sculpture (e.g., Figs. 21, 27, 41 for comparison of shell parameters).

*Adamietta* species formerly assigned to *B. costula*, such as *A. infracostata* (Mousson, 1849), differ in embryonic shell morphology (Köhler & Glaubrecht, 2001, for the "*Brotia testudinaria*-group").

*Brotia dautzenbergiana* (Morlet, 1884)  
(Figs. 22–24)

*Melania dautzenbergiana* Morlet, 1884: 399, 400, pl. 8, fig. 1a–c ("Les ruisseaux se jetant dans le Prec-Thenot, sur sa rive droite dans les environs de Kompong Tull" = streams discharging into the Prec-Thenot on its right bank near Kompong Tull, Cambodia), lectotype and three paralectotypes MNHN (designated by Köhler & Glaubrecht, 2002a) (Fig. 22A); types seen; Fischer-Piette, 1950: 154.

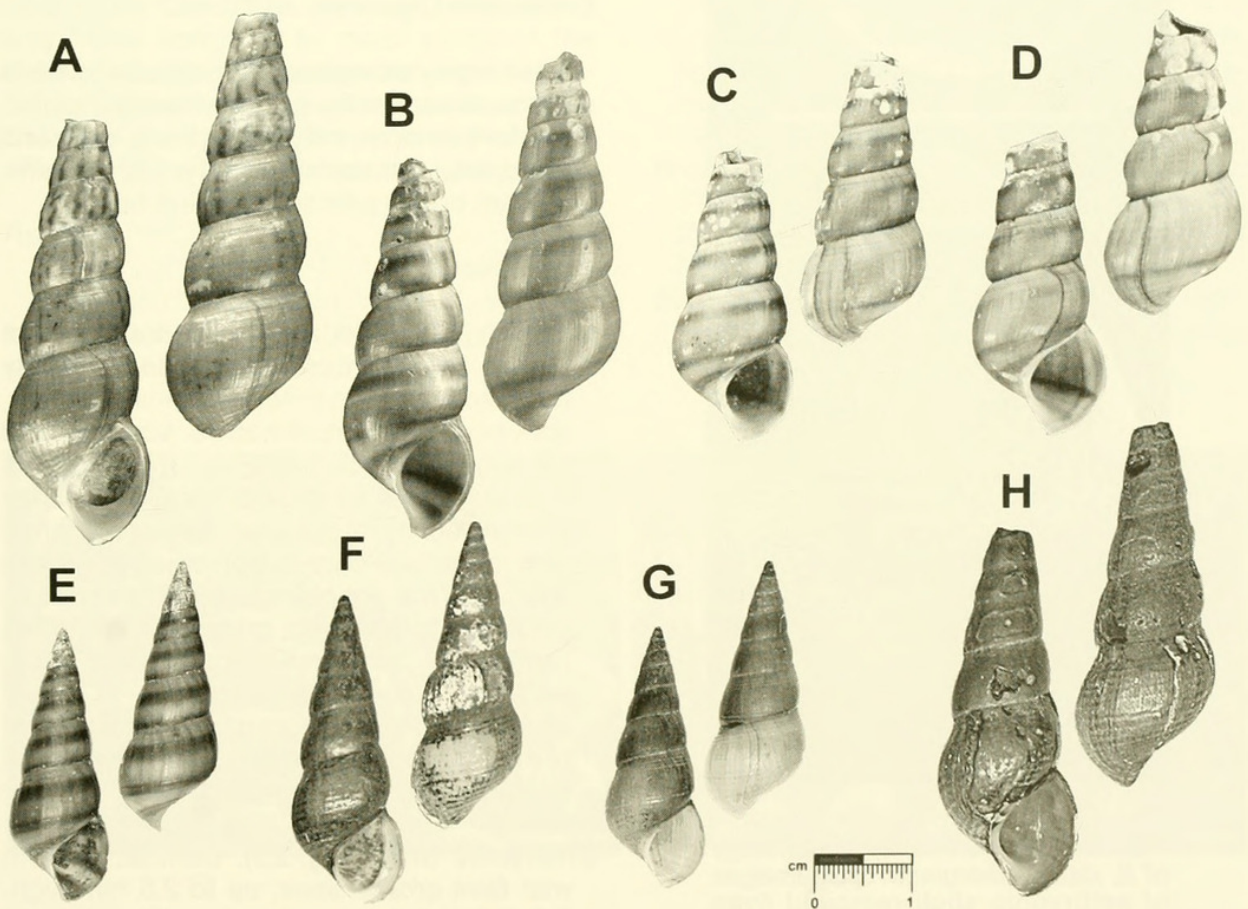


FIG. 22. Shell morphology of *B. dautzenbergiana*. A: Lectotype of *M. dautzenbergiana* MNHN; B: Lectotype of *M. dugasti* MNHN; C–D: Paralectotypes of *M. dugasti* BMNH; E: Myanmar (ZMB 49.626); F–G: Thailand, Lampang (ZMB 200.229); H: Thailand, Thoern (ZMB 200.213). Scale = 10 mm.



*Stenomelania dautzenbergiana* – Habe, 1964: 55, pl. 1, fig. 19.

*Brotia dautzenbergiana* – Köhler & Glaubrecht, 2002a: 133, fig. 10.

*Melania dugasti* Morlet, 1893: 153, 154, pl. 6, fig. 1 ("Laos, Nam-Si, affluent du Nam Moun" = Laos, River Nam Si, affluent of the Nam Moun), lectotype MNHN, four paralectotypes MNHN, three paralectotypes BMNH 1893.12.8.117-119, three paralectotypes MHNG (designated by Köhler & Glaubrecht, 2002a) (Figs. 22B–D); types seen; Fischer-Piette, 1950: 160.

*Brotia citrina* – Brandt, 1974: 179, pl. 13, figs. 33, 34 (*non M. citrina* Brot, 1868).

## Taxonomy and Systematics

*Melania dugasti* is considered as a junior synonym of *M. dautzenbergiana* for the most similar shell. Brandt (1974) assumed that both taxa are synonyms of *B. citrina*. However, the species can be distinguished by several morphological features. Treatment as distinct species is corroborated by molecular phylogenetic data (Figs. 78, 79).

## Material Examined

Myanmar: North Shan, affluent to the Salween, Meungyaw (ZMB 46.626, 200.293), Nampai river, Lashio (ZMB 49.627); Mandalay (ZMB 200.264); Thailand: Prov. Chiang Mai, Lampang River in Lampang (ZMB 200.225-6), bridge 20 km from Lampang, highway to Uttaradit, 18°7.89'N, 99°97.33'E (ZMB 200.229), bridge at highway 106 near Thoern, 17°39.31'N, 98°7.91'E (ZMB 200.213); Prov. Kamphaeng Phet, Huai Hin Fon near Mae Sot (ZMH); Prov. Nan, Thung Thing (RMNH 71320); Huai Mae Lau (ZMH).

## Differential Diganosis

Shell highly elongated, thin, slender; whorls well rounded; suture narrow, deeply incised. Sculpture smooth, only with growth lines and spiral lines, surface not glossy. Light brown, with dark brown patches or spiral band.

## Description

*Shell* (Fig. 22): Medium sized, solid but not thick; elongately turreted, cylindrical, mostly truncated with five to ten remaining regular, convex whorls. Suture narrow, accompanied by subsutural depression. Upper whorls smooth except for growth lines, last whorls sculptured by numerous fine spiral lines forming regular pattern with crossing growth lines. Surface not glossy; colour of periderm yellowish to brownish green or olive, often with broad, dark brown spiral band, occasionally with dark axial flames at upper whorls. Shells often grey or black due to layer of mineral deposits. Aperture ovate with protracted base. Size: H = 23–44 mm, B = 10–16 mm.

*Embryonic Shell* (Fig. 23): Conical, smooth with faint growth lines; up to 2.5 mm high, 2.0–2.5 whorls; average proportions: H = 1.8 mm, B = 1.1 mm, HA = 0.21, BA = 0.41, DA = 0.66 (for n = 15).

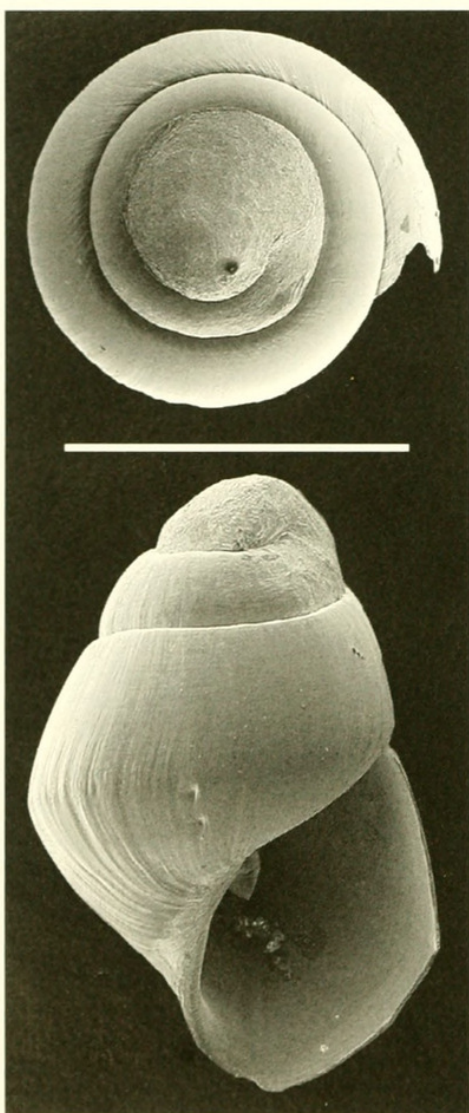


FIG. 23. Embryonic shell morphology of *B. dautzenbergiana*. SEM images of embryonic shell removed from brood pouch (Thailand, Lampang; ZMB 200.229); apical and front view. Scale bar = 1 mm.



*Operculum*: Slightly ovate, up to five fast in diameter increasing whorls, nucleus slightly eccentric.

*Radula* (Fig. 24): Upper rim of rachidian slightly concave, lateral corners not excavated, lower rim rather straight, slightly convex; main cusp flanked by two or three smaller denticles on each side, glabella well rounded at the base, v-shaped, its lateral margins slightly concave. Lateral teeth with main cusp, flanked by two accessory cusps on each side tapering in size. Inner and outer marginal teeth with two cusps, outer cusp broad, rounded; inner cusp pointed, considerably smaller. Outer marginals with conspicuous hooked outer flange.

*Stomach*: Corresponds to *B. citrina* (Fig. 4).

#### Reproductive System

Females (n = 9) contained 11 to 275 juveniles, height 1.0 to 2.5 mm.

#### Distribution (Fig. 36)

Myanmar, central, northern to eastern Thailand, Laos, Cambodia, Vietnam. Widespread and fairly common in most parts of the Indochinese Peninsula. Few more precise localities available, though. River systems of the Salween, and the Chao Praya, as well as some affluents of the Mekong, but not Mekong itself.

#### Remarks

Similar to *B. citrina* from which *B. dautzenbergiana* is distinguished by its more elongated shell, eroded tip, dark brown spiral band. Both

species can be discriminated by shell parameters, although not statistically significant (Table 2).

*Brotia episcopalis* (H. Lea & I. Lea, 1851)  
(Figs. 25, 26, 67A)

*Melania episcopalis* H. Lea & I. Lea, 1851: 184 ("sluggish river, Malakka" = Melaka, Prov. Negeri Melaka; 2°12'N, 102°15'E), lectotype and paralectotype MCZ 221841 (designated by Köhler & Glaubrecht, 2002a) (Figs. 25A, B); types seen; Hanley, 1854: pl. 3, fig. 27; Brot, 1875: 97, 98, pl. 12, figs. 1, 1a.

*Melanoides episcopalis* – H. Adams & A. Adams, 1854: 297.

*Melania (Melanoides) episcopalis* – Chenu, 1859: 288, fig. 1952.

*Melania (Melanoides) variabilis episcopalis* – Nevill, 1885: 256 [partim].

*Brotia costula episcopalis* – Davis, 1971: 53–86.

*Brotia episcopalis* – Köhler & Glaubrecht, 2002a: 134, fig. 1P.

*Melania heros* Brot, 1875: 339, 400, pl. 34, fig. 8 (unknown locality), holotype MHNG (Fig. 25D); type seen.

*Sermyla perakensis* Morgan, 1885: 421, pl. 8, figs. 14a–f ("Perak"), lectotype and paralectotype MNHN (designated by Köhler & Glaubrecht, 2002a) (Fig. 25C); types seen.

*Brotia costula* – Brandt, 1974: 175, pl. 13, fig. 37–39 [partim]; Köhler & Glaubrecht, 2001: 296–299, figs. 1D, 10A–C, G, H [partim] (*non M. costula* Rafinesque, 1833).

*Brotia (Antimelania) costula* – Subba Rao, 1989: 108, 109 [partim] (*non M. costula* Rafinesque, 1833).

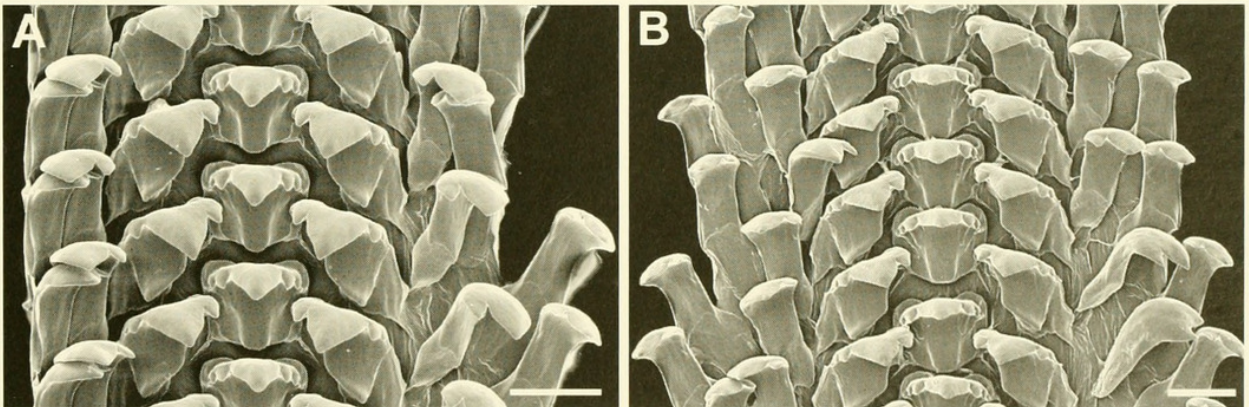


FIG. 24. Radular morphology of *B. dautzenbergiana*. SEM images of radula segments viewed from above. A: Thailand, Lampang (ZMB 200.229); B: Thailand, Thoern (ZMB 200.213).



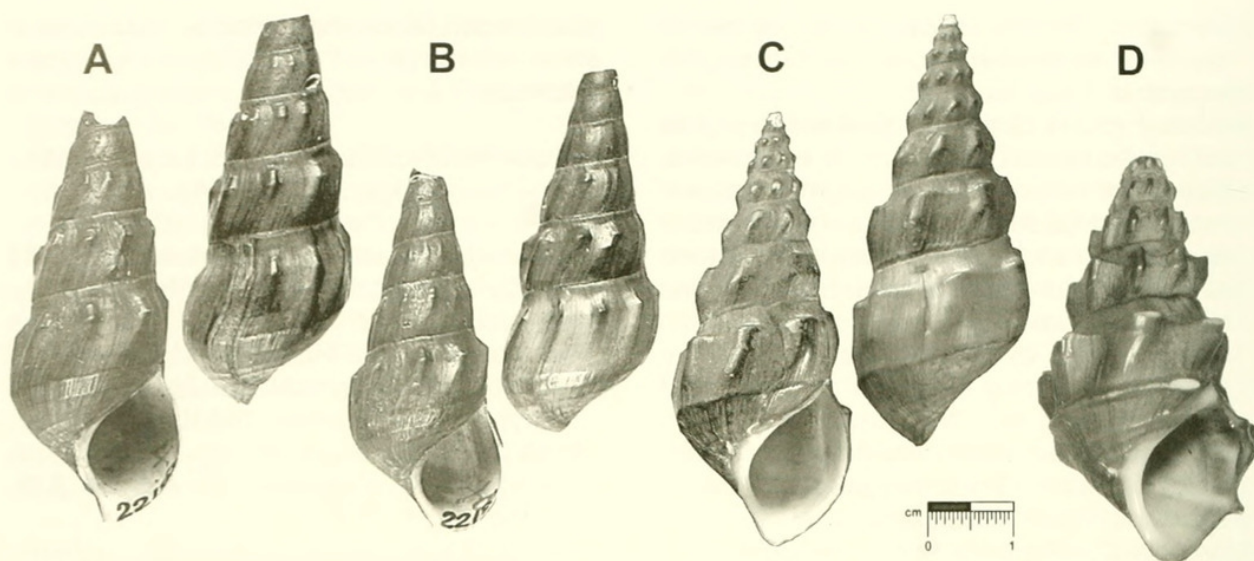


FIG. 25. Shell morphology of *B. episcopalis*. A: Lectotype of *M. episcopalis* MCZ 221841; B: Paralectotype MCZ 221841; C: Lectotype of *Sermyla perakensis* MNHN; D: Holotype of *Melania heros* MHNG. Scale bar = 10 mm.

*Brotia variabilis* – Bequaert, 1943: 433, 434, pl. 33, figs. 11–16 [partim]; Solem, 1966: 15 (*non M. variabilis* Benson, 1836).

#### Taxonomy and Systematics

Frequently subsumed under *B. costula* by 20<sup>th</sup> century authors (Bentham Jutting, 1949, 1956; Brandt, 1968, 1974; Köhler & Glaubrecht, 2001). However, molecular genetic data shows that *B. episcopalis* is distinct (Figs. 78, 79). *Melania heros* and *Sermyla perakensis* are considered as synonyms.

#### Material Examined

Thailand: Prov. Trang: Trang (ZSM 19983228). Prov. Nakhon Si Thammarat: Khlong Nga, Chawang (ZMH); Malaysia: Prov. Kedah: Baling, River to east coast (ZMA). Prov. Pahang, Taman Negara National Park (ZMA; ZMB 200.041, 200.047); Sungei Kenong (ZMB 200.139); Sungei Mantine, affluent to Sungei Serau (ANSP A8907). Prov. Selangor: Sungei Buaya – NW Rawang (ZMA); Sungei Kelang, 17 mi. S Kuala Lumpur (ZMA); rapidly flowing river, 16 mi. N of Kuala Lumpur (CAS 30197). Prov. Negeri Perak: Tong Temple near Ipoh (ZMA; ZMB 200.046); Perak River (ZMB 200.054). Prov. Negeri Melaka: Melaka (ZMB 52.656, 200.047, 200.050, 200.306-7; MHNG).

#### Differential Diagnosis

Shell large, solid; conic, up to 11 whorls, with strong axial ribs. Upper rim of the rachidian flanked by heavily excavated lateral corners.

#### Description

**Shell** (Fig. 25): Large, solid, pyramidal, frequently eroded, 6 to 11 convex, rounded whorls; strong axial ribs, and basal spiral ridges; colour light brown to olive-brown. Aperture wide, oval, well rounded below. Size: H = 34–57 mm, B = 15–24 mm.

**Embryonic Shell:** No own data, but described and depicted by Davis (1971: 60, figs. 2h, i, 11): up to 3.5, perhaps even 4.0 whorls, 2 mm height, rather smooth.

**Operculum:** Oval, multispiral, up to six whorls, sub-central nucleus.

**Radula** (Fig. 67A): Up to 180 rows of teeth, length up to 20 mm, corresponding to about half of shell height. Upper margin of rachidian conspicuously concave, formed by two inflated, well rounded corners. Glabella slightly v-shaped, well rounded at its base, concave lateral margins. Main cusp flanked by mostly two smaller denticles on each side, sometimes only one. Laterals with short lateral extensions, pronounced inner flange, two main cusps flanked by two smaller denticles. Inner and outer marginal teeth with



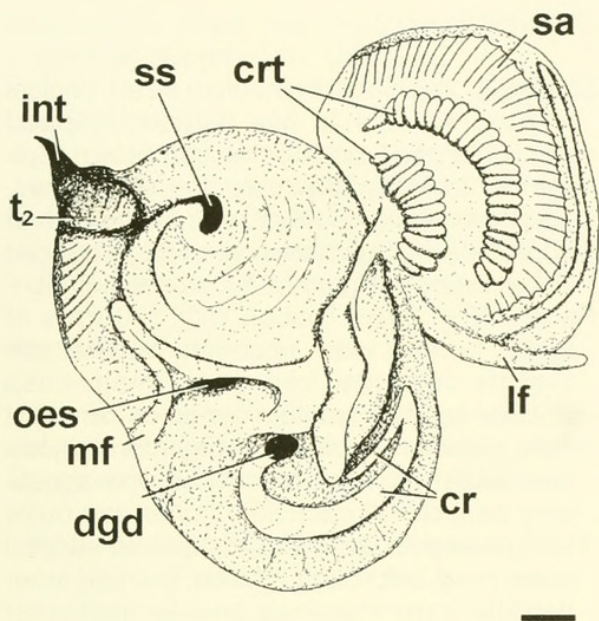


FIG. 26. Stomach anatomy of *B. episcopalis* (Thailand, Nakhon Si Thammarat; ZMH). Scale bar = 1 mm.

two pointed cusps of about same size and shape.

*Stomach* (Fig. 26): Typhlosoles fused at almost entire length of style sac; marginal fold narrowly angled posterior and underneath opening of intestine; flap-like posterior end of

major typhlosole flat, partially covering opening of style sac.

Distribution (Fig. 68)

Southern Thailand and Malaysia: Malay Peninsula, S of Isthmus of Kra. Occurrence in Sumatra unclear.

Habitat

Streams and rivers, only rarely still waters (Davis, 1971; Kruatrachue et al., 1990). In great abundance in the Pahang River system in quiet, marginal waters together with *B. kelantanensis*, which lives among rocks in rapids (Davis, 1982: 392, referring to *B. costula* and "a second spiny species").

Remarks

Frequently confused with *B. costula* and *B. sumatrensis*. *Brotia costula* tends to have a more elongated shell with more closely spaced, regular ribs also on upper whorls. *Brotia sumatrensis* lacks marked transition from smooth upper whorls to strongly sculptured lower whorls and exhibits lesser pronounced axial ribs. Employing statistical analyses, *B. costula*, *B. episcopalis*, and *B. sumatrensis* cannot be discriminated by their morphometry (Fig. 27). A detailed description of morphology, reproductive biology, growth rates, and relevance as intermediate host of the lung fluke *Paragonimus westermanni* is given by Davis (1971). Our observations fit well to the comprehensive data reported in this paper.

*Brotia godwini* (Brot, 1875)  
(Figs. 28, 31A)

*Melania* (*Melanoides*) *hanleyi* Godwin-Austen, 1872: 514, 515, pl. 30, fig. 2 (*non M. hanleyi* Brot, 1860) ("Diyung River, North Cachar hills" = Diyung River, Jaintia-Khâsi hills N of Silchar, Meghalaya, India, 24°48'N, 92°46'E), lectotype BMNH 19991561/A and paralectotype BMNH 19991561/B (designated by Köhler & Glaubrecht 2002a) (Figs. 28A, B); types seen.

*Melania godwini* Brot, 1875: 90, pl. 10, fig. 3 (replacement name for *M. hanleyi* Godwin-Austen, 1872).

*Melania* (*Melanoides*) *variabilis* var. *binodulifera* Nevill, 1885: 259 ("Khasi hills").  
*Brotia godwini* – Köhler & Glaubrecht, 2002a: 136.

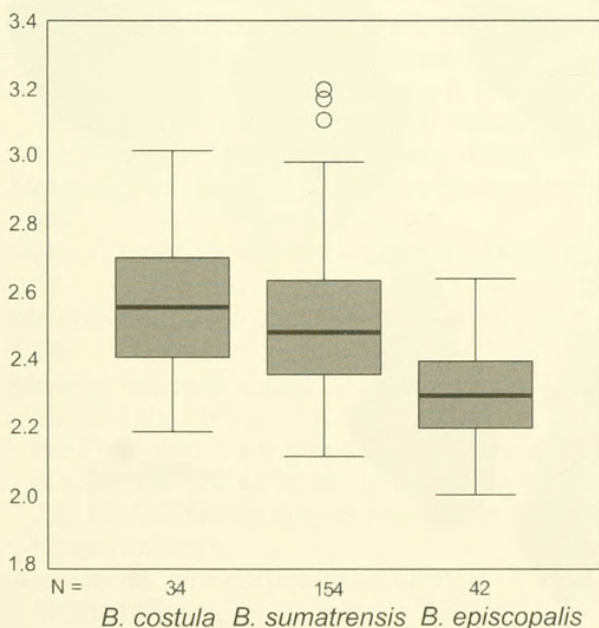


FIG. 27. Comparison of *B. costula*, *B. sumatrensis*, and *B. episcopalis* by means of shell parameter H/B. Box plot diagram showing median, the 25%- and 75%-percentile and largest non-extremes (less than 1.5 times of box height).



## Taxonomy and Systematics

*Melania godwini* Brot, 1875, was employed as replacement name for *M. hanleyi* Godwin-Austen, 1872, being preoccupied by *M. hanleyi* Brot, 1860.

## Material Examined

India: Assam, Lamin (ZMB 94.722); Cachar (ZMB 20.737).

## Differential Diagnosis

Stepped whorls, deeply incised suture, two spiral ridges, lower one at about a third of whorls diameter, upper one at about two thirds, more pronounced. Upper ridge supports spiral row of spiny tubercles; some specimens with axial ribs; aperture very wide.

## Description

**Shell** (Fig. 28): Small to medium sized, conical to turreted, four to five convex, stepped whorls, eroded; colour chestnut brown. Spiral row of spiny tubercles and spiral lines, most prominent at base of shell; last whorl large, inflated; aperture wide, ovate, produced below, comprising up to  $\frac{1}{3}$  of shell height.

**Radula** (Fig. 31A): Ribbon with 120 rows of teeth. Central tooth squarish, anterior rim slightly concave, very large main cusp flanked by two smaller denticles on each side, glabella v-shaped, basally rounded; lateral teeth with main cusp and one accessory denticle on each side; inner and outer marginals with large, broad, spatula-shaped outer cusp and much smaller, pointed inner denticle; inner marginals broader than outer ones.

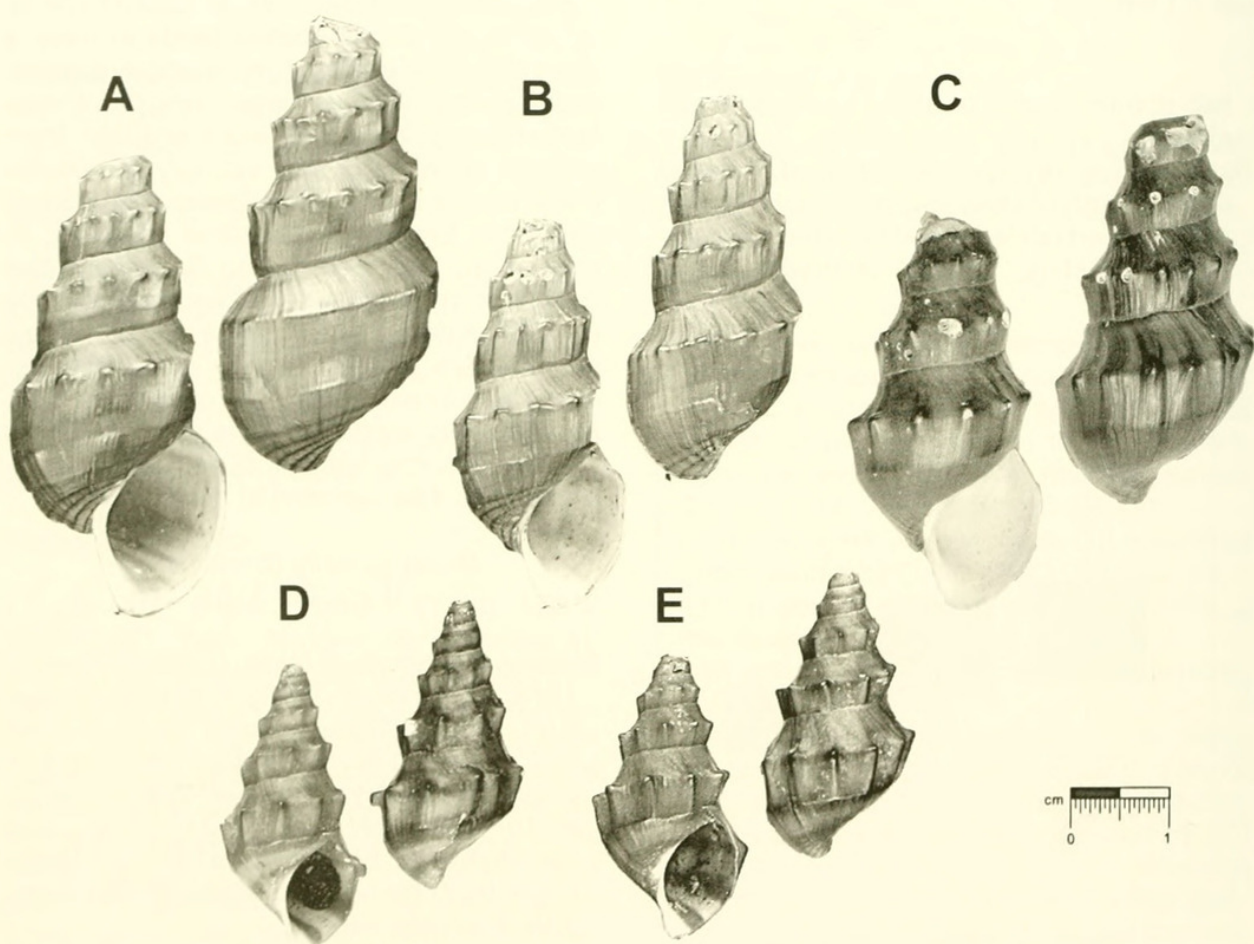


FIG. 28. Shell morphology of *B. godwini*. A: Lectotype of *M. hanleyi* Godwin-Austen BMNH 19991561/A; B: Paralectotype BMNH 19991561/B; C: Assam, Cachar (ZMB 20.737); D–E: Assam (ZMB 97.422). Scale bar = 10 mm.



*Embryonic shell morphology, Soft body anatomy, Operculum*: Unknown.

#### Distribution

India: Meghalaya, Assam, Manipur: tributaries of Brahmaputra (possibly also neighbouring regions of Myanmar and Bangladesh). Seemingly restricted to mountainous regions.

#### Remarks

Similar to spiny morphs of *B. costula*, but shell not as highly turreted, whorls much more stepped; radula differs in shape of glabella.

*Brotia henriettae* (Griffith & Pidgeon, 1834)  
(Figs. 29, 30, 31B, C)

*Melania henriettae* Griffith & Pidgeon, 1834: 598, pl. 13, fig. 2 ("China"), ex Gray ms; lectotype BMNH 19990495/A and paralectotype BMNH 19990495/B (designated by Köhler & Glaubrecht, 2002a) (Figs. 29A, B); types seen; Reeve, 1859: 1.

*Semisulcospira henriettae* – Yen, 1942: 204: pl. 15, fig. 66.

*Brotia henriettae* – Köhler & Glaubrecht, 2002a: 137, 138, fig. 2D.

*Melania baccata* Gould, 1847: 219 ("Thoungyin River, branch of the Salween, Burma"), Lectotype MCZ 169052 and paralectotype USNM 611239 (designated by Johnson, 1964) (Fig. 29E); types seen; Brot, 1875: 81, 82, pl. 9, fig. 6; Hanley & Theobald, 1873: 32, pl. 75, figs. 1, 2, 4; Annandale, 1918: 115, pl. 7, fig. 9; Johnson, 1964: 45.

*Melania (Melanoides) baccata* – Nevill, 1885: 262.

*Melania (Brotia) baccata* – Martens, 1899: 35, 36.

*Melanoides (Tiara) baccata* – Preston, 1915: 26.

*Melania baccata* subsp. *elongata* Annandale, 1918: 115, 116, pl. 7, figs. 3, 3a, 4–7 ("He-Ho Plain and Yawnghwe River" = He ho, N of Lake Inle, 20°44'N, 96°49'E), two syntypes ZSI 11155/2, according to Annandale (1918); types not seen.

*Acrostoma elongatum* – Annandale & Rao, 1925: 117.

*Melania persculpta* Ehrmann, 1922: 18–23, fig. 8 ("Loikaw-Fluß, Süd-Schan-Staaten" = Loikaw River, Southern Shan States, Myanmar), lectotype SMF 221813, 20 paralectotypes SMF 221814–5 (designated by

Köhler & Glaubrecht, 2002a) (Fig. 29D); types seen.

*Acrostoma baccata* – Rao, 1928: 442–445, figs. 17, 18.

*Brotia baccata* – Bequaert, 1943: 431; Morrison, 1954: 384; Johnson, 1964: 45.

*Brotia (Brotia) baccata* – Brandt, 1974: 178, pl. 13, fig. 32.

*Melania reticulata* I. & H.C. Lea, 1851: 193 ("China"), holotype USNM 119663 (Fig. 29C); type seen.

*Melanoides reticulata* – H. Adams & A. Adams, 1854: 297.

*Melania baccata* var. *pyramidalis* Martens, 1899: 36.

*Melania variabilis* var. *pyramidalis* – Theobald, 1865: 274, fig. 7

*Melania variabilis* var. *glabra* Theobald, 1865: 273.

*Melania variabilis* var. *vittata* Theobald, 1865: 273, fig. 4; Nevill, 1885: 263.

*Melania variabilis* var. *turrita* Theobald, 1865: 273, 274, fig. 5.

*Melania variabilis* var. *baccifera* Theobald, 1865: 274, fig. 6.

*Melania (Melanoides) baccata* subvar. *recta* Nevill, 1885: 262 ("Upper Salween").

*Melania (Melanoides) subasperata* Nevill, 1885: 262 ("Shan States").

*Melania (Melanoides) subasperata* var. *sublaevigata* Nevill, 1885: 263 ("Shan States").

#### Taxonomy and Systematics

Noticing the confusing variety of different shell forms that also lead 19<sup>th</sup> century authors to introduce a plethora of names, Annandale (1918) wondered whether these forms should be regarded as representing one highly variable species or a flock of morphologically similar species. Indeed, the diversity of shell forms attributed to this species might be indicative for the existence of more than a single species. However, the question whether and, if so, how many different species are currently subsumed under the concept of *B. henriettae* cannot be answered satisfactorily since only dry shell material is available from Myanmar. Unless more detailed morphological and molecular genetic data will show otherwise, we follow Brot (1875) considering these forms as conspecific. It remains unclear, however, why Brot (1875) referred to *M. baccata* but not to the older name *M. henriettae*. This treatment was followed by later authors, rendering *M. baccata*



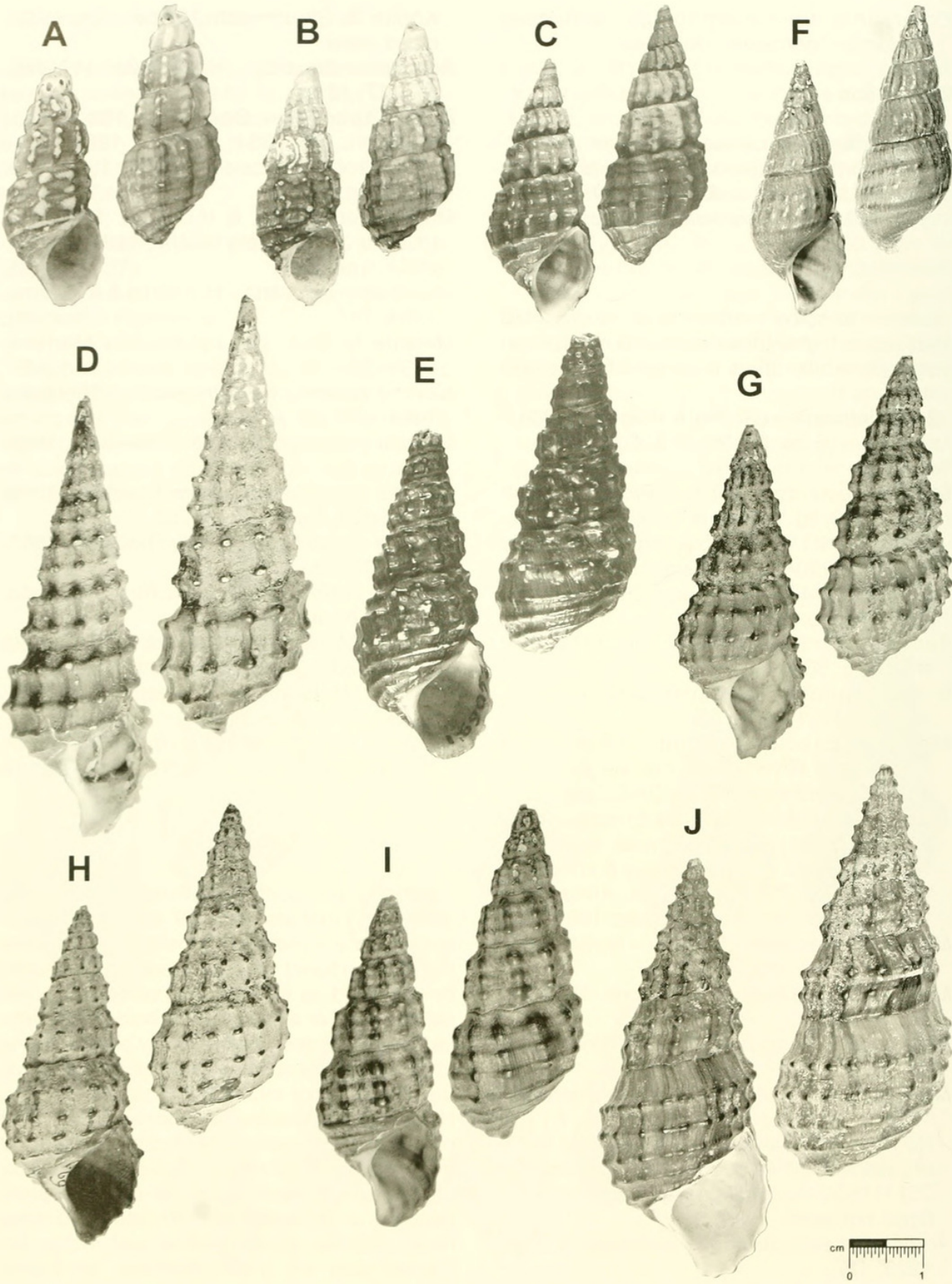


FIG. 29. Shell morphology of *B. henriettae*. A: Lectotype of *M. henriettae* BMNH 1999095/A; B: Paralectotype BMNH 1999095/B; C: Holotype of *M. reticulata* USNM 119663; D: Lectotype of *M. persculpta* SMF 221813; E: Lectotype of *M. baccata* MCZ 169052; F: Thailand, Pai (ZMB 200.221); G: Myanmar, Lashio River (ZMB 49.612); H: Myanmar (ZMB 200.006); I: China, Hienshow (ZMB 62.665); J: Myanmar, Myitnge (ZMB 49.613). Scale bar = 10 mm.



a name most commonly employed. Nonetheless, the name *M. henriettae* Griffith & Pidgeon, 1834, being available has priority over *M. baccata*.

*Brotia henriettae* is type species of *Wanga* Chen, 1943, by original designation. This genus is considered a junior synonym of *Brotia*.

#### Material Examined

China: Yunnan, Yaylayman (ZMB 27.511); Hienshow River (ZMB 52.665). Myanmar: Shan states (BMNH 1907.12.30.210; ZMB 200006-7); North Shan States: Lashio River at Myitnge (ZMB 49.616), Lashio River (ZMB 49.612, 200.076, BMNH 1899.6.21.72-5), Nampai River near Lashio (ZMB 49.611, BMNH

1899.6.21.90-91), tributary of the Nampai near Lashio (ZMB 49.615), small stream at Meungyaw (ZMB 49.618), Myitnge (ZMB 49.613, 200.004, 200.140), tributary of the Myitnge at Bagwyo near Thibaw (ZMB 49.614), small stream near Bangwyo (ZMB 200.002; ZMB 200.005); Chindwin, tributary of the Irawaddy at Matu (ZMB 49.620); affluent of the Salween near Lashio (ZMB 49.619, BMNH 1899.6.21.76-79); tributary of the Salween (ZMB 200.000), Gotheik cave (ZMB 200.001), Thoungyin River (BMNH 1888.12.4.1767-8); Thailand: Prov. Chiang Mai, Pai River in Pai, 19°21.57'N, 98°26.62'E (ZMB 200.221); Prov. Mae Hongson, Som River at Ban Som (ZSM 19983220); Prov. Kamphaeng Phet, Moei River, 30 km S of Mae Sot, boarder to Myanmar, 16°26.96'N, 98°39.27'E (ZMB 200.210).

#### Diagnostic Characteristics

Pyramidal turreted, solid, flattened whorls, narrow suture; spiral lines support two or three spiral rows of closely spaced tubercles; in some specimens tubercles replaced by axial ribs; aperture well produced with sharp peristome; body whorl relatively large; operculum round with up to eight whorls, considerably smaller than aperture; embryonic shells with axial ribs from second whorl on.

#### Description

**Shell** (Fig. 29): Medium sized, solid; spire oval to cylindrical or highly turreted; six to eight flattened whorls, suture deeply incised; strong spiral cords support more or less distinct nodules. Two to three nodules frequently arranged in vertical rows, sometimes forming axial ribs. Aperture rather narrow, peristome thin, sharp. Colour light to chestnut brown. Size: H = 30–64 mm, B = 13–25 mm.

**Embryonic Shell** (Fig. 30): Conic to turreted, penultimate whorl with smooth sculpture, following whorls with strong axial ribs. Average proportions: H = 3.0 mm, B = 1.9 mm, HA = 0.24 mm, BA = 0.40 mm, DA = 0.90 mm (for n = 6) up to 3.5 whorls.

**Operculum**: Round, up to eight regular whorls, almost central nucleus; much smaller than aperture.

**External Anatomy**: Animal black with yellowish to light brown patches.

**Radula** (Figs. 31B, C): Up to 150 rows of teeth; radulae from different localities vary in breadth

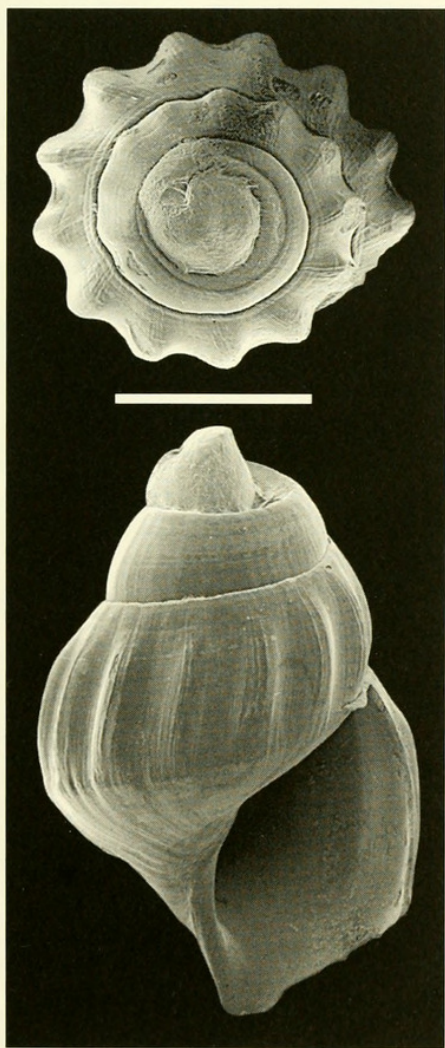


FIG. 30. Embryonic shell morphology of *B. henriettae*. SEM images of embryonic shell removed from dried shell (ZMB 49.613); apical and front view. Scale bar = 1 mm.



and shape of main cusp. Generally, central tooth with concave upper rim, relatively broad central cusp flanked by two accessory denticles tapering in size, glabella with concave to angled lateral margins, basely well rounded. Lateral tooth with broad main denticle flanked by two inner and one or two outer accessory denticles. Inner and outer marginals with two cusps, outer one broad, spatula-shaped, inner one small, pointed. Inner marginals broader.

*Stomach*: Typical, as in *B. citrina* (Fig. 4); typhlosoles unfused.

#### Distribution (Fig. 36)

China (southern China), particularly Yunnan; Myanmar (Northern and Southern Shan states); Thailand (northern and western Thailand); river system of the Irawaddy and Salween.

#### Habitat

Clear mountain rivers and streams with strong current, attached to stones and rocks.

In the Maenam Moei (= Thoungyin River) co-occurring with *B. pagodula* and *B. herculea*.

#### Fossil Record

In Tertiary and Pleistocene cave deposits of Myanmar (Bequaert, 1943); sub-fossil shells reported by Annandale (1918) from Myanmar.

#### Remarks

Similar sculpture in *B. iravadica*, frequently being smaller and more conical in shape, with fewer whorls.

*Brotia herculea* (Gould, 1846)  
(Figs. 32–34)

*Melania herculea* Gould, 1846: 100 ("Tavoy River, British Burma" = Tavoy, Myanmar, 14°05'N, 98°12'E), lectotype MCZ 169436, two paralectotypes MCZ 87933, 17 paralectotypes MCZ 169437, two paralectotypes USNM 611234 (designated by Johnson, 1964) (Fig. 32A); types seen; Reeve, 1859:

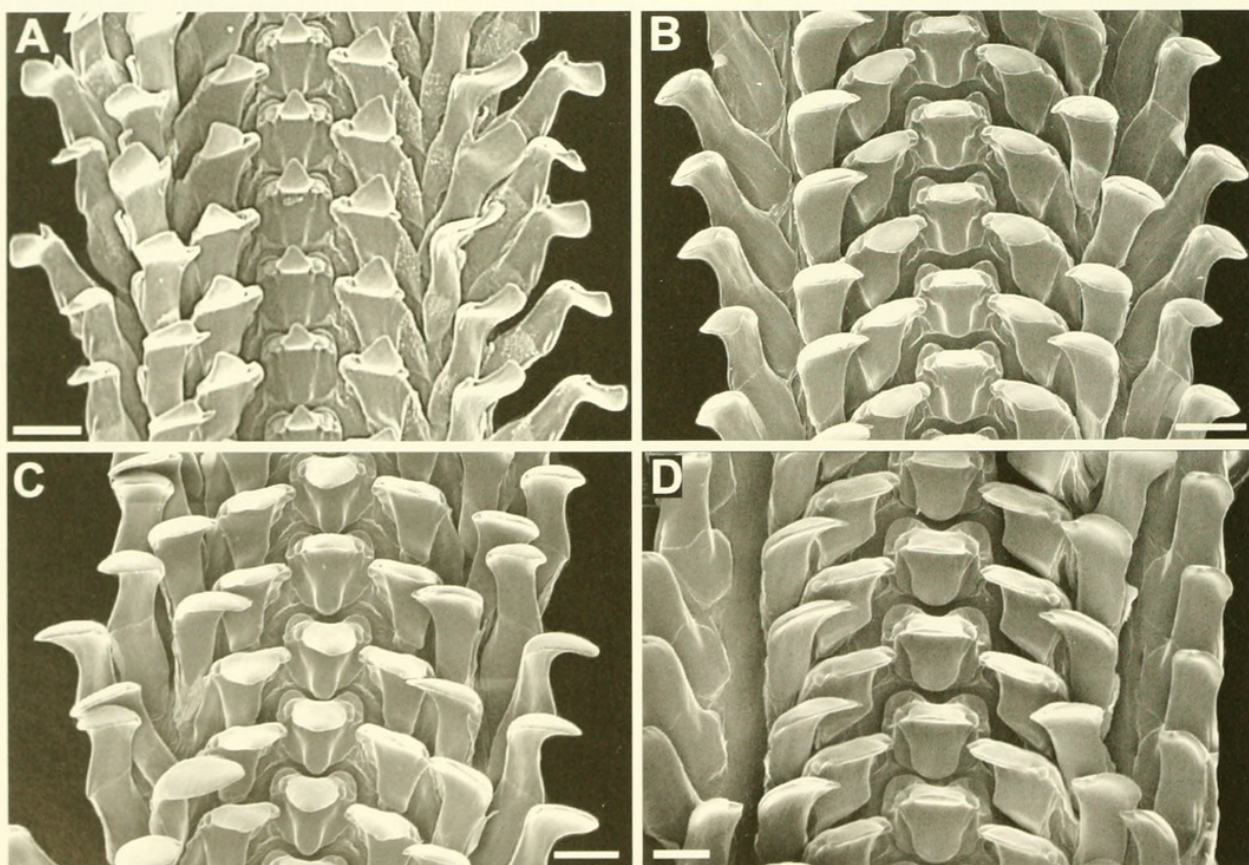


FIG. 31. Radular morphology of *B. godwini*, *B. henriettae*, and *B. jullieni*. A: *B. godwini* (Assam; ZMB 97.422); B: *B. henriettae* (Thailand, Pai; ZMB 200.221); C: *B. henriettae* (Thailand, Mae Sot; ZMB 200.210); D: *B. jullieni* (Cambodia; ZMH). Scale bars = 0.1 mm.



pl. 2, fig. 4; Hanley & Theobald, 1873: 31, pl. 72, fig. 5; Johnson, 1964: 87, pl. 35, fig. 10.  
*Melanoides herculea* – H. Adams & A. Adams, 1854: 297.

*Melania (Melanoides) herculea* – Nevill, 1885: 251.

*Melania balteata* Reeve, 1860: pl. 20, species 144 (*non M. balteata* Philippi, 1858) (no locality given), lectotype ÜMB TK 304/1 and paralectotype ÜMB 308/1 (designated by Knipper, 1958, referring to *M. reevei*) (Figs. 32B, C); types seen.

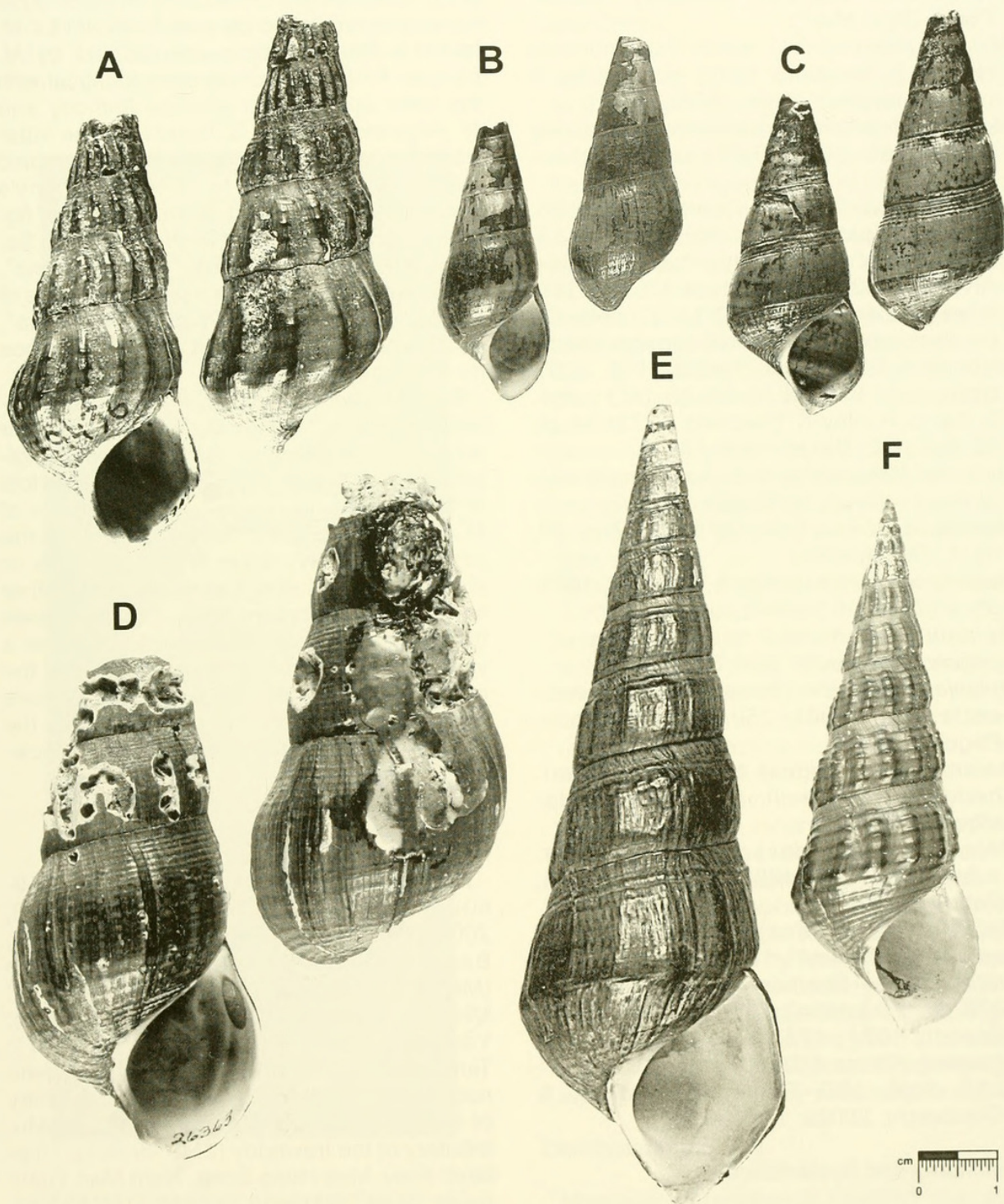


FIG. 32. Shell morphology of *B. herculea*. A: Lectotype of *M. herculea* MCZ 169436; B: Lectotype of *M. balteata* Reeve ÜMB TK 304/1; C: Paralectotype ÜMB TK 308/1; D: Lectotype of *M. gloriosa* ANSP 26363; E: Thailand, Raheng (MHNG); F: Thailand, Sai Yok (ZMB 200.235). Scale bar = 10 mm.



- Melania reevei* Brot, 1862: 46 (replacement name for *M. balteata* Reeve); Brot, 1875: 95, 96, pl. 11, figs. 4, 4a, pl. 13, fig. 6; Hanley & Theobald, 1876: 61, pl. 153, fig. 1.
- Melania (Melanoides) reevei* – Nevill, 1885: 248.
- Melania (Melanoides) reevei* var. *lanceolata* Nevill, 1885: 248, 249 (“Mandalay; Hezada, Pegu; Thyet Myo”).
- Melania (Melanoides) reevei* var. *imbricata* Hanley & Theobald, 1876: pl. 153, fig. 4 (without locality); Nevill, 1885: 249.
- Melania (Melanoides) reevei* var. *soliduscula* Nevill, 1885: 249, 250 (“Pegu, Nong-ben-Ziek”).
- Melania (Brotia ?) reevei* – Martens, 1899: 36.
- Melania gloriosa* Anthony, 1865: 207, pl. 18, fig. 3 (“Pegu” = Pegu, Myanmar), lectotype ANSP 26363, paralectotype MCZ 74106, three paralectotypes MCZ 74107, potential paralectotype MCZ 315666 (designated by Köhler & Glaubrecht, 2002a) (Fig. 32D); types seen; Brot, 1875: 94, 95, pl. 11, figs. 3, 3a, b; Hanley & Theobald, 1873: 31, pl. 72, figs. 1, 2; Baker, 1964: 190.
- Melania (Melanoides) tourannensis* var. *gloriosa* – Nevill, 1885: 250.
- Melania variabilis* – Brot, 1875: 85–87, pl. 10, fig. 1, 1a–d [partim].
- Melania peguensis* Hanley & Theobald, 1873: 31, pl. 72, fig. 6 [nomen nudum].
- Melania (Melanoides) tourannensis* var. *peguensis* – Nevill, 1885: 250.
- Melania (Melanoides) tourannensis* var. *compacta* Nevill, 1885: 250, 251 (“Henzada, Pegu”).
- Melania (Melanoides) tourannensis* var. *beddomeana* Nevill, 1885: 251 (“near Moulmein”).
- Melania (Melanoides) variabilis* subvar. *subvaricosa* Nevill, 1885: 252, 253 “Arakan, Pegu”).
- Melania (Melanoides) variabilis* subvar. *semilaevigata* Nevill, 1885: 252.
- Brotia costula* – Benthem Jutting, 1956: 374–378, fig. 76 [partim]; 1959: 92–95 [partim]; Brandt, 1974: 175, pl. 13, figs. 37–39 [partim]; Köhler & Glaubrecht, 2001: 296–299, figs. 10D–F [partim]; Köhler & Glaubrecht, 2002a: 132 [partim].

#### Taxonomy and Systematics

Treated as synonym of *Brotia costula* by, for example, Benthem Jutting (1956, 1959) and Brandt (1974), this taxon is considered herein as a distinct species since *B. costula* and *B.*

*herculea* occupy different positions in the phylogenetic trees (Figs. 78, 79). Together with its distinct shell morphology, this is reason enough to not treat *B. herculea* conspecific with the former.

A second taxon, *Melania reevei* Brot, has also frequently been considered a synonym of *B. costula* by 20<sup>th</sup> century authors. This name was employed as a replacement for *M. balteata* Reeve, being preoccupied by *M. balteata* Philippi. Most certainly identical with the latter are *Melania gloriosa* Anthony and *M. peguensis* Hanley & Theobald. The latter was introduced in error by Hanley & Theobald (1873), who intended to refer to Anthony's original figure but mixed up the legends of figures 2 and 3 of pl. 18 of Anthony's work. So, they employed the name “*M. peguensis*”, which however referred to a bivalve species of *Monocondylaea*, instead of “*M. gloriosa*”, which would have been the correct reference for the species of *Melania*.

Both *M. reevei* and *M. gloriosa* are tentatively subsumed under *B. herculea* for their somewhat similar shell and since both originate from the same area, Pegu. The type lots of *M. herculea* on one hand and the types of *M. reevei* and *M. gloriosa*, respectively, on the other hand mainly differ in the presence or absence of axial ribs. Examination of further series of dry shells from Pegu, though, reveals that the presence of ribs seems to be rather a variable feature, not sufficient to indicate the existence of two individual species. A more reliable decision on this aspect awaits the study of new alcohol preserved material, however.

#### Material Examined

Myanmar (BMNH; ZMB 49.621, 200.059–60): Pegu (ZMB 41.199, 200.051, 200.060, 200.065–6, 200.305; BMNH 1838.12.4.1757); Bassein District, Pegu (BMNH); Prome (MHNG); Mandalay (ZMB 47.125, 49.623; MHNG); Myadung (ZMB 27.512, 49.623); Yangon (ZMB 200.055–6, 200.067); Tenasserim (ZMB 200.304; BMNH); Chindwin near Matai (ZMB 49.624); Yu River, tributary of the Chindwin (ZMB 49.622, 49.625); Mu, tributary of the Irawaddy (ZMB 49.621); Thailand: Prov. Mae Hong Song, Nam Mae Yuam near Mae Sariang (ZSM 19983228, 19983247); Prov. Chiang Mai, Pai River approximately 20 km E Pai, 19°17.83'N, 98°27.93'E (ZMB 200.219), Pai River in Pai, 19°21.57'N, 98°26.62'E (ZMB 200.220); Mae



Ping, 60 km N Chiang Mai (MNHN; AMS 146766); bridge at the street from Samoeng to Chiang Mai, 18°44.23'N, 98°55.87'E (ZMB 200.253); Prov. Kanchanaburi, Sai Yok Falls 1 at Nam Tok, 14°14.16'N, 99°3.24'E (ZMB 200.235-7); Prov. Kamphaeng Phet, Maenam Moei, about 30 km S Mae Sot, boarder to Myanmar, 16°26.96'N, 98°39.27'E (ZMB 200.209); Prov. Tak, Mae Dao River, Mae Sot (AMS 146762), Maenam Moei, 8 km N Mae Ramat (AMS 146765).

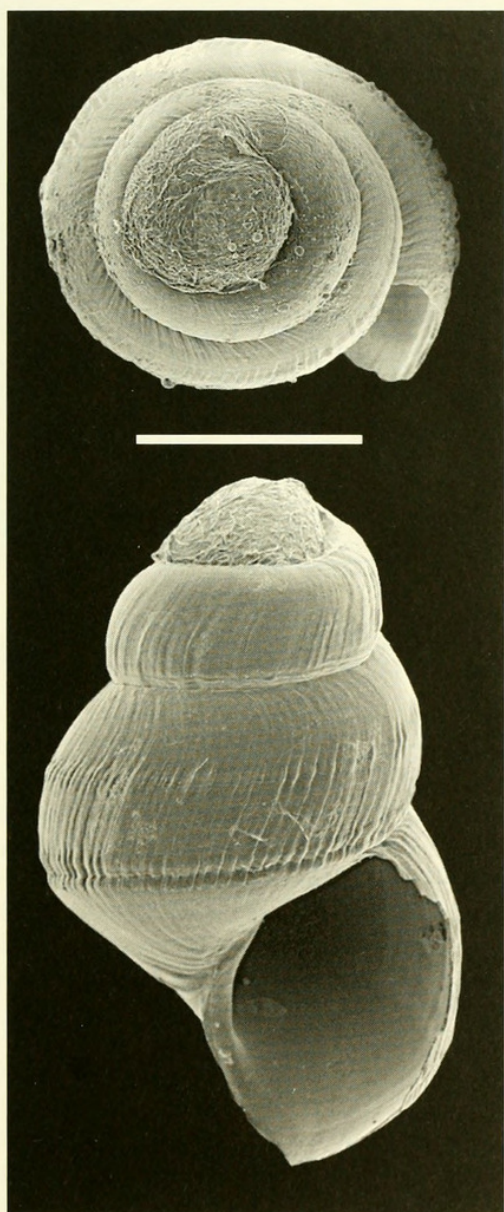


FIG. 33. Embryonic shell morphology of *B. herculea*. SEM images of embryonic shell removed from dried shell (ZMB 49.623); apical and front view. Scale bar = 1 mm.

#### Differential Diganosis

Shell robust, highly turreted, up to 12 flattened whorls, the basal ones convex, more or less rounded in diameter; aperture wide with protracted base. Strong axial ribs, that may also lack completely; spiral lines.

#### Description

*Shell* (Fig. 32): Large to very large, shell solid to thick, spire pyramidal turreted, up to 12 whorls, eroded tip; colour hazelnut to dark brown; spiral ridges most prominent at the base, in some specimens very conspicuous, in others almost completely absent; strong axial ribs may be present. Whorls flattened in diameter, with subsutural depression. Size: H = 28–98 mm, B = 10–34 mm.

*Embryonic Shell* (Fig. 33): Smooth, covered with axial wrinkles. Average proportions: H = 1.7 mm, B = 1.0 mm, HA = 0.25 mm, BA = 0.40 mm, DA = 0.61 mm (for n = 15), up to 3.5 whorls.

*Operculum*: Slightly oval, four to six whorls, central nucleus; almost fits aperture.

*External Morphology*: Uniformly coloured, dark grey to black; grey foot sole with scattered light spots.

*Radula* (Fig. 34): Ribbon length of up to 30 mm, corresponding to about half of the shell height, about 180 rows of teeth. Rachidian with single main cusp, three smaller denticles on each side tapering in size; upper margin concave by inflated, rounded corners; lower rim rounded; glabella narrow, well rounded at its base, lateral margins slightly concave. Laterals with main cusp flanked by three smaller denticles. Inner and outer marginals with two to three denticles, somewhat pointed, of about same size and shape.

*Stomach* (Fig. 35): Typhlosoles fused at almost entire length of style sac; opening to style sac partly covered by fleshy, flap-like proximal end of major typhlosole; proximal end of minor typhlosole thickened; crescent ridges below opening of digestive gland duct undulated; crescent pads adjacent to sorting area well developed, heavily undulated or ribbed.

#### Distribution (Fig. 20)

Myanmar and northwest Thailand: river systems of the Irawaddy, Chindwin, and Salween (with Moei River), and Chao Praya (with Ping and Nan Rivers).



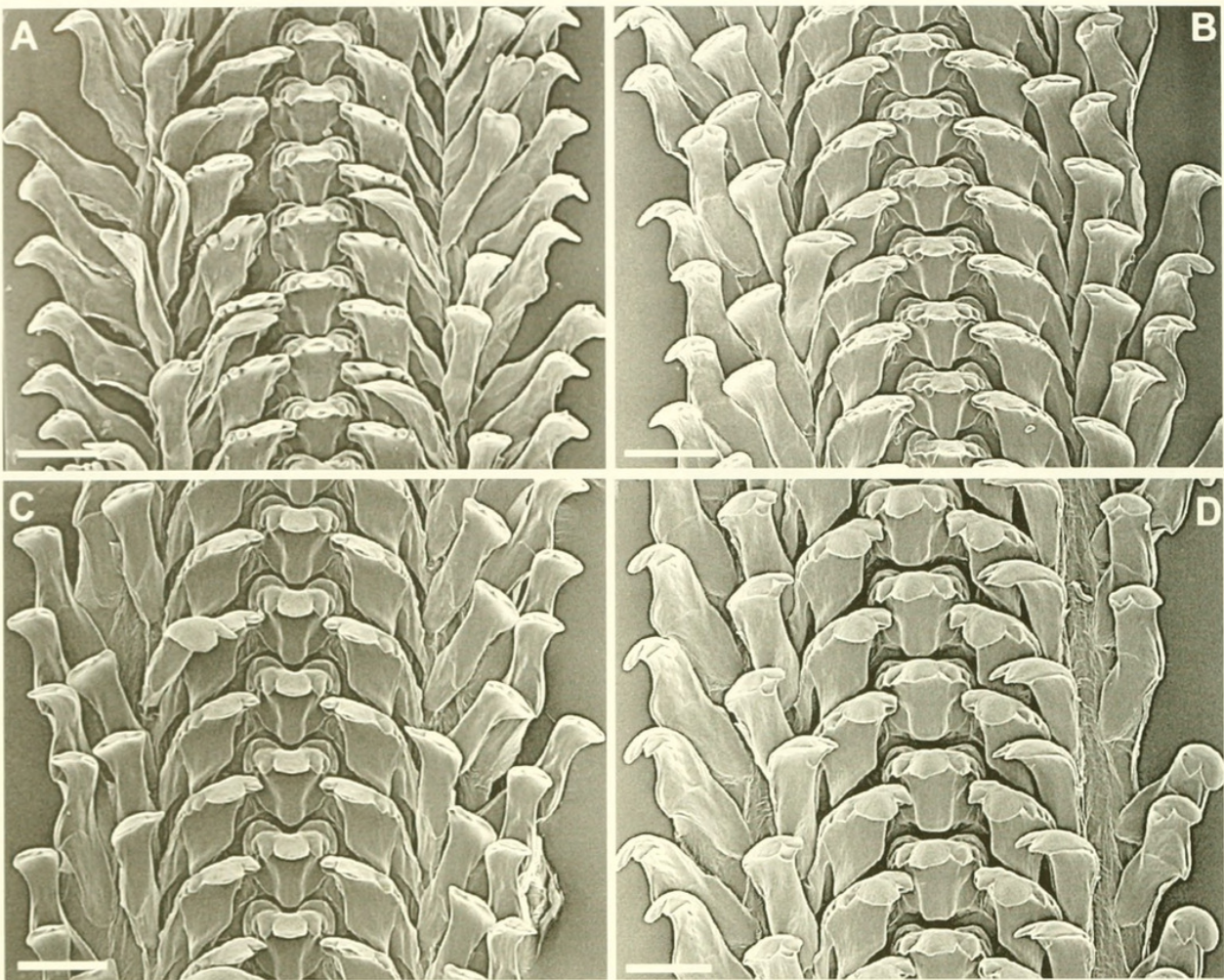


FIG. 34. Radula morphology of *B. herculea*. Radula segments viewed from above. A: Myanmar, Pegu (ZMB 41.199); B: Thailand, Pai (ZMB 200.220); C: Thailand, Sai Yok Falls, Nam Tok (ZMB 200.237); D: Thailand, Pai (ZMB 200.219). Scale bars = 100  $\mu$ m.

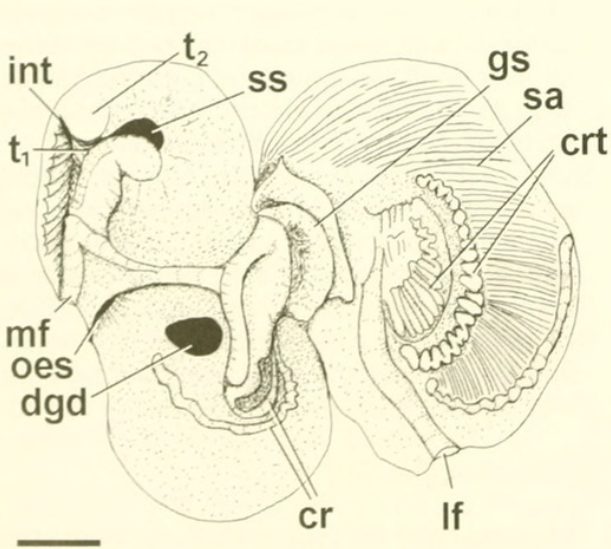


FIG. 35. Stomach anatomy of *B. herculea* (ZMB 200.209; Thailand). Scale bar = 5 mm.

Habitat and Ecology

Clear creeks and rivers on rock, mud, sand, roots, under and among piles of leaf litter in the water (Davis, 1982, referring to *B. costula*), what can be confirmed from own observations in Thailand. May be infested by drilling sabellids (Nematoda).

Remarks

Largest species of the genus. *B. costula* differs statistically significant in shell parameters H/B, H/LA, N (e.g., Fig. 21).

*Brotia indragirica* (Martens, 1900)  
(Fig. 37)

*Melania indragirica* Martens, 1900: 10, 11  
("Indragiri-Fluß, Sumatra" = Indragiri River,



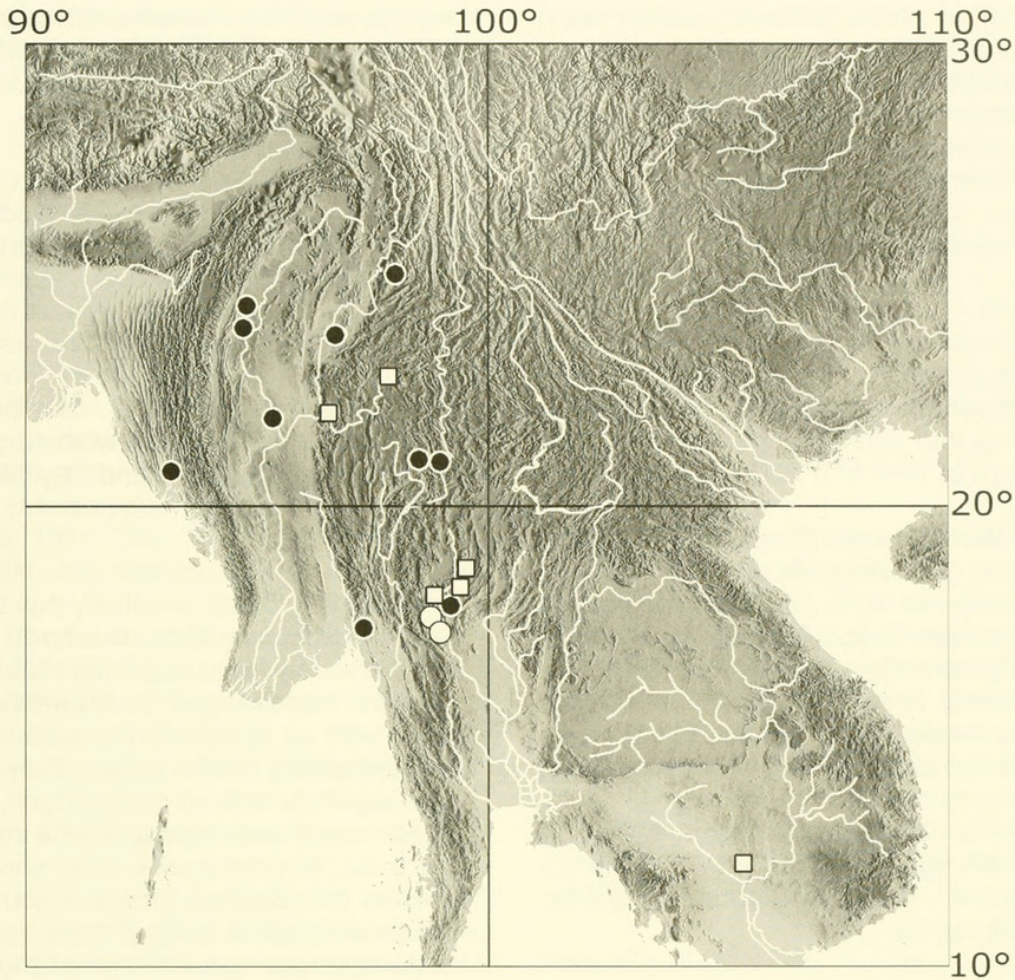


FIG. 36. Distribution of *B. citrina* (open circles), *B. dautzenbergiana* (open squares) and *B. henriettae* (close circles).

Sumatra (Indonesia), lectotype ZMB 51.777a, three paralectotypes ZMB 51.777b, five paralectotypes NMB 1202q (designated by Köhler & Glaubrecht, 2002a) (Fig. 37); types seen; Bullen, 1906: 14 (including an unnamed variety). *Brotia indragirica* – Köhler & Glaubrecht, 2002a: 139, fig. 2L.

#### Taxonomy and Systematics

Only known from the types. For this reason, soft body, radula, and embryonic shells unknown. Shell clearly pachychilid being reason for affiliation with *Brotia* as the only pachychilid taxon known from Sumatra.

#### Differential Diganosis

Highly turreted, convex whorls flattened in diameter, keeled or angled; prominent, wavy spiral bands or ridges, along keel of the whorl spiral row of spiny nodules; aperture wide, well rounded.

#### Description

*Shell* (Fig. 37): Small, not thick but solid; spire turreted, eroded tip, four to five convex whorls,



FIG. 37. Shell morphology of *B. indragirica*. Lectotype of *M. indragirica* ZMB 51.777a.



upper half of whorls flattened; conspicuous, wavy spiral ridges, weak axial ribs; spiral row of spiny nodules at centre of whorls where spiral ridge meets axial ribs. Aperture wide, ovate, produced below. Colour yellowish brown. Size: H = 23–36 mm, B = 10–15 mm. *Embryonic Shell, Operculum, Radula, Soft Body*: Anatomy unknown.

#### Distribution

Sumatra (provinces of West-Sumatra and Riau): Indragiri River and its affluent Kwantan, discharging into South China Sea (approximate centre of river at 0°33'S, 102°03'E).

*Brotia insolita* (Brot, 1868)  
(Fig. 38)

*Melania insolita* Brot, 1868: 11, pl. 3, fig. 4 ("Inde?"), lectotype and seven paralectotypes MHNG, Brot collection, "Siam" (designated by Köhler & Glaubrecht, 2002a) (Fig. 38); types seen; Brot, 1875: 107, 108, pl. 13, fig. 7.

*Brotia (Brotia) insolita* – Brandt, 1974: 176, 177, pl. 13, figs. 29, 30.

*Brotia insolita* – Köhler & Glaubrecht, 2002a: 139, 140, fig. 2J.

#### Taxonomy and Systematics

Brot (1868) stated that the species originated from India, which was later corrected to Thailand (Brot, 1875). This corresponds with labelling of the types. Because the type locality could not further be specified, the So Pa Falls,

Kaek River (Prov. Phitsanulok, central Thailand) were subsequently designated as the type locality by Brandt (1974: 177).

#### Material Examined

Thailand (ZMB 31.172); Cambodia (ZMB 26.870). Without locality (MHNG, Brot collection; labelled "*M. gloriosa*").

#### Differential Diganosis

Relatively small, conical, thin but solid; whorls well rounded; yellowish to greenish brown, dark brown spiral band may be present.

#### Description

*Shell* (Fig. 38): Small, relatively thin but solid. Shell conical in shape, the body whorl is comparatively large and inflated, while subsequent whorls taper considerably in size. Spire with up to six whorls, eroded. Sculpture consisting of faint growth lines and delicate regularly spaced spiral ridges, in some specimens these ridges become stronger at the base, inconspicuous axial ribs may be present too. Surface glossy, colour yellowish brown a spiral band of darker coloration may be present at the mid of the whorls. Aperture wide, oval and well rounded and produced at the base.

*Embryonic Shell, Operculum, Radula, Soft Body*: Anatomy unknown.

#### Distribution

Central Thailand to Cambodia, only vague.

#### Remarks

We were neither able to trace voucher material of Brandt from the Kaek River nor to find this species during our own field work. For this reason, we cannot confirm the occurrence in the Kaek River. Brandt (1974) described *B. manningi*, the shells of which are at best hard to distinguish from *B. insolita*. To complicate matters, *B. insolita* closely resembles some, but not all specimens of the type series of *B. siamensis*, among them the lectotype. The difficulties to reliably discriminate all these taxa will likely persist unless material suitable for studies on soft body morphology and molecular genetic is available. For the time being, we follow the treatment of Brandt (1974).

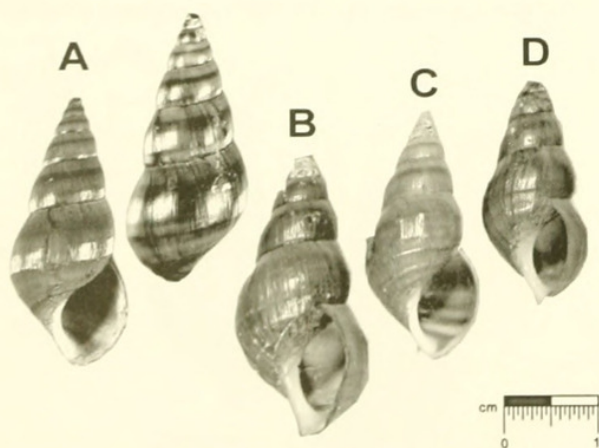


FIG. 38. Shell morphology of *B. insolita*. A: Lectotype of *M. insolita* MHNG; B–D: Three paralectotypes MHNG. Scale bar = 10 mm.



*Brotia siamensis* tends to be more elongate, often exhibiting axial ribs at the upper whorls. Whorls of *B. manningi* are flattened in diameter.

*Brotia iravadica* (Blanford, 1869)  
(Fig. 39)

*Melania iravadica* Blanford, 1869: 445 ("Burma, Upper Irawaddy at Malé and Bhamo"), three syntypes BMNH 1888.12.4.1808-10; types not seen; Hanley & Theobald, 1873: 30, pl. 71, fig. 1.

*Melania irawadica* [sic!] – Brot, 1872: 34; Brot, 1875: 111, 112, pl. 14, figs. 7, 7a.

*Melania (Melanoides) baccata* var. *iravadica* – Nevill, 1885: 262.

*Melania (Melanoides) iravadica* – Nevill, 1885: 33.

*Melania (Brotia) baccata* var. *iravadica* – Martens, 1899: 35, 36.

*Tiara (Melanoides) baccata* var. *irawadica* [sic!] – Preston, 1915: 27.

*Acrostoma iravadica* – Rao, 1928: 446, 447.

#### Taxonomy and Systematics

Mostly treated as subspecies or variety of morphologically relatively plastic *B. henriettae*. We suggest this taxon represents a distinct species because of its deviant shell. Exceptionally known from the Irawaddy, but not from its tributaries where *B. henriettae* occurs. Whether both species occur in sympatry remains unclear.

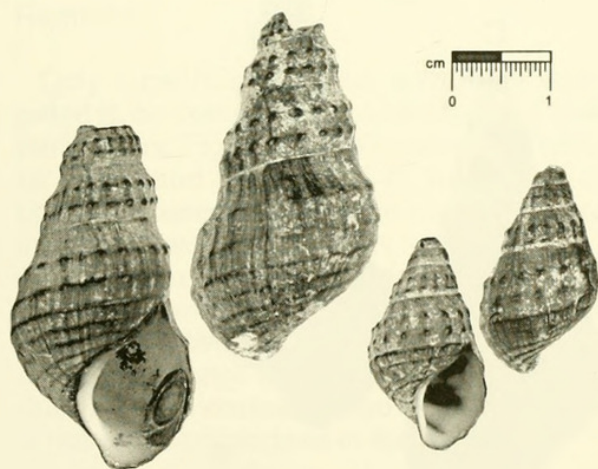


FIG. 39. Shell morphology of *B. iravadica* (Myanmar, Irawaddy; ZMB 49.617).

#### Material Examined

Myanmar: Irawaddy (BMNH 1899.21.6.76-79, ZMB 200.010), Irawaddy near Yenyangyoung (ZMB 49.617, 200.005); Pegu (BMNH 1871.9.23.49). Shan States (BMNH 1888.12.4.1440).

#### Differential Diganosis

Relatively small, broadly conical, truncated, with two to four remaining whorls; two spiral bands of closely spaced nodules.

#### Description

**Shell** (Fig. 39): Relatively small, conical, truncated with two to four remaining whorls. Body whorl comparatively large compared to shell. Two spiral cords support rows of more or less developed nodules as well as some conspicuous spiral cords at base of shell. Aperture wide, produced below, columellar margin thin. Shell size: H = 18–33 mm, B = 9–19 mm.

**Operculum**: Round, central nucleus, considerably smaller than aperture.

**Embryonic shell morphology, Radula, Soft body anatomy**: Unknown.

#### Remarks

Can be distinguished from *B. henriettae* by its smaller and more conical shell and less pronounced sculpture.

*Brotia jullieni* (Deshayes, 1874)  
(Figs. 34D, 40)

*Melania jullieni* Deshayes, in Deshayes & Jullien, 1874: 115, pl. 7, figs. 7–9 ("Thio-Compilh, Cambodge" = Thio Compilh, Sâmbok at the Mekong, Cambodia, 12°34'N, 106°01'E), lectotype and three paralectotypes MNHN (designated by Köhler & Glaubrecht, 2002a) (Fig. 40A); types seen; Morlet, 1889: 145.

*Melania jullieni* [sic] – Brot, 1875: 93, 94, pl. 11, figs. 2, 2a.

#### Taxonomy and Systematics

Commonly treated as synonym of *B. costula* (e.g., Brandt, 1968, 1974; Davis, 1982), but herein considered distinct for its peculiar shell and radula.



## Material Examined

Laos: Muong-Bet sur le Song-Ma (MNHN); Mekong (MNHN). Cambodia: Mekong near Pakse (ZMH); Vietnam: Environs de Gang, Tonkin (MNHN); Song Ya near Yuong-Het, Tonkin (MNHN).

## Differential Diganosis

Extraordinarily large and robust; aperture wide, basely produced; strong axial ribs, fine spiral lines. Radular teeth each with a very broad, rounded main denticle.

## Description

*Shell* (Fig. 40): Large, broadly pyramidal, eroded tip; aperture wide, comprising about

$\frac{1}{4}$  of shell height; whorls rounded, suture thin; strong axial ribs and thin spiral ridges, at least at base of shell; colour yellowish to chestnut brown. Size: H = 55–65 mm, B = 24–30 mm.

*Radula* (Fig. 31D): Lateral corners of rachidian conspicuously enlarged; very broad, spatula shaped main cusp flanked by two much smaller, pointed accessory denticles; glabella almost squarish, well rounded at its base, concave lateral edges. Lateral teeth with very broad main cusp flanked by two smaller denticles on each side, short lateral extensions. Inner and outer marginals with broadly rounded outer cusp and tiny pointed inner cusp. Inner marginals broader than outer ones.

*Embryonic shell morphology, Soft body anatomy*: Unknown.

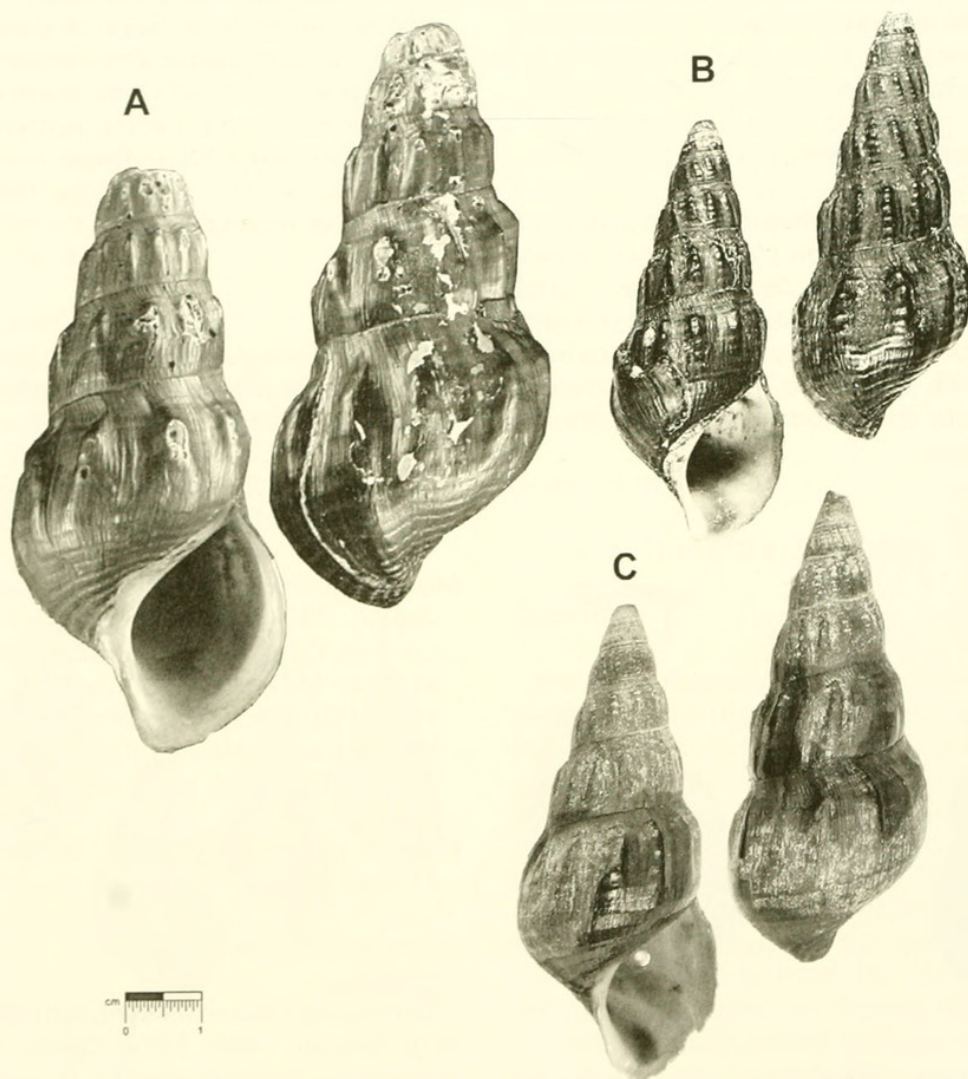


FIG. 40. Shell morphology of *B. jullieni*. A: Lectotype of *M. jullieni* MNHN; B: Cambodia (ZMZ 522392); C: Laos, Pakse (ZMH). Scale = 10 mm.



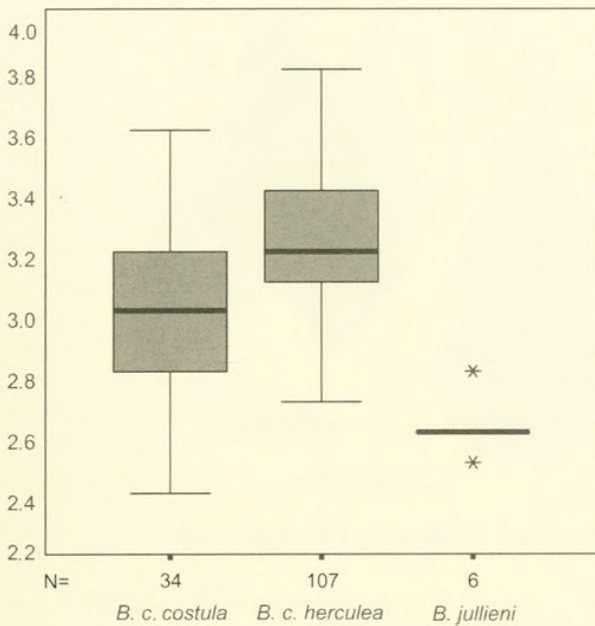


FIG. 41. Comparison of *B. costula* and *B. jullieni* by means of shell parameter H/LA. Box plot diagram showing median, the 25%- and 75%-percentile and largest non-extremes (less than 1.5 times of box height).

#### Distribution

Laos, Cambodia, Vietnam, perhaps also northeast Thailand; Mekong River system.

#### Ecology

Frequently infested by drilling sabellids (*Caobangia* spec., Nematoda).

#### Remarks

Only superficially similar with more elongated *B. herculea* (statistical analyses of shell parameters: Fig. 41). Main cusps of the radular teeth and glabella of *B. jullieni* much broader, possessing only one accessory cusp instead of two in *B. herculea*.

A report from the Ping River near Tak, Thailand, by Morlet (1891: "Riviere de Menam-Pinh, de Raheng à Xieng-Moi") refers to *B. herculea*. Brandt (1974) and Davis (1982), referring to *B. costula*, stated that this species is the only cerithioidean in the Mekong.

*Brotia kelantanensis* (Preston, 1907)  
(Figs. 42, 43A)

*Melania kelantanensis* Preston, 1907: 267, text-fig. ("Kelantan, Malay Peninsula"), types not seen.

#### Taxonomy and Systematics

Ignored by later authors, this species was reported only once by Davis (1982) mentioning an unidentified, spiny species in the Pahang River system. Herein assigned to *Brotia* for its characteristic morphology.

#### Material Examined

Malaysia: Pahang, Taman Negara National Park (ZMA).

#### Differential Diganosis

Shell comparatively small, broadly conical, no more than four whorls; prominent spiral cord at the centre of the whorls supporting spiral row of strong, pointed spines or nodules.

#### Description

**Shell** (Fig. 42): Medium sized, pyramidal, conical, decollated, four remaining whorls; prominent spiral cord at centre of whorls supports spiral row of strong, pointed nodules, additional, weak spiral ridge on upper sector. Colour chestnut brown. Aperture round, relatively small compared to body whorl, slightly produced below. Shell size: H = 31 mm, B = 18 mm (n = 2).

**Operculum**: Oval, four whorls, central nucleus.

**Radula** (Fig. 43A): Ribbon 16 mm long, corresponding to about half of shell height, 100 rows of teeth (n = 1). Rachidian with two conspicuously excavated upper corners, concave upper rim; main cusp flanked by two smaller, accessory denticles; glabella narrow, well rounded below with concave lateral margins. Inner and outer marginals with two cusps, outer one broadly spatulate.

**Embryonic Shell**: Unknown.

#### Distribution

Malaysia (Malay Peninsula): Federal State of Pahang; Pahang River system.

#### Habitat

On rocks in rapids (Davis, 1982: 392).

#### Remarks

Hardly to be mistaken for any other species. Occurs in sympatry with *B. episcopalis*, which is more elongated and differs in average number of whorls and sculpture.



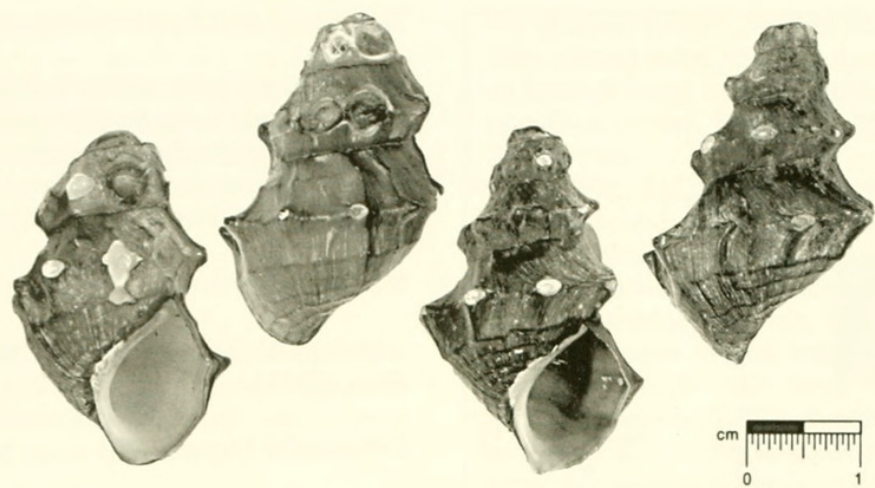


FIG. 42. Shell morphology of *B. kelantanensis* (Malaysia, Pahang; ZMA).

*Brotia manningi* Brandt, 1968  
(Figs. 43B, 44)

*Brotia (Brotia) manningi* Brandt, 1968: 272, pl. 10, fig. 58 (“Thailand: Huai Lan at Ban Dam Pon, Lom Sak District, Phetchabun Province”), holotype SMF 197376, 22 paratypes MCZ 288652, 22 paratypes ZSM 19983239, 20 paratypes RMNH 55289/20 (Fig. 44); types seen; Brandt, 1974: 179, 180, pl. 13, fig. 35.

*Brotia manningi* – Köhler & Glaubrecht, 2002a: 141.

Taxonomy and Systematics

In absence of additional information and material, we follow the statement of Brandt (1968, 1974).

Differential Diganosis

Shell elongate conic with flattened, slightly convex whorls; aperture produced; almost smooth, only with faint spiral lines and growth lines.

Description

*Shell* (Fig. 44): Medium sized, spire conic with up to seven flattened whorls; suture narrow; smooth, faint growth lines; colour brown to olive, dark brown spiral band may be present. Aperture oval, well rounded to produced below. Size: H = 24–38 mm, B = 11–15 mm.  
*Operculum*: Oval, up to four fast in diameter increasing whorls, sub-central nucleus.  
*Radula* (Fig. 43B): Ribbon about 12 mm long with 80 rows of teeth (n = 1). Rachidian elon-

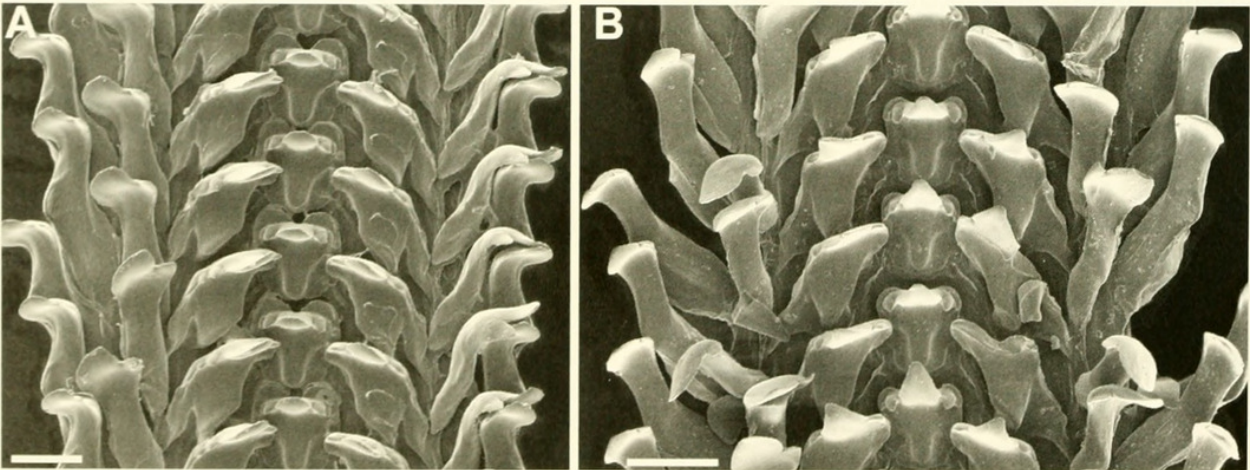


FIG. 43. Radula morphology of *B. kelantanensis* and *B. manningi*. A: *B. kelantanensis* (Malaysia, Pahang; ZMA); B: *B. manningi*, paratype ZSM 19983239). Scale bars = 100 µm.



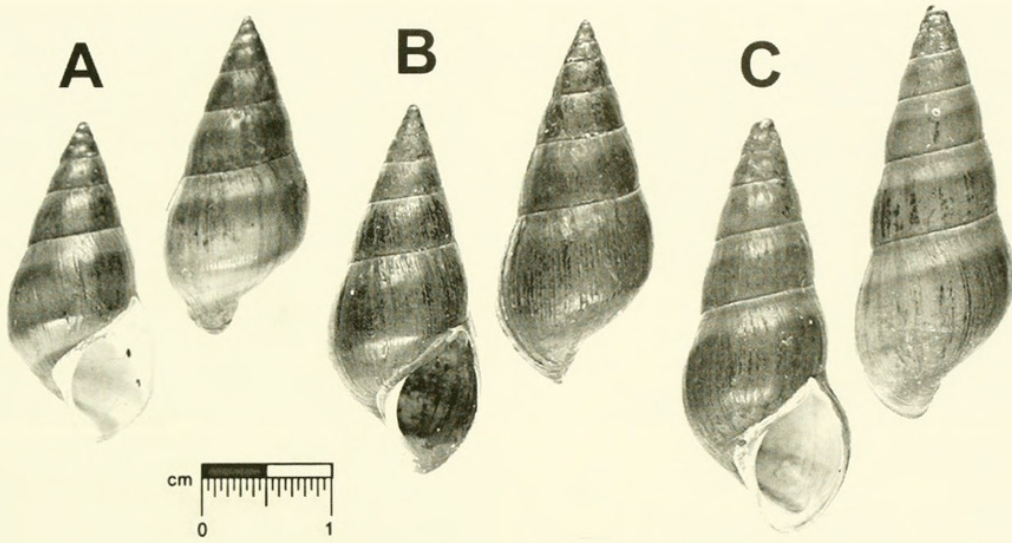


FIG. 44. Shell morphology of *B. manningi*. A–C: Paratypes ZSM 19983239. Scale = 10 mm.

gate, anterior rim slightly concave, inconspicuously excavated upper lateral corners; cutting edge with pronounced main denticle flanked by two, much smaller accessory denticles on each side; glabella narrow, rounded below, not reaching basal margin of rachidian. Laterals with very large main denticle. Inner and outer marginals relatively long, slender, broad outer cusp, smaller, spiny inner denticle.

*Embryonic Shell*: Unknown.

#### Distribution

Thailand: Central Thailand, Provinces of Nan, Loei, and Phetchabun (Brandt, 1974).

#### Remarks

Belongs to a group of taxa from central Thailand with similar shells. To be distinguished from *B. insolita* and *B. siamensis* only by subtle morphological differences. Distinct status requires confirmation by examination of further material suitable for morphological and molecular genetic studies. We were not able to trace material from the Kaek River, central Thailand, a locality reported by Brandt (1974).

*Brotia microsculpta* Brandt, 1968  
(Figs. 45, 46A)

*Brotia microsculpta* Brandt, 1968: 272, pl. 10, fig. 59 ("Thailand: Maenam Kaek, in Thung Salaeng Luang Botanical Garden, 80 km E of Pitsanulok" = Kaek River, Thung Salaeng

Luang NP, Prov. Phitsanulok), holotype SMF 197378/1, 10 paratypes SMF 205356/10 (Fig. 45); types seen; Köhler & Glaubrecht, 2002a: 141; Glaubrecht & Köhler, 2004: 289–291. *Brotia (Brotia) microsculpta* – Brandt, 1974: 180, pl. 13, fig. 36.

#### Taxonomy and Systematics

Revised by Glaubrecht & Köhler (2004) based on morphological and molecular genetic data. Accordingly, *B. microsculpta* belongs to the Kaek River species flock in Central Thailand.

#### Material Examined

Thailand: Prov. Phitsanulok, Kaek River: Resort 53 km E Phitsanulok (ZMB 200.266); Poi Falls (ZMB 200.200); Sopha Falls, 71 km E of Phitsanulok (ZSM 19983240); Thung Salaeng Luang NP (ZMB 200.191).

#### Differential Diganosis

Shell small, conical to elongated, mostly three remaining, slightly rounded whorls; smooth sculpture. Aperture round, not produced. Operculum round, not oval as other Kaek River species. Radula relatively short, closely spaced rows of teeth, marginal teeth prolonged.

#### Description

*Shell* (Fig. 45): Relatively small, conic to elongate conic, not thick but solid; truncated,



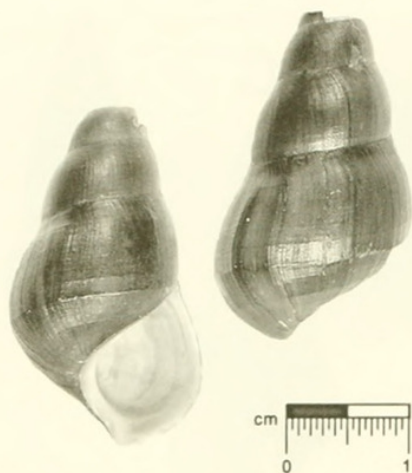


FIG. 45. Shell morphology of *B. microsculpta*. Holotype SMF 197378/1. Scale = 10 mm.

mostly three remaining, convex whorls; smooth, fine axial growth lines, faint spiral lines. Aperture almost round, relatively small compared to shell, basely rounded but not produced. Size: H = 10–25 mm. B = 8–15 mm.

*Operculum*: Round to only slightly oval, 5–6 regular whorls, central nucleus.

*Radula* (Fig. 46A): Length of ribbon  $m = 11.8$  mm ( $sd = 1.7$  mm;  $n = 3$ ), about 190 closely spaced rows of teeth. Radular teeth comparatively small. Rachidian relatively broad, main cusp flanked by three accessory denticles on each side, glabella narrow, with straight lateral margin, cut basal rim, not reaching base of rachidian. Inner and outer marginals very long, narrow, curved, large, broad outer cusp, one to three tiny inner accessory denticles.

*Stomach*: Typical, as in *B. citrina* (Fig. 4).

*Embryonic Shell*: Morphology unknown.

#### Habitat

Buried into sandy substrata in quiet parts of the swift river.

#### Distribution

Thailand: Prov. Phitsanulok: Endemic to Kaek River and its northern tributary Huai Chieng Nam (Brandt, 1974).

#### Remarks

Recognizable by its smaller shell, round operculum, and typical radula. *Brotia pseudosulcospira* is more conical, thicker, whorls

more flattened. Only Kaek River species occurring on soft substrata.

*Brotia pagodula* (Gould, 1847)  
(Figs. 46B, 47, 48)

*Melania pagodula* Gould, 1847: 219 (*non M. pagodulus* Reeve, 1860) ("Thoungyin-River, tributary of the Salween River, Burma"), lectotype MCZ 169276 and paralectotype USNM 611238 (designated by Johnson, 1964) (Fig. 47A); types seen; Brot, 1875: 102, 103, pl. 13, fig. 2, Hanley & Theobald, 1876: 61, pl. 153, fig. 3.

*lo pagodula* – H. Adams & A. Adams, 1854: 300; Reeve, 1859: pl. 3, fig. 10.

*Tiara (Acrostoma) pagodula* – Preston, 1915: 32.

*Brotia pagodula* – Morrison, 1954: 382; Johnson, 1964: 121, pl. 44, fig. 2; Köhler & Glaubrecht, 2001: 292–295, figs. 1A, 9A–F; Köhler & Glaubrecht, 2002a: 142; Glaubrecht & Köhler, 2004: 283.

*Brotia (Brotia) pagodula* – Brandt, 1974: 173, 174, pl. 12, fig. 25.

#### Taxonomy and Systematics

Type species of *Brotia*.

#### Material Examined

Myanmar: (ZMB 26.708); Salween River, Tavoy (BMNH); Thailand: Prov. Kamphaeng Phet: Maenam Moei approximately 20 km E Mae Sot, 16°45.82'N, 98°45.14'E (ZMB 200.205), Maenam Moei approximately 30 km S Mae Sot, boarder to Myanmar, 16°26.96'N, 98°39.27'E (ZMB 200.208), Maenam Moei (USNM 776062), Maenam Moei, 8 km W of Mae Ramat (ZSM 19983241; ZMH; RMNH 71319); soft bodies already removed from the shells, without location (ZMH).

#### Differential Diganosis

Conical shell sculptured by spiral row of conspicuous spines; aperture wide, rhomboid, well produced below; radular teeth with very broad, enlarged main cusp; comparatively large juveniles in brood pouch.

#### Description

*Shell* (Fig. 47): Medium sized, spire broadly conical, decollated, up to five flattened whorls, narrow suture, spiral row of long, pointed



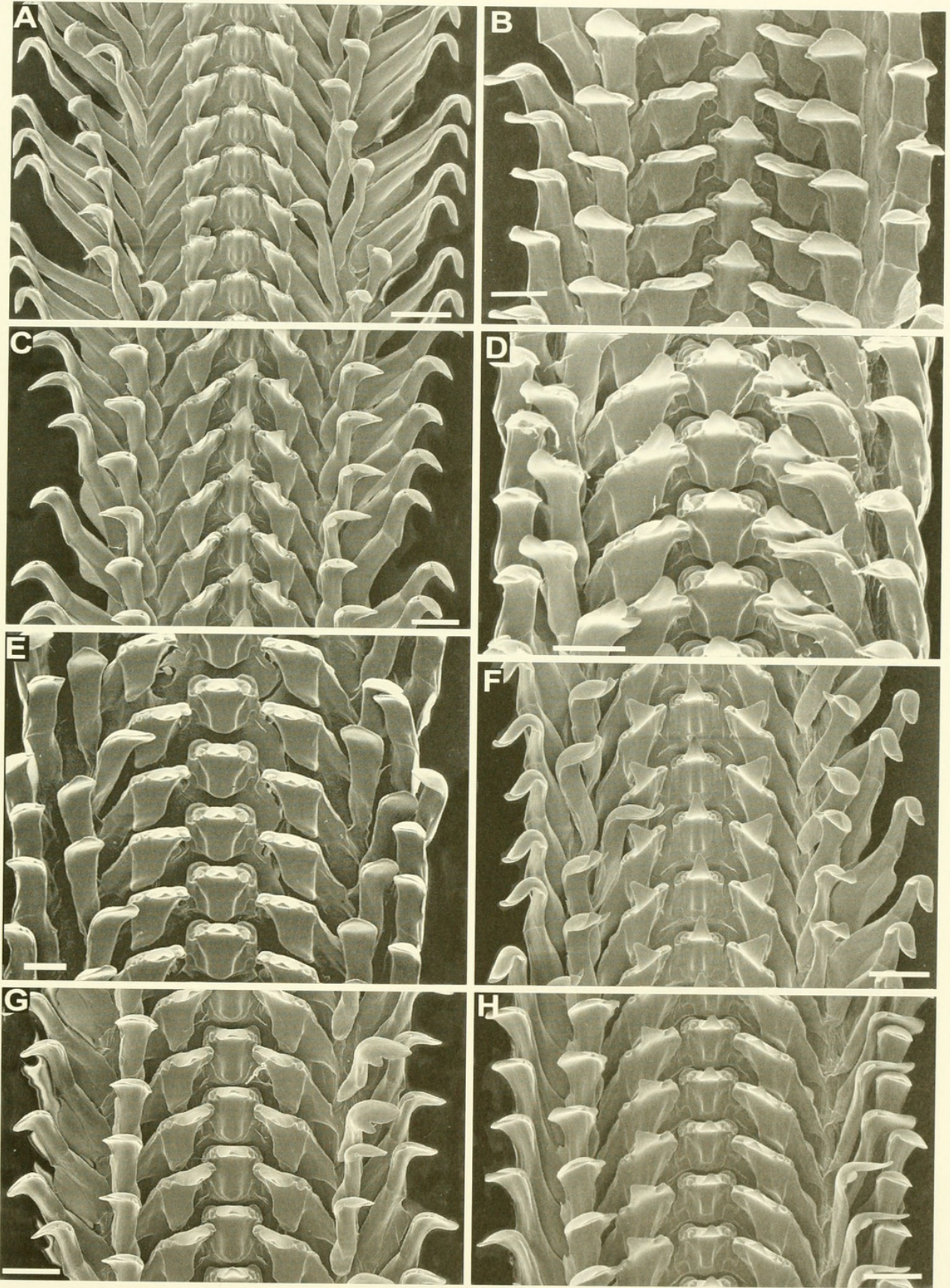


FIG. 46. Radular morphology of several *Brotia* species. A: *B. microsculpta* (Thailand, Kaek River; ZMB 200.200); B: *B. pagodula* (Thailand, Moei River; ZMH); C: *B. paludiformis* (Thailand, Kaek River; SMF 215963); D: *B. peninsularis* (Thailand, Surat Thani; ZMB 200.242); E: *B. praetermissa*, Paratype BMNH 20010482/B; F: *B. pseudosulcospira* (Thailand, Kaek River; ZMH); G: *B. solemiana* (Thailand, Pong River; SMF 193585); H: *B. subgloriosa* Paratype ZSM 19983219. Scale bars = 0.1 mm.



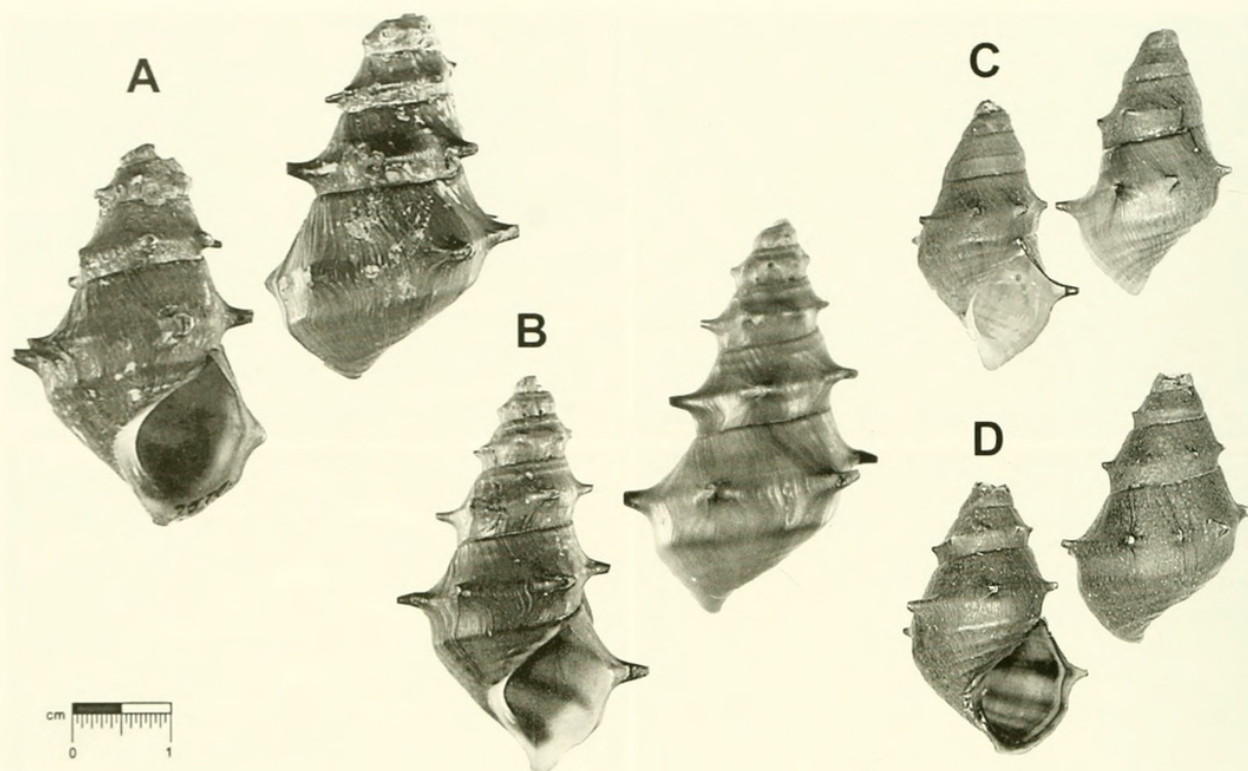


FIG. 47. Shell morphology of *B. pagodula*. A: Lectotype of *M. pagodula* (MCZ 169276; Thougyin); B: Thailand (ZMB 26.708); C: Thailand, Moei River (ZMB 200.205); D: Thailand, Moei River (ZMB 200.208). Scale = 10 mm.

spines; fine spiral lines at base of shell; light to chestnut brown colour, dark brown spiral band may be present. Aperture ovate with angular margin below, inside greyish white with brown bands. Size: H = 18–44 mm, B = 13–26 mm.

**Embryonic Shell** (Fig. 48): Smooth; up to four rapidly increasing whorls, comparatively large compared to adult as well as to other species.

**Operculum**: Round, 6 to 8 regularly increasing whorls; central nucleus; clearly smaller than aperture.

**Radula** (Fig. 46B): 125 to 170 rows of teeth, length of up to 20 mm, corresponding to half of shell height. Rachidian with straight upper rim, base convex by basally extending, broad glabella with more or less straight lateral margins and cut lower rim; very large main denticle flanked by two smaller denticles on each side. Laterals with large, broadly triangular main cusp flanked by two or three minute denticles on inner side and one or two at outer side. Inner and outer marginals broadly spatulate, with large main cusp and tiny inner denticle.

**Stomach**: Stomach as in *B. citrina* (Fig. 4), except for typhlosoles fused at almost entire length of style sac.

#### Reproductive System

Females contain between 1 and 50 juveniles (n = 6) varying in height between 3.5 and 6 mm.

#### Habitat

Attached to rocks in sectors with swift current.

#### Ecology

Specimens collected during a field trip in 2001 frequently infested with drilling sabellids (*Caobangia* spec., Nematoda).

#### Distribution (Fig. 49)

Myanmar, Thailand: Restricted to Salween and its tributary Thoungyin (= Maenam Moei), forming the border between Thailand and Myanmar.

#### Remarks

Can hardly be confused with any other species for its spiny shell. Spines of other species are considerably smaller (e.g., *B. binodosa*, *B. costula*, *B. spinata*).



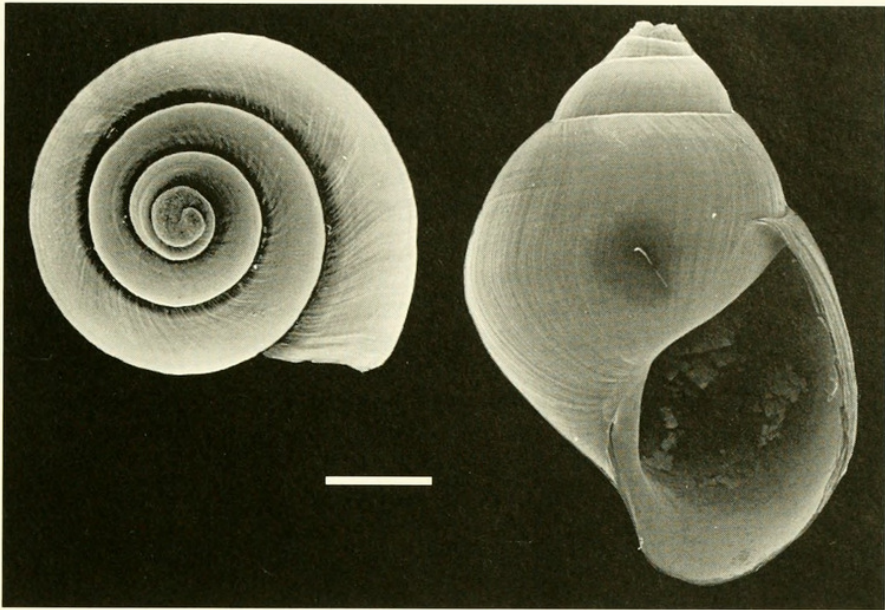


FIG. 48. Embryonic shell morphology of *B. pagodula*. SEM images of embryonic shell removed from brood pouch (ZMH); apical and front view. Scale bar = 1 mm.

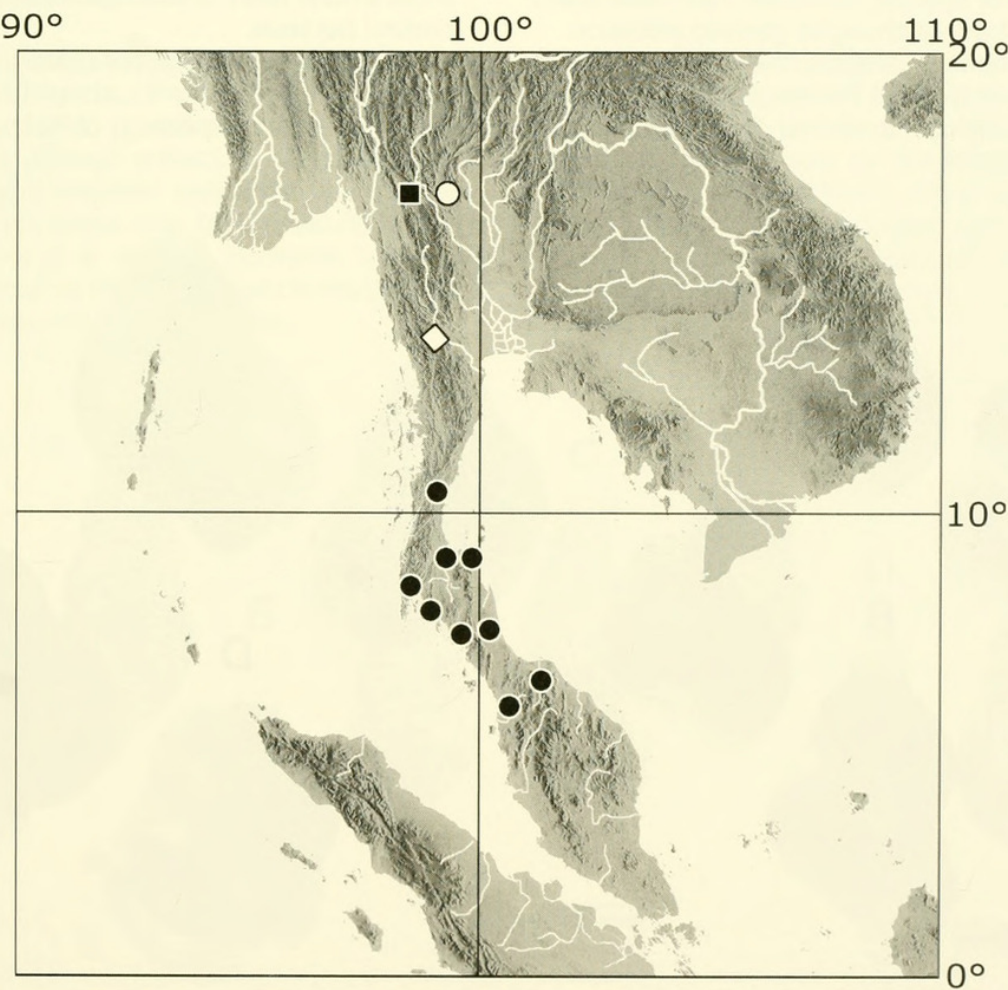


FIG. 49. Distribution of *B. peninsularis* (close circles), *B. siamensis* (open circle), *B. pagodula* (close rectangle) and *B. wykoffi* (open rectangle).



*Brotia paludiformis* (Solem, 1966)  
(Figs. 46C, 50)

*Paracrostoma paludiformis* Solem, 1966: 17, pl. 1, figs. H–J, text-fig. 2 (*non Semisulcospira paludiformis* Yen, 1939) ("Thailand, Provinz Phitsanulok: Kaek River at the Thung Salaeng Luang Falls"); types not seen.

*Paracrostoma paludiformis paludiformis* – Brandt, 1974: 187, pl. 14, fig. 45.

*Paracrostoma paludiformis* – Köhler & Glaubrecht, 2002a: 121–156.

*Brotia paludiformis* – Glaubrecht & Köhler, 2004: 291, 292.

### Taxonomy and Systematics

For specimens from the Kaek River, the name "*Paracrostoma paludiformis*" was first employed by Solem (1966) in reference to a presumably pleurocerid species from Hainan described by Yen (1939). Although, Solem (1966) erred in assuming that both taxa are conspecific, the name introduced by him is available as the species epitheton has been used in context with a changed generic affiliation.

This species belongs to the Kaek River species flock in Central Thailand and was revised and transferred to *Brotia* by Glaubrecht & Köhler (2004).

### Material Examined

Thailand: Prov. Phitsanulok: Kaek River: Sopha Falls, 71 km E of Phitsanulok (ZMH; BMNH; SMF 215963).

### Differential Diagnosis

Shell conical, thick, very robust; two or three convexly rounded whorls; body whorl conspicuously inflated; entirely smooth except for growth lines; aperture broadly oval.

### Description

**Shell** (Fig. 50): Medium sized to large, broadly ovate, two or three well rounded, convex whorls; spire eroded; body whorl large, inflated; smooth sculpture consisting of faint growth lines, only rarely with spiral row of small, rounded nodules; colour chestnut brown; aperture wide, oval, well rounded below. Shell size: H = 24–30 mm, B = 18–22 mm.

**Operculum**: Oval to slightly elongated, up to three whorls fast increasing in diameter, sub-central nucleus.

**Radula** (Fig. 46C): Length of ribbon:  $m = 23.4$  mm ( $sd = 1.3$  mm;  $n = 3$ ), about 190 rows of teeth. Denticle morphology corresponding to *B. armata*.

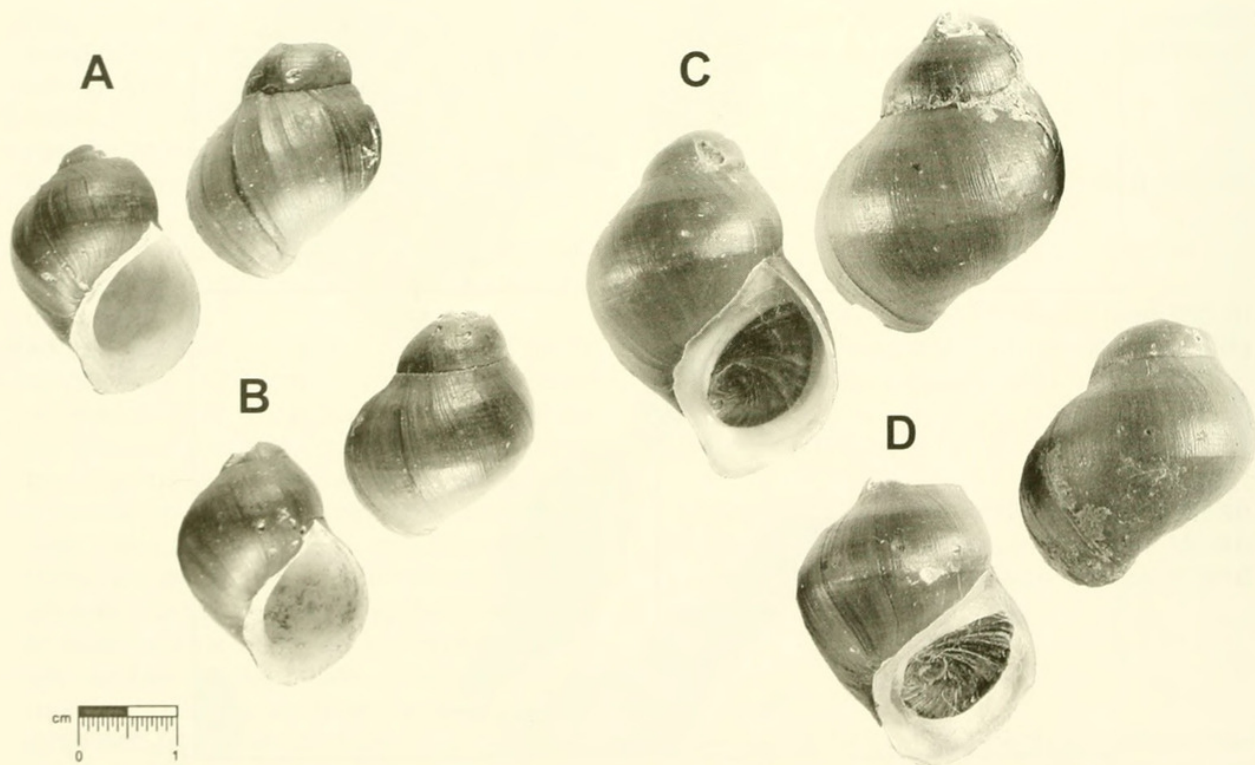


FIG. 50. Shell morphology of *B. paludiformis*. A–B: Thailand, Kaek River, Sopha Falls (SMF 215963); C–D: Thailand, Kaek River, Sopha Falls (ZMH). Scale = 10 mm.



*Embryonic shell morphology, Soft body anatomy*: Unknown.

#### Distribution

Thailand: Prov. Phitsanulok: Endemic to Kaek River; exclusively known from Sopha waterfalls.

#### Remarks

Very distinct species in its globular shape and inflated body whorl. Somewhat similar is *B. pseudosulcospira*, which differs most conspicuously by its more flattened whorls.

*Brotia peninsularis* (Brandt, 1974)  
(Figs. 46D, 51, 52)

*Brotia* (*Brotia*) *costula peninsularis* Brandt, 1974: 183, pl. 1, fig. 17 ("Thailand: Maenam Lampa, Province of Pattalung" = River Lampa, Prov. Phattalung), holotype SMF 220570, 17 paratypes SMF 220571, six paratypes SMF 220572, paratypes ZSM 19983232, paratypes ZMH; types seen.

#### Taxonomy and Systematics

Brandt (1974) mentioned a series of 50 paratypes (Brandt collection 496). Thus, additional type material may exist that was not traced. This taxon has been described as a subspecies of *B. costula*. However, it is considered here as distinct based on morphological and molecular genetic data.

#### Material Examined

Thailand: Prov. Surat Thani, Wiphawadi waterfalls, bridge at highway 401 to Nakhon Si Thammarat, 20 km off Surat Thani, 9°5.88'N, 99°46.33'E (ZMB 200.041-2), Pum Pin near Takuha, km 63.5 (ZMH; ZSM 19983231); Prov. Phang Nga, Khlong Ipan, bridge at street 4035 between Ao Luk and Phrasaeng (ZMB 200.043), Bok Ka Ra Ni falls near Phang Nga (ZMH; ZSM 19983233); Prov. Krabi, street 4 at Ao Luk, 8°91.44'N, 98°34.90'E (ZMB 200.046), creek between Krabi and Baling (ZSM 19982334), Klong Nga opposite Krabi (ZSM 19983230); Klong Sag, Ban Nai Sra (MCZ 288636; marked as paratypes); Yala, creek at new mine, NW Na Pupo (ZMH; ZSM 19983229).

#### Differential Diganosis

Shell rather small, thin but solid, conical; body whorl relatively large; regular spiral lines, rarely axial ribs.

#### Description

*Shell* (Fig. 51): Small, spire oval to conical turreted, moderately thick, up to eight flattened to rounded whorls, narrow suture; regular spiral ridges crossed by growth lines predominant sculpture; rarely, small spiny nodules formed on spiral ridges; colour lightly brown to olive-brown. Aperture oval, well rounded below, pointed above.

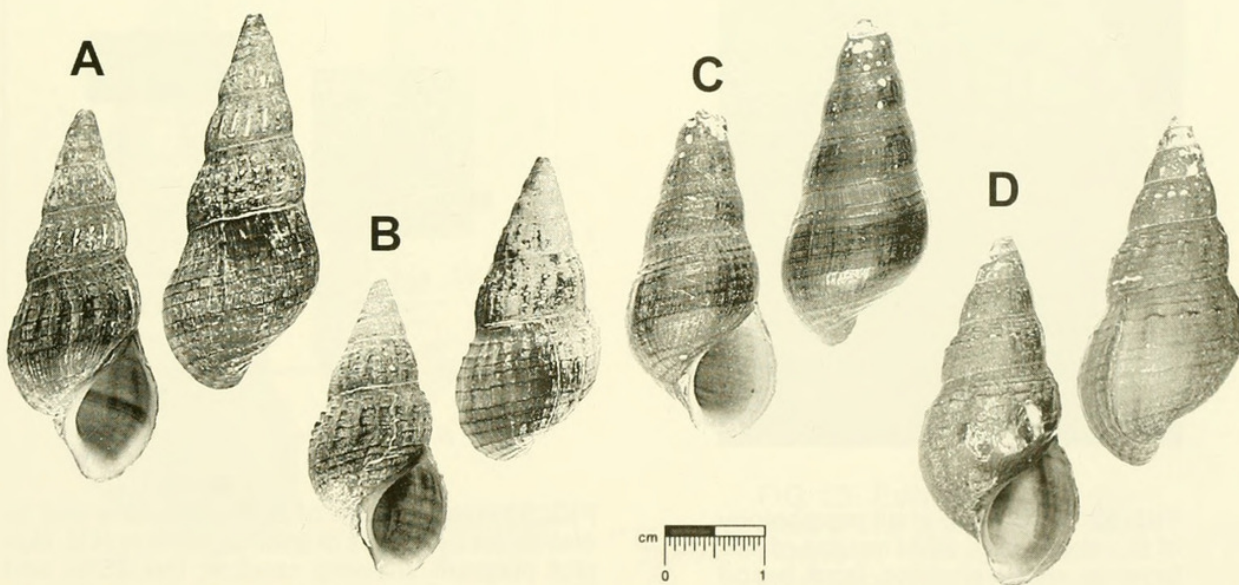


FIG. 51. Shell morphology of *B. peninsularis*. A–B: Paratypes ZMH; C: Paratype ZSM 19983232; D: Thailand, Surat Thani (ZMB 200.242). Scale = 10 mm.



*Embryonic Shell* (Fig. 52): Subsequent whorls smooth, sculptured only by growth lines. Average proportions: H = 3.2 mm, B = 0.4 mm, HA = 0.18 mm, BA = 0.33 mm, DA = 0.65 mm (for n = 10).

*Operculum*: Round to slightly oval, five to six whorls gradually increasing in diameter.

*Radula* (Fig. 46D): Rachidian with slightly concave upper rim, glabella well developed, rounded below, concave lateral margins; main cusp flanked by three smaller denticles on each side. Lateral cusp formula 2–13. Inner and outer marginals with two cusps, the outer one being broader; inner marginal teeth generally broader than outer ones.

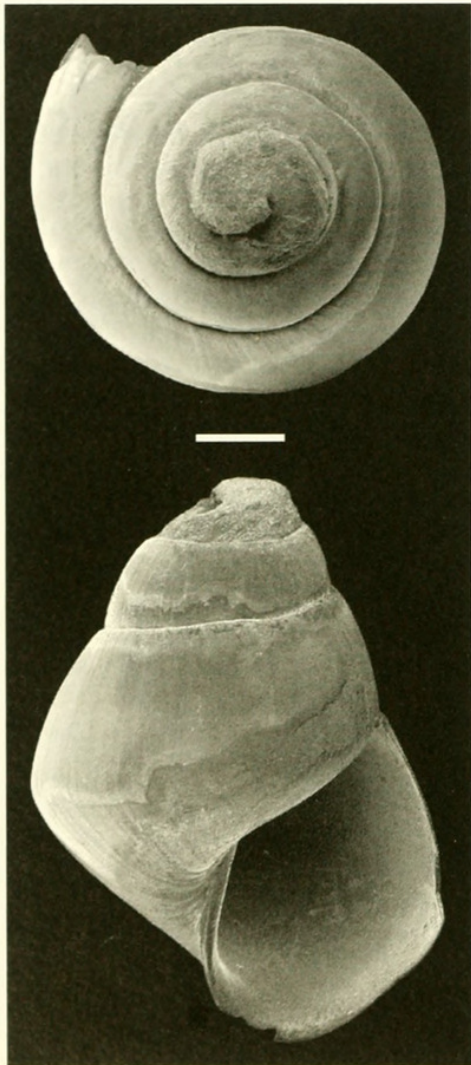


FIG. 52. Embryonic shell morphology of *B. peninsularis*. SEM images of embryonic shell removed from brood pouch (paratype ZMH); apical and front view. Scale bar = 0.3 mm.

*Stomach*: Typical (as in *B. citrina*; Fig. 4); except for both typhlosoles unfused at entire length of style sac.

Reproductive System

One female contained 23 juveniles (ZMB 200.242).

Habitat

Rather small, swift streams on limestone; attached to rocks and boulders, sitting directly in the water current.

Distribution (Fig. 49)

Thailand, Malaysia: Malay Peninsula S of Isthmus of Kra (Thai provinces Chumphon, Surat Thani, Krabi, Phang Nga, and Nakhon Si Thammarat as well as province of Pahang, Malaysia; Brandt, 1974).

Remarks

Type specimens of *B. siamensis* are very similar but can be discriminated statistically significant by parameters N and H/B (Table 3, Fig. 53).

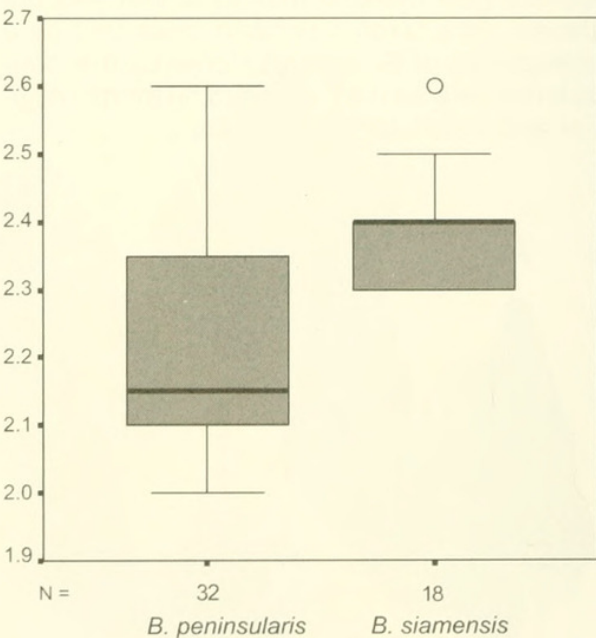


FIG. 53. Comparison of *B. peninsularis* and *B. siamensis* by means of shell parameter H/B. Box plot diagram showing median, the 25%- and 75%-percentile and largest non-extremes (less than 1.5 times of box height).



*Brotia praetermissa* Köhler & Glaubrecht, 2002  
(Figs. 46E, 54–56)

*Brotia praetermissa* Köhler & Glaubrecht, 2002b: 353–355 (“Borneo”), holotype BMNH 20010482/A; three paratypes BMNH 20010482/B (Fig. 54); types seen.

#### Taxonomy and Systematics

This species was described from material in the BMNH and is one of two *Brotia* species recorded from Borneo, even though the locality data is vague.

#### Differential Diganosis

Shell highly turreted, with stepped whorls, conspicuous spiral ridges, one or two spiral rows of spiny nodules; operculum round, relatively small; inner and outer marginal teeth with very broad, oval main tooth, only some outer marginals with accessory cusp at inner side.

#### Description

*Shell* (Fig. 54): Highly turreted, about eight stepped whorls, covered by thick calcareous

deposit; tip eroded; relatively deep suture; sculpture of six strong spiral ridges, most prominent at the base, one or two spiral rows of spiny nodules most prominent at second whorl; early whorls smooth or sculptured by inconspicuous axial ribs only. Colour hazelnut brown to yellowish brown (probably leached due to conservation). Average shell dimensions: H = 58.2 mm, B = 22.3 mm.

*Embryonic Shell* (Fig. 55): Turreted, flattened whorls, smooth texture, faint spiral lines, regular growth lines; about 4 mm in height.

*Operculum*: Round, up to 10 whorls, central nucleus; considerably smaller than aperture.

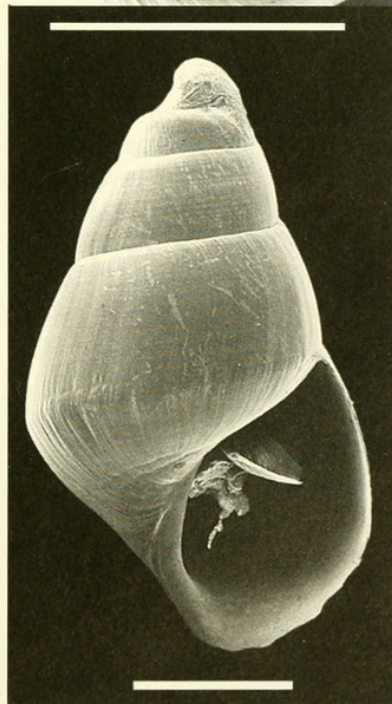
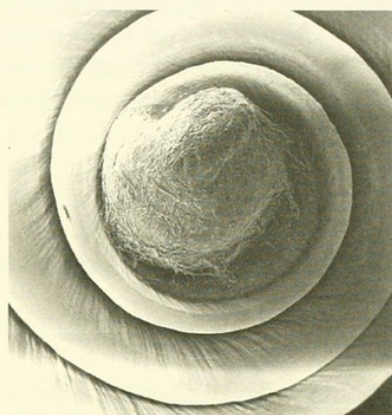


FIG. 55. Embryonic shell morphology of *B. praetermissa*. SEM images of embryonic shell removed from brood pouch (paratype, BMNH 20010482/B); apical and front view. Scale bar = 1 mm.

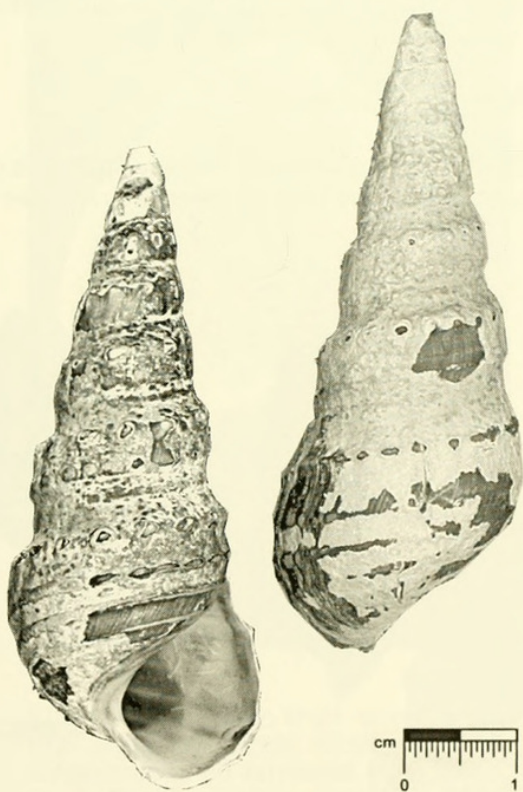


FIG. 54. Shell morphology of *B. praetermissa*. Holotype BMNH 20010482/A. Scale bar = 10 mm.



*Radula* (Fig. 46E): Ribbon about 20 mm long with 120 rows of teeth; rachidian with one main cusp flanked by two smaller denticles on each side that taper in size, glabella well developed with rounded basal margin; anterior rim of rachidian slightly concave by slightly excavated lateral corners, basal rim rounded. Main cusp of laterals flanked by two accessory denticles on each side, glabella well developed comparatively long lateral extensions. Inner marginal tooth with one very broad, spatula-shaped cusp; some of outer marginals in addition possess accessory cusp at inner side. Both, inner and outer marginals, curved or knee-shaped, outer ones with lateral flange at exterior side.

*Stomach* (Fig. 56): Major and minor typhlosole unfused, gastric pad large, sorting area with two well developed crescent septate thickenings.

#### Reproductive System

One female contained 18 shelled juveniles.

#### Distribution

Borneo (locality data vague).

#### Remarks

Somewhat similar is *Jagora asperata* from the Philippines, which can be distinguished by its different soft body, embryonic shell, and radular morphology (Köhler & Glaubrecht, 2003).

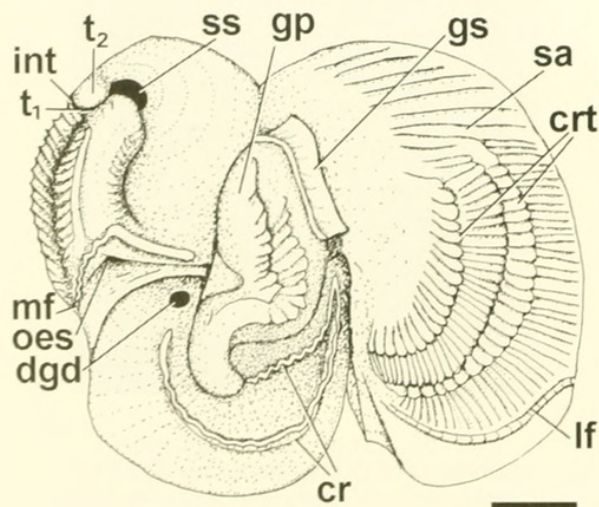


FIG. 56. Stomach morphology of *B. praetermissa*, paratype BMNH 20010482/B.

#### *Brotia pseudoasperata* Brandt, 1968 (Figs. 57–59)

*Brotia (Brotia) pseudoasperata* Brandt, 1968: 270, 271, pl. 10, fig. 57, text-fig. 39 ("Maenam San and its tributary Huai Kao Man", Prov. Loei, Thailand), holotype SMF 197375 ("Huai Kao Man, Phung Song, Loei"), 18 paratypes SMF 19381, 12 paratypes ZSM 19983244, nine paratypes ZSM 19983245, five paratypes RMNH 5240/5, 14 paratypes BMNH 1976072 (Fig. 57); types seen; Brandt, 1974: 177, 178, pl. 13, fig. 31.

*Brotia pseudoasperata* – Köhler & Glaubrecht, 2002a: 144.

#### Taxonomy and Systematics

Brandt (1968) stated that shells from Annam (China) and Laos erroneously attributed to "*Melania asperata*" belong to his species. Another lot of similar shells is known from Mt. Carin (Pegu, Myanmar; ZMB 47.129). However, it is still questionable whether all these references can really be attributed to this species. We rather suspect that *B. pseudoasperata* is restricted to the Heung River system. Species limits by means both of morphology and geographical distribution remain dubious unless material suitable for morphological and molecular genetic analyses will be available.

#### Differential Diganosis

Shell elongate turreted; closely spaced axial ribs that support one to three spiral rows of

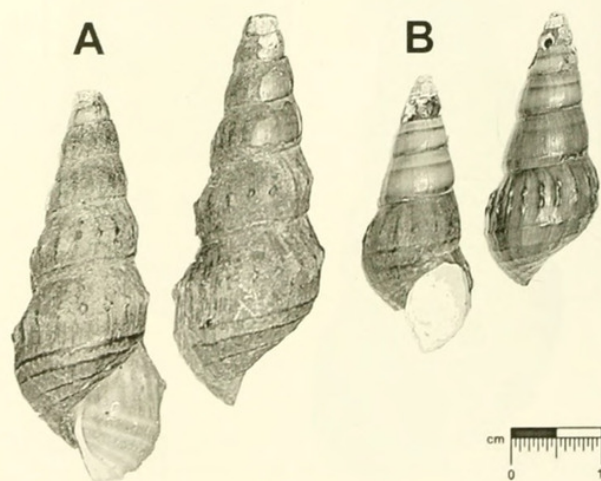


FIG. 57. Shell morphology of *B. pseudoasperata*. A–B: Paratypes ZSM 19983244. Scale bar = 10 mm.



spiny nodules; operculum round with up to eight whorls.

#### Description

**Shell** (Fig. 57): Medium sized, thin but solid, elongate turreted, tip eroded, up to seven convex whorls, narrow suture; thin, regularly spaced axial ribs that support one to three spiral rows of spiny nodules, the first approximately at mid of whorls, the second, if present, at upper half of whorls; upper whorls may be smooth; spiral ridges at base. Colour

hazelnut brown, a dark brown spiral band may be present. Aperture broad, wide, well rounded, produced below. Size: H = 20–27 mm, B = 8–12 mm.

**Embryonic Shell** (Fig. 58): Ovate, smooth except for faint growth lines, comprising 2.0–2.5 whorls. Average proportions: H = 2 mm, B = 1.6 mm, HA = 0.22 mm, BA = 0.33 mm, DA = 0.81 mm (for  $n = 3$ ).

**Operculum**: Round, up to eight gradually increasing whorls, central nucleus; clearly smaller than aperture.

**Radula** (Fig. 59): Ribbon with 90 to 120 rows of teeth. Upper rim of rachidian concave by inflated lateral corners, lower rim almost straight; cutting edge with one main denticle flanked by two smaller ones; glabella narrow, well rounded at base not exceeding lower rim of rachidian, v-shaped with concave lateral margins. Main cusp of laterals flanked by two accessory denticles on each side. Inner and outer marginal teeth with two cusps, outer one broad, rounded, inner one small, pointed.

#### Reproductive System

One female contained 19 shelled juveniles (ZSM 19983244).

#### Distribution

Thailand: With certainty known only from type locality (San River, affluent of Heung River, collecting area of the Mekong), and its tributary Huai Kao Man (Brandt, 1974). Reports from Laos, Vietnam, Myanmar should be treated with caution.

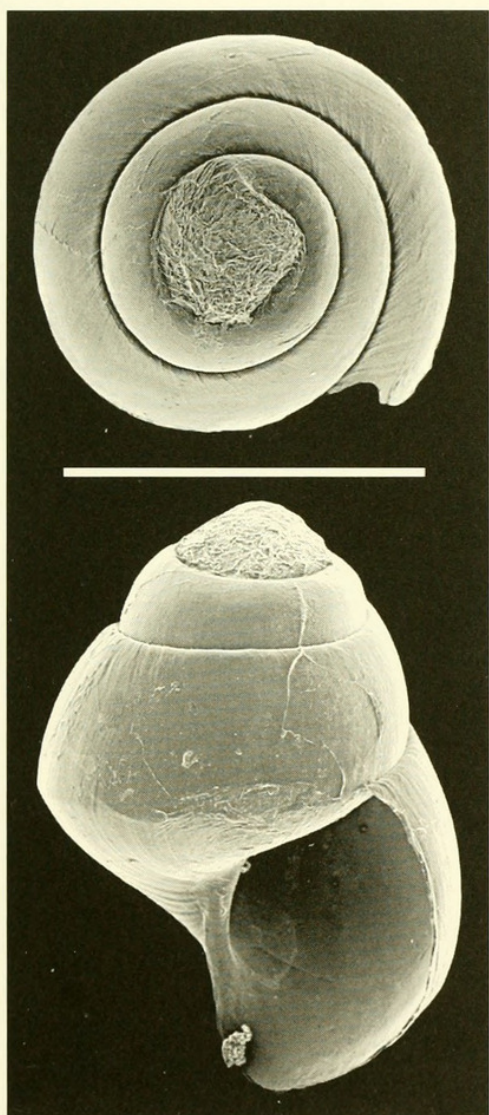


FIG. 58. Embryonic shell morphology of *B. pseudoasperata*. SEM images of embryonic shell removed from dried shell (Thailand, Huai Kao Man, ZSM 19983244); apical and front view. Scale bar = 1 mm.



FIG. 59. Radular morphology of *B. pseudoasperata*, paratype ZMH. Scale bar = 100  $\mu$ m.



*Brotia pseudosulcospira* (Brandt, 1968)  
(Figs. 46 F, 60, 61)

*Brotia* (*Paracrostoma*) *pseudosulcospira*  
Brandt, 1968: 274, 275, pl.10, fig. 61, text-  
fig. 40 ("Maenam Kaek in Pitsanulok Prov.,  
at Wang Nok Nang Aen, Wang Tong District,  
Thailand" = Thailand, Provinz Phitsanulok,  
Wang Tong District, Kaek River at Wang Nok  
Nang Aen), holotype SMF 197379; 23  
paratypes SMF 193586; five paratypes SMF  
194061; 11 paratypes BMNH 1976120; 12  
paratypes ZMH; 11 paratypes ZMH (alc.);  
types seen.

*Paracrostoma pseudosulcospira pseudo-*  
*sulcospira* – Brandt 1974: 185, pl. 13, fig. 42.

*Paracrostoma pseudosulcospira* – Köhler &  
Glaubrecht, 2002a: 144.

*Brotia pseudosulcospira* – Glaubrecht &  
Köhler, 2004: 292.

#### Taxonomy and Systematics

Brandt (1968) described a second subspe-  
cies, *P. p. armata*, which is considered distinct.  
A systematic revision based on morphologi-  
cal and molecular genetic data was presented  
by Glaubrecht & Köhler (2004).

#### Material Examined

Thailand: Prov. Phitsanulok, Kaek River:  
Sakunothayan Falls, 33 km E of Phitsanulok  
(ZMB 200.196, 200.299).

#### Differential Diganosis

Shell conical, up to three flattened whorls,  
rather smooth with growth lines, occasionally  
spiral cords at the base. Aperture widely ovate  
well rounded.

#### Description

*Shell* (Fig. 60): Medium sized, conical, robust,  
frequently with eroded spire, only two re-  
maining, flattened whorls; smooth sculpture  
except for growth lines, occasionally more  
or less developed, regularly spaced spiral  
cords, but not at base of shell. Aperture  
widely ovate well rounded, slightly produced  
below. Size: H = 26–40 mm, B = 18–24 mm.

*Embryonic Shell* (Fig. 61): Smooth, with faint  
growth lines only; size of 2.0–2.5 mm, 2.5  
whorls.

*Operculum*: Oval, up to four whorls fast in-  
creasing in diameter, sub-central nucleus.

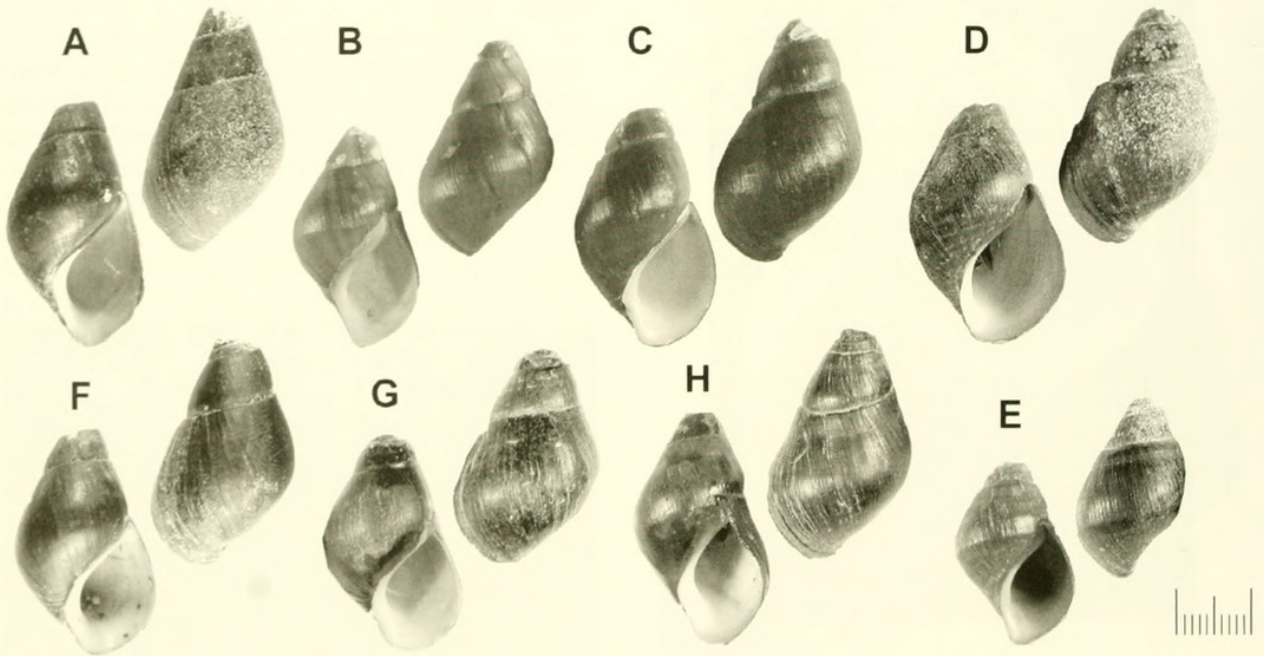


FIG. 60. Shell morphology of *B. pseudosulcospira*. A: Paratype SMF 193586; B–C: Paratypes ZMH; D–E: Paratypes ZMH (alc.); F: Paratype SMF 194061; G–H: Kaek River, Sakunothayan Falls (ZMB 200.299). Scale bar = 10 mm.



*Radula* (Fig. 46F): Length of ribbon:  $m = 25$  mm ( $sd = 2.5$  mm;  $n = 3$ ), up to 180 rows of teeth. Central tooth comparatively broad, glabella very narrow; otherwise similar to *B. armata*.

#### Distribution

Thailand: Prov. Phitsanulok: Endemic to Kaek River, restricted to its westernmost portion (Wang Nok Nang Aen, E of Wang Tong and Sakunothayan Falls close by).

#### Remarks

The shell of *B. pseudosulcospira* is very characteristic. *Brotia paludiformis*, also being smooth, exhibits convexly rounded whorls and an inflated body whorl. It latter lacks spiral lirae

as observed at least in some specimens of *B. pseudosulcospira*. *Brotia armata* has spiny nodules.

*Brotia siamensis* (Brot, 1886)  
(Fig. 62)

*Melania siamensis* Brot, 1886: 90, 91, pl. 7, figs. 3–3b ("Raheng, Siam" = Tak, Prov. Tak, Thailand), lectotype and 18 paralectotypes MHNG, coll. Brot (designated by Köhler & Glaubrecht, 2002a) (Fig. 62); types seen.

*Brotia siamensis* – Köhler & Glaubrecht, 2002a: 147, fig. 3H.

#### Taxonomy and Systematics

Treated in various ways by previous authors, this taxon was considered conspecific with *M. hamonvillei* Brot, 1887, by Bavay & Dautzenberg (1910) for the similar shell. This assumption was also followed by Köhler & Glaubrecht (2002a). In fact, both taxon names are used interchangeably for material in various museum collections (own observations). However, in spite of their conchological similarity, the taxa are not conspecific as is revealed by a different embryonic shell morphology (unpubl. data). *Melania hamonvillei* possesses a protoconch typical for species of *Adamietta* and certainly is not member of *Brotia*.

*Melania siamensis* was further been stated to be identical with *M. jullieni* by Morlet (1891) and *B. costula* by Brandt (1968, 1971). Also Köhler & Glaubrecht (2002a) noticed that some type specimens of *M. siamensis* are similar to *B. costula*, whereas some others are not (Fig. 57). However, this superficial similarity is no reason to assume that both taxa are conspecific, since their distributional areas are separated by a considerable geographic distance. Re-examination of Brandt's voucher material reveals that the author was also not sure how to distinguish between *B. siamensis* and *B. peninsularis*. The latter taxon was treated by him as a subspecies of *B. costula*. Some lots of this species were labelled by him with *B. siamensis*, however. Both taxa are indeed similar. *B. peninsularis* as considered here is restricted to the Malay Peninsula south of the Isthmus of Kra. The only confirmed record of *B. siamensis* is the type locality, Tak, about 700 km N of this isthmus. A reliable decision on the relationships of *B. siamensis* and *B. peninsularis* awaits the examination of well-preserved material from the area of Tak. For

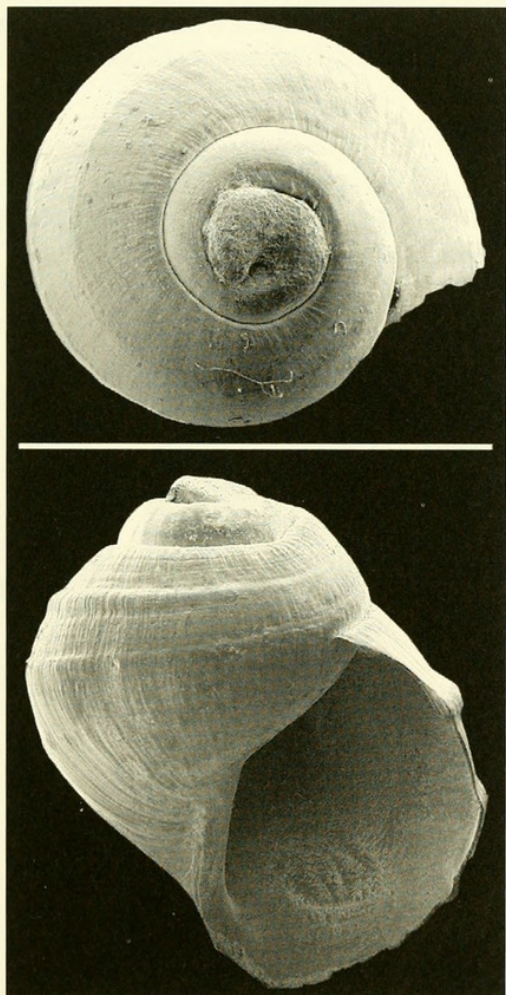


FIG. 61. Embryonic shell morphology of *B. pseudosulcospira*. SEM images of embryonic shell removed from dried shell (paratype ZMH); apical and front view. Scale bar = 1 mm.



TABLE 3. Result of disriminant analysis of shell parameters of *B. peninsularis* and *B. siamensis*.

	Predicted group membership	
	<i>B. peninsularis</i>	<i>B. siamensis</i>
<i>B. peninsularis</i>	29 (93.5%)	2 (6.5%)
<i>B. siamensis</i>	0 (0%)	18 (100%)

the time being, we consider both as distinct species, because they can be discriminated by statistical analyses of shell parameters with significance (Table 3).

Differential Diganosis

Shell variable, rather small, elongate turreted; apex frequently truncated; regularly spaced spiral ridges, sometimes axial ribs, mostly only on upper whorls; greenish to olive brown or dark brown to almost black, brown spiral band may be visible.

Description

*Shell* (Fig. 62): Medium sized, conical to elongate turreted, up to six convex whorls, apex

frequently truncated; regularly spaced spiral ridges, most prominent at the base, axial ribs, mostly on upper whorls, may be lacking. Colour greenish to olive brown or dark brown to almost black; dark brown spiral band may be visible. Size: H = 2639 mm, B = 11–16 mm.

*Embryonic Shell, Radula, Operculum, Soft Body*: Unknown.

Remarks

Similar *B. peninsularis* tends to have larger body whorl compared to the shell height, whorls more rounded in diameter. *Brotia jullieni* has a much larger shell, larger body whorl, wider aperture, protracted basal lip. *Brotia costula* is larger, not truncated, pyramidal turreted, more elongated in shape, different sculpture. “*Melania hamonvillei*” has distinct embryonic shell structure, resembling, for example, *B. testudinaria* (Köhler & Glaubrecht, 2001).

Distribution (Fig. 49)

Thailand: Type locality only known reference: Tak (Prov. Tak, north-central Thailand) at banks of Ping River.

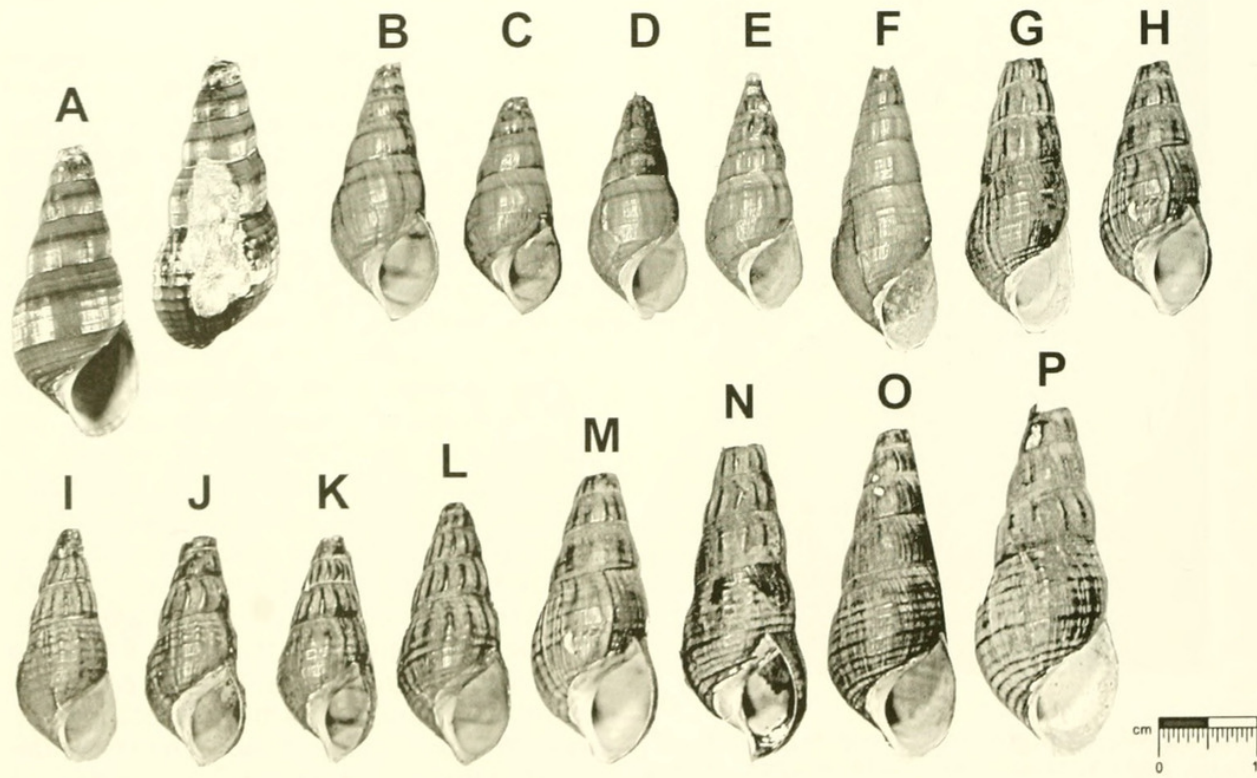


FIG. 62. Shell morphology of *B. siamensis*. A: Lectotype MHNG (front and rear); B–P: Paralectotypes MHNG. Scale bar = 10 mm.



*Brotia solemiana* (Brandt, 1968)  
(Figs. 46G, 63)

*Brotia* (*Paracrostoma*) *solemiana* Brandt, 1968: 273, pl.10, fig. 60 ("Maenam Pong at Ban Pa Nok Kao, Loei Prov." = Thailand, Prov. Loei, Pong River bei Ban Nok Kao), holotype SMF 197377, seven paratypes SMF 193583, six paratypes SMF 193585, two paratypes RMNH 55233/2 (Fig. 63); types seen.

*Paracrostoma solemiana* – Brandt 1974: 186, pl. 13, fig. 44; Köhler & Glaubrecht, 2002a: 147.

*Brotia solemiana* – Glaubrecht & Köhler, 2004: 292, 293.

#### Taxonomy and Systematics

Brandt (1968, 1974) stated a slender shell, flattened whorls, an elongated aperture to be characteristic for this species. Furthermore, he assumed that it is endemic to the Pong River,

between the provinces of Loei and Kon Kaen, central to western Thailand. Glaubrecht & Köhler (2004) attributed specimens also from the Kaek drainage to this species mainly due to a corresponding shell morphology. The description of soft body features is mainly based on these specimens.

#### Material Examined

Thailand: Prov. Loei, Loei River: Tat Kok Falls at the road 2216 near Wang Saphung (ZMB 200.174); Prov. Phitsanulok, upper course of the Kaek River at Sri Dit Falls (ZMB 200.203).

#### Differential Diganosis

Shell conical, two or three flattened whorls, smooth sculpture except for growth lines and occasionally fine spiral ridges, spiral lirae lack at base of shell; aperture widely ovate, acute or produced below.

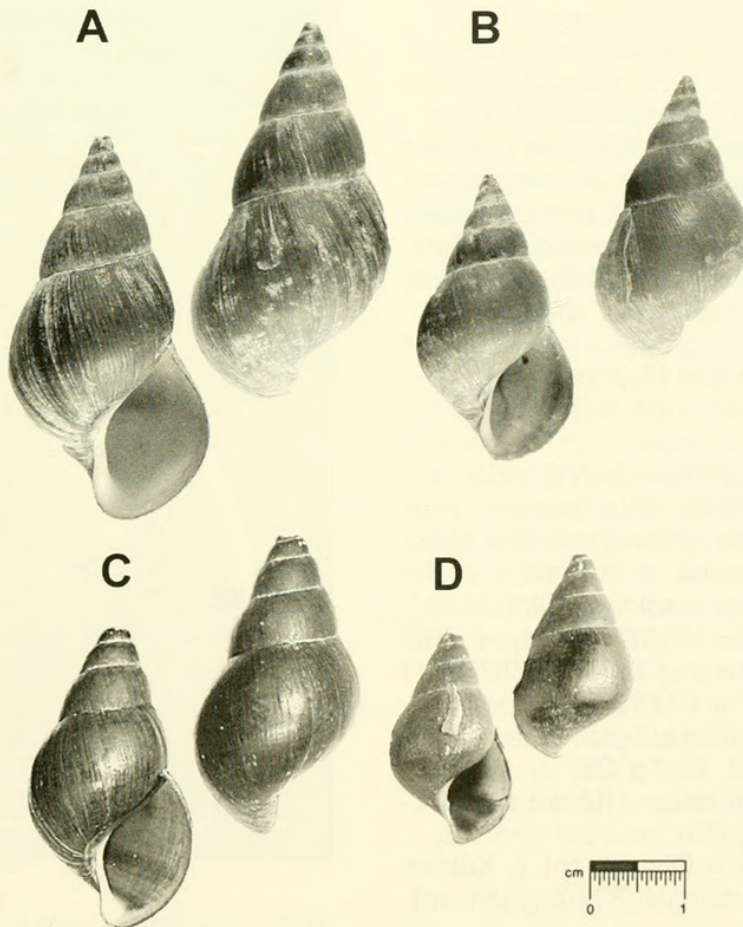


FIG. 63. Shell morphology of *B. solemiana*. A–B: Paratypes SMF 193585; C: Prov. Loei, Tat Kok Falls (ZMB 200.174); D: Kaek River, Sri Dit falls (ZMB 200.203). Scale bar = 10 mm.



## Description

*Shell* (Fig. 63): Medium sized, conical, robust, with two or three flattened whorls, tip eroded; smooth sculpture except for growth lines, in some specimens inconspicuous spiral ridges, spiral lirae lack at base of shell; aperture widely ovate, acute or produced below. Colour yellowish to greenish brown. Size: H = 26–40 mm, B = 18–24 mm.

*Operculum*: Oval, up to four whorls, sub-central nucleus.

*Radula* (Fig. 46G): Length of the ribbon:  $m = 16.0$  mm (sd = 3.4 mm;  $n = 4$ ), 150–160 rows of teeth. Rachidian relatively narrow, otherwise widely corresponding to *B. armata*.

*Stomach*: Typical, as described for *B. citrina* (Fig. 4).

*Embryonic Shell*: Unknown.

## Distribution

Thailand: Loei Prov.: Pong River, Prov. Phitsanulok: Kaek River at Sri Dit Falls in western most headwater.

## Remarks

*Brotia pseudosulcospira* with more flattened whorls, more conical shell; *B. subgloriosa* generally larger, more turreted; *B. microsculpta* with smaller body whorl, rounded aperture, circular operculum. Radula of *B. solemiana* shorter as in other Kaek River species.

*Brotia subgloriosa* (Brandt, 1968)  
(Figs. 46H, 64, 65)

*Brotia binodosa subgloriosa* Brandt, 1968: 269, pl. 10, fig. 56, text-fig. 38 ("Thailand: Huai Chieng Nam, tributary of the Kaek River, about 92 km E of Pitsanulok at the bridge of the Friendship Highway"), holotype SMF 19737, 20 paratypes SMF 193572, paratype ZSM 19983213, six paratypes ZSM 19983219, 11 paratypes ZMH (Fig. 64); types seen.

*Brotia (Brotia) binodosa subgloriosa* – Brandt, 1974: 175, 176, pl. 13, fig. 28.

*Brotia spinata subgloriosa* – Köhler & Glaubrecht 2002a: 129.

*Brotia subgloriosa* – Glaubrecht & Köhler, 2004: 293.

## Taxonomy and Systematics

Described as a subspecies of *B. binodosa*, it was stated that both taxa are connected by in-

termediate morphs (Brandt, 1968). Such intermediates were not found by us among the voucher material examined; their existence is thus contended herein. According to Brandt (1968, 1974), *B. subgloriosa* and *B. binodosa* occur sympatrically in parts of the Kaek River, which conflicts a relation as geographical subspecies. For this reason, *B. subgloriosa* is considered as distinct species, perhaps closely related to *B. binodosa*. According to Glaubrecht & Köhler (2004) this species likely is member of the Kaek River species flock.

## Differential Diganosis

Shell elongate turreted, entirely smooth, aperture elongate produced and relatively narrow.

## Description

*Shell* (Fig. 64): Medium sized, solid, elongate turreted; up to five convex, rounded whorls, truncated tip; smooth except for thin growth lines. Colour olive-brown, often covered with dark mineral deposits. Basal whorl relatively large. Aperture wide, elongate, produced below. Size: H = 25–45 mm, B = 16–24 mm.

*Embryonic Shell* (Fig. 65): Conical, up to 3.5 whorls; smooth sculpture with faint growth lines.

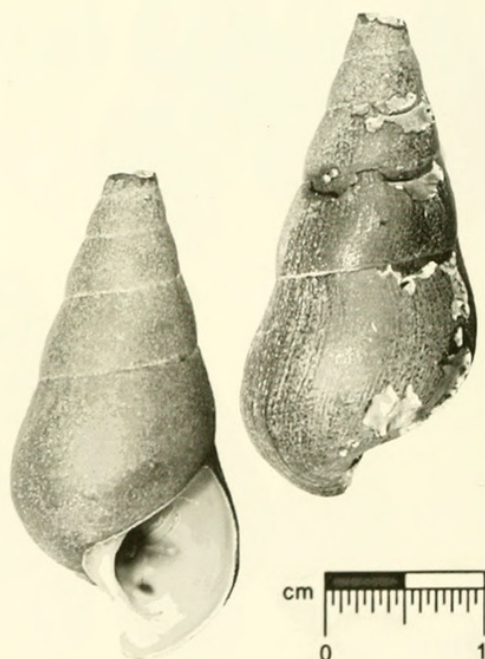


FIG. 64. Shell morphology of *B. subgloriosa*. Paratype ZSM 19983213. Scale bar = 10 mm.



*Operculum*: Oval, up to five whorls gradually increasing in diameter, nearly central nucleus.

*Radula* (Fig. 46H): Length of ribbon: 18 mm ( $n = 1$ ), 220 rows of teeth. Central tooth comparatively broad, glabella very narrow; otherwise corresponding to the radula of *B. armata*.

#### Reproductive System

Two dried shells (ZSM 19983219) contained 130 and 156 shelled juveniles, respectively that varied in height between 0.5 and 1.5 mm.

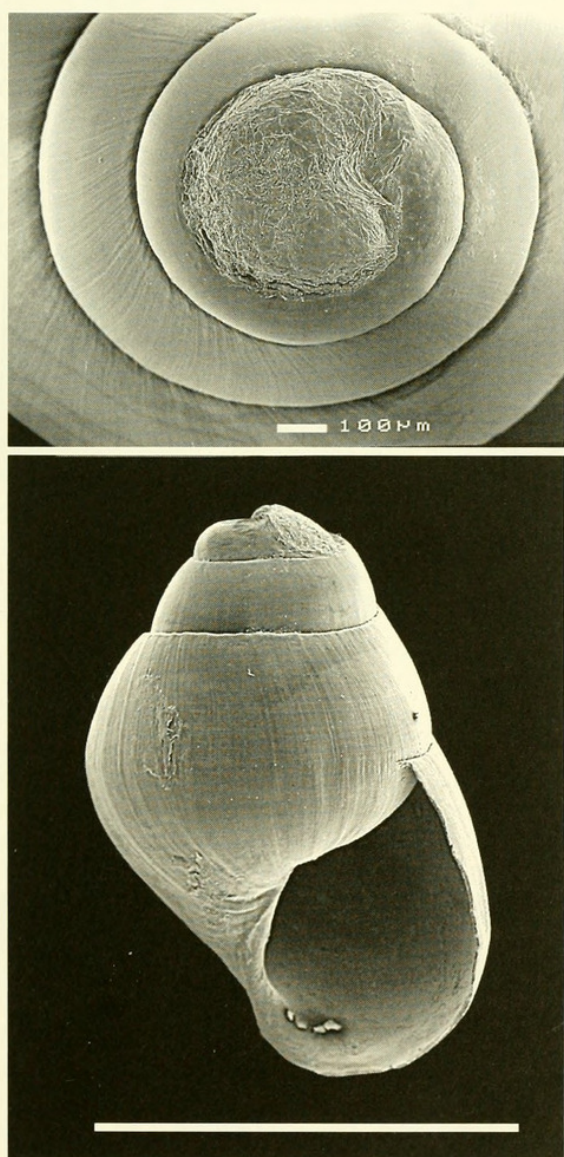


FIG. 65. Embryonic shell morphology of *B. subgloriosa*. SEM images of embryonic shell removed from dried shell (paratype ZSM 19983213); apical and front view. Scale bars = 0.1 mm (above), and 1 mm (below).

#### Distribution

Thailand: Endemic to Kaek River, between 65 km (at Sopha Falls) and 92 km E of Phitsanulok, and tributary Huai Chieng Nam (Brandt, 1968: 270).

#### Remarks

Superficially similar to other Thai species with smooth shells. *Brotia microsculpta* much smaller, with comparatively smaller, rounded aperture and operculum; *B. pseudosulcospira* more conical in shape with flattened whorls; *B. solemiana* more compact with comparatively broader but shorter shell.

*Brotia sumatrensis* (Brot, 1875)  
(Figs. 66, 67B–E)

*Melania* (*Melanoides*) *sumatrensis* Brot, 1875: 87, pl. 10, fig. 2b, pl. 13, figs. 1a, b ("Sumatra: Palembang"), three syntypes MHNG, Brot collection, one syntype MCZ 112689 (Figs. 66A–C); types seen.

*Melania sumatrensis* – Schepman, 1886: 13.

*Melania boeana* Brot, 1881: 154, 155, pl. 6, fig. 1 ("Boea, Sumatra" = Bua, Sumatra), lectotype and four paralectotypes MHNG, Brot collection (designated by Köhler & Glaubrecht, 2002a) (Figs. 66F–J); types seen.

*Melania* (*Brotia*) *episcopalis* – Martens, 1900: 10.

*Melania* (*Melanoides*) *palembangensis* Strubell, 1897: 12 ("Südsumatra" = South Sumatra); types not seen.

*Brotia costula* – Benthem Jutting, 1956: 374–378, fig. 76 [partim]; Benthem Jutting, 1959: 92–95 [partim]; Brandt, 1974: 175, pl. 13, figs. 37–39 [partim]; Köhler & Glaubrecht, 2001: 296–299, figs. 1D, 10A–C, G, H [partim] (*non M. costula* Rafinesque, 1833).

*Brotia* (*Antimelania*) *costula* – Subba Rao, 1989: 108, 109 [partim] (*non M. costula* Rafinesque, 1833).

*Brotia variabilis* – Rensch, 1934: 239 [partim]; Bequaert, 1943: 433, 434, pl. 33, figs. 11–16 [partim]; Solem, 1966: 15 (*non M. variabilis* Benson, 1836).

#### Taxonomy and Systematics

*Brotia sumatrensis* has been subsumed under *B. costula* by most previous authors (see also under that species), but molecular genetic



data shows that the Sumatran species is distinct. Problems of earlier authors to satisfactorily diagnose this species persist to the present due to lack of well-preserved soft body material. Shells examined from various museum collections are remarkably plastic, which may indicate the existence of yet undiscovered, morphologically similar species on Sumatra. This renders a correct characterisation and delineation of *B. sumatrensis* problematic and provisional. For the time being, we assign similar shells to *B. sumatrensis*, as representing the

oldest available name. Future studies may reveal a higher diversity of similar *Brotia* species on Sumatra. Brot (1875) struggled with the diagnosis of *B. sumatrensis* and was unsure whether this species should instead be considered a synonym of *M. infracostata* from Java. Schepman (1886: 13, 14, pl.1, figs. 3a, b, 4a, b) described and depicted a new var. *mitescens* for material with smooth shells, using a manuscript name of Martens. This variety is considered a synonym of *M. torquata* for its rather round, small operculum and fragile shell. *Mela-*

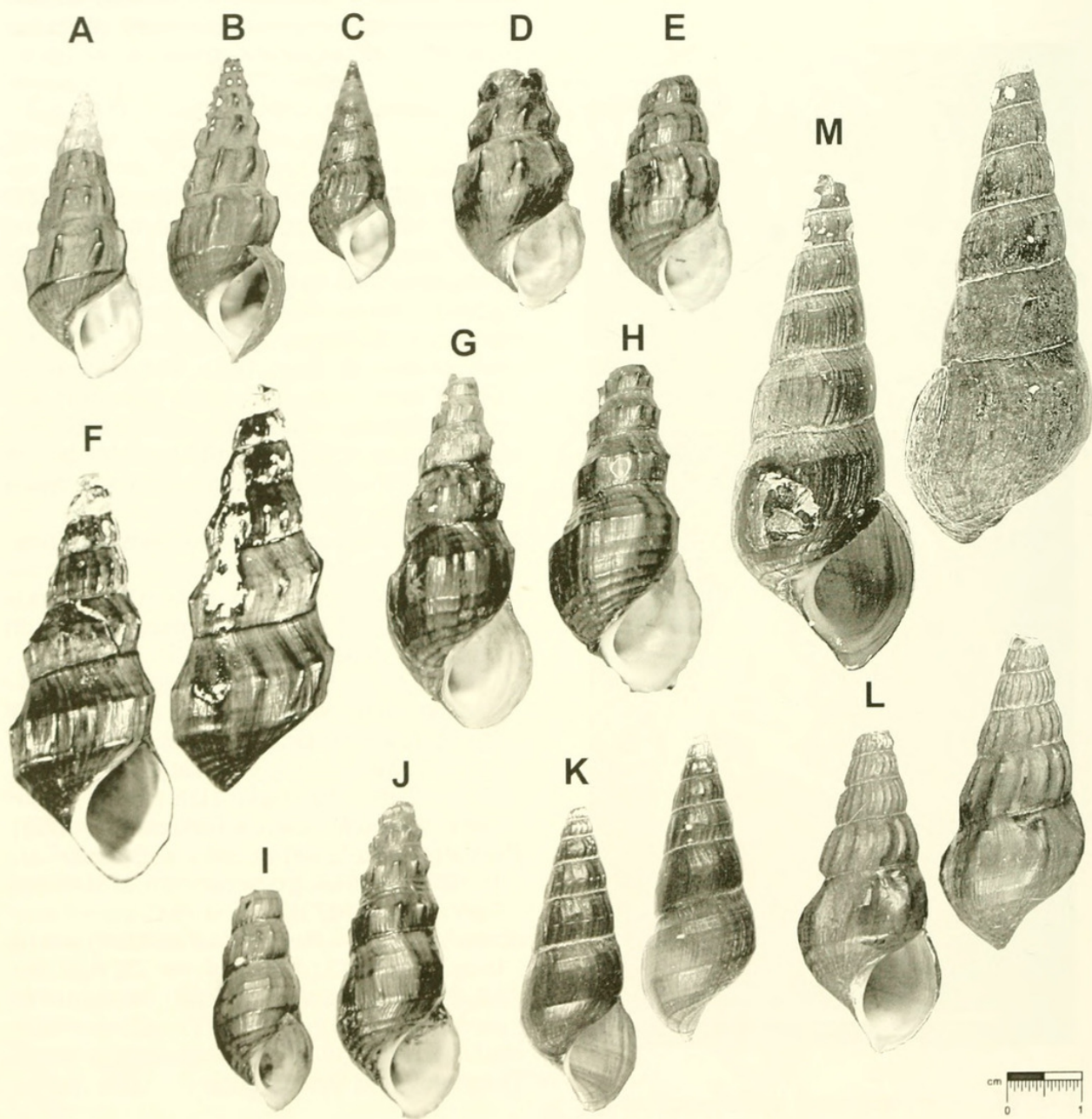


FIG. 66. Shell morphology of *B. sumatrensis*. A–C: Syntypes of *M. sumatrensis* MHNG; D–E: Sumatra (MHNG, coll. Brot); F: Lectotype of *M. boeana* MHNG, front and rear view; G–J: Paralectotypes MHNG; K: Sumatra, Lake Ranau (MZB); L: Sumatra, Jambi (MZB 9013); M: Sumatra, Lake Toba, Parapat (ZMB 200.119).



*nia boeana* Brot, 1881, is considered a synonym of *B. sumatrensis*, because we are not able to establish a significant distinction. The original series in the MHNG comprises in total seven specimens. Two of them originally are assigned to a var. b and, thus, not qualified as types (ICZN, Art. 72.4.1.). The type locality "Bua" is a common local village name that occurs several times in Sumatra. Consequently, the type locality of this taxon cannot be specified more accurately.

#### Material Examined

Indonesia: Sumatra (ZMB 200.045; BMNH 1890.2.21.1-4): Tandjung djatti (ZMA); Suengei Ketil, Kampung (ZMA); Sungei Mentjirin near Kampung (ZMA); Kepahiang (ZMB 26.715, 200.039; MHNG); Bengkajang (ZMB 200.040); Sungei Kalau (ZMA); Sungei Minahol (ZMA); Tibitinggi (ZMB 26.717, ZMB 27.680); Demarguri (ZMB 35.819). Prov. Aceh (ZMB 76671; ZMA; MZB 8786): Tributary of Alas River, Ketombe, SE Aceh (MZB 8624); Lake Takengon (ZMB 76.673, 200.136). Prov. Sumatera Utara: Trans-Sumatra highway, bridge 150 km N Bukittinggi, 1°28.28'N, 99°19.41'E (ZMB 200.116); Lake Toba, harbour of Parapat, 2°49.17'N, 98°56.22'E (ZMB 200.119); Trans-Sumatra highway, 1°40.04'N, 99°10.05'E (ZMB 200.120); Sungei Belawan (ZMB 51.776); Sungei Kopas, Kisaran, east coast (ZMA); Tandjung Langkat (ZMA); Laut Tawar, N Sibangun (ZMA; ZMB 87.409, 200.124); Bukit Lawang, at the Wisma Cottage (ZMB 200.125); Bukit Lawang (MZB 7058); Bohorok river (MZB; ZMA); Berastagi, Mt. Sinabung, Gunung Leuser NP (ZMB 200.124); Medan (NMB); Sungei Rambai near Langkat (ZMA), Sungei Deli near Medan (ZMA). Prov. Sumatera Barat: small stream at Pajakumbuh, N Bukittinggi, 0°27.31'S, 100°36.2'E (ZMB 200.122); Danau di Atas (ZMB 200.069, 200.154; RMNH; ZMA); Sumpur (MZB); Ambulutu (MZB 4361); river in Pajakumbuh, N Bukittinggi, 0°27.31'S, 100°36.2'E (ZMB 200.122); Pajakumbuh (RMNH); Lake Maninjau (MZB 8632); Lake Singkarak (ZMA). Prov. Riau: Arau River (MZB 9009); Kampar River, Pulau Jadang (MZB 9010). Prov. Jambi (NMB): Lake Kerinci (RMNH; MZB 4901, 9022); Sungei Merangiu, Gunung Raya (MZB 9013). Prov. Sumatera Selatan, Pagaralam (ZMA), Palembang (RMNH; NMB); Lake Ranau (ZMB 76.288-9; MZB); Sungei Lapan, Langkat (ZMA); Simpang (ZMB 76.296); Sumani (ZMB 200.070); Sungei Musi, Muara Klingi (ZMB 76.295), Air Putih, Tjurup (ZMB 76.298). Prov. Lampung (MZB 7028).

#### Differential Diganosis

Shell elongate turreted, thin but solid, slender, up to nine whorls; sculpture variable, from smooth to ribbed; no marked transition from smooth to ribbed whorls.

#### Description

*Shell* (Fig. 66): Relatively large, elongate turreted, slender in shape, up to nine whorls, rather thin. Sculpture variable; whorls either smooth or with axial ribs; no transition from smooth upper to ribbed lower whorls. One colour, chestnut brown. Shell size: H = 24–75 mm, B = 10–27 mm.

*Operculum*: Oval, four to six whorls, central nucleus.

*Radula* (Figs. 67B–E): Up to 200 rows of teeth; ribbon length up to 30 mm, corresponding to more than half of shell height. Upper margin of rachidian concave by two inflated, well rounded corners; lower corners slightly angled; glabella slightly v-shaped, narrow, well rounded at base, its lateral margins concave. Cutting edge of rachidian with single main cusp and two or three smaller denticles on each side of it; some specimens with single flanking denticle. Laterals with short lateral extensions, pronounced inner flange, two main cusps flanked by two smaller denticles. Inner and outer marginals with two cusps, pointed, of about same size and shape.

*Stomach*: Corresponds to *B. episcopalis* (Fig. 26).

*Embryonic Shell*: Unknown.

#### Distribution (Fig. 68)

Indonesia: Sumatra.

#### Habitat

From fast running, clear forest streams with sandy or stony bottom to muddy irrigation channels in rice fields; even in lakes with polluted waters (e.g., harbour of Parapat, Lake Toba).

#### Remarks

*Brotia costula* tends to be larger and more elongate, axial ribs are regular; *B. episcopalis* differs mainly by a marked transition from smooth upper whorls to strongly sculptured lower whorls, with lesser pronounced axial ribs.



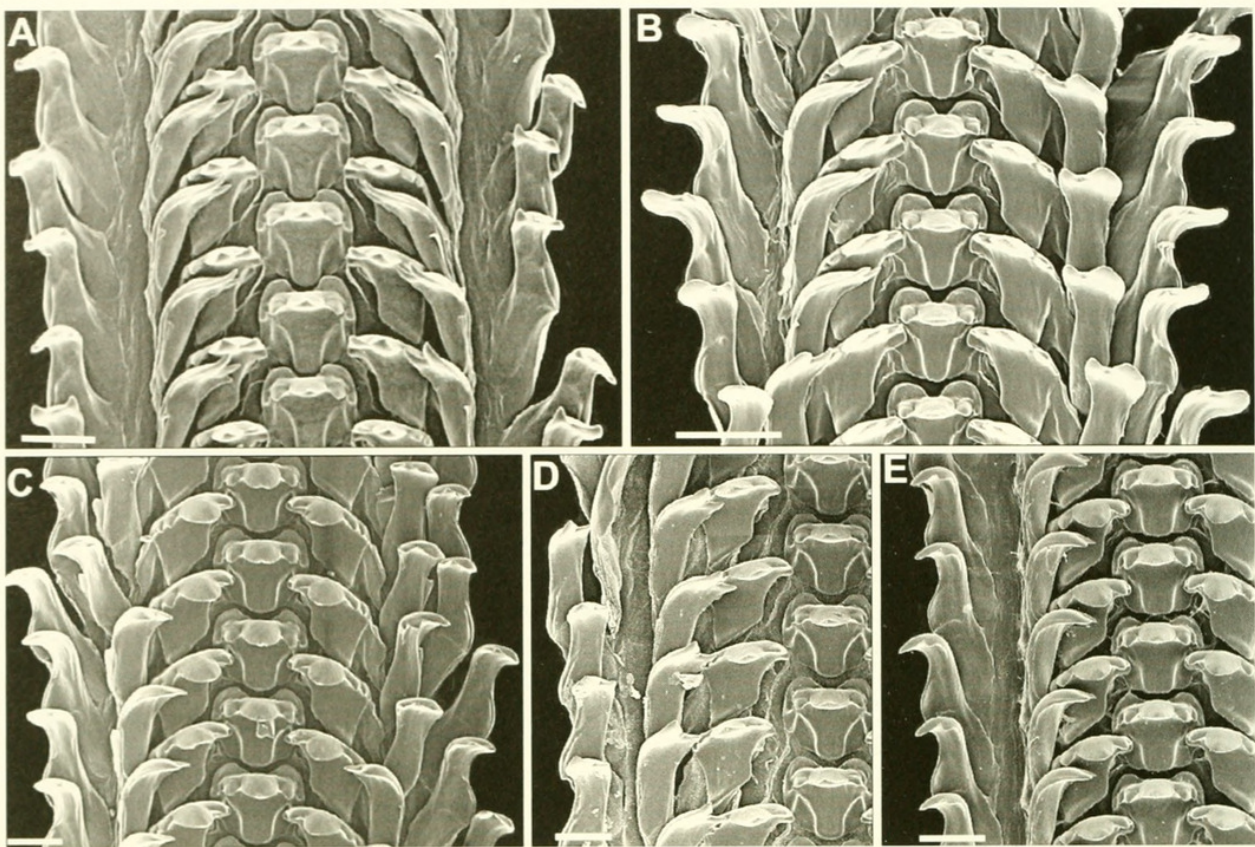


FIG. 67. Radular morphology of *B. episcopalis* and *B. sumatrensis*. A: *B. episcopalis*, Thailand, Nakhon Si Thammarat (ZMH); B: *B. sumatrensis* (Sumatra, Lampung; MZB 7028); C: South Sumatra (ZMB 200.116); D: Sumara, Lake Toba (ZMB 200.119); E: Trans-Sumatra highway (ZMB 200.120).

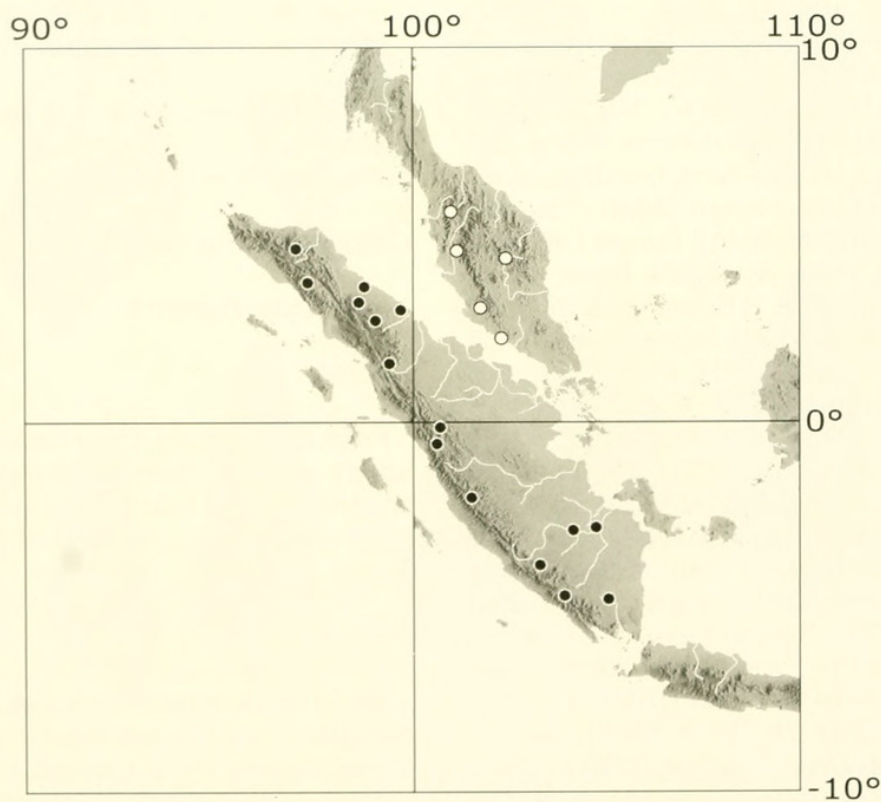


FIG. 68. Distribution of *B. sumatrensis* (close circles) and *B. episcopalis* (open circles).



*Brotia torquata* (Busch, 1842)  
(Figs. 69, 70, 71A)

*Melania torquata* Busch, 1842 – In: Philippi, 1842: 3, pl. 1, fig. 18 (“Java”), lectotype ÜMB TK 291/1 (designated by Knipper, 1958) (Fig. 69A); type seen; Mousson, 1849: 70; Brot, 1870: 281; Brot, 1875: 110, 111, pl. 14, fig. 5, 5a [partim].

*Melanoides torquata* – H. Adams & A. Adams, 1854: 297.

*Brotia torquata* – Köhler & Glaubrecht, 2002a: 150.

*Melania zollingeri* Brot, 1868: 42, pl. 2, fig. 4 (“Java”), holotype MHNG, coll. Brot (Fig. 69B); type seen; Brot, 1875: 111, pl. 14, fig. 6;

Schepman, 1886: 14; Leschke, 1914: 252; Degner, 1928: 374; Benthem Jutting, 1959: 93.

*Brotia zollingeri* – Köhler & Glaubrecht, 2002a: 152, fig. 3Q.

*Melania subplicata* Schepman, 1886: 14, pl. 1, fig. 6 (“Bedar Alam” = Sumatra, SW part of Riau, Bedar Alam, 0°45'S, 102°15'E), lectotype ZMA and four paralectotypes RMNH 71330 (designated by Köhler & Glaubrecht, 2002a) (Figs. 69E, F); types seen; Martens, 1897: 37, pl. 2, fig. 15, pl. 4, fig. 26; Bullen, 1906: 15; Leschke, 1914: 218, 252; Degner, 1928: 374; Benthem Jutting, 1959: 93.

*Melania sumatrensis* var. *mitescens* Schepman, 1886: 13, 14 (“Soepajang en nabij

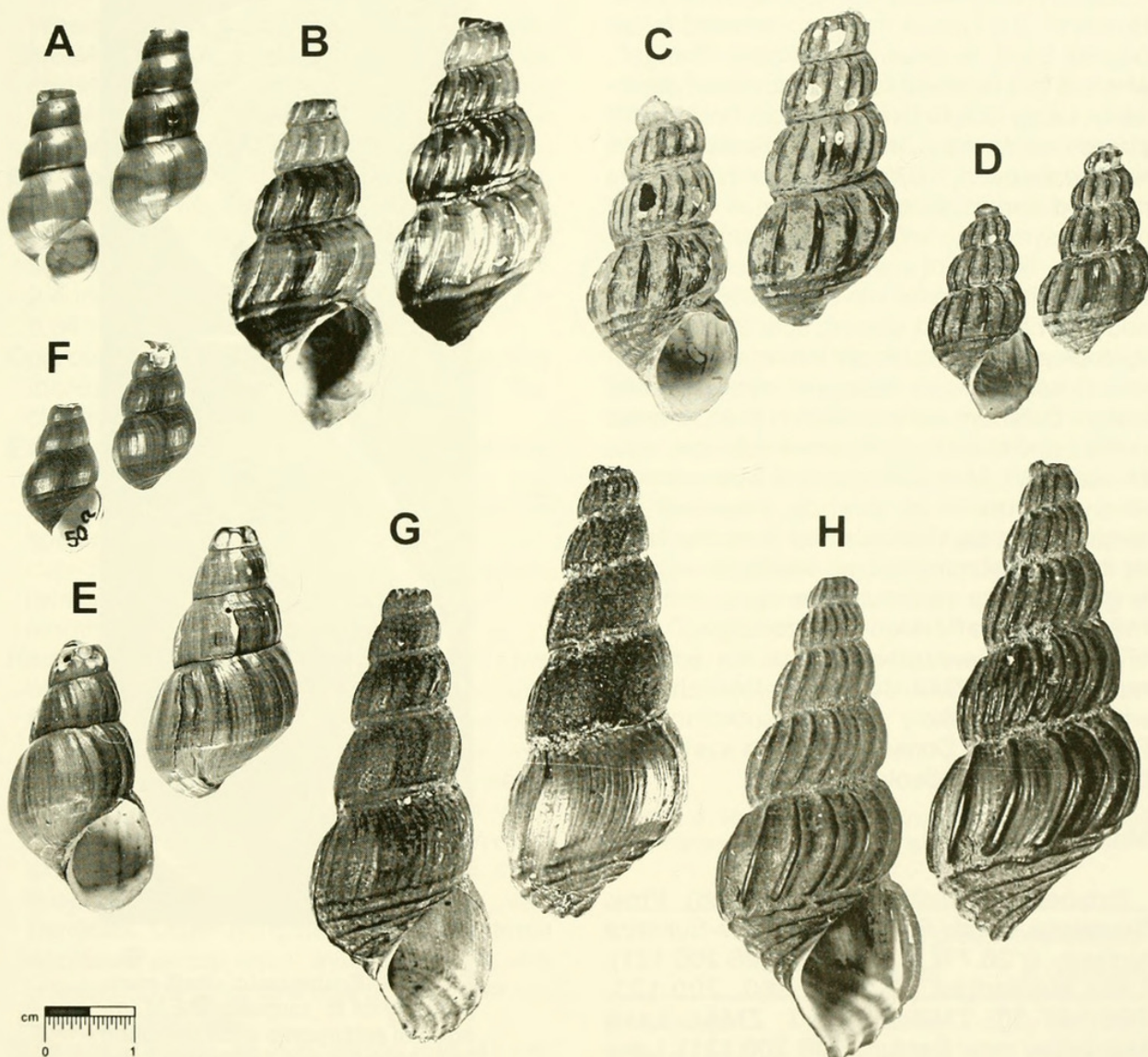


FIG. 69. Shell morphology of *B. torquata*. A: Lectotype of *M. torquata* ÜMB TK 291/1; B: Holotype of *M. zollingeri* MHNG; C: Lectotype of *M. curvicosta* ZMA; D: Paralectotype of *M. curvicosta* ZMA; E: Lectotype of *M. subplicata* ZMA; F: Paralectotype of *M. subplicata* ZMA; G–H: West Sumatra, Fort Kok (RMNH 71331). Scale bar = 10 mm.



Alahan pandjang" = Supajang and Alahan pandjang, nearby); types not seen.

*Melania curvicosta* Martens, 1897: 36, pl. 2, fig. 14, pl. 4, fig. 27 ("See von Manindjau, Sumatra = Laker Manindjau, Sumatra), lectotype, paralectotype ZMA, 12 paralectotypes ZMA (alc.), three paralectotypes ZMB 54.364 (designated by Köhler & Glaubrecht, 2002a) (Figs. 69C, D); types seen; Bullen, 1906: 15; Degner, 1928: 374.

*Melania curvicosta* var. *prestoniana* Bullen, 1906: 15, pl. 2, fig. 8; types not seen; Degner, 1928: 374.

*Brotia costula* – Knipper, 1958 [partim].

### Taxonomy and Systematics

Busch (1842) stated type locality to be Java. However, the type is not accompanied by an original label. A newer label states "Bengal", which is not believed to represent the type locality. Likely due to this confusion, Brot (1875) stated that *M. torquata* is conspecific with *M. terebra* Benson, 1836, from Bengal. This is rejected herein, since the latter is a thiarid, neither sympatric with nor even similar to *B. torquata*. Studies of shell series show that several described taxa fall into a joint morphospace and that ribbed and smooth specimens occur syntopically, connected by intermediates. For this reason, these taxa are synonymized herein. Benthem Jutting (1956, 1959), Knipper (1958), and Brandt (1974) treated *M. torquata*, *M. zollingeri*, *M. subplicata*, and *M. curvicosta* as synonyms of *B. costula*. However, *B. torquata* can be distinguished from the latter by its different morphology; additional support is gained from molecular genetics. Rensch (1934: 233) affiliated "*M. zollingeri*" with "*Tiaropsis*". Re-examination of his voucher material in the ZMB shows that Rensch dealt with a thiarid, likely *Melania subcancellata* Boettger, 1890. Consequently, his systematic conclusions are obsolete.

### Material Examined

Indonesia: Sumatra (ZMB 200.156). Prov. Sumatera Barat: Rao at the Trans-Sumatra highway, 0°26.7'N, 100°2.4'E (ZMB 200.121); Lake Manindjau (ZMB 54.360, 200.123, 200.147-50, ZMB 200.053; ZMA); Lake Manindjau near Banjur (ZMB 200.131); Lake Manindjau at Manindjau, 0°19'S, 100°22'E (ZMB 200.117); Fort Kok (RMNH 71331).

### Differential Diganosis

Mostly small, delicate to thin, smooth or sculptured by convex, closely spaced axial ribs; operculum round; embryonic shells with more or less developed axial ribs from second whorl on; cutting edge of inner marginal teeth with two accessory cusps at inner side.

### Description

*Shell* (Fig. 69): Small, thin, often even fragile, highly turreted, spire mostly eroded; three to five whorls; strong, closely spaced axial ribs, spiral striae at base, or entirely smooth.

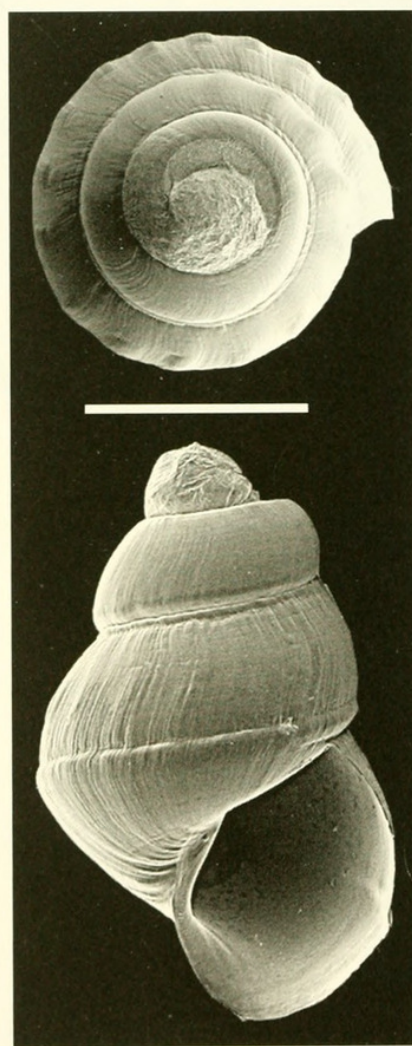


FIG. 70. Embryonic shell morphology of *B. torquata*. SEM images of embryonic shell removed from brood pouch (Sumatra, Lake Manindjau; ZMB 200.117); apical and front view. Scale bar = 1 mm.



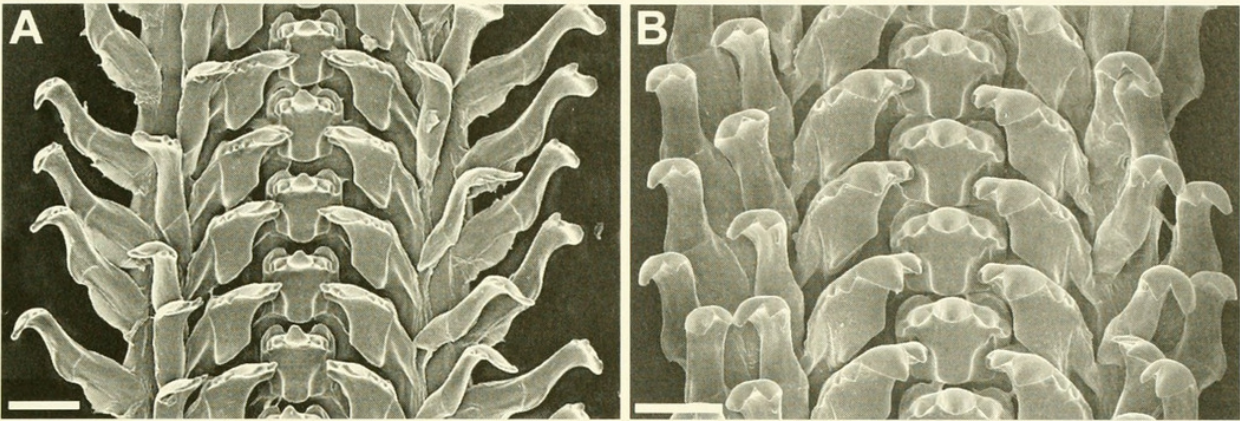


FIG. 71. Radular morphology of *B. torquata* and *B. verbecki*. A: *B. torquata* (Sumatra, Lake Maninjau; ZMB 200.117); B: *B. verbecki* (Sumatra, Lake Singkarah; ZMB 200.118). Scale bars = 10  $\mu$ m.

When present, axial ribs curved across entire whorl from one suture to the other. Colour chestnut to dark brown. Aperture wide, basely rounded, pointed above. Size: H = 25–48 mm, B = 6–23 mm.

*Embryonic Shell* (Fig. 70): Conical turreted, three to four whorls; fine vertical growth lines, in some specimens distant axial ribs from the second whorl on. Average proportions: H = 2.4 mm, B = 1.7 mm, HA = 0.22 mm, BA = 0.34 mm, DA = 0.68 mm (for n = 9).

*Operculum*: Round, with about six regularly increasing whorls, central nucleus, flat, clearly smaller than aperture.

*External Morphology*: Animal small, up to four whorls; one colour dark grey to black; egg transfer groove beneath right tentacle inconspicuous and short; mantle cavity short occupying about 2/3 of first whorl; osphradium relatively short corresponding to 1/3 to 1/2 of length of ctenidium.

*Radula* (Fig. 71A): Ribbon with about 100 rows of teeth. Upper margin of rachidian concave by two inflated, rounded corners; lower corners of basal plate rounded; glabella well rounded at base, its lateral margins concave; cutting edge of rachidian with single main cusp flanked by two accessory cups on each side that taper in size. Laterals with main cusp flanked by two inner and three outer denticles. Outer marginals with two pointed denticles, almost equal; inner marginals with pointed outer cusp and one or two inner accessory denticles.

*Stomach*: Typical, as in *B. citrina* (Fig. 4); except for unfused typhlosoles at entire length of style sac.

Distribution

Indonesia: Java, West-Sumatra. The only known reports from Java refer to types of *M. torquata* and *M. zollingeri*. Either these reports are in error or the species have become extinct or extremely rare. All other material from West-Sumatra.

Remarks

Somewhat similar to *B. verbecki* when considering similar shape and size of shell. Some specimens of *B. verbecki* even exhibit marked axial sculpture otherwise typical for most specimens of *B. torquata*. Shells of *B. torquata* are thinner and generally lack more pronounced spiral elements except for basal lirae. The two species can significantly be discriminated by shell morphometry (Table 4). The report of Leschke (1914) on *M. subplicata* from Bogor is incorrect; the voucher material in the ZMB is re-determined as *Adamietta testudinaria*.

TABLE 4. Result of disriminant analysis of shell parameters of *B. torquata* and *B. verbecki*.

	Predicted group membership	
	<i>B. torquata</i>	<i>B. verbecki</i>
<i>B. torquata</i>	10 (90.9%)	1 (9.1%)
<i>B. verbecki</i>	1 (2.6%)	37 (97.4%)



*Brotia verbecki* (Brot, 1886)  
(Figs. 71 B, 72, 73)

*Melania verbecki* Brot, 1886: 90, pl. 6, figs. 9–9b (“Lac de Singkarah, gouvernement de Padang, Sumatra occid.” = Lake Singkarah, Padang distr., West Sumatra), lectotype, 11 paralectotypes MHNG, coll. Brot, paralectotype MCZ 112682 (designated by Köhler & Glaubrecht, 2002a) (Figs. 72A–D); types seen; Martens, 1897: 38.

*Melania verbecki* var. *laevis* Martens, 1897: 38 (Lake Singkarah), 32 syntypes ZMB 200.152.

*Brotia verbecki* – Köhler & Glaubrecht, 2002a: 151, 152, fig. 3P.

*Melania papillosa* Martens, 1897: 38, 39, pl. 2, fig. 21 (“See Singkarah, Sumatra” = Lake Singkarah), lectotype ZMA, 18 paralectotypes ZMA, 15 paralectotypes ZMB 200.025 (designated by Köhler & Glaubrecht, 2002a), (Figs. 72F–K); types seen.

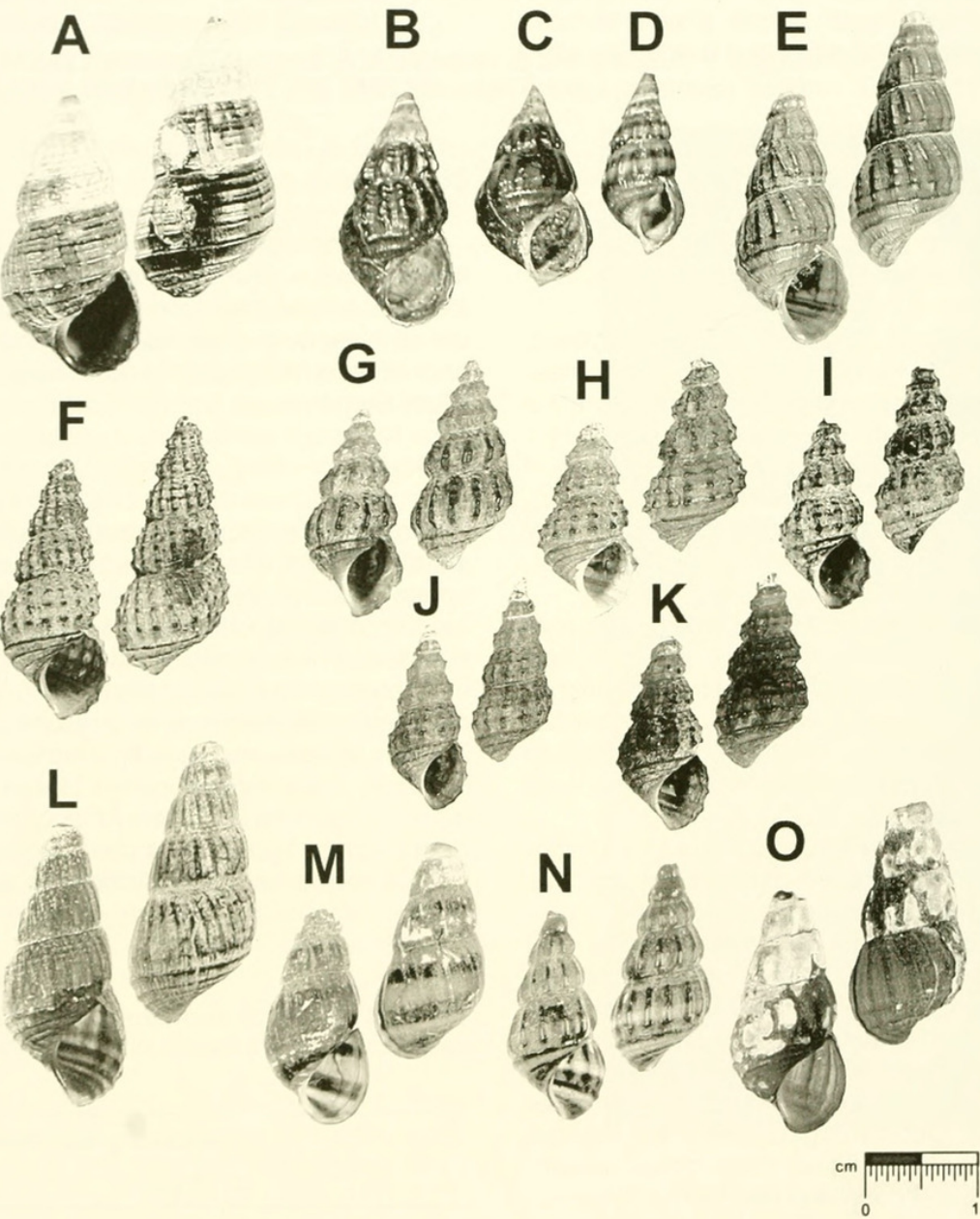


FIG. 72. Shell morphology *B. verbecki*. A: Lectotype of *M. verbecki* MHNG; B–D: Paralectotypes MHNG; E: Lectotype of *M. stricticosta* ZMB 200.102; F: Lectotype of *M. papillosa* ZMA; G–K: Paralectotypes ZMB 200.103; L–O: Sumatra, Lake Singkarah (ZMB 200.118). Scale bar 10 mm.



*Melania stricticosta* Martens, 1897: 39, 40, pl. 2, figs. 22–26 (“See Singkarah, Sumatra” = Lake Singkarah, Sumatra), lectotype and two paralectotypes of *M. stricticosta* ZMB 200.102, 16 paralectotypes ZMB 200.103, two potential paralectotypes ZMB 200.151 (designated by Köhler & Glaubrecht, 2002a) (Fig. 72 E); types seen.

#### Taxonomy and Systematics

Brot described this species from Lake Singkarah, West-Sumatra (Indonesia) using a manuscript name of Boettger. From the same locality, Martens (1897) described not only a new var., *laevis*, but also two new species, *M. papillosa* and *M. stricticosta*, for subtle conchological differences. Examination of the type series shows that the named taxa only delineate conchological varieties of a single, albeit somewhat variable species. The different morphs occur frequently and syntopically in the lake with intermediate forms, and there is no evidence that they represent distinct species.

#### Material Examined

Indonesia, Sumatra: Lake Singkarah (ZMB 76.290-4, 200.118, 200.126, 200.155, 200.157-60).

#### Differential Diganosis

Shell small, thin but solid, conical to elongate turreted, pronounced sculpture of either strong spiral ridges, axial ribs, or combination of both; frequently with spiny nodules where spiral lines and axial ribs meet; operculum round; embryonic shells frequently with two spiral rows of nodules from second whorl on.

#### Description

**Shell** (Fig. 72): Small, relatively thin to delicate, broadly conic to elongate turreted, up to five flattened whorls; more or less prominent spiral lines or cords, especially at base, in some specimens dominating; mostly with strong axial ribs. In several specimens axial rows of three to four tubercles where spiral lines and axial ribs meet. Colour yellowish brown to olive brown. Aperture widely oval, well rounded to slightly produced below. Size: H = 12–36 mm, B = 6–16 mm.

**Embryonic Shell** (Fig. 73): Conical turreted, three to four whorls; fine vertical growth lines, in many specimens, double spiral row of distant, rounded nodules from second whorl on. Average proportions: H = 2.9 mm, B = 1.7 mm, HA = 0.17 mm, BA = 0.32 mm, DA = 0.66 mm (for n = 6).

**Operculum**: Round, up to eight whorls, central nucleus, smaller than aperture.

**Radula** (Fig. 71B): Ribbon with about 100 rows of teeth. Rachidian with slightly concave upper rim by only slightly inflated lateral corners. Cutting edge with main cusp flanked

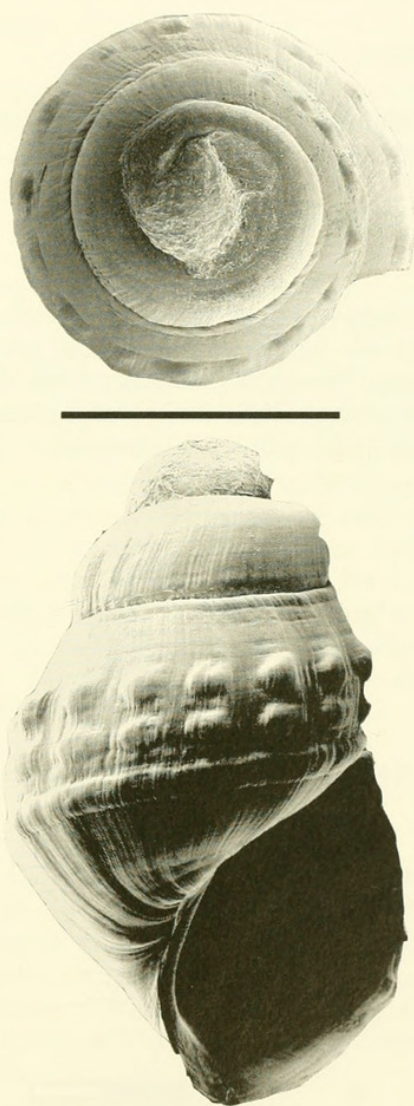


FIG. 73. Embryonic shell morphology of *B. verbecki*. SEM image of shell removed from brood pouch (Sumatra, Lake Singkarah; ZMB 200.118). Scale bar = 1 mm.



by three smaller denticles on each side. Glabella rather straight at its basal end, with concave lateral margins. Lateral teeth with main cusp flanked by two to three smaller denticles. Inner and outer marginals with two pointed cusps, the outer one being broader. *Stomach*: Typical, as in *B. citrina* (Fig. 4); except for both typhlosoles unfused at entire length of style sac.

Reproductive System

Females contained between 19 and 75 shelled juveniles ( $n = 4$ ), forming cohorts with heights between 1.5 and 2.5 mm.

Distribution

Indonesia, West-Sumatra: Only known from Lake Singkarah.

*Brotia wykoffi* (Brandt, 1974)  
(Figs. 74–76)

*Brotia* (*Senckenbergia*) *wykoffi* Brandt, 1974: 184, pl. 13, fig. 41 (“Creek at Sai Yok, Kanchanaburi Province”), holotype SMF 197268, four paratypes RMNH 55244/4; types seen. *Brotia wykoffi* – Köhler & Glaubrecht, 2002a: 152.

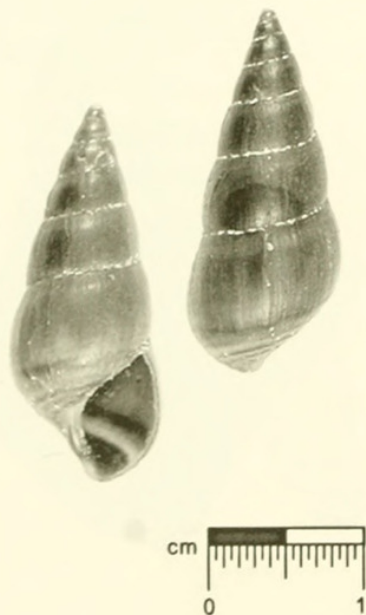


FIG. 74. Shell morphology of *B. wykoffi* (Thailand, Nam Tok; ZMB 200.132).

Taxonomy and Systematics

Brandt (1974) affiliated this species to *Senckenbergia* Yen, 1939, and treated this taxon as a subgenus of *Brotia*. However, *Senckenbergia* is not considered a pachychilid (Köhler & Glaubrecht, 2002a).

Material Examined

Thailand: Prov. Kanchanaburi, Sai Yok Falls 2 (Sai Yok NP), Nam Tok, 14°26.3'N, 98°51.0'E (ZMB 200.131-2).

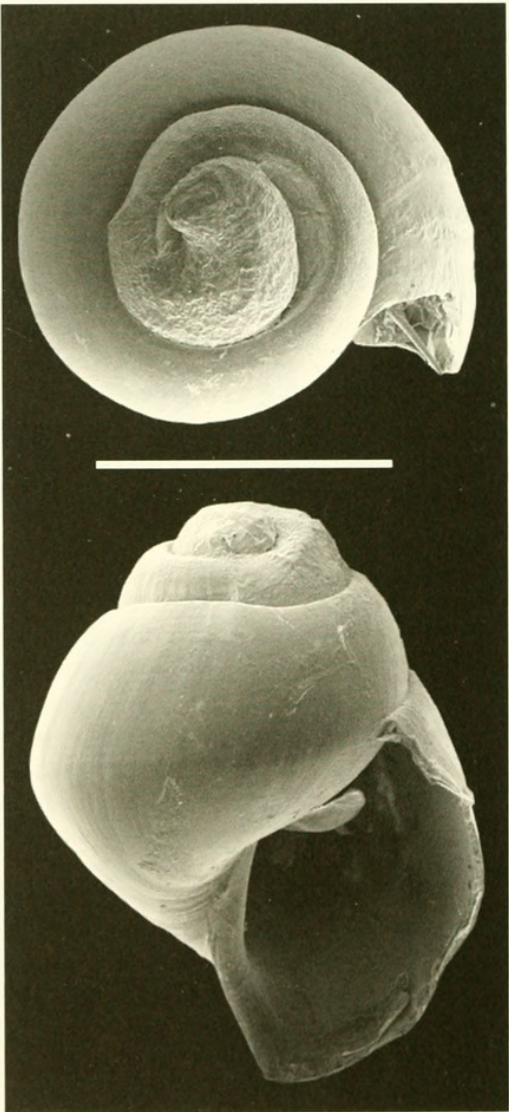


FIG. 75. Embryonic shell morphology of *B. wykoffi*. SEM images of embryonic shell removed from brood pouch (Thailand, Nam Tok; ZMB 200.132); apical and front view. Scale bar = 1 mm.



## Differential Diganosis

Shell smooth, rather small, thin but solid, conical turreted; whorls flattened, only slightly convex; colour olive brown with lightly green spiral bands; aperture inside olive green with yellowish bands.

## Description

*Shell* (Fig. 74): Small, thin but solid; spire conical turreted, up to eight flattened, only slightly convex whorls; smooth sculpture except for growth lines, weak spiral lirae at base. Colour olive brown with lightly green spiral bands. Aperture relatively narrow, angled below, pointed above, inside olive green with yellowish bands.  $H = 22\text{--}30\text{ mm}$ ,  $B = 9\text{--}11\text{ mm}$ .

*Embryonic Shell* (Fig. 75): Broadly ovate, three whorls; smooth sculpture; aperture wide. Average proportions:  $H = 2.0\text{ mm}$ ,  $B = 1.4\text{ mm}$ ,  $HA = 0.15\text{ mm}$ ,  $BA = 0.28\text{ mm}$ ,  $DA = 0.62\text{ mm}$  (for  $n = 10$ ).

*Operculum*: Round, up to eight regular whorls, central nucleus.

*Radula* (Fig. 76): Ribbon with about 120 rows of teeth. Rachidian with slightly concave upper rim by inflated lateral corners. Cutting edge with one main cusp flanked by two smaller denticles on each side. Glabella straight at its base, relatively long, with straight lateral margins. Laterals with main cusp flanked by two smaller denticles on each side, rather long lateral extensions. Inner and outer marginal teeth with two to three pointed cusps, the outer one being broader.

*Stomach*: Typical, as in *B. citrina* (Fig. 4); except for both typhlosoles unfused at entire length of style sac.

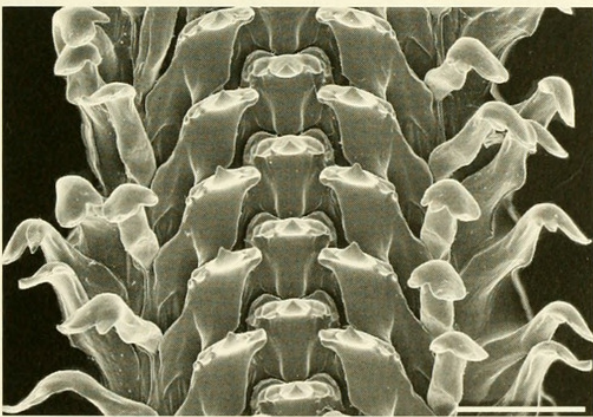


FIG. 76. Radular morphology of *B. wykoffi*. SEM image of segment viewed from above (Thailand, Nam Tok; ZMB 200.132). Scale bar = 100  $\mu\text{m}$ .

## Reproductive System

A female contained 21 juveniles of more or less of same size (ZMB 200.232).

## Distribution

Thailand: Prov. Kanchanaburi, known only from type locality (Sai Yok Falls, Nam Tok).

## Habitat

Small, tangled, swift stream discharging into Kwa Noi River.

## Remarks

Somewhat similar to *B. dautzenbergiana*, which is much larger, juveniles more slender.

## INCERTAE SEDIS

In the following, a number of taxa are listed that are members of the Pachychilidae, as can be judged from features of their shell, operculum and/or radula. However, an unequivocal affiliation with *Brotia* is not possible for lack of crucial information on diagnostic features, such as embryonic shell morphology or reproductive anatomy. Because the species originate from localities where other pachychilid genera may occur, such as, for example, *Adamietta*, we refrain from a formal treatment under *Brotia*, although it appears plausible for most of the following taxa that they are members of this genus.

*Brotia* (?) *angulifera* (Brot, 1872)  
(Figs. 77A, B)

*Melania* (*Pachychilus*) *angulifera* Brot, 1872: 32, pl. 2, fig. 9 ("Java"), lectotype and paralectotype MHNG, coll. Brot (designated by Köhler & Glaubrecht, 2002a) (Figs. 77A, B); types seen; Brot, 1875: 51, 52, pl. 6, fig. 5. *Brotia angulifera* – Köhler & Glaubrecht, 2002a: 126, 127, fig. 1B.

## Taxonomy and Systematics

Bentham Jutting (1956) considered this species a synonym of "*B. testudinaria*". However, the shells of both species are easy to distinguish. *B. angulifera* is considered here a distinct species. Details of soft body, radula, and embryonic shell remain unknown, which hin-



ders a systematic decision. Not identical with *Melania* (*Plotia*) *scabra* var. *angulifera* Martens, 1897.

#### Differential Diganosis

Shell conical turreted, one colour dark greenish to olive brown with convex, rounded to slightly shouldered whorls, sculptured by fine spiral lirae; spiral depression below suture.

#### Description

*Shell* (Figs. 77A, B): Medium sized, oval to conical turreted, solid, with six convex, well rounded to slightly shouldered whorls, narrow suture; with fine spiral lirae and faint vertical growth lines. Colour greenish to olive brown. Body whorl comparatively large. Aperture medium sized, oval, well rounded, slightly produced below. Columella thick. Size of lectotype: H = 33 mm, B = 14 mm.

*Embryonic shell morphology, Operculum, Radula, Soft body anatomy*: Unknown.

#### Distribution

Indonesia: Java, the type locality as only known record.

*Brotia* (?) *assamensis* (Nevill, 1885)  
(Figs. 77C, D)

*Melania* (*Acrostoma*) *assamensis* Nevill, 1885: 271 ("Delaima River, North Cachar"), four syntypes IMC, according to Nevill (1885); types not seen.

*Tiara* (*Acrostoma*) *assamensis* – Preston, 1915: 31.

*Paracrostoma assamensis* – Köhler & Glaubrecht, 2002a: 128.

#### Taxonomy and Systematics

Specimens in the BMNH apparently were not available to Nevill (1885), who mentioned only four specimens in the IMC. Placed in *Paracrostoma* because of a close similarity to its type species, *P. huegeli* (Philippi, 1843), by Köhler & Glaubrecht (2002a) and because *Acrostoma* Brot, 1870, is a synonym of *Paracrostoma* Cossmann, 1900 (Köhler & Glaubrecht, 2002a). However, *Paracrostoma* is endemic to southern India (federal states of Karnataka, Kerala, and Tamil Nadu) and most likely does not occur in Assam, from where otherwise some *Brotia* species are known (unpubl. data). For this circumstantial evidence,

we suggest to treat this species as a member of *Brotia*.

#### Material Examined

India: Assam, Delaima River, North Cachar (= Delaima River, N of Silchar; BMNH 19991534 (12 shells originating from the Godwin-Austen collection, same series as types; Figs. 77C, D).

#### Differential Diganosis

Shell elongate, conical with rounded whorls, surface smooth and glossy; one colour dark brown, sculptured by faint spiral lirae and growth lines only; aperture wide, angularly produced below; body whorl comparatively large compared to shell height.

#### Description

*Shell* (Figs. 77C, D): Medium sized, spire conically turreted, eroded, with three to five slightly convex to flattened whorls, sculpture smooth except for faint spiral lines and growth lines. All one colour, chestnut brown. Aperture elongate oval with produced to slightly angled lower margin, columellar margin inconspicuous, peristome sharp.

*Embryonic Shell, Operculum, Radula, Soft Body*: Anatomy unknown.

#### Distribution

India: Assam, Delaima River as the only known locality.

#### Remarks

Similar to *Paracrostoma huegeli*, but more slender in shape, coloration lacks spiral flames, body whorl not as inflated as in the former. *P. huegeli* lacks glossy surface.

*Brotia* (?) *beaumetzi* (Brot, 1887)  
(Fig. 77H)

*Melania beaumetzi* Brot, 1887: 34, 35 ("Baie du Touranne", in error, replaced by "environs de Than Moi" by Dautzenberg & Hamonville, 1887 = Thanh Mòi, about 200 km NE of Hanoi, Vietnam, 21°37'N, 106°32'E), holotype MNHN (Fig. 77H); type seen; Dautzenberg & Hamonville, 1887: 219; Fischer-Piette, 1950: 160, pl. 5, fig. 4.

*Brotia beaumetzi* – Köhler & Glaubrecht, 2002a: 129, fig. 1D.



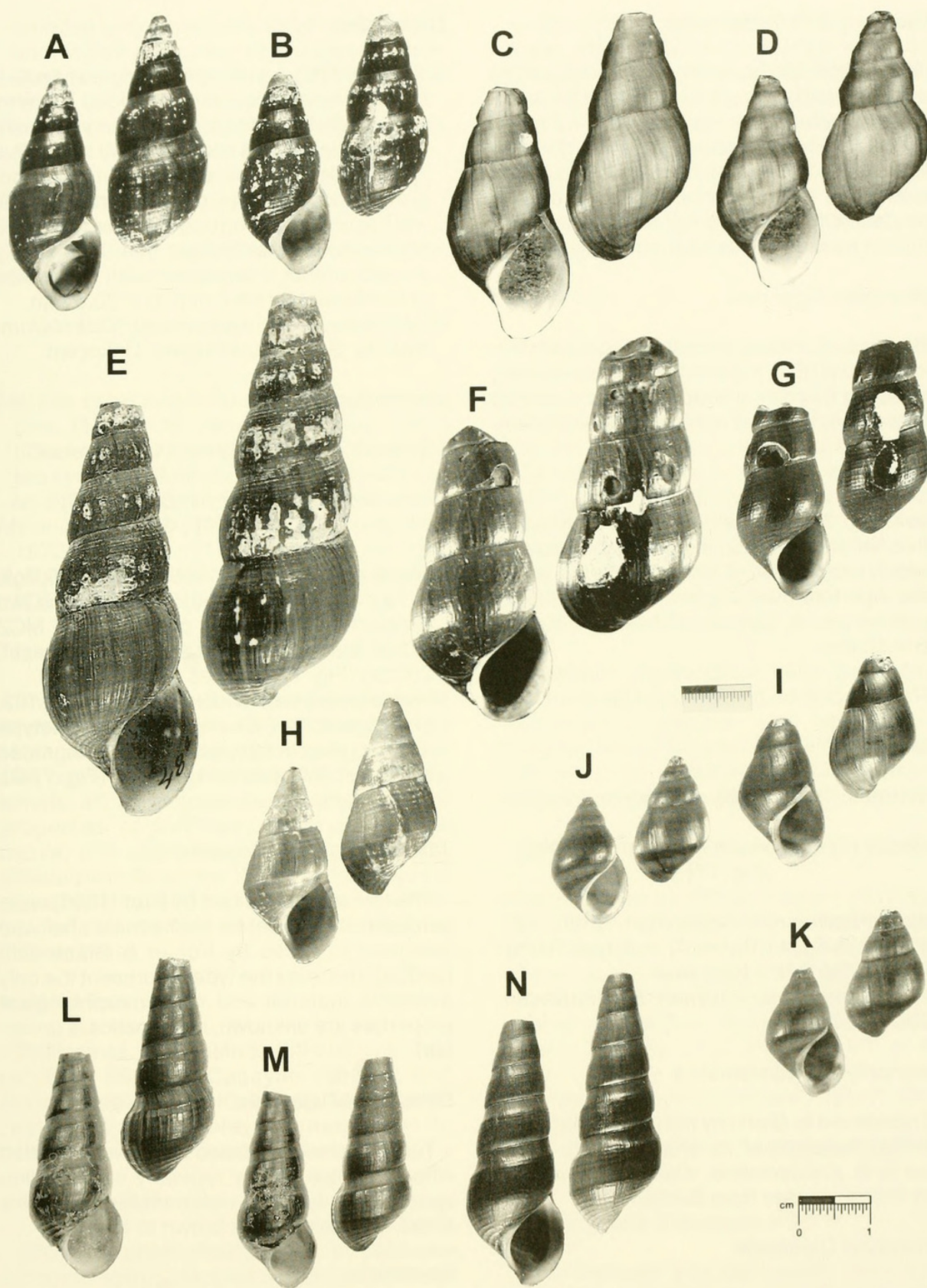


FIG. 77. Shell morphology of several species with uncertain classification. A: Lectotype of *M. angulifera* MHNG; B: Paralectotype MHNG; C–D: *Brotia* (?) *assamensis* (Assam, North Cachar, Delaima River; BMNH 19991534); E: Holotype of *M. borneensis* RMNH 71325; F: Lectotype of *M. cylindrus* MHNG; G: Lectotype of *M. subcylindrica* MHNG; H: Holotype of *M. beaumonti* MNHN; I: Lectotype of *M. zonata* von dem Busch, 1842 ÜMB TK 271/1; J–K: Paralectotypes ÜMB TK 272/2; L–M: Syntypes of *Melania canaliculata* Reeve, 1869 (BMNH 20050105, ex coll. Cuming, = *Melania sooloensis* Reeve, 1860); N: *Brotia* (?) *soloensis* (Philippines, Sulu Islands; ZMB 59.161).



## Taxonomy and Systematics

Brot (1887: 34) gave "Baie du Touranne" as the type locality. This was stated to be incorrect and replaced by "Environs de Than-Moi (leg. M. de Merlaincourt)" (Dautzenberg & Hamonville, 1887), which corresponds to the label of the type material. The species was transferred to *Brotia* by Köhler & Glaubrecht (2002a) because of its characteristic shell.

## Differential Diganosis

Shell small, robust, broadly conical with flattened whorls; thin, regularly spaced spiral lirae; distinct by its conical shape, tiny size, keeled basal whorl, fine and regular spiral sculpture.

## Description

*Shell* (Fig. 77H): Small, conical turreted with five flattened whorls, inconspicuous suture; regular spiral lirae. Colour light brownish olive. Aperture oval, angled, produced below, pointed above. Size of holotype: H = 20 mm, B = 10 mm.

*Embryonic shell morphology, Operculum, Radula, Soft body anatomy*: Unknown.

## Distribution

Vietnam: Type locality only known record.

*Brotia* (?) *borneensis* (Schepman, 1896)  
(Fig. 77E)

*Melania borneensis* Schepman, 1896: 137, 138, pl. 2, fig. 4 ("Borneo"), holotype RMNH 71325 (Fig. 77E); type seen.

*Brotia borneensis* – Köhler & Glaubrecht, 2002a: 130.

## Taxonomy and Systematics

Transferred to *Brotia* by Köhler & Glaubrecht (2002a) because of its characteristic shell. Next to *B. praetermissa*, it would be the second *Brotia* species from Borneo.

## Differential Diganosis

Shell relatively large, highly turreted with convex, well rounded whorls, sculptured by spiral lines most conspicuously below suture, and faint axial growth lines; aperture wide, well produced below.

## Description

*Shell* (Fig. 77E): Large, spire elongate turreted, five remaining, regularly rounded, convex whorls; shell solid to thick; colour yellowish-olive; upper whorls sculptured by numerous spiral striae, more conspicuous on last whorl, growth lines inconspicuous. Aperture ovate, well rounded, produced below, pointed above; columellar margin thin, moderately curved; inferior of aperture bluish white. Size of holotype: H = 54.7 mm, B = 20.6 mm.

*Embryonic shell morphology, Operculum, Radula, Soft body anatomy*: Unknown.

## Distribution

Borneo: Type locality only known record.

*Brotia* (?) *cylindrus* (Brot, 1886)  
(Figs. 77F, G)

*Melania cylindrus* Brot, 1886: 92, 93, pl. 6, figs. 7, 7a ("Siam" = Thailand), lectotype and two paralectotypes MHNG, paralectotype MCZ 11268 (designated by Köhler & Glaubrecht, 2002a) (Fig. 77F); types seen.

*Melania subcylindrica* Brot, 1886: 102, 103, pl. 6, figs. 2, 2a ("Chine" = China), lectotype and two paralectotypes MHNG (designated by Köhler & Glaubrecht, 2002a) (Fig. 77G); types seen.

## Taxonomy and Systematics

The two taxa described by Brot (1886) were considered identical for their similar shell and assigned to *Brotia* by Köhler & Glaubrecht (2002a). Because the types represent the only available material and most morphological properties are unknown, systematics is uncertain.

## Differential Diganosis

Turreted shell, truncated spire, well-rounded whorls, sculptured by regularly spaced, fine spiral lines; aperture well rounded, relatively small; one colour dark brown to black.

## Description

*Shell* (Figs. 77F, G): Highly turreted, frequently truncated after second or third whorl, whorls well rounded in diameter, sculptured by regularly spaced, fine spiral lines; aperture well



rounded below, relatively small compared to body whorl; one colour dark brown to black. Shell size: H = 27.5–42 mm, B = 13.5–19.7 mm.

*Embryonic shell morphology, Operculum, Radula, Soft body anatomy*: Unknown.

#### Distribution

Vague: “Siam” and “China” as only known records.

*Brotia* (?) *sooloensis* (Reeve, 1859)  
(Figs. 77L, M)

*Melania canaliculata* Reeve, 1859: pl. 6, species 31 (*non M. canaliculata* Say, 1821) (“Sooloo Islands” = Sulu Islands, Philippines); two syntypes BMNH 20050105 (Sulu Islands, ex coll. Cuming) (Fig. 77L, M), types seen.

*Melania sooloensis* Reeve, 1860: errata; Brot, 1870: 281; Brot, 1875: 105, 106, pl. 14, fig. 3.

*Brotia sooloensis* – Köhler & Glaubrecht, 2002a: 147, 148.

#### Taxonomy and Systematics

The name *M. sooloensis* was employed by Reeve (1860: errata) as replacement name for *M. canaliculata* Reeve, 1859, being preoccupied by *M. canaliculata* Say, 1821. The systematic affinity is suspicious due to unknown properties of soft body, embryonic shell, radula, and operculum. Herein preliminarily affiliated with *Brotia*, but this treatment requires critical revision as the Zulu Archipelago, Philippines, is not within the range of *Brotia* as defined here.

#### Material Examined

Philippines: Sulu Islands (MHNG, coll. Taylor; ZMB 59.161); Cagayan (MHNG; coll. Norris); Isabella (MHNG; leg. Semper), herein restricted to Isabela, Basilan (6°41'N, 118°58'E).

#### Differential Diagnosis

Shape of shell unmistakable; in particular elongate spire, stepped whorls, subsutural depression or shoulder.

#### Description

*Shell* (Fig. 77L–N): Elongate turreted, solid but not thick, up to six whorls, deep suture,

mostly truncated tip; whorls well rounded at base, upper whorls convex but more flattened than basal ones; subsutural depression, most prominent on last two or three whorls; smooth sculpture, basal spiral ridges, faint growth lines, faint spiral lines; surface glossy. Aperture oval, well rounded below. Shell size: H = 31–38 mm, B = 13–15 mm.

*Embryonic shell morphology, Radula, Soft body anatomy*: Unknown.

#### Distribution

Reports on this species refer to Sulu Islands, Philippines; neither known from Mindanao nor Borneo. Two islands in the Sulu Sea are named Cagayan. The island Cagayan-Sulu (material in MNHG) in N of Borneo (Sarawak), more than 300 km W of Sulu archipelago (6°59'N, 118°28'E); Cagayan Island in central Sulu Sea is even more remote, between Palawan and Negros (9°35'N, 121°28'E), about 600 km NW of the Sulu archipelago. Occurrence on both islands seems dubious and requires confirmation.

#### Remarks

Somewhat similar are species of *Pseudopotamis* (Glaubrecht & Rintelen, 2003). Well preserved material of *B. sooloensis* is needed to clarify its systematic position.

*Brotia* (?) *spinata* (Godwin-Austen, 1872)

*Melanoides spinata* Godwin-Austen, 1872: 514, pl. 30, figs. 1, 1a (“Kopili River, North Cachar hills, a tributary of the Brahmaputra” = Kopili River, Jaintia-Khâsi hills N of Silchar, federal state of Meghalaya, India); types not seen; Hanley & Theobald, 1874: pl. 109, fig. 1.

*Melania spinata* – Brot, 1875: 89, 90, pl. 10, figs. 2, 2a.

*Melania* (*Melanoides*) *spinata* – Nevill, 1885: 261.

*Brotia spinata* – Köhler & Glaubrecht, 2002a: 148 [partim].

#### Taxonomy and Systematics

Type material was not traced. Shell only known from original figure. Attributed to *Brotia* by Köhler & Glaubrecht (2002a) as being typical for *Brotia*. Geographical distribution well within range of the genus. Köhler & Glaubrecht (2002a) assumed that *B. binodosa* is conspecific for the similar shell. However, in their re-



vision of the Kaek River species flock, Glaubrecht & Köhler (2004) show that *B. binodosa* is endemic to central Thailand and, thus, not conspecific with *B. spinata*.

Differential Diganosis

Highly turreted shell with two spiral rows of spiny nodules supported by more or less prominent spiral cords; body whorl large compared to shell; aperture wide, produced below.

Distribution

India, Meghalaya: Known from type locality only.

Remarks

Similar to *B. binodosa*, which has a more slender shell.

*Brotia* (?) *zonata* (Benson, 1836)  
(Figs. 77I–K)

*Melania zonata* Benson, 1836: 747 (no figure); types not seen.

*Melania zonata* Busch, 1842 – In: Philippi, 1842: 3, pl. 1, fig. 12 (“Bengalia”), lectotype ÜMB TK 271/1, two paralectotypes ÜMB TK 272/2 (designated by Knipper, 1958) (Figs. 77I–K); types seen.

*Melanella zonata* – H. Adams & A. Adams, 1854: 296.

*Brotia zonata* – Köhler & Glaubrecht, 2002a: 152.

Taxonomy and Systematics

Benson described this species from a collection of freshwater shells originating from Bengal and Sylhet, but did not explicitly mention a type locality. *Melania zonata* Busch (1842) was stated to be junior synonym by objective homonymy (Reeve, 1859; Brot, 1875; Knipper, 1958; Köhler & Glaubrecht, 2002a).

Differential Diganosis

Shell rather small, broadly conical, truncated after third whorl, strong, sculpture smooth except for growth lines, glossy surface, two chestnut brown spiral bands, aperture widely oval and well produced below.

Description

*Shell* (Figs. 77I–K): Relatively small, broadly conical with three whorls, shell robust; sculpture smooth except for faint growth lines, body whorl comparatively large; colour greenish brown with chestnut brown spiral bands; aperture oval, wide inside whitish with brown bands.

*Embryonic shell morphology, Radula, Soft body anatomy*: Unknown.

Distribution

India, Bangladesh: Bengal.

Remarks

Similar to *B. pseudosulcospira* and *B. microsculpta* in its smooth and conical shell; the spiral brown band being unique, though.

MOLECULAR GENETICS

Sequence Analysis

Separate sequence alignments comprise 646 bp (COI) and 826 bp (16S), respectively. Plotting rates of transitions (s) and transversions (v) against sequence divergence for both genes separately indicates that sequences are not saturated and, thus, accommodate phylogenetic analyses. A partition homogeneity test as implemented in PAUP\* showed that the two data partitions (COI and 16S) are not significantly incongruent at the 99% level ( $P < 0.01$ ). The analysis software MrModeltest (Nylander, 2002) revealed an invariant + gamma distributed model of sequence evolution (GTR+I+ $\Gamma$ ; Gu et al., 1995) as the best fitting model for both sequence data sets. Accordingly, this model was chosen to calculate pair wise genetic distances shown in Table 5. The model was also implemented in distance based analyses (NJ and BI). Pair wise genetic distances were calculated separately for each of the partial genes. With one exception, in COI intraspecific distances usually do not exceed 16% (in *B. citrina*) and mostly range between 0 and 6%. The high sequence divergence in *B. sumatrensis* is very striking. Since a similar divergence is not observed in 16S, we assume that the one sequence of *B. sumatrensis* high-



TABLE 5. Genetic distances (GTR+I+Γ) within and between *Brotia* species for COI (upper rows) and 16S (lower rows) (N = number of sequences analysed per species; printed in bold = infraspecific distances; \* dubious value, see discussion).

	N	<i>armata</i>	<i>binodosa</i>	<i>citrina</i>	<i>dautzenbergiana</i>	<i>henriettae</i>	<i>herculea</i>	<i>microsculpta</i>	<i>pagodula</i>	<i>peninsularis</i>	<i>solemiana</i>	<i>sumatrensis</i>	<i>torquata</i>
<i>armata</i>													
COI		<b>0-0.07</b>	0-0.06	0.17-0.26	0.19-0.22	0.18-0.22	0.19-0.24	0.00-0.06	0.24-0.29	0.16-0.20	0.06-0.08	0.17-1.38*	0.17-0.19
16S	6	<b>0-0.03</b>	0.01-0.03	0.14-0.18	0.21-0.23	0.16-0.17	0.17-0.20	0.01-0.02	0.17-0.19	0.14-0.15	0.02-0.03	0.10-0.12	0.11-0.12
<i>binodosa</i>													
COI			<b>0-0.15</b>	0.16-0.26	0.20-0.21	0.18-0.22	0.22-0.25	0-0.06	0.24-0.28	0.16-0.20	0.05-0.08	0.17-0.20	0.13-0.14
16S	5		<b>0-0.02</b>	0.14-0.17	0.0-0.23	0.15-0.16	0.17-0.19	0-0.02	0.17-0.19	0.13-0.14	0.01-0.02	0.10-0.12	0.11-0.12
<i>citrina</i>													
COI				<b>0-0.16</b>	0.17-0.20	0.19-0.25	0.18-0.25	0.17-0.26	0.14-0.18	0.14-0.18	0.18-0.27	0.17-2.41*	0.18-0.26
16S	2			<b>0-0.10</b>	0.19-0.22	0.19-0.20	0.14-0.19	0.14-0.17	0.10-0.15	0.17-0.18	0.14-0.18	0.20-0.22	0.20-0.24
<i>costula</i>													
COI		0.22-0.24	0.22-0.23	0.19-0.25	0.25	0.25-0.26	0.25-0.26	0.22-0.24	0.23	0.17-0.19	0.24	0.18-1.36*	0.16-0.18
16S	1	0.10-0.11	0.10-0.11	0.16-0.17	0.25-0.26	0.16	0.19	0.10	0.20	0.16	0.10	0.14	0.14
<i>dautzenbergiana</i>													
COI				<b>0-0.02</b>	<b>0-0.02</b>	0.22	0.16-0.17	0.20-0.22	0.21-0.24	0.15	0.18-0.20	0.19-1.68*	0.16-0.18
16S	3			<b>0-0.02</b>	<b>0-0.02</b>	0.20-0.22	0.13-0.15	0.20-0.23	0.20-0.22	0.23-0.24	0.19-0.21	0.23-0.24	0.27-0.29
<i>henriettae</i>													
COI						<b>0-0.05</b>	0.20-0.23	0.19-0.21	0.22-0.24	0.17-0.21	0.18-0.22	0.17-1.32*	0.17-0.20
16S	2					<b>0-0.02</b>	0.17-0.19	0.15-0.16	0.21-0.22	0.17-0.19	0.15-0.16	0.18-0.19	0.21-0.22
<i>herculea</i>													
COI						<b>0-0.09</b>	<b>0-0.05</b>	0.20-0.24	0.21-0.27	0.15-0.16	0.21-0.25	0.23-1.92*	0.21-0.25
16S	5					<b>0-0.05</b>	<b>0-0.05</b>	0.16-0.18	0.18-0.20	0.17-0.20	0.15-0.16	0.20-0.21	0.22-0.24
<i>microsculpta</i>													
COI								<b>0-0.05</b>	0.26-0.29	0.16-0.20	0-0.08	0.17-1.38*	0.17-0.20
16S	3							<b>0-0.02</b>	0.16-0.19	0.13-0.15	0-0.02	0.10-0.11	0.10-0.12
<i>pagodula</i>													
COI									<b>0-0.13</b>	0.17-0.18	0.24-0.28	0.19-1.58*	0.18-0.23
16S	2								<b>0-0.10</b>	0.18-0.20	0.15-0.18	0.20-0.23	0.23-0.25
<i>peninsularis</i>													
COI										<b>0-0.02</b>	0.16-0.20	0.17-1.55*	0.16-0.17
16S	2									<b>0-0.005</b>	0.12-0.13	0.20	0.18-0.19
<i>pseudosulcospira</i>													
COI		0.00-0.06	0.02	0.14-0.17	0.22	0.18-0.22	0.21-0.25	0.02-0.06	0.27-0.28	0.16-0.19	0.06-0.07	0.18-1.29*	0.17-0.19
16S	1	0.00-0.04	0.01-0.03	0.15-0.17	0.22-0.23	0.16	0.19-0.20	0.01-0.02	0.18-0.20	0.15	0.01-0.02	0.11	0.12
<i>solemiana</i>													
COI										<b>0-0.06</b>	<b>0-0.06</b>	0.17-1.31*	0.16-0.18
16S	2									<b>0-0.01</b>	<b>0-0.01</b>	0.10	0.10
<i>sumatrensis</i>													
COI											<b>0-0.49*</b>	<b>0-0.49*</b>	0.10-0.98
16S	2										<b>0-0.004</b>	<b>0-0.004</b>	0.08-0.09
<i>torquata</i>													
COI												<b>0-0.06</b>	<b>0-0.06</b>
16S	2											<b>0-0.03</b>	<b>0-0.03</b>
<i>verbecki</i>													
COI		0.17-0.21	0.17	0.20-0.29	0.20	0.19-0.20	0.23-0.24	0.17-0.20	0.23-0.25	0.21-0.22	0.18-0.19	0.10-0.93*	0.06
16S	1	0.10-0.11	0.11	0.18-0.21	0.25-0.26	0.20-0.21	0.20-0.21	0.10-0.11	0.21-0.22	0.19	0.10	0.08	0.05-0.06
<i>wyckoffi</i>													
COI		0.21-0.22	0.21-0.22	0.19-0.25	0.20-0.22	0.19-0.21	0.21-0.23	0.21-0.22	0.24-0.27	0.17	0.18-0.21	0.19-1.57*	0.07
16S	1	0.10-0.17	0.17	0.18-0.20	0.24	0.13	0.19	0.17	0.23-0.25	0.18	0.17	0.22	0.25-0.26



TABLE 6. Sequence data analysed in this study with GenBank accessions and inventory numbers.

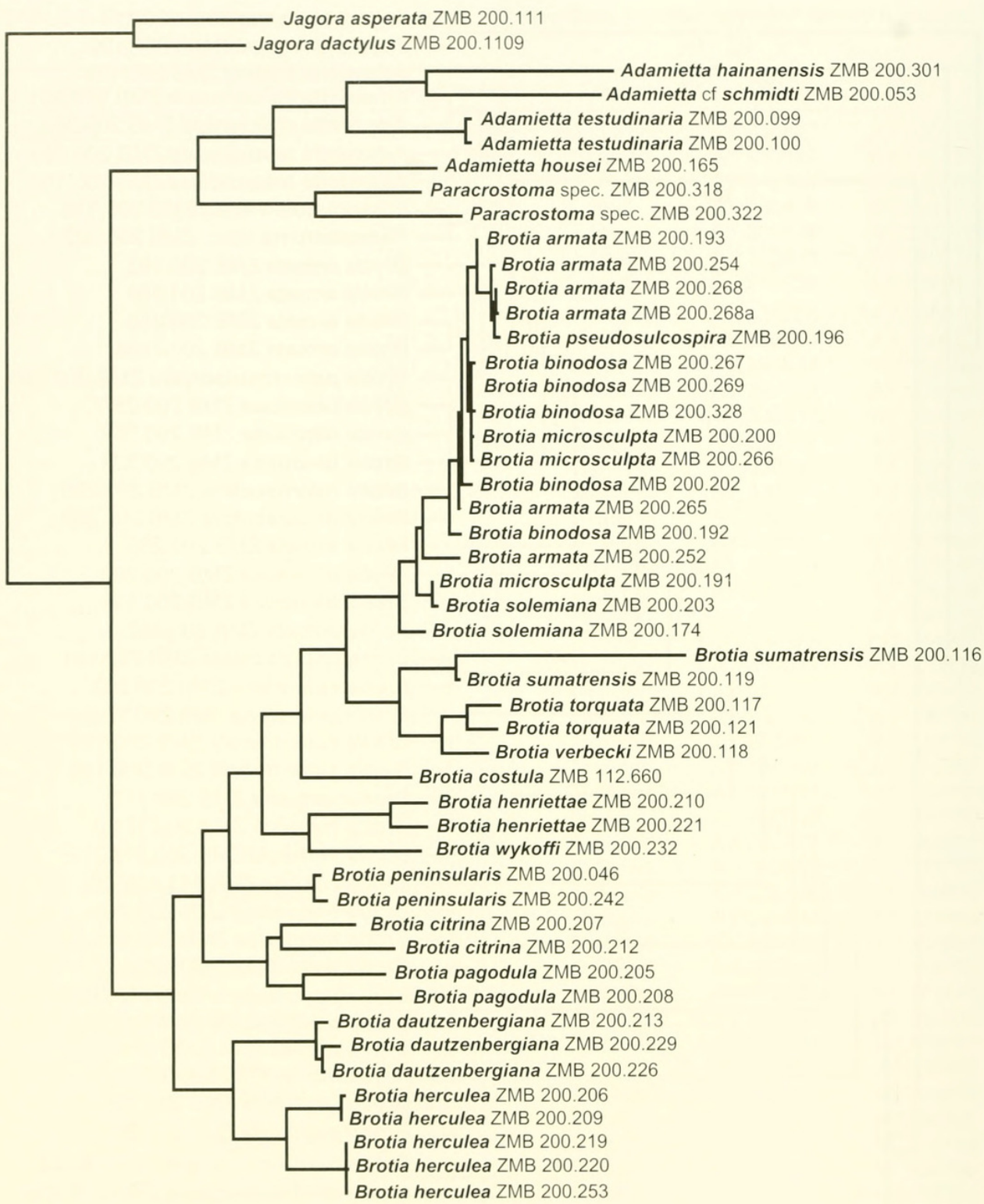
Genus	Species	Inventory No.	Origin	COI	16S
Adamietta	<i>A. hainanensis</i>	ZMB 200.301	Hong Kong	AY 330827	AY 330778
	<i>A. housei</i>	ZMB 200.165	Thailand	AY 330823	AY 330774
	<i>A. provisoria</i>	ZMB 200.053	Borneo	AY 242951	AH 012869
	<i>A. testudinaria</i>	ZMB 190.415	Java	AY 330825	AY 330777
		ZMB 190.416	Java	AY 330826	AY 330776
		ZMB 200.099	Java	AY 330824	AY 330775
		ZMB 200.100	Java	AY 242950	AY 242949
Brotia	<i>B. armata</i>	ZMB 200.193	Thailand	AY 330853	AY 330810
		ZMB 200.252	Thailand	AY 330854	AY 330809
		ZMB 200.254	Thailand	AY 330834	AY 330808
		ZMB 200.265	Thailand	AY 330855	AY 330806
		ZMB 200.268	Thailand	AY 330837	AY 330807
		ZMB 200.268a	Thailand	AY 330856	AY 330811
	<i>B. binodosa</i>	ZMB 200.192	Thailand	AY 330857	AY 330815
		ZMB 200.202	Thailand	AY 330859	AY 330819
		ZMB 200.267	Thailand	AY 330860	AY 330818
		ZMB 200.269	Thailand	AY 330861	AY 330820
		ZMB 200.328	Thailand	AY 330858	AY 330816
		ZMB 200.207	Thailand	AY 330829	AY 330798
	<i>B. citrina</i>	ZMB 200.212	Thailand	AY 330830	AY 330799
		ZMB 112.660	Nepal	DQ 284985	DQ 284986
	<i>B. dautzenbergiana</i>	ZMB 200.226	Thailand	AY 330831	AY 330802
		ZMB 200.229	Thailand	AY 330832	AY 330800
	<i>B. henriettae</i>	ZMB 200.210	Thailand	AY 330845	AY 330793
		ZMB 200.221	Thailand	AY 330846	AY 330794
	<i>B. herculea</i>	ZMB 200.206	Thailand	AY 330841	AY 330787
		ZMB 200.209	Thailand	AY 330842	AY 330789
		ZMB 200.219	Thailand	AY 330843	AY 330790
		ZMB 200.220	Thailand	AY 242972	AY 242971
		ZMB 200.253	Thailand	AY 330844	AY 330788
		ZMB 200.191	Thailand	AY 330836	AY 330805
	<i>B. microsculpta</i>	ZMB 200.200	Thailand	AY 330833	AY 330804
		ZMB 200.266	Thailand	AY 330835	AY 330803
		ZMB 200.205	Thailand	AY 330847	AY 330795
	<i>B. pagodula</i>	ZMB 200.208	Thailand	AY 172453	AY 172443
		ZMB 200.046	Thailand	AY 330850	AY 330792
	<i>B. peninsularis</i>	ZMB 200.242	Thailand	AY 330841	AY 330791
		ZMB 200.196	Thailand	AY 330862	AY 330797
	<i>B. pseudosulcospira</i>	ZMB 200.174	Thailand	AY 330849	AY 330814
		ZMB 200.203	Thailand	AY 330848	AY 330812
	<i>B. sumatrensis</i>	ZMB 200.116	Sumatra	AY 330838	AY 330784
		ZMB 200.119	Sumatra	AY 330840	AY 330785
	<i>B. torquata</i>	ZMB 200.117	Sumatra	AY 330864	AY 330781
		ZMB 200.121	Sumatra	AY 330865	AY 330782
	<i>B. verbecki</i>	ZMB 200.118	Sumatra	AY 330863	AY 330779
	<i>B. wykoffi</i>	ZMB 200.232	Thailand	AY 330866	AY 330796
Paracrostoma	<i>P. spec.</i>	ZMB 200.318	South India	AY 330821	AY 330770
	<i>P. spec.</i>	ZMB 200.322	South India	AY 330822	AY 330773
Jagora	<i>J. asperata</i>	ZMB 200.311	Philippines	AY 172447	AY 172439
	<i>J. dactylus</i>	ZMB 200.109	Philippines	AY 172444	AY 172438





FIG. 78. Confidence limits on the topology of the MP strict consensus cladogram of concatenated data set of 16S and COI expressed by branch support values mapped on respective branches (above: MP bootstrap values, middle: NJ bootstrap values, below: BI posterior clade probabilities).





— 50 changes

FIG. 79. Bayesian inference phylogram of concatenated data set of 16S and COI.



lighted as genetically very distinct is deficient. It will thus not be considered in further discussion.

Pair wise genetic distances between different *Brotia* species range between the maxima of 8 and 29% when considering species from outside the Kaek River, and between 0 and 8% when comparing endemic species in the Kaek River.

In COI, pair wise genetic distances between species from different genera are even higher, with 28–40%, when comparing *Jagora* and *Brotia*, 20–47% when comparing *Adamietta* and *Brotia*, and 24–42% when comparing *Paracrostoma* and *Brotia*.

Similar genetic distances are observed also in 16S with an infraspecific level of sequence divergence of up to 10%, interspecific distances of up to 8% among Kaek River species and up to 25% between other *Brotia* species as well as divergence rates between 30 and 56% when comparing species of different genera with each other.

### Phylogenetic Analyses

The concatenated sequence data set was analysed using MP, NJ, and BI methodology.

603 positions of the concatenated data set with a total length of 1,472 bp are constant, 222 variable but parsimony uninformative, and 647 variable and parsimony informative. MP analysis delivers 6 most parsimonious trees; the strict consensus tree is shown in Fig. 78 (numbers mapped on the tree indicate branch support for the depicted topology by MP bootstrap values [above lines], NJ bootstrap values [on lines], and Bayesian posterior clade probabilities [below lines], respectively). All trees were rooted with species of *Jagora* as outgroup since this genus is among the most basal groups among the Pachychilidae (Köhler et al., 2004). The topologies of two distance based trees, the NJ phylogram (not shown) and the BI phylogram (Fig. 79), do widely correspond to the MP tree. However, in contrast to the MP tree, these reconstruction show both *Adamietta* and *B. citrina* as monophyletic groupings, the latter being sister to *B. pagodula*.

All trees corroborate the monophyly of *Brotia* as delineated according to morphological characteristics in respect to the other pachychilid genera included into the analysis, that is, *Jagora*, *Paracrostoma*, and *Adamietta*. The monophyly of *Adamietta* is not unambiguously

corroborated since it is not shown as a monophylum in the MP tree. However, this is not relevant in regard to the monophyly of *Brotia*. Within *Brotia* some well supported sub-groupings are shown, such as the Kaek River species flock, and a Sumatra clade. Only the species of the Kaek River species flock do not appear as monophyletic entities in either of the trees. These species also show low genetic distances, as has been mentioned above.

## DISCUSSION

### Evaluation of Morphological Characters

#### (1) Adult Shell

Traditionally, in classifications and taxon descriptions of gastropods the shell is emphasized. It bears many characters that are most convenient for taxonomic purposes and that are accessible even from dry material and fossils (for examples, Smith, 1981; Ridgeway et al., 1998). Also in pachychilids, shell features are essential to distinguish species, and morphometry is often useful for species discrimination. On the other hand, the shell may particularly be prone to environmental pressures such as wave action (Reid, 1986: 8 for *Littorina*) or predation (Vermeij & Covich, 1978) by birds (Reed & Janzen, 1999) or by crabs and crayfish (Reid, 1992; Warner, 1996). Therefore, divergent shells may represent just phenotypic variation. In addition to that, even relatively complex shell structures may have evolved in analogy as has been discussed for the clausilial apparatus in the Clausiliidae (Moorsel et al., 2000).

Shell features, such as shape, size, thickness, and sculpture, vary considerably among species of *Brotia*. This diversity provoked earlier authors to describe many new species based solely on the shell, and a few of them carried this to excess by introducing a vast number of taxonomic names for subtle conchological differences (e.g., Nevill, 1885). This procedure reflects the essentialist view of many systematists at this time (see Haffer, 1997 for examples from ornithology; Glaubrecht, 2004, for malacology).

Since the 1930's, when authors began to acknowledge the existence of intraspecific variation, it has frequently been assumed that



*Brotia* species are remarkably plastic not only in their phenotypic appearance. Similar taxa have in the following been considered conspecific, which has bloated the synonymies (e.g., Rensch, 1934; Benthem Jutting, 1956; Brandt, 1974). However, in many cases it remained unclear (and unattended) to which extent shell parameters really varied within single species. Most recent data suggests that intraspecific variability of morphological characters including the shell frequently was overemphasized, which has led to erroneous taxonomic conclusions. This has been exemplified also for other pachychilids, such as *Jagora* by Köhler & Glaubrecht (2003). Consequently, one of the main results of the current study is the conclusion that in *Brotia*, 20<sup>th</sup> century authors have frequently gone too far in synonymizing taxa for exhibiting a similar shell. Instead, a quite contrasting picture is revealed herein showing that *Brotia* species in general are much more restricted by means of their morphological variability as well as their distributional range than assumed before.

**Shell Shape:** Most pachychilid species have highly turreted shells with about up to 12 whorls. This feature is found in all major clades as a predominant character. Few species have conical or even globular shells, such as *B. armata*, *B. paludiformis*, or *B. pagodula*. These species live attached to stones and boulders in swiftly flowing streams while other species are found buried in or crawling on substrata of all kinds.

It has been shown by Urabe (1998) for *Semisulcospira reiniana* that individuals inhabiting riverine habitats have a more conical shell than specimens from stagnant waters as a phenotypic response to environmental pressures. Although this observation refers to phenotypic responses only, a conical shell can be considered as adaptation to strong water currents repeatedly obtained by Asian pachychilids.

**Size and Thickness:** In general, shell size and thickness may be controlled by the availability of nutrients (Frömming, 1956), but also by the harshness of physical environmental factors (Vermeij, 1972), parasitism (Wright, 1966), or predation (Zipser & Vermeij, 1978; Reimchen, 1982; Reid, 1986). Nevertheless, there is substantial evidence that shell growth rate and adult size are also under genetic control (Vermeij, 1980). In *Brotia*, variability in shell size among conspecific

specimens of same age is considered lower than formerly supposed. Only in few cases, shells may vary for about the twofold between populations from different environments: Specimens of *B. torquata* from Lake Manindjau are considerably smaller than those from adjacent rivers. In other cases, however, inhabitants of lakes are larger than riverine forms (e.g., *B. sumatrensis* from Lake Toba). A possible explanation could include the limitation of certain nutrients due to interspecific competition in one case and the presence of predators, such as shell crushing crabs as discussed for *Tylomelania* in Sulawesi (Rintelen et al., 2004) or simply the fact that large shells are prone to dislodgement in rivers but not in lakes in the other case.

**Sculpture:** Freshwater gastropods in general are notorious for their plasticity in form and sculpture (e.g., Davis, 1971; Fretter & Graham, 1984; Urabe, 2000). Similarly, among *Brotia* shell sculptures vary considerably and are used as a conspicuous feature to distinguish among species. Shells may be completely smooth or sculptured by strong axial ribs, spiral cords, spiny nodules, and/or spines. The degree of intraspecific variability, however, seems to differ greatly. In general, variation of the shell morphology, and thus also sculpture, has been considered to have a genetic basis and a strong sculpture shall be adaptive against predators or physical environmental factors (e.g., West & Cohen, 1996). It has been shown that sculptured shells are more tolerant of a crushing load than are smooth shells with the same shell mass (Urabe, 2000). Some studies have further demonstrated that shell morphology shows a great deal of phenotypic plasticity controlled by physical or biological factors (e.g., De Wolf et al., 1997), such as the substratum (Urabe, 2000). While phenotypic plasticity within single species has not been addressed in this study, it can be confirmed that shell form and sculpture are correlated to the substratum: species with smooth shells were always found on sandy or pebble substrata, whereas species with armed shells live on gravel, stony bottoms or sit on boulders (Glaubrecht & Köhler, 2004, for *Brotia* species of the Kaek River). It is assumed that a sculpture not only prevents the animals from being preyed upon, which seems to be a rather imaginary threat when sitting directly in the water current, but



from the influence of physical forces. A well-developed sculpture, however, is unfavourable when crawling in the sand as it would increase the friction with the substratum. Accordingly, different shell sculptures may have evolved as result of ecological and morphological diversification, in some cases induced by competitive interaction between the different species.

**Colour.** In *Brotia* shell colour is uniform, from yellowish brown to olive brown, dark brown or almost black and overall not very helpful for species recognition. In some species, dark spiral bands may be present; axial flames that can be observed in other pachychilids, such as *Pachychilus*, *Adamietta*, and *Paracrostoma*, are generally lacking.

## (2) Embryonic Shell

*Brotia* shows a remarkable modification of the ontogeny that is also imprinted in the embryonic shell structure (Köhler & Glaubrecht, 2001): In early ontogenetic stages, soft tissue protrudes from the apical whorl of the forming shell. This tissue is believed to have nutritive function for the encapsulated embryo. A secondary shell layer closes at the apex not before this tissue is entirely consumed. Protruding tissue and uncalcified apex was first noted by Morrison (1954) in embryonic shells of "*Brotia baccata*" (= *B. henriettae*). The uncalcified apex was called by him an "open" or "soft apex" and stated to be a characteristic feature of *Brotia*. Subsequently, Solem (1966: 16, fig. 1) depicted several embryonic stages of *B. binodosa* with protruding soft tissue and open apex; this was followed by a report an "asymmetric" apical portion of the juvenile shell of *B. episcopalis* (Davis, 1971: fig. 11).

A storage structure similar to the tissue observed in *Brotia* was described for numerous other "prosobranchs", functioning as a substructure for the formation of the digestive gland (Fioroni & Schmekel, 1976: 129 ff.). The "yolk sac" of *Brotia*, which originates from the yolk supply of the egg capsule, is believed to be of same morphological and functional origin.

Riedel (1993) has hypothesized that delayed calcification of the apical whorl and a shrinking visceral mass in *Melanoides tuberculata* result in a wrinkled shell structure. This pattern is also observed in *Brotia*, in which the process of shell calcification is retarded and overlaps with the shrinking of the yolk sac by consumption of nutritive material. However,

while delayed shell calcification is known from a number of gastropods (Eyster, 1986: 224–226), among them also some Thiaridae (Riedel, 1993; Glaubrecht, 1996), nutrition via a large, protruding yolk sac is unique among freshwater gastropods in the pachychilid genera *Brotia* and *Jagora* (description of the latter: Köhler & Glaubrecht, 2003). However, the phylogenetic relationships between these two genera indicate that open apex and protruding yolk sac have evolved independently (Köhler et al., 2004). This is suggested also by a different appearance of the apical portion of the embryonic shell in the two taxa. While in *Brotia* the apical whorl is wrinkled and appears irregular when viewed from above, in *Jagora* it is comprised by a lid-like structure that does not resemble a whorl at all (figured in Köhler & Glaubrecht, 2003).

Embryonic shells of all other Asian Pachychilidae can easily be distinguished from *Brotia* by the lack of wrinkles. A comparative overview of different embryonic shell morphologies in the Pachychilidae is provided by Köhler & Glaubrecht (2005). Consequently, in all other pachychilid taxa shell calcification is not retarded, but complete and continuous, a protruding yolk sac is not present.

## Operculum

Next to the shell, the operculum is a feature that has long been used as diagnostic character for the classification of "melaniid" gastropods. For example, Troschel (1857–58) based his classification of the "Melaniidae" in part on opercular features. P. Sarasin & F. Sarasin (1898) distinguished between "Neomelanien" and "Palaeomelanien" on basis of a different operculum. Later, all palaeomelanian species were transferred to *Brotia* by Thiele (1928, 1929). While this decision has proven erroneous, the two species groups delineated by P. Sarasin & F. Sarasin (1898) still are considered to largely represent groups recognised by modern systematics: Pachychilidae and Thiaridae, respectively (Glaubrecht, 1999). Even taxa more closely related to the Pachychilidae, such as *Faunus ater* and the Melanopsidae, possess a paucispiral operculum (Houbrick, 1991; Glaubrecht, 1996). Consequently, a multispiral operculum with a central or subcentral nucleus is considered as autapomorphy of the Pachychilidae. Within this family, however, operculum morphology is a conservative character, and only in some species it may be used for species determination.



## Radula

In general, the molluscan radula is considered a conservative character with little variation on the species level (Fretter & Graham, 1994). Nevertheless, the importance of radular characteristics, at least in higher level classifications, has been acknowledged early on (Troschel, 1856–1863; Thiele, 1928, 1929–1935). At high levels of taxonomic hierarchy, several of the radular patterns first described by 19<sup>th</sup> century morphologists still correspond largely or entirely with monophyletic clades recognised by modern cladistic analyses. Also at lower levels, recent cladistic analyses of morphology have frequently included radular characters (Glaubrecht, 1996; Reid, 1996; Ponder & Lindberg, 1997; Simone, 2001; Strong, 2003). Though, it became evident that radular characters, as any other morphological feature, may be prone to adaptation, parallelism and convergence and that intraspecific variability and plasticity may be considerable (Padilla, 1998; Reid & Mak, 1999; Reid, 2000). Therefore, before radular features can be used in phylogenetic studies, the extent of intraspecific variation must be carefully assessed, as is standard practise for shell characters.

The pachychilid radula is of the generalised taenioglossate type. Each row consists of a central rachidian, flanked on each side by a lateral and an inner and outer marginal tooth. All these teeth bear a number of cusps. Comparison of radulae of different pachychilid genera, such as *Pachychilus* (Troschel, 1858: pl. 9; Fischer & Crosse, 1892: pl. 49, fig. 14; Simone, 2001: figs. 95, 96), *Doryssa* (Simone, 2001: figs. 89–92), *Potadoma* (Glaubrecht, 1996: pl. 5, figs. 7, 8), *Jagora* (Köhler & Glaubrecht, 2003), *Sulcospira* (Troschel, 1858: pl. 9, fig. 6; Köhler & Glaubrecht, 2005), *Pseudopotamis* (Glaubrecht & Rintelen, 2003), and *Tylomelania* (Rintelen & Glaubrecht, 2005), shows little variation of radula patterns within the family. Nonetheless, it has also been shown that denticle shape and size as well as radular length may vary considerable even between closely related species if they occur in sympatry but feed on different substrata (Glaubrecht & Köhler, 2004; Rintelen et al., 2004; Rintelen & Glaubrecht, 2005).

The generalized radular pattern observed in most *Brotia* species comprises a central tooth with a well-developed glabella and a cutting edge comprising one main denticle flanked by up to three accessory cusps that taper in size,

a lateral tooth exhibiting a glabella and a main denticle flanked frequently by two inner and two to three outer accessory cusps, as well as the inner and outer marginals, each with two cusps. These cusps may be rather of the same size or the outer cusp is enlarged. There are several other structures, for example, lateral extensions of the central and lateral tooth or a lateral flange of the marginal teeth that show a certain degree of variability among different species. Furthermore, the shape of the glabella of the main denticle varies among species. In general, the range of variation within *Brotia* is rather small, though, and only rarely some radular features are species specific. Most conspicuous modifications of the radula are connected to the substratum (Glaubrecht & Köhler, 2004; Rintelen et al., 2004). In rock-dwelling species, cusps may be enlarged, blunt or broadly round (e.g., in *B. pagodula*), whereas species living on soft substrata may possess much smaller denticles as well as radular teeth (e.g., *B. microsculpta*).

## Gross Anatomy

The general appearance of the soft body and general organisation of the mantle cavity is rather constant among southeast Asian pachychilids and corresponds largely to the description given for *Brotia*. A feature typical for the Pachychilidae is the smooth mantle edge, which clearly differs from the papillated mantle edge found in Thiaridae. Among Pachychilidae, *Jagora*, *Tylomelania*, *Melanatria*, and *Pachychilus* differ from *Brotia*, *Adamietta*, and *Paracrostoma* in possessing a fleshy flap at the inner surface of the mantle roof. It has been suggested that this flap has a function for the formation of clutch masses during egg laying; therefore, it would have no function in viviparous species (Houbbrick, 1991). In *Jagora*, it still might be functional, perhaps to prevent egg capsules and juveniles from becoming dislocated from the mantle cavity in which they are retained. Another structure connected to reproduction is the genital groove at the right side of the head, which is found not only in pachychilids, but also Melanopsidae and Potamididae. While in egg laying species, this groove is involved in egg deposition, in *Brotia* it is needed to transfer eggs from the pallial oviduct to the brood pouch (Fig. 5F).

**Reproductive Organs:** These are the most informative for pachychilid systematics (Köhler et al., 2004). Although all Asian Pachy-



chilidae are viviparous, brooding structures are not homologous among several groups. The subhaemocoelic brood pouch found in *Brotia* was first mentioned by Martens (1897: 29). Later, Moore (1899: 161, 162; pl. 14, fig. 13; pl. 16, fig. 2), Morrison (1954: 383), Davis (1971: 69), and Köhler & Glaubrecht (2001) described this pouch in more detail. A homologous brood pouch is found in *Adamietta* (Brandt, 1974) and *Paracrostoma* (unpubl. data) and is considered as a synapomorphy of the Asia mainland clade among the Pachychilidae (Köhler et al., 2004).

No homologous incubatory structures are possessed by other Asian Pachychilidae or other freshwater cerithioideans. The Philippine pachychilid *Jagora* broods in the mantle cavity (Köhler & Glaubrecht, 2003), while pachychilid *Pseudopotamis* and *Tylomelania* possess a uterine brood pouch (Glaubrecht & Rintelen, 2003; Rintelen & Glaubrecht, 2005). Since oviparity is suggested to represent a plesiomorphic character state in the Pachychilidae, brooding in turn must have evolved three times independently in this family (Köhler et al., 2004). In the Thiaridae and viviparous Planaxidae, a subhaemocoelic brood pouch very similar to that of *Brotia* is found. While this brood pouch was discussed as representing a possible synapomorphy of a clade comprising Planaxidae and Thiaridae (e.g., Houbrick, 1988; Glaubrecht, 1996; Simone, 2001), recent phylogenetic studies suggest that these are convergent (Lydeard et al., 2002; Köhler et al., 2004). The presence of a subhaemocoelic brood pouch in *Brotia* was furthermore a reason for erroneously placing *Brotia* within the Thiaridae (e.g., Morrison, 1954; Benthem Jutting, 1956; Brandt, 1968, 1974).

Other informative structures of the reproductive morphology include the pallial oviduct and the arrangement of the gonads. Among Asian Pachychilidae, *Brotia* possesses the simplest pallial oviduct. *Paracrostoma* differs by a distinct organisation of the sperm gutter (unpubl. data), which is located more posteriorly. *Adamietta* possesses a seminal receptacle in addition to a spermatophore bursa, which is present also in *Brotia* (Köhler & Glaubrecht, 2001, for the *Brotia testudinaria* group). Again, *Jagora*, *Pseudopotamis*, and *Tylomelania* possess oviduct morphologies that significantly deviate from *Brotia* (Glaubrecht & Rintelen, 2003; Köhler &

Glaubrecht, 2003; Rintelen & Glaubrecht, 2005).

**Stomach:** Midgut morphology recently emerged as an yet untapped source of phylogenetic information, at least when groups of higher taxonomic ranks are compared (e.g., Simone, 2001; Strong, 2003). Various features of the stomach, such as a laminated crescent sorting area with two adjacent crescent and septate thickenings, a lateral and marginal fold, a single digestive gland duct, and two crescent ridges posterior to the opening of the digestive gland duct are considered synapomorphic among Pachychilidae (Strong & Glaubrecht, 1999). However, these features show little variation among the different genera as can be judged from the figures and descriptions for *Potadoma* (Binder, 1959), *Pachychilus* (Simone, 2001), *Jagora* (Köhler & Glaubrecht, 2003), and *Tylomelania* (Rintelen & Glaubrecht, 2005), and we were not able to identify characters that can be considered as diagnostic for species of *Brotia*.

#### Molecular Phylogeny of *Brotia*

The number of species included into phylogenetic analyses of molecular data is limited because of the restricted availability of material suitable for sequencing. For instance, it was not possible to extract high molecular DNA from preserved museum material. Nonetheless, mitochondrial DNA from a total of 48 samples of 16 Thai and Sumatran *Brotia* taxa, as well as 6 further pachychilid taxa from Asia mainland, were sequenced and analysed. Sequences of two *Jagora* species were included as outgroup representatives.

The mitochondrial trees unambiguously corroborate the monophyly of *Brotia* as restricted herein by morphology with regard to other pachychilid genera included in the analyses (i.e., *Jagora*, *Paracrostoma*, *Adamietta*). In this respect, it is important to bear in mind that also the concepts of the latter two genera – *Paracrostoma* and *Adamietta* – are subject to changes in regard to previous treatments, for example, by Solem (1966) and Brandt (1968, 1974). For instance, some species that were affiliated with *Paracrostoma* because of their conical shell were transferred to *Brotia* by Glaubrecht & Köhler (2004). *Paracrostoma* is now restricted to its type species, *P. huegellii*, and some yet undescribed species (Köhler, unpubl. data) endemic to southern India.



While on generic level the phylogeny strongly supports the classification based on the morphology, problems mainly occur as to the identification of some species-level taxa, in particular among the Kaek River radiation (Figs. 78, 79). This radiation comprises at least seven species recognized by a divergent shell and radular morphology, such as *B. armata*, *B. binodosa*, and *B. microsculpta*. However, sequence divergence among these taxa is very low, which is considered the main reason for the observed mismatch between the topology of the mitochondrial gene tree and the presumed species identity of these taxa as based on their morphology. Low genetic divergence indicates a relatively recent origin of the Kaek River radiation, and incomplete lineage sorting is the most likely explanation for the unresolved mitochondrial gene tree (Glaubrecht & Köhler, 2004). In order to get better resolved molecular reconstructions, it has been suggested to analyse different genetic markers and to use a different methodology, that is, AFLP genotyping.

Looking beyond the Kaek River species flock, all other *Brotia* species recognized by their morphology are also resolved as monophyletic entities in the mitochondrial gene trees. There is only one exception, *B. citrina*, the two sequences of which are shown as a paraphylum in the MP tree. In the distance-based trees, however, these sequences cluster together as a sister pair, which supports our treatment of the two populations as being conspecific. The mismatch in the MP tree therefore is no reason to doubt in the correct determination of *B. citrina*.

Intraspecific sequence divergence among *Brotia* species calculated under the GTR+I+ $\Gamma$  model of sequence evolution does not exceed a maximum of 16% in COI and 29% in 16S, but mostly values are clearly smaller. Not considered is the unusual high sequence divergence of one of the two sequences of *B. sumatrensis*, which is caused by numerous peculiar substitutions in this sequence. Since a similar divergence is not observed in 16S, technical failure in sequencing cannot be ruled out.

Rates of sequence divergence reported here for *Brotia*, although difficult to compare since different models of gene evolution were applied by different studies, does exceed the limits observed in other freshwater cerithioideans (e.g., Pleuroceridae; Lydeard et al. 1997; Holznagel & Lydeard, 2000), but is similar to infraspecific sequence divergences observed

in other Pachychilidae (e.g., Köhler & Glaubrecht, 2003; Glaubrecht & Rintelen, 2003).

Interestingly, in *Brotia* morphological disparity and genetic differentiation obviously are not linked to each other. Instead, two extremes are observed with the morphologically diverse but genetically rather undifferentiated Kaek River species flock on one hand and with species such as *B. citrina* and *B. pagodula* on the other, which show a low degree of morphological plasticity but a high degree of genetic differentiation. This phenomenon can probably be explained by strong competition and low prezygotic isolation (by means of geographical separation) between different sympatric taxa in the first case and absence of competition and relatively strong geographical separation between different conspecific populations in the latter case. This significant variation of infraspecific sequence divergences among *Brotia* shows with which problems approaches are fraught that aim at delimiting species only by the use of genetic distances (for further discussion of the merits and limits of DNA taxonomy the reader is referred to the contributions of, e.g., Lipscomb et al., 2003; Seberg et al., 2003; Tautz et al., 2003; Blaxter, 2004).

## Systematic Implications

### (1) Family Placement

The familiar placement of *Brotia* was subject to controversy caused by a mélange of rival systematic opinions as well as taxonomic difficulties. In an attempt to clarify the confusion, we shortly revise phylogenetic and systematic aspects on one hand and taxonomic issues on the other.

In the first attempts to classify what we call today cerithioidean freshwater gastropods all species were placed in a single group called Melanien or melanians, later also Melaniidae (e.g., Lamarck, 1822; Brot, 1874). This huge assemblage was subsequently subdivided into different groupings according to diagnostic features of their shell, operculum, and radula (e.g., Troschel, 1856–1863; Fischer & Crosse, 1891–1892; Thiele, 1928, 1929–1935); but Melaniidae were still considered a large monophylum. Fischer & Crosse (1891–1892) as well as Thiele (1928, 1929–1935) recognized six different lineages within the Melaniidae, among them a group already characterized by Troschel (1857) as “Pachychili” that comprises, for example, *Pachychilus*, *Potadoma*, *Melanatria*, and *Sulcospira*. This



group was ranked as a subfamily Pachychilinae of the Melaniidae according to the name introduced by Troschel. Morrison (1954), however, who strongly influenced most 20<sup>th</sup> century authors, recognized only three lineages and placed representatives of the "Pachychili" within two different clades, that is, the Pleuroceridae (*Pachychilus* and *Potadoma*) and the Thiaridae (*Sulcospira*, *Antimelania*, and *Brotia*). Later authors followed Morrison and treated Neotropical taxa as member of the Pleuroceridae (e.g., Vaught, 1989; Simone, 2001), but Asian taxa as Thiaridae (e.g., Solem, 1966; Davis, 1971; Brandt, 1968, 1974; Burch, 1980). This concept initially seemed to gain support even from a first cladistic analysis of morphological data presented by Houbrick (1988). In this analysis, which was to a large part based on morphological data presented by Morrison (1954), two major and independent freshwater lineages within the Cerithioidea were recognized, that is (1) Pleuroceridae + Melanopsidae and (2) Thiaridae. *Brotia* was affiliated with the latter for possessing a subhaemocoelic brood pouch. First doubts in this view have been raised by another cladistic analysis of morphological data (Glaubrecht, 1996), which revealed a new group besides Thiaridae and Melanopsidae (while Pleuroceridae were not included): the Pachychilidae. However, in this study only the oviparous taxa *Pachychilus*, *Doryssa*, *Melanatria*, and *Potadoma* were subsumed under the Pachychilidae, whereas the viviparous *Brotia* still was considered a thiarid. A third cladistic analysis of morphological data (Simone, 2001) supports the existence of exactly this monophyletic freshwater group comprising *Pachychilus* and *Doryssa* as being clearly distinct from the Thiaridae (with *Melanoides* and *Aylacostoma*). However, in this study the (wrong) name "Pleuroceridae" was employed for this lineage.

Molecular genetic studies helped much to clarify aspects of cerithioidean phylogeny. The most comprehensive phylogeny based on mitochondrial sequence data was so far presented by Lydeard et al. (2002). This study provided further evidence for the existence of at least three distinct freshwater lineages, (1) the Thiaridae, (2) the Melanopsidae + Pleuroceridae, and (3) an unnamed group comprising *Pachychilus* and *Paracrostoma*. This clear evidence unfortunately was obscured by application of a misleading taxonomy: Although forming a distinct lineage,

*Pachychilus* and *Paracrostoma* were uncritically treated as members of Pleuroceridae and Thiaridae, respectively. As a consequence, all freshwater cerithioidean lineages were seemingly rendered polyphyletic, while a more restricted application of names would have unmistakably shown that they are in fact all monophyletic.

Direct comparison of the different phylogenetic studies is complicated by their deviant taxon composition. However, a closer look reveals that there is strong evidence for the existence of a monophyletic freshwater lineage beside the (1) Thiaridae and (2) Pleuroceridae + Melanopsidae, constituted by taxa such as *Pachychilus*, *Doryssa*, or *Paracrostoma* (Glaubrecht, 1996; Simone, 2001; Lydeard et al., 2002). All three studies failed to name this lineage properly, though. The names Thiaridae and Pleuroceridae although formerly used certainly are not available for this group, since they refer to the other two freshwater clades.

As the oldest name for this "new" lineage the name "Pachychili" was introduced by Troschel (1857) and later used as Pachychilinae by Fischer & Crosse (1891). Thiele (1921), who believed the name Pachychilinae to be invalid since he erroneously considered the generic name *Pachychilus* Lea, 1850, for neotropical "melaniids" as being preoccupied by *Pachychila* Eschscholtz, 1831, also recognized this taxon but suggested "Melanatriinae" as a replacement name. For a different reasoning against the validity of the name "Pachychilidae" with Troschel (1857) as author, see Bouchet & Rocroi (2005) as well as the introductory remarks in this article.

In contrast to Thiele (1921, 1925, 1928) we consider the name Pachychilidae as available and valid. Consequently, Melanatriinae is a synonym of Pachychilidae (Köhler & Glaubrecht, 2002, 2002a).

Eventually, Thiele (1925: 83) noticed that *Brotia* is member of this group besides, for example, *Pachychilus* and *Melanatria*, based on radular and opercular features. This is supported by a molecular phylogeny showing the close affinity of the Asian taxa, such as *Brotia*, with the Neotropical taxa, such as *Pachychilus*. This provided strong evidence for the existence of the clade named Pachychilidae (Köhler et al., 2004). As a consequence, the view of Morrison (1954) and Houbrick (1988), who strongly emphasized features of the soft body, in particular of the reproductive tract, on the systematic position of *Brotia* is refuted.



Morphological comparison of *Brotia* with other freshwater cerithioideans reveals that it shares as a synapomorphic character a widely corresponding operculum and radular morphology with oviparous pachychilids, such as *Pachychilus*. This also means that a subhaemocoelic brood pouch in *Brotia* has evolved in convergence to a similar structure found in the Thiaridae (Köhler & Glaubrecht, 2001; Köhler et al., 2004).

## (2) Phylogenetic Relationships among Asian Pachychilidae

Traditionally almost all Asian pachychilid species sooner or later were attributed to *Brotia* by one or the other author. This was done in absence of a phylogenetic reconstruction, which would allow to identify autapomorphic features and lead to an inflated concept of *Brotia*, which in its conventional understanding by Rensch (1934), Abbott (1948), Benthem Jutting (1956), Brandt (1968, 1974), and Davis (1971) is rendered a polyphyletic grouping.

In a preliminary study, Köhler & Glaubrecht (2001) identified four different species groups among what was previously considered as constituting *Brotia*, which most conspicuously are characterized by peculiarities of their reproductive tract, their incubatory anatomy, and their embryonic shell. In concert with molecular genetic analyses it has been shown that these groups represent independent and monophyletic evolutionary lineages. The conspicuous morphological differences between and different evolutionary histories of these lineages justify the treatment as independent genera (Köhler & Glaubrecht, 2003; Glaubrecht & Rintelen, 2003; Köhler et al., 2004; Rintelen & Glaubrecht, 2005). According to this revised and more specific concept, *Brotia* is here restricted to pachychilid species possessing diagnostic characteristics, such as a wrinkled apical whorl of the embryonic shell and a simple pallial oviduct with a deep, ciliated spermatophore bursa but without a seminal receptacle. Besides *Brotia* there are six further pachychilid genera mainly recognized on basis of a divergent reproductive and embryonic shell morphology. Some of them have already been systematically revised, such as (1) *Jagora* endemic to the Philippines (Köhler & Glaubrecht, 2003), (2) *Tylomelania* endemic to Sulawesi (Rintelen & Glaubrecht, 2005), (3) *Pseudopotamis* endemic to the Torres Strait Islands (Glaubrecht & Rintelen, 2003), and (4)

*Sulcospira* endemic to Java (Köhler & Glaubrecht, 2005). Irrespective of the fact that a formal revision of the two remaining genera, (5) *Adamietta* and (6) *Paracrostoma*, still is pending, it is suggested on basis of a molecular phylogeny of the Pachychilidae that they are also distinct (Köhler et al., 2004). This suggestion is corroborated by published and also unpublished morphological data (Köhler & Glaubrecht, 2001; Köhler, unpubl. data).

Together with these latter two genera *Brotia* forms a monophyletic lineage, the Southeast Asia mainland clade, which is characterized by possession of a subhaemocoelic brood pouch as synapomorphic feature (see Köhler et al., 2004).

## Revised Concept of *Brotia*

What remains of *Brotia* under the restricted concept, still is a diverse group comprising at least 27 species that ranges from northeast India through Bangladesh, Myanmar, Thailand, and the Malaysian Peninsula to Sumatra, Borneo, and perhaps even Java. Systematic affinities of eight additional species remain to be clarified.

A subdivision into three subgenera as suggested by Brandt (1974) is refuted by the current study. Brandt suggested ranking two taxa, *Paracrostoma* and *Senckenbergia*, as subgenera of *Brotia*. This treatment is supported neither by morphological nor by molecular genetic data. In fact, *Paracrostoma* represents a monophyletic group closely related to *Brotia* but definitely distinct, as is revealed by the mitochondrial phylogeny (Figs. 78, 79; Köhler et al., 2004). All Thai species affiliated with *Paracrostoma* by Solem (1966) and Brandt (1968, 1974) are members of *Brotia* since they are not closely related to *Paracrostoma* from southern India but cluster together within *Brotia* (Glaubrecht & Köhler, 2004).

Type species of *Senckenbergia* is *Melania pleuroceroides* Bavay & Dautzenberg, 1910, a species from the Yangtze-Kiang. This species was stated to possess an operculum similar to *Semisulcospira*, which is a pleurocerid (Yen, 1939: 55). Since the Yangtze-Kiang is far out of the range of *Brotia*, and since also the operculum of its type species is of a pleurocerid type, *Senckenbergia* cannot be considered as a member of *Brotia*. A species originally assigned to *Senckenbergia* by Brandt (1974) is herein treated as *Brotia wykoffi* in regard to its morphology and position in the molecular trees.



In comparison to concepts used by former revising authors, that is, mainly Brandt (1968, 1974), the current study shows that assumptions on the morphological variability and geographical range of single species were exaggerated. For instance, Rensch (1934), Benthem Jutting (1956), and Brandt (1974) believed *B. costula* to be a highly variable species that occurs across entire Southeast Asia from India to the Philippines and even on some oceanic islands. It has been shown, however, that this species is much more restricted in its occurrence and also in respect to its morphological properties. Still, there are a number of named forms that preliminary remain as synonyms of this as well as of other species, although their distinct shells might indicate that they in fact represent independent species. This holds true, for example, for *B. reevei* (treated as synonym of *B. herculea*) and *B. elongata* (treated as synonym of *B. henriettae*). However, any decision on the status of these and other named forms in absence of properly preserved material would be rendered rather a matter of opinion. For this reason and in order to not further complicate the taxonomy of this group, we here follow the usual treatment of those taxa by former authors. In this respect, we are convinced that future studies will be able to recognize further, yet vaguely defined or unknown species within *Brotia*.

### Conclusions

In summary, 27 species of *Brotia* are recognized in this work and eight additional species are presented with uncertain affinities. Using morphological and molecular data, the characteristics of *Brotia* are specified, and many species are newly delimited. Former systematic concepts are discussed and corrected accordingly. The current study results in an altered and more restricted concept of *Brotia* in comparison to former suggestions. It further shows that the subdivision into several subgenera as suggested by Brandt (1974) is erroneous. The new systematic concept is relevant also from a biogeographical perspective. While it has been assumed before that the range of *Brotia* covers almost entire South and Southeast Asia, it now becomes clear that its distribution is actually much more restricted. Thus, *Brotia* appears to be distributed mainly to the west of continental Southeast Asia ranging from northeast India (Assam, Sikkim, Meghalaya) and Bangladesh to central Thailand and the Malaysian Peninsula in the east.

It is in the latter area where *Brotia* reaches its highest diversity. In the south, Sumatra, Java, and Borneo, comprising parts of former Sundaland, are within its distributional area. Among these three areas, Sumatra supports the highest diversity of species, forming a monophyletic subgroup, while from Java and Borneo only few species are known. As a rule, reports from Java and Borneo are not confirmed by collections after about 1920. If and how far the distribution of *Brotia* ranges towards the east of continental Asia (to Laos, Cambodia, southern China, and Vietnam) remains to be studied.

### ACKNOWLEDGEMENTS

For technical assistance, we record our gratitude to the colleagues at the Natural History Museum, Berlin, in particular to Gabriele Drescher, Robert Schreiber, Sabine Schütt, and Christine Zorn. Special thanks we owe to Yves Finet (Geneva), David Reid and David Brown (London) for various advices in tracing material and literature as well as for valuable comments. Ellen Strong shared her insights into gastropod morphology, and Thomas von Rintelen his knowledge in molecular genetics.

Types and various other materials examined in this study were provided from various museum collections worldwide. Therefore, we thank Adam Baldinger (Cambridge, Mass.), Philippe Bouchet (Paris), Yves Finet (Geneva), Edmund Gittenberger, Jeroen Goud, and Wim Maassen (Leiden), Ambros Hänggi (Basel), Bernhard Hausdorf (Hamburg), Robert Hershler (Washington), Roland Janssen (Frankfurt/Main), Edward Kools (San Francisco), Elisabeth Kuster-Wendenburg (Bremen), Ristiyanti Marwoto (Bogor), Trudi Meier (Zurich), Robert Moolenbeek (Amsterdam), Gary Rosenberg (Philadelphia), Bernhard Ruthensteiner (Munich), Winston Ponder and Ian Loch (Sydney) as well as Fred Naggs, Joan Pickering, and Kathie Way (London) for making available materials from collections in their charge. Ulrich Bößneck kindly provided some material from his private collection, which facilitated the study of *Brotia costula*.

A number of photographs were kindly provided for publication by Vera Heinrich (Berlin), Pierre Lozouet (Paris), C. Ratton (Geneva), and the Natural History Museum (London). Financially this study was supported by a post-graduate scholarship and a travel



grant of the Konrad-Adenauer-Stiftung to FK as well as by a research grant of the Deutsche Forschungsgemeinschaft (DFG) to MG (GL 297/4-1 and 4-2), which is thankfully acknowledged. Visits of the first author to the Natural History Museum, London and the Museum National d'Histoire Naturelle, Paris were financed by the Bioresource and the Parsyst Programme of the European Union, respectively. David Reid, Chris Jones, and Zeta Field (London) as well as Philippe Bouchet and Virginie Héros (Paris) offered kind support during these visits.

Most valuable comments of three referees, George M. Davis, and Eugene V. Coan helped much to improve the quality of this article. Their effort to critically and carefully read the entire manuscript is most thankfully acknowledged.

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