INTRODUCTION

On the mainland of Southeast Asia, in the Indo-Malay Archipelago and on the Philippine Islands, freshwater gastropods of the superfamily Cerithioidea are conspicuously and substantially represented by viviparous species of the genus *Brotia* H. Adams, 1866 (Fig. 1).

Approximately 90 nominal species have been named, based almost exclusively on the highly variable adult shell, essentially under a typological species concept in the early taxonomic works of the nineteenth century (e.g. Lamarck, 1822; Deshayes & Milne Edwards, 1838; Reeve, 1859–60; Brot, 1862, 1868, 1870, 1872, 1874; Martens, 1897; Sarasin & Sarasin, 1898). This procedure has been continued into recent times. For example, Brandt (1968, 1974) described several new *Brotia* taxa from Thailand. However, the validity of these morphospecies remained enigmatic resulting until today in a most confusing usage of species names in biological and palaeontological accounts. In addition, due to the lack of detailed systematic and phylogenetic studies of *Brotia*, there is confusion as to the limits of this genus as well as its generic and familial affinities.

What today is considered to constitute the genus *Brotia* has been subsumed, to various extents, under *Melania* Lamarck, 1799, an invalid generic name for...
Thiara Röding, 1798. The former was long assumed to comprise most if not all freshwater Cerithioidea. Thus, the so-called ‘Melaniidae’ of earlier authors such as Reeve (1859–60), Brot (1874), Fischer (1887), Martens (1897) and Thiele (1928, 1929) were long held to form a more or less homogeneous and monophyletic group. This concept was followed uncritically by many malacologists far into the twentieth century, even after the establishment of the valid familial name Thiaridae Troschel, 1857 (e.g. Rensch, 1934; Benthem Jutting, 1956; Solem 1966; Brandt, 1968, 1974). However, Houbrick (1988) explicitly stated that this large family in particular is only poorly known.

For a long time there has been much confusion about the systematics of this heterogeneous assemblage of freshwater Cerithioidea. Recently, Glaubrecht (1996, 1999) has reviewed the changing concepts and confusing usage of the so-called ‘Melaniidae’ or Thiaridae sensu lato. With respect to the present question of the fusing usage of the so-called ‘Melaniidae’ or Thiaridae 1999) has reviewed the changing concepts and con-

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Later, based again on characters of the operculum and the radula, Thiele (1921: 142; see also later in Thiele, 1925: 83; 1928: 381; 1929: 189) formally established a subfamily Melanatriinae explicitly within the Melaniidae for a group of pantropical distributed freshwater Cerithioidea that in Southeast Asia also comprises Brotia. He erroneously considered the generic name Pachychilus Lea, 1850 for neotropical ‘melaniids’ to be preoccupied by Pachychilus sensu stricto. A comprehensive phylogenetic analysis of about 180 morphological characters provides further evidence for the differentiation of Thiele’s subfamily as a monophyletic group separated from the Thiaridae (Glaubrecht, 1999; Strong & Glaubrecht, 1999; Glaubrecht et al., unpubl. data). In addition, this analysis established characteristics which allow the inclusion of Brotia sensu lato together with the other genera to constitute Thiele’s ‘Melanatriinae’. Since Pachychilus Lea, 1850 is the oldest valid generic name, we here prefer Pachychilidae over Melanatriidae for this clade whose present distribution suggests a Gondwanan origin (Glaubrecht, 2000a,b).

Until now, details on the systematics and evolution of the Southeast Asian taxa have received only cursory attention (e.g. Morrison, 1954; Brandt, 1974; Glaubrecht, 1996). Not only did the relationships of the species within Brotia remain unclear, but also the taxonomic status and the phylogenetic affinities of those Southeast Asian taxa traditionally grouped with Brotia, viz. Sulcospira Troschel, 1857, Pseudopotamis Martens, 1894, Paracrostoma Cossmann, 1900, Senckenbergia Yen, 1939 and Adamietta Brandt, 1974. Most accounts consider only shell features, and since comparative anatomical investigations are not available, the taxono-

momic treatment of these taxa as either genera, sub-
genera or synonyms of Brotia by various authors is highly arbitrary and equivocal (e.g. Morrison, 1954; Benthem Jutting, 1956; Solem, 1966; Brandt, 1968, 1974; Vaught, 1989).
Similarly, the alpha-level taxonomy is unclear since it is undetermined how many and which of the described taxa belong to *Brotia* and actually represent valid species. For example, Sarasin & Sarasin (1898) postulated a species radiation of ‘melaniid’ gastropods assigned to *Brotia* and *Tylomelania* within the central lakes on Sulawesi (Brooks, 1950; Rintelén & Glaubrecht, 1999). Brandt (1968, 1974) suggested a so-called ‘Rassenkreis’, i.e. a single polytypic species for *B. costula* from Thailand. Davis (1982: 392) assumed a radiation of *Brotia* in streams and rivers in Southeast Asia, with at least nine species in Thailand and 11 species that have radiated in lakes on Sulawesi plus an additional four species outside the lakes. For various reasons we consider all these given species numbers in need of reconsideration (see more under Discussion).

Confusion also exists concerning the fossil record of *Brotia* from the Neogene. For example, shells from the Upper Miocene of the Mediterranean region were repeatedly attributed to this genus, e.g. by Lörenthey (1902), Wenz (1938), Papp (1953), Willmann (1980, 1981) and Fischer (1994). However, the genetic relationship with the Recent Southeast Asian taxon remains highly questionable (see discussion in Glaubrecht, 1996: 378). This also holds true for some fossil taxa described as *Brotia* from Mio-Pliocene sediments from Java (Martin, 1905; Oostingh, 1935; Skwarko & Sufiati, 1994; details under the generic diagnosis for *Brotia*).

Anatomical and ecological studies of *Brotia* and other pachychilids are rare and only provide scattered information (Rensch, 1934; Benthem Jutting, 1956; Solem, 1966; Brandt, 1968, 1974; Davis, 1971, 1982; Dudgeon, 1982, 1989; Rintelén & Glaubrecht, 1999). In addition, there is a persistent lack of other vital biological information, e.g. the degree of intraspecific variability, geographic distribution, sympatric and syntopic occurrences etc. Nevertheless, viviparity in *Brotia* has often been stressed as a characteristic feature (e.g. Martens, 1897; Moore, 1899; Rensch, 1934; Morrison, 1954; Benthem Jutting, 1956; Solem, 1966; Brandt, 1968, 1974; Davis, 1971; Glaubrecht, 1996). However, only the possession of a ‘brood pouch’ has been noted and it was consistently referred to as being similar to the subhaemocoelic brood pouch known from Thiaridae (e.g. *Melanoides* Olivier, 1804 and *Thiara*). In fact, female *Brotia* retain shelled juveniles in a specific incubatory structure. As we will show in the present study, the incubatory structure in Southeast Asian *Brotia* is not always a subhaemocoelic brood pouch. We will illustrate the reproductive anatomy and correlated protoconch morphology of representative species of *Brotia* and show significant differences in the reproductive strategy within the genus as currently perceived.

As a first step towards a thorough systematic revision and phylogenetic analysis of the Southeast Asian Pachychilidae and the freshwater Cerithioidea in general, we here present a framework for the genus *Brotia* based on conchology, anatomy, histology and geographic distribution of six species covering the whole distributional area of the genus (Fig. 1), viz. *B. pagodula* (Gould, 1847), *B. costula* (Rafinesque, 1833), *B. pageli* (Thiele, 1908), *B. testudinaria* (von dem Busch, 1842), *B. hainanensis* (Brot, 1872), and *B. asperata* (Lamarck, 1822), which we compare to the pachychilid taxa on Sulawesi. Distributional data are compiled, and the limited ecological information is reviewed. Finally, the analysis of phylogenetic affinities and the spatial distribution of *Brotia* will be set in the framework of an historical biogeography for Southeast Asia. This is one of the most geologically complex regions of the world, especially ‘Wallacea’, the transition zone between the Oriental and Australian regions.

**MATERIAL AND METHODS**

This account is based on examination of all material in the collection of the Museum für Naturkunde, Berlin (formerly Zoological Museum Berlin, ZMB), supplemented by types and materials from the Australian Museum, Sydney (AMS), the Natural History Museum, London (BMNH), the Academy of Natural Sciences, Philadelphia (ANSP), California Academy of Sciences, San Francisco (CAS), the Museum of Comparative Zoology, Cambridge, Mass. (MCZ), the Muséum d’Histoire Naturelle, Genève (MHNG), the Musée National d’Histoire Naturelle, Paris (MNHP), Zoological Museum, Bogor (MZB), the Überseemuseum, Bremen (ÜMB), the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), the Zoölogisch Museum, Amsterdam (ZMA), the Zoologisches Museum und Institut, University of Hamburg (ZMH), the Zoologisches Museum, Zürich (ZMZ) and the Zoologische Staats-sammlung, München (ZSM). Collections of specimens were made by the authors in Indonesia (Sumatra, Java, Borneo, Sulawesi), on the Philippines and in Hong Kong; voucher material is deposited with the ZMB. Some shells were cracked to allow complete fixation of the soft-tissue and preservation in 70% ethanol.

The dimensions of the shell and, on SEM photographs of the protoconch were measured with callipers to 0.1 mm. Since a distinct and abrupt transition from the protoconch, i.e. the primary or larval shell, to the teleoconch of the adult as found in most marine gastropods is lacking in viviparous freshwater Cerithioidea (due to the abbreviation or loss of early ontogenetic stages; see Glaubrecht, 1996: 298–320), we apply the more general term ‘embryonic shell’ and ‘juvenile
shell' for early and later shelled developmental stages in the brood pouch. The height (HA), breadth (BA) and diameter of the apical whorl (DA) is measured according to Glaubrecht (1996: 28). The shell height (H) is the maximum dimension parallel to the axis of coiling, the breadth (B) the maximum dimension perpendicular to H. The length of the aperture (LA) is the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip, the width of the aperture (WA) the greatest length perpendicular to LA. The height of the bodywhorl (BW) is the maximum dimension from the lower margin of the aperture to the upper suture delimiting the first whorl. Anatomy was studied using a stereo microscope with a camera lucida. Extracted radulae were cleaned by heating to about 60–80°C in 5% KOH solution and by ultrasound or by soaking in 1% hypochlorite solution at room temperature for 5 minutes and rinsing in distilled water (see Reid, 1986: 5). Radulae were mounted on aluminium specimen stubs using adhesive splicing tape and coated with gold for examination with a Jeol JSM 6300 scanning electron microscope. Juvenile shells were taken from brood pouches of fixed or dried specimens, cleaned by ultrasound and hypochlorite solution and prepared for SEM as described above. Some samples of soft tissues were critical point dried with hexamethyldisilazane (method in Nation, 1993). For histology, fixed specimens were embedded in paraffin. Serial sections with a thickness of 7 to 10 µm were prepared with a sliding microtome and stained with haematoxylin and eosin (HE). Sex ratio was determined as propor-

RESULTS

**Brotia** H. Adams, 1866


*Wanga* Chen, 1943—type species, by original designation: *Melania henriettae* Gray, 1834.

**Taxonomic remarks:** The genus *Brotia* was established by Adams (1866) for *M. pagodula* Gould, 1847 for having a round and multispiral operculum, in contrast to the paucispiral operculum of other so-called ‘melaniids’. Adams’ description of the new genus, however, was incomplete and, thus, received little attention subsequently. For example, Brot (1874: 102–103), who assumed a simple mix-up of the peculiar circular and multispiral operculum, considered *Brotia* as synonym of *Melania* since he regarded the shell of the type *B. pagodula* as of ‘the typical habitus of a melaniid’. Sarasin & Sarasin (1898), who described a number of species from the central lakes on Sulawesi under ‘*Melania*’, refrained from assigning these to *Brotia* since they believed that a round and multispiral operculum could be found frequently among ‘melaniid’ taxa.

In contrast, Martens (1897: 33) separated *Brotia* as a natural group of ‘knobby melaniids’, ‘die vom östlichen Ende des Himalaya bis Borneo reich, aber in Java nur schwach vertreten ist’ [that occurs with many forms from eastern Himalayas to Borneo, but is rare in Java]. Eventually, following Martens’ view, it was Thiele (1925: 83; 1928, 1929) who conceded *Brotia* independent generic status and differentiated other pachychilids

![Figure 2](image-url)
from Southeast Asia as of subgeneric or generic status related to *Brotia* within the subfamily ‘Melanatrinae’. Martens’ and Thiele’s suggestion has subsequently been followed by most authors until Morrison (1954) proposed an alternative hypothesis (review in Glaubrecht, 1999).

Several controversial generic and/or subgeneric arrangements among the Oriental pachychilids have been suggested since then, resulting in a still unresolved confusion concerning the taxonomy of the genus. Most recently, Brandt (1968, 1974) proposed that *Brotia* comprises three subgenera, viz. *Brotia*, *Paracrostoma* and *Senckenbergia*. However, his reasoning as well as that of earlier authors was mostly based on radular and operculum features. We suggest, that these characters represent symplesiomorphic character states within the Pachychilidae and are therefore not suitable for a characterization of genera within the family.

Brot (1870) described a new genus *Acrostoma*, with the type species *M. huegeli* Philippi, 1843, on the basis of shell and operculum characteristics. As this name is preoccupied by *Acrostoma* Fischer, 1826 (‘vermes’) it was renamed *Brotheria* by Rovereto (1899), which is itself preoccupied by *Brotheria* Kaup, 1858 (‘fish’). Cossmann (1900) corrected the change of the name with *Paracrostoma*. Unaware of the complicated taxonomic history, some authors (e.g. Prashad, 1921; Annandale, Prashad & Amin-Du-Din, 1921; Annandale & Rao, 1925) referred to the invalid generic name *Acrostoma* for *Brotia* species. Brandt (1968: 273) treated *Paracrostoma* first as a subgenus of *Brotia*. Later, Brandt (1974: 184) considered it to be a genus on its own and assumed that it is closely related to *Sulcospira*. For the latter genus, Davis (1971: 69) saw no reason for it to be treated as distinct; in contrast Benthem Jutting (1956: 378) treated it as a separate genus. Due to the fact that no anatomical and histological examinations have been completed on *P. huegeli*, and because the radula and the operculum of *Paracrostoma* and *Sulcospira* seem to be less distinctive among the Pachychilidae than originally thought, the systematic placement of both genera requires critical re-examination. For the time being, we consider neither *Paracrostoma* nor *Sulcospira* as a synonym of *Brotia*.

Fischer & Crosse (1892) suggested the name *Antimelania* for several species with an Oriental distribution (*M. asperata*, *M. filocarinata* Brot, 1874, *M. dactylus* I. Lea & H.C. Lea, 1850, *M. cancellata* Benson, 1836, and *M. variabilis* Benson, 1836) mainly according to radular characteristics, which they found to be similar to *Pachychilus* from South America. Later, Pilsbry & Bequaert (1927: 300) designated *M. variabilis*, which is identical with *B. costula*, as the type species of *Antimelania*. Consequently, we consider *Antimelania* here to be a synonym of *Brotia*, as suggested by Brandt (1974).

The genus *Pseudopotamis* described by Martens (1894: 83–96) has been treated by Thiele (1928) as a subgenus of *Brotia*. However, based on new studies and the finding of unique features of the radula and the reproductive anatomy (Glaubrecht & Rintelen, unpublished data) we also consider *Pseudopotamis* to be distinct from *Brotia*.

Brandt (1974: 184) regarded *Senckenbergia* Yen, 1939—with the type species *M. pleuroceroides* Bavay & Dautzenberg, 1910—to be a subgenus of *Brotia* because of the possession of a subhaemocoelic brood pouch and a similar radular morphology. However, the anatomy of *S. pleuroceroides* from Indochina is still unknown and thus, as in the case of *Paracrostoma*, the systematic affinity remains hypothetical.

Based on our study of the type material we regard *Wanga* Chen, 1943 as a synonym of *Brotia*, since the type species *M. henriettae* Gray, 1834 has to be considered conspecific with *B. baccata* (Gould, 1847); see also Morrison (1954).

**Diagnosis:**

*Shell*: Relatively large, often up to 4 or 5 cm. Moderately thick, broadly to elongately conic with a turreted spire and a generally eroded apex. The sculpture is rather variable, but prominent axial ribs, sometimes even with nodules, and spiral ridges at the base are frequent and characteristic elements. The body whorl is comparatively large, the aperture is oval, well rounded or angled below and pointed above (Fig. 1).

*Protoconch and juvenile shell*: Embryonic shells are large, with an average of height to width of about 200 μm to 435 μm and a diameter of the first whorl of the protoconch of 645 μm; see Table 1 for parameters of the six species. Juvenile shells retained in the brood pouch comprise up to four whorls. The apical whorls of the juveniles have distinct sculptures and shapes, according to species. For example, in *B. pagodula* and *B. costula* the embryonic shell is asymmetrically and irregularly wrinkled (Figs. 9 B–C; 10 D–F). This initial shell with its wrinkled texture is clearly delimited from subsequent whorls with a more or less smooth sculpture with only regular growth lines and spiral elements. Since the first one to one and a half whorl(s) are disproportionately large, the initial part of the juvenile shell appears slightly asymmetrical in relation to the regularly increasing later whorls (e.g. Fig. 9 B). In addition to *B. pagodula*, wrinkled protoconchs also occur in *B. henriettae*, *B. binodosa* (Blanford, 1903), *B. pseudo-
**MORPHOLOGY AND SYSTEMATICS OF BROTIA**

Table 1. Mean shell dimensions of juvenile shells removed from the brood pouch (or mantle cavity in *B. asperata*) with standard deviation in parentheses. Juvenile shell: H—height, B—breadth; protoconch: HA—height, BA—breadth, DA—diameter.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>H [mm]</th>
<th>B [mm]</th>
<th>HA [µm]</th>
<th>BA [µm]</th>
<th>DA [µm]</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. pagodula</em></td>
<td>1</td>
<td>5.6</td>
<td>3.8</td>
<td>171</td>
<td>257</td>
<td>586</td>
</tr>
<tr>
<td><em>B. costula</em></td>
<td>10</td>
<td>2.4</td>
<td>1.2</td>
<td>237 (±48)</td>
<td>484 (±61)</td>
<td>622 (±46)</td>
</tr>
<tr>
<td><em>B. pageli</em></td>
<td>10</td>
<td>1.2</td>
<td>1.0</td>
<td>238 (±36)</td>
<td>556 (±58)</td>
<td>747 (±44)</td>
</tr>
<tr>
<td><em>B. testudinaria</em></td>
<td>8</td>
<td>1.3</td>
<td>1.0</td>
<td>217 (±37)</td>
<td>549 (±27)</td>
<td>677 (±19)</td>
</tr>
<tr>
<td><em>B. hainanensis</em></td>
<td>5</td>
<td>1.0</td>
<td>0.8</td>
<td>192 (±33)</td>
<td>458 (±35)</td>
<td>611 (±49)</td>
</tr>
<tr>
<td><em>B. asperata</em></td>
<td>5</td>
<td>1.7</td>
<td>1.2</td>
<td>190 (±66)</td>
<td>309 (±24)</td>
<td>628 (±34)</td>
</tr>
</tbody>
</table>

*A. asperata* Brandt, 1968 and *B. manningi* Brandt, 1968 from Thailand and Myanmar, in *B. costula* of the Malaysian Peninsula and Sumatra (Fig. 10 D–F), and *B. asperata* from the Philippines (Fig. 16 A–D).

Embryonic and juvenile stages of critical point dried specimens show that during ontogeny in some species of *Brotia* soft tissue protrudes from the apex of the shell. Thus, the protoconch in these taxa is open and this presumably nutritive material, or ‘yolk sac’ is clustered about the shell apex; studied in detail in *B. costula* and *B. asperata* (further explanation under these species). This phenomenon is also known from *B. binodosa* and other members of the *B. pagodula*-group. In contrast, other species from Java, Borneo and South China, such as *B. testudinaria*, *B. pageli*, *B. pontificalis* (von dem Busch, 1853) and *B. hainanensis*, as well as the species endemic to Sulawesi exhibit a distinct sculpture lacking the strongly wrinkled texture. In these taxa the initial cap is more or less smooth with only faint irregular striae and continues without sharp transition to subsequent whorls which are generally smooth with only axial growth lines (Figs. 11 C–D; 14 A, B, D; 15 C–E). In these species no protruding soft tissue was observed.

**Operculum:** Either round with up to eight whorls and a central nucleus, as in *B. pagodula* (Fig. 3 C), or slightly oval for the last whor which increases in diameter (Fig. 3 D–H) comprising up to six whorls.

**External morphology** (see Fig. 3 B, for *B. hainanensis*): The animals are light to dark brown, dark grey or black, often with light patches. They have a broad and furrowed snout. The cephalic tentacles are moderately long, each with a tiny eye on the side of the peduncular base. In females with a subhaemocoelic brood pouch, the ‘egg transfer’ or ‘genital groove’ on the right side of the head foot connects the pallial oviduct and the pore of this pouch near the base of the right tentacle. This groove is also present in males. The mantle margin is smooth, and the mantle cavity occupies approximately two thirds of the first whorl. The osphradium forms a narrow ridge embedded in a shallow trench and lies adjacent to the anterior part of the ctenidium; it is delicate and often slightly undulating. The ctenidium begins shortly behind the mantle edge, extending posteriorly almost the entire length of the cavity; it is large, broad and tapers posteriorly. On average the gill is twice as long as the osphradium. The hypobranchial gland is inconspicuous and lies adjacent to the large and wide rectum. The anus is located well behind the mantle edge.

**Nervous system:** (Fig. 4) The cerebral commissure is long while the cerebro-pleural connectives are short. The sub-oesophageal ganglion is fused with the left pleural ganglion. The pedal ganglia are deeply embedded in the muscle of the propodium and connected to the pleural and cerebral ganglia with relatively long connectives. The pedal ganglia are closely joined and statocysts are located basally.

**Radula:** The taenioglossate radula (Fig. 9 D–F for *B. pagodula*) is relatively large and robust. It is up to 30 mm long corresponding to half of the shell height. Posteriorly, the radula is embedded in connective tissue and coiled behind the buccal mass in the radular sac. In general, the rachidian tooth is squarish with a pronounced, more or less pointed central denticle flanked by up to three accessory denticles that taper in size. A glabella (terminology by Troschel, 1857) is always present. The anterior margin of the rachidian tooth is concave or straight, the lower rim concave by the postero-rially extending glabella. The lateral teeth have a rounded swelling on their face (glabella) as well and the major denticle is flanked by two or three smaller cusps on each side. The inner marginal teeth are hooked and generally have two denticles. Both marginals possess a simple flange or ledge at their outer margin. This feature is more pronounced in the outer marginal teeth.
**Alimentary system:** The oesophagus is longitudinally folded and transverse septae are not present. The stomach of *Brotia* exhibits features typical of other Pachychilidae, as described by Strong & Glaubrecht (1999, and in prep.). These include: unique modifications of the sorting area, a single digestive gland duct, a narrow glandular pad, a cuticular gastric shield, and a crescentic ridge and groove. The major and minor typhlosoles are fused in several species including *B. pagodula*, *B. costula*, and *B. pageli*. The epithelium of the style sac is heavily ciliated giving the surface a golden gloss. A crystalline style is present and is cylindrical or club-like in shape.

**Reproductive biology:** Typically, *Brotia* species possess a subhaemocoelic brood pouch that is located dorsally in the neck region and occupies almost the entire visceral cavity of the head foot (Fig. 7). This incubatory structure is compartmentalized with lamellae of thin adventitious tissue within which the embryos are embedded (see Fig. 8). Generally, juveniles found within the pouch are at the same ontogenetic stage, forming a cohort. This type of a subhaemocoelic brood pouch is present in all *Brotia* species described here except for taxa endemic to Sulawesi and the Philippines. The distinct incubatory structures and correlated strategies of these two groups will be described under the species in question.

The comparatively large gonad is located adjacent to and dorsal of the digestive gland (Fig. 3 A). It is orange to light brown in females and consists of broad lobes. The testis is light yellow and consists of highly branched thin tubes. The pallial gonoduct is open in both sexes. The pallial oviduct comprises a deep oviductal groove bounded by parallel laminae. The capacious spermatophore bursa lies within the median lamina that forms a fleshy flap. Histological sections of the pallial oviduct of *B. pagodula* are shown in Fig. 5. Both the median and the lateral laminae are ciliated along the inner surface of the oviductal groove. The large albumen...
gland extends from the base for almost the entire length of the pallial oviduct. A ciliated sperm gutter forms along the free edge of the medial lamina (Fig. 5 B). This gutter opens to the papillated spermatophore bursa approximately at two thirds of the oviductal length (Fig. 5 C). Based on these findings, a schematic reconstruction of the pallial oviduct is given in Fig. 6. Modifications of the gonoduct anatomy in other taxa will be described under the relevant species sections.

Generally, Brotia species are gonochoristic and the sex ratio is balanced in most species examined, with the exception of the type species B. pagodula and B. asperata, where it is skewed towards the females (Table 3). These two species seem likely to reproduce parthenogenetically, but since sample size is only small, examination of more material is required.

Ecology: Brotia species inhabit freshwater biotopes ranging from small and clear mountain streams to large muddy rivers and even ponds and lakes. Some species are restricted to specific habitats, while others have a much wider ecological tolerance. Rarely more than one, two at the most, species are found co-occurring together in a given habitat.
**Distribution** (Fig. 2): Southeast Asia, ranging from North East India and Bangladesh to Burma, Thailand, Indochina and South China, the Malaysian Peninsula as well as to Sumatra, Java and Borneo. *B. asperata* is endemic to the Philippines, particularly to the islands of Luzon, Samar, Leyte, Bohol, and Cebu. The species traditionally referred to as *Brotia* and *Tylomelania* from Sulawesi are not considered here in detail because they represent an independent clade (Rintelen & Glaubrecht, 1999).

**Fossils:** Some fossil gastropods from the Cenozoic in Europe were originally referred to as *Melania*, and were later regarded as being related to the Recent *B. asperata*; for example, *M. melanioides* Sowerby, 1816 and *M. inquinata* Defrance, 1793 from the Eocene of the Paris Basin and England (e.g. Deshayes, 1837; Philippi, 1842). *Brotia escheri* (Brongniart, 1822) and *B. vasarhelyii* (Hantken, 1887) are known from Panonian deposits (Upper Miocene) near Budapest, Hungary (e.g. Höhnes, 1857; Lörenthey, 1902), Upper Miocene of Burgenland, Austria (e.g. Fischer, 1994) and the so-called ‘Cerithienschichten’ (Upper Oligocene to Lower Miocene) of Mainz Basin, Germany (Kadolsky, 1995). Given the considerable degree of conchological variability, Höhnes (1857) suggested that these and other Miocene fossil taxa from Europe should be subsumed under *Melania escheri* (discussion in Fischer, 1994). Papp (1953), who transferred these Neogene forms to *Brotia*, also suggested the subgeneric division of *Tinnyea* (after the location Tinnye in Hungary). However, since these species were placed in

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**Figure 5.** Histological sections of the pallial gonaduct of *B. pagodula* (ZMH, Myanmar); scale bars = 1.0 mm. **A.** Cross-section at the anterior end of the pallial gonaduct showing the lateral lamina to be fused with the mantle tissue and the free and simple medial lamina. **B.** Cross-section at about one third of the oviductal length showing the heavily ciliated sperm gutter formed by the medial lamina. **C.** Cross-section at about the half of the oviductal length showing the spermatophore bursa formed by the medial lamina and the capsule gland comprising the base of the oviductal groove. **D.** Cross-section at about two thirds of the oviductal length showing the ciliated spermatophore bursa. Abbreviations: cg—capsule gland, ft—foot muscle, ll—lateral lamina, ml—medial lamina, mr—mantle roof, og—oviductal groove, sb—spermatophore bursa, sg—sperm gutter.
Brotia simply due to conchological similarities, despite uncertainties concerning the freshwater origin of the deposits, these reports and their taxonomic assignments should be reviewed carefully.

In Southeast Asia the fossil record of Brotia extends back to the Pliocene (and possibly Miocene?). Annandale (1919) reported on fossil Brotia from Miocene and Pleistocene sediments of Lower Burma, e.g. B. variabilis from the Miocene of the Pegu district, and B. bacata near Lake Inle in the Shan States of presumably post-Pleistocene age. From the latter deposits, Bequaert (1943) noted three forms of Brotia (Antimelania) and Sulcospira, respectively, that persist to the recent. For details see under the species.

Martin (1905), Oostingh (1935) and recently Skwarko & Sufiati (1994) reported on fossil taxa which they refer to as Brotia, from the Miocene and Pliocene of Java. However, the dating of the sediments has been questioned (e.g. Oostingh, 1935: 2). Although the Martin collection has recently been re-examined (Hoek

**Figure 6.** Schematic reconstruction of the pallial gonoduct of *B. pagodula*. Abbreviations: cg—capsule gland, ll—lateral lamina, ml—medial lamina, og—oviductal groove, osb—opening to spermatophore bursa, sb—spermatophore bursa, sg—sperm gutter.
Ostende, Leloux & Wesselingh, in press), the systematic placement of some of the fossil taxa in question remains to be solved. For example, judging from the figures and description given, we do not regard *B. oppenoortii* Oostingh, 1935 as congeneric with the Recent *Brotia*. Instead, it probably represents a thiarid taxon, most likely *Sermyla*.

**Brotia pagodula** (Gould, 1847)

*Melania pagodula* Gould, 1847: 219, no figure, not *Melania pagodulus* Reeve, 1860 (*Thoungyin-River, tributary of the Salween River, Burma*; lectotype MCZ 169276, paralectotype USNM 611238); Brot, 1874: 102, pl. 13, fig. 2.

*Io pagodula*—Reeve, 1859: pl. 3, fig. 10.

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


**Taxonomic remarks:** *B. pagodula* is the type species of the genus. The lectotype has been designated and depicted by Johnson (1964).

**Shell** (Fig. 1 A): The shell is solid and broadly conical. Its spire is decollated and consists of up to five flattened whorls with a spiral row of long and pointed spines. It is covered by fine spiral lines at the base and has a light to chestnut brown colour. A dark brown spiral band may be present. The whorls are separated by a narrow suture. The aperture is ovate with an angular margin below, grey white in colour, with brown bands inside. Mean shell dimensions (for n = 15; standard deviation in parentheses): H = 29.2 (± 5.7) mm,

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**Figure 7.** The subhaemocoelic brood pouch of *Brotia*. A. Schematic reconstruction of the head foot of *B. testudinaria* opened dorsally, showing the location of the subhaemocoelic brood pouch. Abbreviations: ba—buccal apparatus, bp—subhaemocoelic brood pouch, etg—egg transfer groove, ey—eye, pr—protoconch shells, rad—radula, sg—salivary glands, sn—snout.
Figure 8. Histological sections of the head foot of *B. testudinaria* (ZMB 200100, Java); scale bars = 0.5 mm. A. Cross-section of the head foot showing the anterior part of the subhaemocoelic brood pouch near the brood pouch pore at the right side of the head. The brood pouch filled with egg capsules lies dorsal of the buccal mass. B. Section through the central part of the subhaemocoelic brood pouch comprising most of the visceral cavity. Abbreviations: ba—buccal apparatus, bp—brood pouch, eg—egg capsule, ft—foot muscle, mr—mantle roof, oe—oesophagus, ra—radula.
Protoconch and juvenile shell (Fig. 9 A–C): The juvenile shell comprises four rapidly increasing whorls and is large compared to the adult and other congeneric forms. The initial cap of the asymmetrical protoconch exhibits a wrinkled sculpture. The dimensions of the only juvenile shell available: \( H = 5.6 \text{ mm}, B = 3.8 \text{ mm}, DA = 586 \mu \text{m} \) (Table 1).

Operculum (Fig. 3 C): Round, multispiral with a central nucleus. It consists of six to eight regularly increasing whorls and is clearly smaller than the aperture.

External morphology: The animal has a light brownish to grey colour with yellowish patches. It is medium sized and comprises two to three whorls. The mantle cavity occupies approximately two thirds of the first whorl.

Radula (Fig. 9 D–F): The radula comprises about 125 to 170 rows of teeth and is 16 to 20 mm long, corresponding to approximately half of the shell height. The upper rim of the rachidian tooth is straight, the base is

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**Figure 9.** SEM images of juvenile shell and radula of *B. pagodula* (ZMH, Myanmar). A. Lateral view of the juvenile shell; scale bar = 1.0 mm. B. Apical view of the same shell; scale bar = 1.0 mm. C. Lateral view of the apical area of the protoconch; scale bar = 0.1 mm. D. Segment of the radula; scale bar = 0.1 mm. E. Laterals, inner and outer marginal teeth; scale bar = 0.1 mm. F. Rachidian tooth; scale bar = 0.01 mm.
convex and includes the basal extension of the broad glabella with more or less straight sides. The lateral sides of the rachidian are also straight, with a notch formed at the lower third, and very inconspicuous lateral extensions. The cutting edge consists of one very large main denticle and two much smaller flanking cusps. The major cusp of the lateral teeth is large, broadly triangular, flanked by two or three minute cusps on the inner side and one or two at the outer side. The marginal teeth are shaped broadly spatulate, with only a tiny lateral cusp on the inside.

**Stomach:** Stomach morphology is consistent with the general description given above for the genus. The typhlosoles are fused to each other and their proximal ends are thickened.

**Reproductive biology:** The subhaemocoelic brood pouch of one female contained only a single large shelled juvenile; all other females had empty pouches. The pallial oviduct corresponds to the description given for the genus (Figs. 5 A–D, 6). Among a total of 12 specimens one was male (Table 3).

**Ecology:** These snails live attached to rocks as well as on sandy bottoms (Brandt, 1974).

**Distribution** (Fig. 2): *B. pagodula* is restricted to the Thounyin River, a tributary of the Salween River (called Maenam Moei in Thai according to Brandt, 1974), forming the border between Thailand and Myanmar.

**Material examined:** Myanmar: (ZMB 26708); Salween River (BMNH). Thailand: Thounyin-River (= Maenam Moei) (USNM 776062); Maenam Moei, 8 km W of Mae Ramat Mae Sot (ZSM 19983241; ZMH); soft bodies already extracted from the shells, without location (ZMH).

**Brotia costula** (Rafinesque, 1833)

*Melania costula* Rafinesque, 1833: 166, no figure (‘Ganges’).

*Brotia costula*—Benthem Jutting, 1956: 374–378, fig. 76 (partim); Brandt, 1974: 175, pl. 13, fig. 37–39 (partim).


*Melania carolinae* Gray, 1834—In: Griffith & Pidgeon, 1834: 598, pl. 13, fig. 3 (locus typicus not given; holotype BMNH 1874.10.12.11).

*Melania variabilis* Benson, 1835: 746, no figure (‘Tolly Nullah, Jaunpur and Goomti River near Calcutta’; 1 syntype BMNH 1872.12.2.2); Brot, 1874: 85, pl. 10, fig. 1a-d.

*Melania (Melanoides) variabilis*—Nevill, 1884: 251.


*Acrocomia variabilis*—Amandale, Prashad & Amin-Du-Din, 1921: 560, pl. 6, fig. 3–6; Prashad, 1921: 485–488 (partim).
sider that many of the taxa he synonymised under *B. costula* are not conspecific. In addition, for example, *M. varicosa* was originally described from the Ganges River in India, but not from Java, as also erroneously stated by Mousson (1849). Thus, to use the name *varicosa* for a subspecies occurring on Java and Borneo is misleading. The classification of Brandt (1974) remains questionable and this complex systematic and taxonomic situation awaits systematic revision. Accordingly, the synonymy list given above is not necessarily complete.

**Shell** (Fig. 1 D): The solid shells have 6 to 11 whorls and a pyramidal, turretted and frequently eroded spire with a light brown to olive-brown coloration. The sculpture consists of axial ribs, occasionally comprising nodules, and basal spiral ridges. Mean shell dimensions (standard deviation in parentheses): \( H = 39.5 \pm 9.1 \) mm, \( B = 15.7 \pm 3.4 \) mm, \( LA = 13.7 \pm 2.9 \) mm, \( WA = 8.1 \pm 1.9 \) mm, \( BW = 21.7 \pm 4.6 \) mm (n = 81).

**Protoconch** (Fig. 10 A–F): The apical whorl is wrinkled; Fig. 10 A–C shows critical point dried juvenile shells with protruding soft tissue at the apical portion of the protoconch. During ontogeny the embryos within their egg capsules originally have an uncalcified apex with nutritive tissue, a so-called ‘yolk sac’, protruding out of the developing juvenile shell. This sac gradually decreases in size during development. Eventually, the apical opening is covered by shell material, thus the apex closes by secondary calcification resulting in the typical wrinkled texture of the asymmetrical protoconch (Fig. 10 D). Mean dimensions of juvenile shells are given in Table 1.

**Operculum** (Fig. 3 E): Round to slightly oval comprising four to six whorls and a central nucleus.

**External morphology:** The animal is uniformly coloured, dark grey to black. The sole is grey with scattered light spots.

**Radula** (Fig. 10 G, H): The radula has about 180 rows of teeth and a length of up to 30 mm, corresponding to even more than half of the shell height. The upper margin of the rachidian tooth is concave, formed by two inflated rounded corners. The lower corners of the basal plate are rounded to slightly angled. The glabella is slightly v-shaped, narrow with a tongue-like projection along its base. The cutting edge of the rachidian consists of a single main cusp and up to two or three smaller denticles on each side. In some specimens from Sumatra only a single flanking denticle was found. The laterals have short lateral extensions, a pronounced inner flange, and two main cusps flanked by two smaller denticles. The two cusps of the inner and outer marginal teeth are pointed and of about the same size and shape.

**Stomach:** The typhlosoles are fused. The opening to the style sac is partly covered by the flattened flap-like proximal end of the major typhlosole. The proximal end of the minor typhlosole is thickened.

**Reproductive biology:** Females possess a subhaemo- coelic brood pouch containing up to more than a hundred juveniles (Table 2). The gonoduct corresponds to the description given for the genus. In a total of four populations, nearly 50% of the animals were male (Table 3).

**Ecology:** *B. costula* is eurytopic, living in habitats ranging from clear, narrowly tangled jungle creeks with sandy bottoms to large muddy rivers (Abbott, 1948; Davis, 1971). According to Davis (1982) the species lives on rocks, mud, sand, root systems, under and among piles of leaf litter in the water, as was confirmed by our own observations. *B. costula* occurs in great abundance in the Pahang River system, Malaysia together with a second spiny *Brotia* species (Davis, 1982: 392). Davis found *B. costula* in quiet, marginal waters whereas the spiny form lives among rocks in the rapids. According to Krutatrachue, Upatham, Vichasri & Baidikul (1990) the species inhabits mainly streams and rivers, only rarely still waters, while Subba Rao (1989) states that *B. costula* lives in ponds and does not occupy swift streams. We found specimens in museum collections that confirm the occurrence of *B. costula* in lakes on Sumatra: e.g. Lake Toba, Lake Singkarah, Lake Maninjau and Lake Ranau. Recent samplings by the first author were taken in Lake Toba, clear streams and muddy irrigation channels of rice fields on Sumatra.

**Fossils:** Fossils of similar shape have been depicted, as *B. variabilis*, from Tertiary and Pleistocene sediments of lake basins in Yawngwhe, South Shan, Myanmar (Annandale, 1919; Bequaert, 1943). Reports on fossils exist from cave deposits near Guong Pondok (Perak, Malaysia) (Benthem Jutting, 1949).

**Distribution** (Fig. 2): The occurrence of *B. costula*, as conceived of here, is fairly widespread, including North East India (Ganges, Assam, Manipur, Meghalaya, Mizoram, Sikkim, West-Bengal), Bangladesh, Burma, Thailand, the Malaysian Peninsula and Sumatra, as
Figure 10. SEM images of juvenile shell and radula of *B. costula*. A-C. Critical point dried probes: A. Lateral view of the apical whorl of the juvenile shell, note that soft tissue is attached to the apical portion and shell is not completely calcified at this stage (ZSM 19983237, Thailand); scale bar = 0.1 mm. B. Lateral view of early stage of juvenile shell partly covered by membrane; for further explanation see text (ZMH, Thailand); scale bar = 1.0 mm. C. Lateral view of later stage of juvenile shell (ZSM 19983237, Thailand); scale bar 1.0 mm. D, E. Apical whorl of juvenile shell with completely calcified shell, note wrinkled texture (ZMB 200051, Myanmar); scale bar = 0.1 mm. F. Lateral view of later stage of juvenile shell with completely calcified apical part (ZMB 200051, Myanmar); scale bar = 1.0 mm. G. Segment of the radula (ZMH, Thailand); scale bar = 0.1 mm. H. Half row of radula showing rachidians, laterals and inner and outer marginals (ZMH, Thailand); scale bar = 0.1 mm.
well as Cambodia and Vietnam. It has been reported from the Mekong where it is the only cerithioidean species found (Brandt, 1974; Davis, 1982).

**Remark:** We consider reports from Sri Lanka (Annan-dale, 1920), Java (Rensch, 1934; Benthen Jutting, 1956) and Borneo (e.g. Brandt, 1974) as dubious due to confusion with other species. The occurrence of *B. costula* on Java reported by some 19th century authors, Rensch (1934: 340; based on a single specimen from Bogor!) and Benthen Jutting (1956), is not yet confirmed; for further discussion see the latter author. The report of *M. variabilis* from Melanesia (Abbott, 1948) as representing a species of *Brotia* are incorrect. A report on habitat preferences of a misidentified *Brotia aff. costula* in a river on Cebu Island, Philippines, by Bandel & Riedel (1998) clearly refers to *B. asperata* judging from the figures provided. *B. costula* is intermediate host of the parasites *Cercaria indica* (Kruatrachue et al., 1990) and *Paragonimus westermani* (Hoa & Liat, 1969; Davis, 1971; Brandt, 1974).

**Table 2.** Number and mean size of egg capsules, embryos, and juveniles retained in the brood pouch (or mantle cavity) of *Brotia* species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Juveniles or egg capsules per female</th>
<th>Height of juvenile shells</th>
<th>Size of egg capsules</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. pagodula</em> (n = 1)</td>
<td>1 juvenile</td>
<td>5.6 mm</td>
<td>–</td>
</tr>
<tr>
<td><em>B. costula</em> (n = 2)</td>
<td>120 egg capsules</td>
<td>–</td>
<td>1.0 mm</td>
</tr>
<tr>
<td></td>
<td>96 juveniles</td>
<td>2.0–2.5 mm</td>
<td>–</td>
</tr>
<tr>
<td><em>B. pageli</em> (n = 3)</td>
<td>80 egg capsules</td>
<td>–</td>
<td>1.0 mm</td>
</tr>
<tr>
<td></td>
<td>107 juveniles</td>
<td>2.0–2.8 mm</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>320 juveniles</td>
<td>1.2–1.5 mm</td>
<td>–</td>
</tr>
<tr>
<td><em>B. testudinaria</em> (n = 3)</td>
<td>105 egg capsules</td>
<td>–</td>
<td>0.5–0.75 mm</td>
</tr>
<tr>
<td></td>
<td>120 juveniles</td>
<td>1.3 mm</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>120 juveniles</td>
<td>0.9–1.1 mm</td>
<td>–</td>
</tr>
<tr>
<td><em>B. hainanensis</em> (n = 3)</td>
<td>66 juveniles</td>
<td>1.0 mm</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>152 juveniles</td>
<td>1.0–1.5 mm</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>248 juveniles</td>
<td>1.5 mm</td>
<td>–</td>
</tr>
<tr>
<td><em>B. asperata</em> (n = 1)</td>
<td>270 juveniles</td>
<td>1.7–2.0 mm</td>
<td>–</td>
</tr>
</tbody>
</table>

**Table 3.** Sex ratios in *Brotia* from Southeast Asia, given as the proportion of males of the entire sample.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample</th>
<th>Males : Females per sample</th>
<th>Sex ratio (for all individuals of each species)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. pagodula</em></td>
<td>Myanmar (ZMH)</td>
<td>0 : 6</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>Myanmar (USNM 776062)</td>
<td>1 : 3</td>
<td></td>
</tr>
<tr>
<td><em>B. costula</em></td>
<td>Thailand (ZMH)</td>
<td>4 : 3</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>Thailand (ZMH)</td>
<td>1 : 1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sumatra (ZMA)</td>
<td>3 : 1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sumatra (ZMA)</td>
<td>0 : 1</td>
<td></td>
</tr>
<tr>
<td><em>B. pageli</em></td>
<td>Borneo (ZMB 102083)</td>
<td>2 : 2</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>Borneo (ZMB 200092)</td>
<td>4 : 5</td>
<td></td>
</tr>
<tr>
<td><em>B. testudinaria</em></td>
<td>Java (ZMB 200099)</td>
<td>1 : 4</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td>Java (ZMB 200100)</td>
<td>4 : 3</td>
<td></td>
</tr>
<tr>
<td><em>B. hainanensis</em></td>
<td>Hong Kong (ZMB 200094)</td>
<td>4 : 5</td>
<td>0.44</td>
</tr>
<tr>
<td><em>B. asperata</em></td>
<td>Bohol (AMS 324129)</td>
<td>1 : 5</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>Luzon (AMS 324130)</td>
<td>0 : 3</td>
<td></td>
</tr>
</tbody>
</table>

**Material examined:** India: (ZMB 200044; ZM 522372; CAS 6199); Assam (ZMB 200042, 200052; BMNH 1935.10.9.5-17, 1888.12.4.1492-3); Durang (BMNH); Himalaya (BMNH 1841.7.23.9); Manipur (BMNH); Keladye River (BMNH 1899.12.4.1761-2); Calcutta (BMNH; CAS 25326); Bengal (BMNH 1888.12.4.1480-2; ZM 522371); River Toolsi Ganga, Bengal (BMNH); River Atrai, Bengal (BMNH); Basudepur, Rajshaye (BMNH); Malaudi, Rajshaye (BMNH); River Jumna (BMNH 1907.12.30.207); Gowa-hati, Assam (ZM 522377); Settlepore (ZM 522372); Jonapore (ZM 522370); Khasi hills (BMNH); Bhutan: Doobars, West Bhutan (BMNH). Myanmar: Cuchar hills (ZMB 20737); Pegu (ZMB 200051; BMNH 1838.12.4.1757);
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Bassein District, Pegu (BMNH). Bangladesh: Chittagong (BMNH). Thailand: Guang River near Lampun (ZSM 19983246); Nam Mae Yum near Mae Sariang, Prov. Mae Hongsong (ZSM 19983247, 19983228); Mae Nam Ram, Prov. Trang (ZSM 19983228); Mae Ping (MNHP). Malaysia: Perak (BMNH 1885.8.21-3, 1886.8.2.41-46, 1897.3.15-45-7); Perak River (ZMB 200054); Larut, Perak (BMNH 1886.8.2.50-6); Ipoh, Perak (ZMB 200046); Tong Temple near Ipoh (ZMA); Tenasserim (BMNH); River near Jemphol at Batu Kiker Negri Sembilan (ZMA); River Buaya, NW Rawang, Selangor (ZMA); rapidly streaming river, 16 miles N of Kuala Lumpur (CAS 30197); Arwing River at Kelantau, 17 miles S Kuala Lumpur (ZMA). Vietnam: Environ de Gang, Tonkin (MNHP); Song Ya bei Yuong Raya, Jambi (MZB 9013).near Solok (ZMB 200070); Tandjung djatti (ZMA); Gun-Tibintingi and Kepahiang (ZMB 27680); Musi near Muara Trussan near Tibintingi (ZMB 26717); Ramanta between Island, Riau (MZB 9010); Kepahiang (ZMB 26715, 200039); Gadang Island, Riau (MZB 9009); Kampar River, Jadang Bengkajang (ZMB 200040); Arau River, Bengkinang, River, Muaramat, tributary of Alas River (MZB 7311); Alam (ZMA); Lake Kerinci (ZMB 4901, 9022); Merangiu Lawang (MZB 7058); Deli River near Medan (ZMA); East Belawan River (ZMB 51776); Bohorok River, Bukit 87409); Northeast coast, small creek near Lunfa Peli (ZMB 200047). Laos: Laos Occidentale, Menam Pinh, Xieng Moi 200050; MHNG); Malakka, Gunuong Tahon (ZMB 200041, Kanpong, Pahang (ANSP A8907); Malakka, Gunuong Tahon (ZMB 200041, 200047). Thailand: Guang Fiver near Lampun (ZSM 17.3 200047). Malaysia: Sumatra: (ZMB 200043, 200045; BMNH 1890.2.21.1-4); Aceh (MZB 8786); Southeast Aceh (MZB 8624); Lake Takengon, Aceh (ZMB 76673); Laut Tawar, North Sumatra (ZMB 87409); Northeast coast, small creek near Lunfa Peli (ZMB 43442); Belawan River (ZMB 51776); Bohorok River, Bukit Lawang (MZB 7058); Deli River near Medan (ZMA); East Sumatra (MZB 4361), Lake Manindjau (MZB 8632); Pager Alam (ZMA); Lake Kerinci (MZB 4901, 9022); Merangiu River, Muaramat, tributary of Alas River (MZB 7311); Bengkajang (ZMB 200040); Arau River, Bengkinang, Gadang Island, Riau (MZB 9009); Kampar River, Jadang Island, Riau (MZB 9010); Kepahiang (ZMB 26715, 200039); Trussan near Tisburyt (ZMB 26717); Ramanta between Tisburyt and Kepahiang (ZMB 27680); Musi near Muara Klini (ZMB 76295); Danau di Atas (ZMB 200069); Sumani near Solek (ZMB 200070); Tandjung djatti (ZMA); Gunung Raya, Jambi (MZB 9013).

Brotia pageli (Thiele, 1908)

Melania (Brotia) pageli Thiele, 1908—In: Thiele & Martens, 1908: 268, pl. 5, fig. 5 (‘British North Borneo’; 9 syntypes ZMB 59654, 102083).

Melania schmidtii Martens, 1908—In: Thiele & Martens, 1908: 267, pl. 5, fig. 3 (West-Kalimantan: ‘Guleh River near Sangkulirang-Bay’; 3 syntypes ZMB 200072, 200073).

Taxonomic remarks: There remains great confusion in the literature concerning the taxonomy of various species which were described from the Greater Sunda Islands Sumatra, Java and Borneo. Due to conchological resemblance, species from Borneo and Java in particular have repeatedly been synonymized with B. costula from the Asian mainland. Rensch (1934) was the first to note the distinction between the shell of B. costula from the Southeast Asian mainland including Sumatra and the shell of forms originally described as Melania infracostata from Java and M. pontificalis and M. brookei Reeve, 1860 from Borneo. This finding is supported by personal investigations showing that B. costula differs morphologically from the Bornean and Javanese taxa (see below). In particular the Bornean taxa show enormous phenotypic plasticity that renders decisions on the taxonomy difficult. For example, while shells of B. pageli are essentially smooth with a fine, regular spiral sculpture on the basal whorl (see Fig. 1 C), the sculpture of forms like B. pontificalis is dominated by strong axial ribs and exhibit a pronounced subsutural depression particularly on the last whorl. It remains unclear whether these forms represent ecophenotypes, geographical variations or distinct biospecies. Accordingly, we refrain here from synonymizing B. pageli with B. pontificalis which is the oldest available name for Brotia from Borneo. We attribute the material from Sabah and Southeast Kalimantan, on which our study is based, to B. pageli for conchological reasons and restrict our description here to this particular taxon. We have also examined the type material of Melania provisoria Brot, 1881 in the MNHN that has (perhaps erroneously?) been described from Sumatra. These shells are extremely similar to those of B. pageli, but again we refrain from considering both as conspecific as long as soft body material of M. provisoria is not available.

Shell (Fig. 1 C): Medium to large and highly turreted, comprising five to eight rounded whorls. The spire often is truncated. The aperture is oval and angular inside it is bluish white. The peristome is chestnut to dark brown. The sculpture is rather smooth consisting only of spiral striae at the base; occasionally distinct axial ribs are present on the body whorl. The sides of the first whorls are flattened while the last three whorls are rounded, often exhibiting a prominent ridge two millimetres from the suture. Juveniles always have the first whorls are flattened while the last three whorls are rounded, often exhibiting a prominent ridge two millimetres from the suture. Juveniles always have growth lines; neither axial nor spiral elements are present. The apical whorl exhibits only faint wrinkles along growth lines; neither axial nor spiral elements are present. The apical whorl exhibits only faint wrinkles along
initial cap appears large, covering most of the apex; viewed laterally, the apex is rounded and dome-shaped (Fig. 11 C, D). Subsequent whorls are smooth with no dominant sculpture, except for a faint subsutural groove in some specimens. Because of the large, dome-shaped expansion of the initial cap, the apex appears as if the juvenile shell changes its direction of spiralling, resulting in a slightly ‘pseudo-heterostrophic’ appearance as is also observed in the following species. Mean dimensions of juvenile shells are: \( H = 1.2 \text{ mm}, \) \( B = 1.0 \text{ mm}, \) \( DA = 747 \mu \text{m} \) (for \( n = 10 \)) (Table 1).

**Operculum** (Fig. 3 F): Oval with a slightly eccentric nucleus. The last 3 to 3 ½ whorls increase rapidly in diameter.

**Radula** (Fig. 11 A, B): Comprises about 150 to 170 rows of teeth and has a length up to 30 mm, corresponding to approximately half of the shell height. The squarish rachidian tooth has a broad glabella with a truncated basal margin, extending beyond the lower margin of the more or less straight basal plate. The upper margin is slightly concave, with inflated and rounded corners. The lateral sides of the basal plate lack a notch and extend in thin lateral extensions. The cutting edge is formed by one pronounced denticle.

**External morphology:** The colour is brown to dark grey with yellowish patches; the sole is dark grey and lightly spotted.

Figure 11. SEM images of radula and juvenile shell of *B. pageli* (ZMB 200092, Borneo). **A.** Detail of rachidian and marginal teeth; scale bar = 0.1 mm. **B.** Segment of the radula; scale bar = 0.1 mm. **C.** Lateral view of the juvenile shell; scale bar = 1.0 mm. **D.** Apical view of the juvenile shell; scale bar = 1.0 mm.
flanked by two smaller denticles on each side. The lateral tooth has two main cusps with one smaller cusp on the inside and one or two tapering cusps on the outside. The inner lateral margin forms an angled flange. The inner and outer marginal teeth each have two pointed cusps of similar shape and size, and are hooked and curved or slightly angled.

**Stomach**: The typhlosoles are fused separating intestinal groove and style sac.

**Reproductive biology**: Mature females contain up to several hundred embryos (Table 2) in their subhaemo-coelic brood pouch, all of equal size, reaching about 2.5 whorls before they are released. The sex ratio observed was 0.46 (Table 3). The pallial oviduct differs in some respects from that found here in *B. pagodula* and *B. costula*. Anteriorly, the medial lamina consists of a thin flap bearing a deep sperm gutter. The gutter deepens and eventually opens at about one third of the oviducal length to the papillated spermaphor bursa. A second slit-like and shallow gutter with a thin flap projecting into the lumen of the oviduct runs posteriorly, remaining open until about half of the length of the gonoduct, before terminating as a blind sac that is here tentatively considered a seminal receptacle. On the basis of histological sections (Fig. 12 A–D), a schematic reconstruction of the pallial oviduct is shown in Fig. 13.

**Ecology**: The species inhabits small, clear mountain streams with rocky and/or pebble substrates. At Gamantong Cave, Kinabatang River in Sabah, it lives in creeks draining into the main stream. It is mainly found under dead leaves, on stones, or buried in mud.

**Distribution** (Fig. 2): Mountain streams on Borneo, from Sabah to South Kalimantan.

**Material examined**: Borneo (ZMB 200074). Malaysia: Sabah (ZMB 59654, 102083; creek at Gamantong Cave, near Kinabatang River (ZMB 200092-3); Madai (BMNH 1894.10.6.3-4); Penokok River, near Mt. Kinabalu, altitude 4000 m (CAS 32618); North Borneo: Tabin river (USNM 75671); Kota Belud, Kadamain river (USNM 756667); Indonesia: Guleh River, near Sangkulirang Bay (ZMB 200072-3, 36937); South Kalimantan: Mountain creeks near Loksado, NE Banjarmasin (ZMB 200053, 200097).

*Brotia testudinaria* (von dem Busch, 1842)

*Melania testudinaria* von dem Busch, 1842—In: Philippi, 1842: 3, pl. 1, fig. 14 (*Java*; lectotype ÜMB TK 271/1, 1 paralectotype ÜMB TK 273/1, 1 paralectotype MCZ 74859); von dem Busch—In: Philippi, 1847: 176; Mousson, 1849: 66, pl. 11, fig. 1–3; Reeve, 1860: pl. 21, fig. 154 *Melania junghuhni* Schepman, 1896: 135–136, pl. 2, fig. 1 (*Java*) non Martin, 1879. *Melania martini* Schepmann, 1898: 84 (replacement name for *M. junghuhni*; 42 syntypes RHNL 71326, var. *flammulata*: 16 syntypes RHNL 71327; 3 syntypes MCZ 96926, var. *fasciata*: 18 syntypes RHNL 71328; 24 syntypes ZMA; 8 syntypes MCZ 96989)


**Taxonomic remarks**: The lectotype of *B. testudinaria* was designated and depicted by Knipper (1958). For their different coloration Schepmann (1896) described two variants (viz. *flammulata* and *fasciata*) of his new species, *Melania junghuhni*. However, the name is preoccupied by *M. junghuhni* Martin, 1879 for a fossil species from Tertiary sediments of Java. Therefore the name was changed to *M. martini* (Schepmann, 1898).

The descriptions of numerous forms by Schepmann (1896), Mousson (1849) and Oostingh (1935) show that the shell of *B. testudinaria* is rather variable; the extensive synonymy in Benthem Jutting (1956) indicates serious problems with species discrimination. Rensch (1934) briefly discussed the conchological variability and some of its taxonomic implications. Some authors (Oostingh, 1935; Adam & Leloup, 1938) even place this species within the genus *Sulcospira* due to its similar shell. Benthem Jutting (1956) synonymized *M. agrestis* Reeve, 1860 from Borneo with *B. testudinaria* and argued that the type locality of *M. agrestis* was erroneous. In contrast, we found that *M. agrestis* is similar to snails we found on Borneo and which are clearly distinct from *B. testudinaria*.

**Shell** (Fig. 1 F): The shell morphology is quite variable, solid but not thick, conical to pyramidal, turreted and light green to olive brown in colour, occasionally covered by an almost black periostracum. Dark axial flames, visible especially in juveniles, are frequently present. The spire is more or less conical in shape and has up to 10 regular more or less flattened whorls. The sculpture is smooth and consists only of some basal spiral bands. The aperture is ovate and rounded below. Mean shell dimensions (standard deviation in parentheses): H = 29.8 (± 3.4) mm, B = 12.1 (± 1.7) mm, LA = 10.3 (± 2.1) mm, WA = 6.0 (± 0.9) mm, BW = 17.6 (± 2.0) mm (n = 25).

**Protoconch and juvenile shell** (Fig. 14 A, B, D): The protoconch corresponds to the description given for
B. pageli. The surface of the large apical cap is only slightly wrinkled and granular. Subsequent whorls are smooth, with only faint growth lines. The entire juvenile shell including protochonch comprises little more than two whorls. Mean dimensions: $H = 1.3\, \text{mm}$, $B = 1.0\, \text{mm}$, $DA = 677\, \mu\text{m}$ ($n = 5$) (Table 1).

Operculum (Fig. 3 D): Circular, consisting of up to five regularly increasing whorls with a central nucleus.

External morphology: Animals are dark grey with light patches.

Radula (Fig. 14 C): There are about 120 rows of teeth; the entire radula has a length of up to 15 mm, corresponding to half of the shell height. The rachidian tooth has one main cusp flanked by three tapering denticles. The anterior margin is concave with inflated and rounded corners. The glabella is broad and well rounded at its lower margin. The laterals have one large main cusp flanked by two or three smaller denticles on each side. The inner and outer lateral teeth each have two cusps, the outer one being more pronounced and somewhat rounded.

Stomach: Style sac and intestinal groove are open to each other. The proximal tip of the major typhlosole forms a flap partly covering the opening to the style sac. The inner crescent fold underneath the opening to the digestive gland duct is undulated.

Reproductive biology: The subhaemocoelic brood pouch of the females contains up to 120 eggs or juveniles (Table 2). The sex ratio observed was 0.42.

Figure 12. Histological sections of the pallial gonoduct of B. pageli (ZMB 200092, Borneo); scale bars = 1.0 mm. A. Cross-section of the anterior part of the pallial gonoduct showing sperm gutter formed in the medial lamina and the capacious capsule gland comprising the base of the oviductal groove. B. Cross-section at about one third of the oviduct showing spermatophore bursa formed in the medial lamina; note the continuous second gutter. C. Cross-section at about two thirds of the oviduct with the spermatophore bursa and a blind ending sac. D. Cross-section at the posterior part of the oviduct showing the papillated spermatophore bursa and the capsule gland (note that the mantle tissue is mostly destroyed). Abbreviations: cg—capsule gland, ft—foot muscle, ll—lateral lamina, ml—medial lamina, og—oviductal groove, sb—spermatophore bursa, sg—sperm gutter, sr—seminal receptacle.
The anatomy of the pallial oviduct corresponds to *B. pageli*.

*Ecology:* This species was found in a wide range of freshwater habitats on Java; in running as well as stagnant water between sea level and 1500 m altitude and is evidently eurytopic (Rensch, 1934: 243; Benthem Jutting, 1956). However, this species seems to be less common than it once was judging from difficulties in finding populations on West-Java during a field trip in 1999. Even well known populations, e.g. in the Botanical Garden of Bogor, seem to be extinct, probably due to pollution of the habitats.

*Fossils:* Oostingh (1935) described several phenotypically distinct forms of *Sulcospira testudinaria* from Pliocene sediments from Java, of which only some resemble the Recent *Brotia testudinaria* (e.g. Oostingh,
1935: pl. 4, figs. 44–52). However, Oostingh figures (pl. 3, figs. 39–41) shells with pronouncedly angled whorls, identified partly as Sulcospira foeda and S. testudinaria, that clearly represent a different form and should not be assigned to B. testudinaria.

Distribution (Fig. 2): Known from Java, some of its satellite islands, and South Sumatra.

Material examined: Java: (ZMB 2238-9, 4073, 12333, 26739, 76308, 200081, 200083-4, 200086); Tandjung Priok, Jakarta (ZMB 94821); Cianjur near Bogor (ZMB 26884); Cisarua near Bogor (ZMB 200099); Cungengan near Bogor (ZMB 200100); Badung (ZMA); Sukabumi (ZMB 52783); Sidanglaya (ZMB 76302-3); Semarang (ZMB 200079); Rembang (ZMB 26881); Malang, East Java (ZMA); Lake Pakis (ZMB 76301, 76307, 200088); Lake Bedali (ZMB 76309-12, 76476); Berbek (ZMB 26883); Pumekusan, Madura (ZMB 52782); Sumatra: Lake Ranau (MZS 8787).

**Brotia hainanensis** (Brot, 1872)

Melania (Sulcospira) hainanensis Brot, 1872: 32, pl. 3, fig. 11 (‘Hainan’; 2 syntypes MHNG; 1 paratype SMF 39107, vide Yen, 1939).

Melania hainanensis—Brot, 1874: 60, pl. 6, fig. 15; Brot, 1883: 82, 83; Brot, 1886: 98, pl. 4, fig. 3, 3a.


Melania ebenina Brot, 1883: 83, no fig. (‘the mainland NE Hong Kong’; lectotype SMF 39077, 9 paralectotypes SMF 39079, 39105; 3 paralectotypes MHNG).

Melania subcylindrica Brot, 1886: 102–103, pl. 6, fig. 2, 2a (‘China’; 3 syntypes MHNG).

Taxonomic remarks: The lectotype of *M. ebenina* was designated and depicted by Yen (1939: pl. 5, fig. 17). We consider this taxon as a synonym of *B. hainanensis* despite Brot’s (1886) statement that the former is characterized by a different microsculpture.

Shell (Fig. 1 B): The shell is ovate, elongately conical; after truncation of the apex frequently only three to
five whorls remain. The colour is olive-brown. The sculpture consists of growth lines, fine transverse costae and spiral ridges at the base. The suture is well defined but narrow and the whorls are rounded in cross-section. The last whorl is comparatively large and the aperture is narrow and elongate, pointed above and well rounded below. The columella is turned, slightly thickened and has a simple and sharp margin. Mean shell dimensions (standard deviation in parentheses): $H = 34.6 (\pm 8.9)$ mm, $B = 15.9 (\pm 3.4)$ mm, $LA = 14.0 (\pm 2.8)$ mm, $WA = 8.2 (\pm 1.9)$ mm, $BW = 22.6 (\pm 4.5)$ mm ($n = 59$).

Protoconch and juvenile shell (Fig. 15 C–E): Similar to *B. pageli* and *B. testudinaria* its apex is only slightly wrinkled to smooth, comprising up to two whorls with a more or less pronounced sculptural transition at about 1 to 1.25 whorls. The first whorl is dome-shaped and appears to change coiling as described for *B. pageli*. Mean dimensions are: $H = 1.0$ mm, $B = 0.8$ mm, $DA = 611 \mu$m ($n = 5$) (Table 1).

**Operculum** (Fig. 3 G): Multispiral, slightly oval with a central nucleus and about six whorls with a hyaline growth zone along the posterior side.

**External morphology:** (Fig. 3 A) The animal is dark grey to black with light patches. The light grey coloured tentacles are relatively short.

**Stomach:** Major and minor typhlosole are not fused.

**Radula** (Fig. 15 A–B): The radula consists of about 140 to 170 rows of teeth and has a length of up to 18 mm, corresponding to half of the shell height. The teeth closely resemble those of *B. pageli*.

**Reproductive biology:** Females retain between 60 to 250 juveniles in their subhaemocoelic brood pouch (Table 2). Sex ratio within the population examined was more or less even with proportions of males being 0.44 (Table 3). The anatomy of the pallial oviduct corresponds to the description given for *B. pageli*.

**Ecology:** *B. hainanensis* is confined to stony mountainous streams and the upper courses of rivers (Dudgeon, 1982, 1989). We found a population in the New Territories of Hong Kong in a mountainous creek, shaded by large trees and rich in leaf material, where the snails dwell on muddy to pebbly substratum among boulders.

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**Figure 15.** SEM images of radula and juvenile shell of *B. hainanensis* (ZMB 200094, Hong Kong). A. Segment of the radula; scale bar = 0.1 mm. B. Detail of rachidian and lateral teeth; scale bar = 0.1 mm. C. Lateral view of the juvenile shell. D. Apical view of the juvenile shell; scale bar = 0.1 mm. E. Lateral view of the juvenile shell.
Distribution (Fig. 2): South China to North Vietnam and Hainan.

Remarks: Brot (1883: 83), describing additional specimens from Canton and Hong Kong, also commented on the type locality ‘Hainan’, originally given by a shell dealer, as being uncertain. However, we found material from Hainan in the ZMB, confirming that the island might actually be within the species range. Brot (1883) also reported an operculum with only three slowly increasing whorls, while we found up to six whorls here. According to Dudgeon (1982, 1989), B. hainanensis is relatively long lived (up to 3.5 years) and slow growing; sexual maturation is apparently reached at 2.5 years. The highly variable environment (seasonal surges in streams) favours large brood size, recruitment of two seasonal cohorts each year and, thus, iteroparity.

Material examined: China: Hong Kong (MHNG; CAS 6127); Hong Kong, New Territories: Wukau Tang, Mirrow Pool (ZMB 200094-5); Hainan (ZMB 200096; MHNG), Canton (MHNG); Amoy (MHNG); Lo Tou Shan (MHNG); Lilong, north of Canton (MHNG).

**Brotia asperata** (Lamarck, 1822)

*Melania asperata* Lamarck, 1822: 164, no fig. (‘Manille’); holotype MHNG 1093/60; Brot, 1874: 73, pl. 8, fig. 1a–g. *Melania philippinarum* Sowerby, 1838: pl. 1, fig. 1–3 (‘Philippines, Manila’).

*Melania pulchra* von dem Busch, 1848—In: Philippi, 1848: pl. 5, fig. 1 (‘Philippines’; lectotype UMB TK 236/1). *Pachychilus pulcher*—Troschel, 1857: 116, pl. 9, fig. 4.


**Protoconch and juvenile shell** (Fig. 16 A–D): The apical whorl is pronouncedly wrinkled as in *B. pagodula* and *B. costula* and exhibits an ‘open’ apex with protruding soft tissue. Thus, the apical part of the shell calcifies only later in the embryonic development when the apex is sealed by a secondary plug (Fig. 16 D). Subsequent whorls are sculptured by regular spiral ridges crossed by growth lines. Mean dimensions of the juvenile shells: H = 1.7 mm, B = 1.2 mm, DA = 628 µm (n = 10) (Table 1).

**Operculum** (Fig. 3 H): Oval with about three rapidly increasing whorls and a slightly eccentric nucleus.

**External morphology:** Soft body relatively large comprising up to eight whorls. The skin is dark grey. The mantle edge may be slightly papillated as reported by Fischer & Crosse (1892), though, papillae are inconspicuous and not always present. A large, fleshy flap formed by the inner surface of the mantle roof projects from the mantle cavity dorsal of the proximal end of the gonoduct.

**Radula** (Fig. 16 E, F): The radula consists of 130 to 220 rows of teeth and has a length of up to 25 mm, corresponding to half of the shell height. The rachidian tooth has one main cusp flanked by three tapering denticles. The glabella is hourglass-shaped and rounded below. The anterior margin of the rachidian tooth is convex, with rounded corners; lateral extensions as observed in other *Brotia* species are absent. Lateral teeth have one main triangular cusp flanked by two cusps forming a wing shaped plate on the inner side, and up to two or three tapering cusps outside. The inner and outer marginal teeth are curved or hooked and have two
pointed cusps, the outer one being broader. The outer marginals exhibit a pronounced simple flange at their outer side.

Stomach: Minor and major typhlosoles are unfused, thus style sac and intestinal groove communicate.

Reproductive biology: In contrast to other Brotia species, females of B. asperata possess no brood pouch. Instead, up to about 270 juveniles (Table 2) are retained within egg capsules attached to the roof of the mantle cavity, thus exhibiting a unique reproductive strategy. Among nine animals only one was male (Table 3). The pallial oviduct is completely open with the oviductal groove lined by a distal capsule gland. Anteriorly, the medial lamina starts off as a very thin, elongated flap, with a groove forming on the inner side as continuously deepening sperm gutter, at this stage resembling the condition found in B. pagodula. This gutter runs along almost the entire length of the oviduct, becoming voluminous and papillated inside posteriorly, and eventually runs into a small spermatophore bursa. The are additional folds presumably also forming gutters, however further histological details of the gonoduct were not visible due to inadequate preservation of the material.

Figure 16. SEM images of juvenile shell and radula of B. asperata (AMS 324129, Bohol). A. Lateral view of a critical point dried juvenile; note soft tissue extending and attached to the apical portion of the shell; scale bar = 1.0 mm. B. Lateral view of the apical portion; note the already calcified shell. C. Lateral view of the juvenile shell with already calcified shell; scale bar = 0.1 mm. D. Apical view of the juvenile shell; scale bar = 0.1 mm. E. Detail of rachidian and lateral teeth; scale bar = 0.1 mm. F. Segment of the radula; scale bar = 0.1 mm.
Ecology: We found snails in relatively small, fast flowing mountain streams with stony bottoms, as reported by Abbott (1948) and Bandel & Riedel (1998; however, the latter authors erroneously referred to this species from Cebu Island as ‘Brotia aff. costula’; see above). A report by Woltereck (1941) from Lake Laguna, on Luzon, is questioned here, as the species has otherwise not been found there.

Distribution (Fig. 2): Philippines: Luzon and some of its satellite islands as Polillo and St. Cruz Island, Samar, Leyte, Bohol, Cebu, Negros, Guimeras and Siquijor.

Remark: B. asperata is intermediate host of the human lung fluke Paragonimus westermani (Cabrera & Vajrasthira, 1973).

Material examined: Philippines: (ZMB 2222, 77093, 88840, 200012, 200017, 200019, 200022-9, 200031-4, 200041, 200077; CAS 6195-6). Luzon: (ZMB 200014-5; ZMH; BMNH); Manila (ZMB 26714, 200016); Rizal Prov., Antipolo-River, tributary of the Pasig River (BMNH 1913.11.24.33-37; CAS 47627); Prov. Laguna de Bay (ZMB 27268; MHNG; AMS 324130; CAS 11306); Sta. Cruz (ZMB 78325); Calauan (ZMB 26766; MHNG); Jovilar, Alban (CAS 47627); Prov. Albay, Daragu River (ZMB 26768, 200013); Manvelu (ZMB 200011); Sibul (BMNH 1909.10.12.34-44); Brunot Lake, San Pedro (AMS 324135). Polillo (ZMB 200020; MHNG). Insl. Siquijor (BMNH). Samar (ZMB 26767; MHNG); Loqui-locum (ZMB 26765); Basey (CAS 23860). Leyte (ZMB 200035); Bohol: Bilar, Bilar River (ZMB 65288; CAS 116978); San Isidro (AMS 324129). Negros (BMNH). Guimeras (BMNH 19990496; MHNG).

DISCUSSION

In freshwater cerithioidean gastropods the underestimation of their high conchological variability has caused a plethora of species names that does not necessarily reflect the actual biological diversity. Many such taxa may represent ecophenotypes, geographical variations, or allo- and paraspecies within, for example, a superspecies, as has been shown for another supposedly ‘species-rich’ freshwater cerithioidean, the circum-Mediterranean Melanopsis Férussac, 1807 (Glaubrecht, 1993, 1996: 260–297). It is evident from the present study that the actual number of biospecies, or evolutionary entities, of Brotia in various parts of Southeast Asia is yet unknown. Many of the aforementioned estimates of species diversity in Brotia (e.g. Sarasin & Sarasin, 1898; Davis, 1982; Brandt, 1974; see Introduction) require reconsideration. Given the absence of data for sufficient populations of all relevant taxa across the entire geographic range of Brotia, we here refrain from a comprehensive taxonomic treatment at the species level.

The genus was long considered to represent a single, more or less homogeneous and monophyletic clade that, nevertheless, shows remarkable intra- and interspecific variability of conchological features. The morphological data presented show that Brotia, as formerly conceived is a composite of several divergent taxa. Since female Brotia retain their juveniles in specific incubatory structures, their ontogeny provides important anatomical and biological information. We found differences particularly in the reproductive anatomy and ontogenetic strategies, the latter manifested particularly in the embryonic shells. These features allow the differentiation within Brotia sensu lato of at least three major species groups representing separate evolutionary lineages (Table 4), viz. (i) Brotia sensu stricto with the B. pagodula-group and the B. testudinaria-group, (ii) the species synonymized with B. asperata, and (iii) all endemic species from Sulawesi, which are subject of a parallel study (Rintelen & Glaubrecht, 1999) but referred to for comparison. This suggested systematization of Brotia sensu lato is supported by data on molecular genetics (Köhler, Rintelen & Glaubrecht, 2000; and Rintelen & Glaubrecht, unpubl. data).

The new systematization and the evaluation of characters

Brotia was originally established by Adams (1866) for its round and multispiral operculum of the type species B. pagodula. For that reason it was considered as being monotypic (e.g. Brot, 1874) and only later thought to include the ‘Palaeomelanien’ of Southeast Asia (e.g. Martens, 1897; Sarasin & Sarasin, 1898; Thiele, 1925, 1928, 1929). However, as is shown herein, a round operculum as was stated to be a characteristics of Brotia (cf. Adams, 1866) is an exception since most Brotia species actually possess an ovate and multispiral operculum like also other Pachychilidae, e.g. Paracrostoma and the neotropic Pachychilus. A round operculum, though, is present in the endemic species of Sulawesi (Rintelen & Glaubrecht, 1999).

Comparison with other genera reveals that also characteristics of the radula, the stomach, the mantle cavity, the gonoduct and the genital groove on the right side of the head-foot are essentially similar across the Pachychilidae, and thus are likely to represent symplesiomorphies within Brotia. Since most genus-group taxa of Southeast Asian Pachychilidae were described using these ‘diagnostic’ features, the confusion con-
cerning systematics and the placement of *Brotia* becomes understandable. Given the lack of more comprehensive anatomical data for all constituent taxa of the Pachychilidae, a thorough evaluation of characters is currently impossible and awaits the results of cladistic analysis.

From the data presented above, no unequivocal synapomorphic features become evident, either in the anatomy of the pallial oviduct or the protoconch morphology, to support monophyly of *Brotia* sensu lato. The subhaemocoelic brood pouch is considered synapomorphic only for the *B. pagodula*-group and the *B. testudinaria*-group among *Brotia* s.str. (see below).

We refrain from formally revising the taxonomy and naming the Philippine and Sulawesi groups as separate genera here pending a full phylogenetic analysis combining morphological and molecular data.

Nevertheless, we consider the characteristics of the oviduct, the brood pouch and the protoconch as providing consistent and reliable taxonomic features for the subdivision of *Brotia* s.l. suggested here, while other features used previously, such as shell, radula and operculum are uninformative at this level. In concert with the reproductive anatomy, the embryonic shells represent relatively complex characters that are also testimony to different life histories.

Table 4. Suggested systematization of *Brotia* sensu lato and the distinguishing features of representative taxa from Southeast Asia. Taxa in bold described in this study.

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<tr>
<th><em>Brotia</em> sensu stricto</th>
<th><em>B. pagodula</em> – group</th>
<th><em>B. testudinaria</em> – group</th>
<th><em>B. asperata</em> – group</th>
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<td><strong>Species</strong></td>
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<td><em>B. testudinaria</em></td>
<td><em>B. asperata</em></td>
<td><em>Brotia</em> and Tylomelania species endemic to Sulawesi</td>
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<td></td>
<td><em>B. pseudoasperata</em></td>
<td><em>B. proteus</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>B. manningi</em></td>
<td><em>B. tourannensis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Occurrence</strong></td>
<td>mainland Southeast Asia incl. Sumatra</td>
<td>South and Indo-China, Borneo, Java</td>
<td>Philippines</td>
<td>Sulawesi</td>
</tr>
<tr>
<td><strong>Shell</strong></td>
<td>brown, axial elements or spines may be present</td>
<td>brown, axial flames may be present, axial elements frequently absent</td>
<td>brown, axial and spiral elements present</td>
<td>brown, axial and spiral elements may be present</td>
</tr>
<tr>
<td></td>
<td>4–12 whorls</td>
<td>3–10 whorls</td>
<td>8–12 whorls</td>
<td>4–12 whorls</td>
</tr>
<tr>
<td><strong>Operculum</strong></td>
<td>round to ovate, multispiral (6–8 whorls), central nucleus</td>
<td>round to ovate, multispiral (3–6 whorls), central nucleus</td>
<td>ovate, multispiral (3–4 whorls), slightly eccentric nucleus</td>
<td>round, multispiral (4–10 whorls), central nucleus</td>
</tr>
<tr>
<td><strong>Protoconch</strong></td>
<td>wrinkled apical shell surface, ‘soft apex’</td>
<td>smooth shell surface, apex dome-shaped, no ‘soft apex’</td>
<td>wrinkled apical shell surface, ‘soft apex’</td>
<td>smooth shell surface, no ‘soft apex’</td>
</tr>
<tr>
<td><strong>Shape and size of the juvenile shell</strong></td>
<td>relatively large, whorls flattened</td>
<td>relatively small, whorls flattened</td>
<td>relatively small, whorls flattened</td>
<td>relatively large, whorls shouldered</td>
</tr>
<tr>
<td><strong>External anatomy</strong></td>
<td>mantle edge smooth</td>
<td>mantle edge smooth</td>
<td>mantle edge smooth, with flap</td>
<td>mantle edge smooth, with flap</td>
</tr>
<tr>
<td><strong>Stomach</strong></td>
<td>typhlosoles fused</td>
<td>typhlosoles fused or unfused</td>
<td>typhlosoles unfused</td>
<td>typhlosoles unfused</td>
</tr>
<tr>
<td><strong>Brood pouch</strong></td>
<td>subhaemocoelic brood pouch</td>
<td>subhaemocoelic brood pouch</td>
<td>eggs, embryos and juveniles are retained in mantle cavity</td>
<td>uterine brood pouch</td>
</tr>
<tr>
<td><strong>Reproductive system</strong></td>
<td>capacious spermatophore bursa, sperm gutter closes at opening to spermatophore bursa</td>
<td>capacious spermatophore bursa, sperm gutter closes posteriorly of opening to bursa, second gutter closes to a blind sac</td>
<td>small spermatophore bursa, sperm gutter leads almost to the end of the pallial oviduct, additional folds forming gutter</td>
<td>capacious spermatophore bursa, second gutter closes to a blind ending sac, oviductal groove modified into brood pouch</td>
</tr>
</tbody>
</table>

Table 309
\textit{Brotia} sensu stricto: Viviparity and the possession of a brood pouch were often considered as diagnostic features of \textit{Brotia} (e.g. Martens, 1897; Sarasin \& Sarasin, 1898; Moore, 1899; Rensch, 1934; Morrison, 1954; Benthem Jutting, 1956; Solem, 1966; Brandt, 1968, 1974; Davis, 1971, 1982; Glaubrecht, 1996). The brooding structure in the neck region was consistently related to a similar structure known from the Thiaridae. For example, in \textit{Melanooides} and \textit{Thiara} it is situated in the neck region and often extends anteriorly into the right propodium (see Glaubrecht, 1996, 1999; Schütt \& Glaubrecht, 1999). For the Thiaridae and its putative sister taxon, the marine Planaxidae, this peculiar brooding structure was considered as a synapomorphy (e.g. Morris, 1954; Houbrick, 1987, 1988; Ponder, 1991; Glaubrecht, 1996). However, it remained unclear as to which extent this subhaemocoelic brood pouch is homologous within and among the Thiaridae and Pachychilidae (Glaubrecht, 1998, 1999). The present study shows that a subhaemocoelic brood pouch, however, is only shared by species of \textit{Brotia} sensu stricto. Since it is missing in other Pachychilidae, i.e. \textit{Pachychilus}, \textit{Potadoma}, \textit{Melanatrix} (see Glaubrecht, 1996) and \textit{Pseudopotamis} (cf. Glaubrecht \& Rintelen, submitted), it is considered here to represent a synapomorphy only of the \textit{B. pagodula}-group and the \textit{B. testudinaria}-group (Table 4). The subdivision of \textit{Brotia} s.str. into these two species-groups is based primarily on differences in the protoconch morphology and different anatomies of the pallial oviduct as described above.

– The \textit{B. pagodula}-group: In species from the mainland of Southeast Asia and Sumatra, such as \textit{B. pagodula}, \textit{B. costula}, \textit{B. henriettae}, \textit{B. binodosa} and \textit{B. citrina} (Brot, 1868), the apical whorl of the juvenile shell is characterised by a ‘soft apex’ and, as a result (see below), exhibits an asymmetrical protoconch with a wrinkled shell texture (e.g. Fig. 11 D, E). In addition, the pallial oviduct is comparatively simple, with the sperm gutter closing at the opening to the spermatophore bursa.

– The \textit{B. testudinaria}-group: In contrast, species lacking the characteristic wrinkled embryonic shell exhibit a more or less smooth texture of the apical whorl, with an inflated, dome shaped apex lying across the coiling axis of the subterminal whorls (e.g. Fig. 13 A, B, D). A protruding ‘yolk sac’ is apparently lacking. The sperm gutter of the oviduct closes posterior of the opening of the bursa, while a second gutter terminates in a blind sac, presumably the seminal receptacle, the latter lacking in the \textit{B. pagodula}-group. This species group comprises \textit{B. testudinaria} from Java, \textit{B. hainanensis} from South China and \textit{B. pagelli} from Borneo. We also found similar protoconch structures in \textit{B. pontificalis} from Borneo, \textit{B. proteus} (Bavay \& Dautzenberg, 1908) and \textit{B. tourannensis} (Eydoiux \& Souleyet, 1852), both occurring in Indochina.

\textit{B. asperata}: Endemic to the Philippines, \textit{B. asperata} is characterized by the lack of a subhaemocoelic or uterine brood pouch. Instead, egg capsules and juveniles are retained within the mantle cavity. Other peculiarities of \textit{B. asperata}, such as the anatomy of the gonoduct with a small spermatophore bursa at the proximal end and complex additional foldings, as well as the radula with a convex anterior margin of the rachidian tooth, support its separate status. Davis (1971: 69–70) failed to note the distinct gonoduct anatomy and correlated brooding strategy, since he presumably expected to find a subhaemocoelic brood pouch in this species. However, its distinct and unique reproductive biology clearly sets \textit{B. asperata} aside from all other species of \textit{Brotia} sensu lato. Furthermore, we believe that brooding in the mantle cavity represents the ancestral state of viviparity among these freshwater Cerithioidea and might indicate that \textit{B. asperata} is the closest relative to the stemgroup that gave rise to \textit{Brotia}.

\textit{Tylomelania} and \textit{Brotia} endemic to Sulawesi: From Sulawesi, traditionally two pachychild genera are known, viz. the so-called \textit{Brotia} species originally described by Sarasin \& Sarasin (1898) and three species of \textit{Tylomelania}. These approximately 30 named taxa are believed to form an endemic radiation in the central lakes, and are the subject of an ongoing study (Rintelen \& Glaubrecht, 1999). All taxa studied from Sulawesi possess an unique uterine brood pouch and a specific embryonic shell morphology (Rintelen \& Glaubrecht, 1999; and unpubl. data). For this completely distinct and, among \textit{Brotia}, unique brooding strategy as well as additional morphological features (e.g. radula and shell), all species endemic to Sulawesi are distinguished from the remaining \textit{Brotia} species, including \textit{B. asperata} from the Philippines. Investigations on the phylogeny and systematics of the Sulawesi species, including molecular genetic data (Köhler et al., 2000) are in progress (Rintelen \& Glaubrecht, unpubl. data).

\textbf{Reproductive biology, ontogeny, and life history strategy of Brotia}

In the past, authors frequently referred to the viviparity and brood pouch of \textit{Brotia} (e.g. Morris, 1954; Benthem Jutting, 1956; Solem, 1966; Brandt, 1968, 1974; Davis, 1971, 1982), though without sufficient attention to the detailed structure of the anatomical features
In addition, although all members of *Brotia* from Southeast Asia brood, the incubatory structures involved are different between certain groups of taxa. We found that an incubatory pouch can be built in various ways in *Brotia* sensu lato and by no means is always a subhaemocoelic brood pouch. On the other hand, the possession of a subhaemocoelic brood pouch as a consistent feature of *Brotia* sensu stricto is not strictly correlated with a particular shape and texture of the protoconch, as assumed earlier for freshwater Cerithioidea (for review see Glaubrecht, 1996). Since we found individual ontogenetic differences, involving different types of incubatory structures, reproductive strategies and protoconch sculptures, we here view differences of the protoconch shell sculpture as testimony to the various pathways of embryonic development and modes of shell calcification.

For example, within the *B. pagodula*-group (and also in *B. asperata*), formation of the protoconch is linked to ontogenetic peculiarities. In embryonic shells the apical (and thus earliest) part remains uncalcified even after shell formation of subsequent whorl(s) is complete (see Fig. 11 A–C for *B. costula*). From this apical opening soft tissue protrudes to various degrees in different ontogenetic stages. We found growth series of juveniles that demonstrate how the voluminous protruding ‘yolk sac’ continuously decreases in size while the embryos grow. In accordance with Morrison (1954) and Solem (1966) we interpret this protruding tissue to consist of yolkky material, presumably connected to the digestive gland in later stages, and being of nutritive function.

Irrespective of the individual brooding strategy, egg capsules and embryonic shells of *Brotia* in general are exceptionally large compared to other freshwater gastropods (Fioroni & Schmekel, 1976: 108–116; Glaubrecht, 1996). The egg capsules comprise up to 1 mm in diameter (Table 2), and since special nutritive structures of the brood pouch epithelium have not been found, we assume that growth of embryos and juveniles within the pouch is sustained by the nutritional supply of the egg only. This strategy differs from the mechanisms described for some Thiaridae wherein brooding females nourish their embryos via secretory epithelia in the pouch (Glaubrecht, 1996).

In general, shell formation in early embryonic stages of gastropods begins at the ectodermal area of the embryonic visceral mass (shell field) and first produces a conchiolin layer with increasing diameter that remains uncalcified. In later stages the shell gland secretes calcareous material on this layer (Fretter & Graham, 1994: 577). Apparently, in species of the *B. pagodula*-group and in *B. asperata* the apical portion of proto-
conchs of younger stages does not calcify. As a consequence, nutritive tissue of the embryo protrudes through this ‘open’ apex or at least clusters around the uncalcified apical part of the embryonic shell as is revealed by critical point dried samples (Fig. 10). We confirm Solem’s (1966: 17) observation that only in embryos ready to be expelled from the brood pouch the apical part is covered by shell, and hypothesize that the delayed apical shell calcification results in the characteristically wrinkled shell of the protoconch.

A similarly wrinkled apical whorl has also been reported from some other cerithioidean viviparous taxa, such as Melanoideas (cf. Riedel, 1993; Glaubrecht, 1996), Tarebia H. & A. Adams, 1854, Thiara, Lavigeria Bourguignat, 1888 and Potadomoides Leloup, 1953 (cf. Glaubrecht, 1996) and was also explained as a result of delayed calcification of embryonic shells. Riedel (1993) assumed that the development of the wrinkled shell in Melanoideas tuberculata (Müller, 1774) is caused by a retarded agglutination of primarily isolated calcium carbonate crystals during the process of calcification while the visceral mass of the embryo is shrinking due to the consumption of nutritive tissue during larval development. However, protruding soft tissue has not been observed in any other gastropod than Brotia. Since the underlying mechanism of nourishment is apparently different in various Cerithioidea, it is the mode of embryonic nutrition via a large yolk sac and not the wrinkled apical shell itself that is unique to the B. pagodula-group.

Although species of the B. testudinaria-group incubate their embryos in a subhaemocoelic brood pouch as well, a distinct protoconch sculpture and ontogenetic strategy is found. Here, the smooth protoconch lacks the protruding ‘yolk sac’ and ‘open apex’. Hence, the calcification of the embryonic shell is complete and continuous. Presumably these juveniles are provided with a smaller supply of nutritive tissue. Consequently, we would expect them to be smaller when hatching. Our observations (Table 1) fit this hypothesis: Juveniles of the B. testudinaria-group comprise up to 2.5 whorls and 1.3 mm in shell height, while those of the B. pagodula-group reach up to 4 whorls and exceptionally more than 5 mm.

A protruding ‘yolk sac’ and wrinkled protoconch sculpture was also found in B. asperata, whose females incubate their embryos in the mantle cavity. Sizes of the biggest juveniles, presumably close to hatching, lie between those of the B. pagodula-group and the B. testudinaria-group.

Apparently, the number of retained juveniles is connected to the maximum size of the embryonic shells. B. pagodula broods relatively few but large juveniles and the same was found in the pachychilid taxa endemic to Sulawesi, having only between 2 to at most 22 relatively large juveniles per animal (Rintelen & Glaubrecht, 1999). In both cases, the occurrence of only few large juveniles in the brood pouch indicates a k-strategy. In contrast, other Brotia species retain up to several hundred juveniles, which are released from the brood pouch at a smaller size, though. Our observations on the number of juveniles per female are supported, for example, by Abbott (1948) who mentioned ‘some 50 or so’ juveniles, and by Kruatrachue et al. (1990) reporting on an average of 46.3 juveniles per female in B. costula. Similar numbers have also been given for some Thiaridae: In Melanoideas tuberculata between ‘up to some dozen’ (Abbott, 1948), 15 to 20 (Starmühlner, 1969), 24 to 71 (Glaubrecht, 1996: 119), and a maximum of 265 (Starmühlner, 1976); in Thiara scabra (Müller, 1774) between 75 and 110 (Riech, 1937: 45).

For B. hainanensis Dudgeon (1982, 1989) reported 112 to 936 (!) juveniles per female and attributed the wide range to variable habitat conditions, individual nutrition status or size and age of the females. Brooding numerous embryos of a small size, as e.g. B. hainanensis, indicates an ‘r-strategy’ that should result in an increased reproductive potential, a higher dispersal ability and ecological plasticity (MacArthur & Wilson, 1967). If only few embryos are retained, each of them provided with a higher parental investment (i.e. with yolk), a ‘k-strategy’ is pursued, which might be favoured by a more stable environment. Unfortunately, the available data for Brotia is insufficient to decide whether the observed differences between the number of retained juveniles are testament to different life histories, or only reflect the different sample sizes.

Another important aspect concerning reproduction in Brotia is controversial. Some authors assumed parthenogenesis to be the common mode (e.g. Morrisson, 1954; Benthem Jutting, 1956; Brandt, 1968, 1974; Subba Rao, 1997), albeit often as a consequence of the erroneous systematic concept of the Thiaridae, for which parthenogenesis was considered synapomorphic. Brandt (1974) reported an average male frequency of only 3 % in B. costula. However, our data show that in all species males occur much more frequently resulting in a rather balanced sex ratio (Table 3). For B. pagodula and B. asperata, respectively, where only one male was found, we consider sample size as too low for feasible estimates of the sex ratio. Since males actually were found in both these species, and Davis (1971: 70) and Kruatrachue et al. (1990) also noted the existence of males in B. asperata, we expect all Brotia species to be gonochoristic. Clarification of this aspect remains highly desirable since it has import-
ant biological implications. For example, as analogy to the parthenogenetic and today pantropical thiarid *Melanoides tuberculata*, Martens (1897), Morrison (1954), Benthem Jutting (1956) and Davis (1982) attributed the wide geographical range of *B. costula* to its presumed parthenogenetic status. It was hypothesized that parthenogenesis leads to increased dispersal abilities, since each individual has the potential to found a new population.

**Biogeography**

Although largely neglected in this context, freshwater gastropods with their ancient ancestry, rich palaeontological record, habitat specificity and limited dispersal ability have the potential to serve as a model system to provide new biogeographical insight (Glaubrecht, 2000a). However, *Brotia* has previously only rarely been taken into consideration by malacologists interested in biogeography (Martens, 1897; Davis, 1982). Davis (1982: 392) emphasised ecology rather than history as a limit on the distribution of *Brotia* species. Although restricting this question to a comparison with the Pomatiopsidae of the Mekong River, he noticed that mostly only one species of *Brotia* is found per river system and is rarely sympatric with a second one. On the other hand, he pointed out that *Brotia* radiates in some streams and rivers in Thailand. There, especially in the Kaek Noi River (a tributary of the Nan-Chao Phraya River in north central Thailand) five species, subspecies or phenotypically distinct forms described by Brandt (1968, 1974) as forming a 'rassenkreis', are found along the river that flows over numerous small waterfalls. However, since *Brotia* are able to climb waterfalls (Dudgeon, pers. comm; own observ.), it seems dubious that waterfalls could serve as effective barriers to gene flow and so are unlikely to be isolating mechanisms favouring speciation. In addition, Davis (1982: 391) related the extensive distribution of *B. costula* in Southeast Asia to its brooding behaviour, overlooking the fact that other cnergic species are also viviparous without exhibiting such widespread distributions. Thus, a comprehensive zoogeographical understanding of the genus in Southeast Asia is still lacking.

Based on the systematization outlined in the present study, *Brotia* can be utilized within the framework of an historical biogeography of one of the most complex regions of the world, the so-called 'Wallacea', a transitional zone between the Australian and Oriental region (review in Glaubrecht, 2000a). This region was built of oceanic island arcs and drifting continental fragments, with its faunal elements apparently reflecting a complex history of fragmentation and amalgamation by separation and speciation, dispersal and colonization (e.g. Whitmore, 1981, 1987; Hall & Blundell, 1996; Hall & Holloway, 1998; Heaney, 1999).

*Brotia* sensu stricto comprises all taxa from the Southeast Asian mainland as well as Sumatra, Java and Borneo, thus being restricted to the Sunda shelf region, or Sundaland, a discrete land mass during Pleistocene low sea level stands. Therefore, the eastern limits of *Brotia* s.str. is circumscribed by Wallace’s line, a much disputed ‘imaginary’ border that has lost much of its cachet in light of modern biogeographic studies (e.g. Dickerson, 1928; Mayr, 1944; Simpson, 1977; Glaubrecht, 2000a,b). The second group with endemic *Brotia* (and *Tylomelania*) species occurs across the Wallace Line, but exclusively on Sulawesi, an island that remains enigmatic in terms of its biogeography in many respects. Finally, *B. asperata* is isolated from both groups and endemic to the Philippine Islands.

In all three cases our biological data correspond with recent geological findings concerning the palaeogeographical history of these islands and areas. Most importantly, the *Brotia* s.str. clade, characterized by a subhaemocoelic brood pouch, is clearly separated from species on Sulawesi and the Philippines. In contrast, all species east of the Wallace Line (including *Pseudopotamis* on the Torres Strait Islands between Australia and New Guinea) possesses an uterine brood pouch or lack this modified oviduct and brood juveniles in the mantle cavity, indicating an independent evolution of these reproductive characters.

Based on the known distribution of members of the Pachychilidae, indicative of a Gondwanian origin of the family (Glaubrecht, 2000a, b), and on first molecular data that suggests at least an early Tertiary age for several *Brotia* lineages (Köhler et al., 2000; Rintelen, Köhler and Glaubrecht, unpubl. data), we hypothesize that *Brotia* sensu lato might represent an ancient lineage of Tertiary or even Mesozoic origin. In agreement with recently presented geological data (Hall, 1998, 2000; Hall & Holloway, 1998), we further tentatively hypothesize that the phylogeny and distribution of *Brotia* in Southeast Asia might reflect palaeogeographic events during the Cenozoic involving the fragmentation, migration and amalgamation of terranes (tectonic microplates), and does not reflect more recent geological history, such as those events, related to the formation of Sundaland and its drowning during the Plio-Pleistocene. Consequently, we suggest that the distribution of *Brotia* s.l. is an ancient pattern caused by plate tectonics that has not been obscured subsequently. This may be due to their relatively restricted dispersal ability in conjunction with ecological factors, such as the dependence of these snails on smaller,
mountainous creeks and rivers in rainforest areas with high rainfall. In this case, even the interconnection of larger rivers during low-sea level times of the dry-climate Sundaland period (see review in Heaney, 1991) might not have resulted in the dispersal of formerly isolated populations and/or species of *Brotia*.

We have identified a number of important diagnostic features of *Brotia* species in order to provide the framework for continuing investigations towards a thorough systematic revision and historical zoogeography of all constituent members of the Oriental Pachychilidae. Moreover, our conclusions are supported by preliminary molecular sequence data. Nevertheless, a reliable conclusion as to whether or not the systematization suggested here represents monophyletic lineages distinguished by independently derived features awaits further morphological and molecular genetic investigations and finally a comprehensive and simultaneous phylogenetic analysis of the entire group.

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