



# On the morphology and taxonomic position of *Babylonia* (Neogastropoda: Babyloniidae)

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**KEY WORDS:** *Babylonia*, Babyloniidae, taxonomic position, anatomy, phylogenetic analysis, cytochrome c oxidase I sequence.

**ABSTRACT** *Babylonia* Schlüter, 1838 is a conchologically distinctive and commercially important genus of neogastropods traditionally assigned to the family Buccinidae. External morphology and anatomy of several species of *Babylonia* have been studied in detail for the first time. All studied the species of this genus possess an unpaired accessory salivary gland, and two of six studied species (*B. areolata* and *B. japonica*) have a rectal gland. The radula of all species is distinctive and differs markedly from that of any buccinoidean in having cusps along the outer edges of the rachidian teeth, and in the morphology of the three strongly buttressed central cusps, which emanate from the anterior edge of the basal plate. Cladistic analyses of anatomical data as well as of partial DNA sequences of the cytochrome c oxidase I gene revealed that the genus *Babylonia* is not closely related to Buccinoidea, but has close affinities to the volutoidean families Volutidae and Olividae. More detailed comparisons that include a broader representation of volutoidean families will be required to more precisely determine the sister group relationship of the family Babyloniidae Kuroda, Habe and Oyama, 1971.

**RIASSUNTO** *Babylonia* Schlüter, 1838 è un genere di neogastropodi ben caratterizzato conchigliologicamente e di una certa importanza commerciale, tradizionalmente assegnata alla famiglia Buccinidae. In questo lavoro si presentano dati derivati dallo studio della morfologia esterna e dell'anatomia di alcune specie, per la prima volta ad un elevato livello di dettaglio. Tutte le specie studiate posseggono una ghiandola salivare accessoria impari, e due delle sei specie studiate (*B. areolata* e *B. japonica*) hanno una ghiandola rettale. La radula di tutte le specie è nettamente distinta e differisce rimarchevolmente da quella di qualunque buccinoideo nell'avere cuspidi lungo il bordo esterno del dente rachidiano, e nella morfologia delle tre cuspidi centrali, che originano dal bordo anteriore della lamina basale. Un'analisi cladistica dei caratteri anatomici insieme ai dati da sequenze parziali del gene per la citocromo c ossidasi I (COI) mostrano come il genere *Babylonia* non sia strettamente correlato ai Buccinoidea, ma abbia forti affinità con i Volutoidae, in particolare con le famiglie Volutidae ed Olividae. Comparazioni più dettagliate che includano una più ampia rappresentanza delle famiglie volutoidee saranno necessarie per determinare più precisamente le relazioni di sister-group della famiglia Babyloniidae Kuroda, Habe & Oyama, 1971.

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## INTRODUCTION

The genus *Babylonia* Schlüter, 1838, encompasses a group of conchologically distinctive and commercially important neogastropods that inhabit soft bottoms at littoral and sublittoral depths along the western and northern margins of the Indian Ocean, the Indonesian Archipelago, the Philippines, and Japan. While the species level systematics of *Babylonia* is stable and well documented (e.g., HABE, 1965; ALTENA & GITTENBERGER, 1981), the taxonomic rank and relationships of this group within Neogastropoda have a long and convoluted history.

This genus was well known to nineteenth century authors as *Eburna*, originally proposed by LAMARCK (1801:78) to include a single southern Caribbean species, *Buccinum glabratum* Linné, 1758, now referred to the subfamily Ancillinae of the family Olividae. Later, LAMARCK (1822) expanded the genus to contain four additional species today included in *Babylonia*. Lamarck placed *Eburna* within the family Purpurifera, and suggested an affinity to *Buccinum*, noting (LAMARCK, 1822:280) that *Eburna* is "Distinguished from *Buccinum* by the singular position of the umbilicus, of the columella, which is also produced so as to form a canal, which occupies the rest of the left lip" (translation cited from GOULD, 1833). Recognizing that LAMARCK's 1822 formulation of *Eburna* differed markedly from his original usage of the genus, SCHLÜTER, (1838:18) proposed the genus *Babylonia*, without diagnosis or discussion, including only *Buccinum spirata*. Presumably unaware of SCHLÜTER's 1838 work, GRAY (1847) introduced name *Latrunculus*, also without description or discussion,

listing *Eburna*, sp. Lam. 1822, not 1801, in its synonymy. He included this genus within Buccinidae (as Buccinina).

The majority of 19th century iconographies include a monograph of the genus *Eburna* (e.g., KIENER 1835; REEVE, 1849; SOWERBY, 1859; TRYON, 1881). SOWERBY (1859) noted that "Authors have generally agreed to remove from this genus the [type species] *Buccinum glabratum* of Linneus, which is an *Ancillaria*, ... the remaining species form a very compact and well-defined genus." TRYON (1881) recognized that, based on its type species, "*Eburna* must become a synonym of *Ancillaria*" but continued to use *Eburna*, noting that "Naturalists have done much to render science and themselves contemptible by expending their time upon the nomenclature, instead of the structure and habits of the animals." With the increasing codification of nomenclatural protocols toward the end of the 19th century (see MELVILLE, 1995), *Babylonia* gained widespread usage for this group early in the 20th century (e.g., THIELE, 1929; WENZ, 1943).

Most authors have attributed *Babylonia* (some using one of its various synonyms – *Eburna*, *Latrunculus*, *Peridipsacus*) to the family Buccinidae (e.g., GRAY, 1847; H. & A. ADAMS, 1853) based primarily on shell morphology. The gross external morphology of the animal and the radula of several species were described or figured by a number of authors (e.g., KIENER, 1835; ADAMS & REEVE, 1848; EYDOUX & SOULEYET, 1852; SOWERBY, 1902; ALTENA & GITTENBURGER, 1983; RIEDEL, 2000). REEVE (1849) commented that the animal of *Babylonia* is so similar to that of *Buccinum* that the species should hardly be separated, were it not





for differences in shell morphology. Indeed, the distinctive morphology of the shell prompted several authors to erect supra-generic taxa (Eburninae SWAINSON, 1840, as a subfamily of Turbinellidae; Babyloniinae KURODA, HABE & OYAMA, 1971, as a subfamily of Buccinidae; Babyloniidae GORYACHEV, 1987, as a family of Buccinoidea) to encompass this group.

Over the past year, we were able to examine living and preserved specimens of several species of *Babylonia*. Dissections supplemented with histological studies revealed that the anatomical organization of all species of *Babylonia* available to us differs significantly from that of all known buccinoideans, and is incompatible with the inclusion of *Babylonia* within the Buccinoidea. In this paper, we document the anatomical features of six of the 13 Recent species, and present the results of cladistic analyses based on this morphological data in order to discern the phylogenetic relationships of *Babylonia*. These findings are corroborated by phylogenetic analyses of partial sequences of the cytochrome c oxidase I gene of *Babylonia japonica* and representative neogastropod taxa.

## MATERIALS AND METHODS

Specimens of *Babylonia areolata* and *B. spirata* were collected and dissected living. Shells of living *Babylonia japonica* were cracked in a vise and the animals immersed and shipped in 85% ethanol. Samples of the remaining species were received in varying states of preservation.

Ciliary currents in the stomach were traced by applying carmine particles finely dispersed in seawater while dissecting living specimens. When warranted, tissues were embedded in paraffin, sectioned at 10 µm and stained using Masson Triple Stain. Protoconch, shell ultrastructure and radulae were coated with carbon and gold and examined using a Leica Stereoscan 440 Scanning Electron Microscope.

Taxa, characters, and the data matrix used for phylogenetic analyses of the relationships of *Babylonia* based on morphological characters are itemized in Table 1, which also references the sources of data for selected neogastropod taxa used in the analysis. *Splendrillia chathamensis* Sysoev & Kantor, 1989, a primitive member of the Conoidea (TAYLOR, KANTOR & SYSOEV, 1993), the sister taxon or Rachiglossa (TAYLOR & MORRIS, 1988; KANTOR, 1996), was selected to serve as the outgroup for this analysis. Representative taxa from major lineages within Buccinoidea as well as other rachiglossan groups were selected based on availability of published data.

The six species of *Babylonia* that we have studied have identical character state distributions except for the presence or absence of a discernible rectal gland. The data matrix includes *Babylonia areolata* as a representative of species that have a rectal gland (*B. areolata*, *B. japonica*), and *Babylonia spirata* as a representative of species that lack a rectal gland (*B. spirata*, *B. papillaris*, *B. lutosa*). We were not able to determine if *B. zeylanica* has a rectal gland.

DNA was extracted from an ethanol preserved specimen of *Babylonia japonica*. Protocols for DNA extraction, PCR amplification, DNA sequencing, are identical to those reported by HARASEWYCH ET AL. (1997a). Primers for PCR amplification and sequencing of the cytochrome c oxidase I gene fragment are from

FOLMER ET AL. (1994). PCR product was purified using a Wizard PCR Purification Kit (Promega) and sequenced on an Applied Biosystems 377 Fluorescent Sequencer using Prism Sequencing Kits according to the manufacturer's protocols. The partial CO I sequence of *Babylonia japonica* and four buccinoidean taxa were aligned against previously published neogastropod CO I sequences from taxa selected to represent as closely as practical the higher taxa contained in the morphological data set. Table 2 lists the taxa used in this study, their source, voucher specimen information, and GenBank sequence accession numbers. The sequences were aligned using Clustal W (THOMPSON ET AL., 1994) with minor manual adjustments.

Maximum parsimony analyses of the morphological and molecular data were performed using PAUP 4.02 (SWOFFORD, 1998).

## Abbreviations for the museums:

NM – Natal Museum, Pitermaritzburg, South Africa;  
USNM – National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.  
ZMMU – Zoological Museum of Moscow State University, Moscow, Russia.

## RESULTS

### Anatomical Data

Family: BABYLONIIDAE Kuroda, Habe & Oyama, 1971

Synonymy – Eburninae Swainson, 1840:305.

Babyloniinae Kuroda, Habe & Oyama, 1971:250.

Babyloniidae Goryachev, 1987: 35.

*Remarks:* As noted in the introduction, several suprageneric taxa have been proposed for *Babylonia*. The oldest name is Eburninae, which was proposed by SWAINSON (1840) as a subfamily of Turbinellidae. Swainson's generic concept of *Eburna* was identical to the current concept of *Babylonia*, as he included as an example two species, *E. spirata* and *E. pacifica* [= *B. lutosa* (Lamarck, 1822)]. Nevertheless, the name is invalid, since it is based on the genus *Eburna* Lamarck, 1801, which is a valid genus of Olividae.

More recently, KURODA, HABE AND OYAMA (1971) established the subfamily Babyloniinae within Buccinidae. As their diagnosis was provided in Japanese only, we include the English translation here (translated by Paul Callomon): "Shells of medium size, strong and robust; oviform to oval. Spire conical, whorls mildly convex, sutures shallow or forming a groove. Shell surface smooth, with pattern of spots, covered with thick periostracum. Body whorl large, fasciole prominent, umbilicus open or enclosed by extension of apertural margin. Aperture oviform, outer lip curved, inner margin smooth; siphonal canal short, broad and open". No anatomical characters were included in the diagnosis.

GORYACHEV (1987), apparently unaware of KURODA, HABE AND OYAMA's (1971) taxon, proposed the family Babyloniidae within Buccinoidea. As Goryachev's taxon was proposed without diagnosis and description, it should be considered invalid (ICZN Article 13.2). The oldest available name is that of KURODA, HABE AND OYAMA (1971), who should be considered the authors of the family Babyloniidae. This family includes a single genus, *Babylonia* Schlüter, 1838.





### Genus: *Babylonia* Schlüter, 1838

Synonymy - *Eburna* Lamarck, 1822:281 (not Lamarck, 1801).

*Babylonia* Schlüter, 1838:18. [type species, by monotypy, *Buccinum spiratum* Linnaeus, 1758]. *Latrunculus* Gray, 1847: 139. [type species, by subsequent designation (ALTENA & GITTENBERGER, 1981:10), *Babylonia spirata* (Linnaeus, 1758)]. *Peridipsaccus* Rovereto, 1900: 168. [type species, by subsequent designation (ALTENA & GITTENBERGER, 1981:10), *Babylonia spirata valentiana* (Swainson, 1822)].

*Zemiropsis* Thiele, 1929:332. [type species, by monotypy, *Eburna papillaris* Sowerby, 1825].

**Remarks:** ROVERETO (1900) considered *Latrunculus* Gray, 1847 to be the valid generic name for *Babylonia*, and placed *Eburna* Lamarck, 1822 (non 1801) and *Babylonia* Schlüter, 1838, which he considered to be a *nomen nudus* (sic!), in its synonymy. He also introduced the section (=subgenus) *Peridipsaccus* [type species, "*L. mollianus* Chemnitz" = *Babylonia spirata valentiana* (Swainson, 1822)] for the non-umbilicate species, and included *Eburna papillaris* Sowerby, 1825. THIELE (1929) later proposed the monotypic genus *Zemiropsis* [type species, *Eburna papillaris* Sowerby, 1825] and placed it in the subfamily Pseudolivinae of the family Olividae, noting that "the systematic position of this species, which was previously placed in *Babylonia*, is uncertain without knowledge of the animal" [THIELE, 1992:505]. ALTENA AND GITTENBERGER (1981) distinguished *Zemiropsis* from *Babylonia* on the basis of conchological differences as well as on the presence of a pronounced medial pedal tentacle in *Zemiropsis*, and its absence in *Babylonia*.

All species of *Babylonia* that we were able to examine had a medial pedal tentacle. While this tentacle tends to be strongly contracted and weakly discernible in preserved material, it is prominent in living specimens of *Babylonia areolata*, *B. spirata* and *B. zeylanica*. As *B. papillaris* does not differ anatomically from other species of *Babylonia*, we see little justification for retaining the name *Zemiropsis*, which becomes a synonym of *Peridipsaccus* and *Babylonia*.

### *Babylonia (Babylonia) areolata* (Link, 1807)

Figures 1A, 2A-H, 3A-D, 4A-D, 5A-D

**Material examined:** ZMMU Lc-25174 (voucher material — sections and radular preparations), Nha Trang, Central Vietnam, coll. Yu. Kantor, November 1999. 3 ♀ specimens.

**External anatomy:** (Fig. 2A). Soft tissues comprise approximately  $3\frac{1}{2}$  whorls. Mantle cavity spans  $\sim \frac{1}{3}$  whorl. Mantle edge thick, does not cover head. Columellar muscle short, broad, spanning  $\sim \frac{1}{2}$  whorl. Nephridium (Fig. 2A, nep) narrow, covering  $\sim \frac{1}{4}$  whorl. Foot moderately large, elongate, oval (L/W  $\approx 1.75$ ), terminating posteriorly in small pedal tentacle (Fig. 2A, ped.t). Base color of preserved specimen yellowish, with dorsal surfaces of head, tentacles, siphon, posterior part of foot mottled with dark grayish black. Head with conical, tapering tentacles with black eyes at their bases.

Siphon short, muscular. Operculum leaf-shaped, brownish, with terminal nucleus.

**Mantle cavity:** (Fig. 2B). Mantle thick, opaque, with smooth, thickened edge that is outwardly reflected in preserved specimens. Mantle cavity slightly longer than wide. Siphon (Figs. 2A-B, s) short, muscular, thick-walled, extending substantially beyond mantle edge. Osphradium (Figs. 2A-B, os) small, bipectinate, slightly asymmetrical (ventral lamellae slightly larger than dorsal lamellae), with narrow axis, spanning  $\sim 0.4$  mantle cavity length,  $< \frac{1}{2}$  of ctenidium length. Ctenidium (Figs. 2A-B, ct) large, narrow, spanning  $> \frac{3}{4}$  mantle cavity length, more than twice as wide as osphradium. Ctenidial lamellae high, subtriangular posteriorly, become gradually lower anteriorly, with an overhanging extension along their dorsal crests. Hypobranchial gland (Fig. 2B, hg) of three large, thickened, oblique folds, covered by layer of mucus. Rectum (Fig. 2B, re) broad, thick-walled along its entire length, embedded in the capsule gland (Fig. 2, cg), free at terminal end. Rectal gland, short, narrow, tubular, barely visible through mantle wall near anterior margin of rectum. Gland lined with epithelium of low cells with few melanin granules (Fig. 4A-C, rg). Gland opens into mantle cavity by narrow duct posterior to anus. Anal opening (Fig. 2B, a) laterally compressed slit. Capsule gland broad, laterally compressed. Bursa copulatrix large and swollen.

**Alimentary system:** (Figs. 2C-H, 3A-D, 5A-D). Mouth opening (Fig. 2G) in form of vertical slit, unlike mouth of Buccinidae, which is triangular. Retracted proboscis 13 mm long, extended proboscis 26 mm long, with proboscis sheath and rhynchodeum protracted to form proboscis wall. Proboscis wall  $\sim 1.2$  mm thick at its distal most margin, becoming abruptly thinner ( $\sim 0.4$  mm) posterior to buccal cavity, gradually decreasing in thickness, reaching  $\sim 0.2$  mm in thickness at the posteriormost limit of the extended proboscis. Proboscis retractor muscles (Figs. 2C-D, prr) thin, numerous, equal in size, attached to inner proboscis wall in a ring at about  $\frac{1}{3}$  the distance from the proximal to the distal end.

Oesophagus (Fig. 2H, oe) narrow, flattened dorso-ventrally, constricts before passing through nerve ring (Fig. 2D-E, ao), expands posterior to nerve ring (Figs. 2C-E, poe). Epithelium in this expanded oesophagus yellow-orange, producing large amount of orange mucus. Folds on dorsal wall of oesophagus enlarged, seemingly glandular. Posterior region of oesophagus narrow, light yellow, with dorsal folds less prominent, of the same thickness as on the other walls of the oesophagus. The valve of Leiblein and gland of Leiblein absent. Expanded region of oesophagus similar to the *glande framboisée* of Muricidae (e.g. FRETTER & GRAHAM, 1994, fig. 116 — *Nucella lapillus*), but less pronounced.

Salivary glands (Figs. 2C-D, F, sg) very small, fused, with indistinct border, cover most of dorsal surface of nerve ring. Salivary ducts run loosely along both sides of anterior oesophagus, entering into its wall just dorsal to opening of radular diverticulum (Fig. 2H, sd). Accessory salivary gland, single, narrow, tubu-





lar, slightly shorter than retracted proboscis. Duct of accessory salivary gland runs medially under esophagus, entering buccal cavity anterior to radular diverticulum. Salivary glands, nerve ring, posterior esophagus enveloped in dense connective tissue. Buccal mass longer than retracted proboscis, extending beyond its posterior margin. Radular diverticulum (Fig. 2H, rd) very long, equal in length to retracted proboscis. Odontophore equal in length to buccal mass, composed of paired subradular cartilages fused anteriorly. Radula triserial, 9.1 mm long, 1.18 mm wide

(0.031 SL), composed of 40 rows of teeth, of which 3 are nascent. Rachidian teeth with 5 cusps. Three cusps large, closely spaced, equal in length, radiating from midpoint of tooth, one shorter, broader, triangular cusp at each lateral end of tooth. Rachidian teeth attached to radular membrane by very short base, with central cusp buttressed posteriorly (Fig. 5D). Central cusp with deep indentation on its anterior dorsal surface, accommodating central cusp tip of anteriorly adjacent tooth (Fig. 5C-D). Lateral teeth bicuspid, with outer cusp >2 times longer than inner cusp.

Table 1. Data matrix and descriptions of morphological characters and character states used in cladistic analyses. Missing characters are indicated by "?".

Taxa	Characters				Sources of anatomical data:
	1	2	2		
	0	0	4		
<i>Splendrillia chatbamensis</i>	0000200021	013020000?	2011		SYSOEV & KANTOR, 1989
<i>Babylonia areolata</i>	1111120110	1130001101	2110		Herein
<i>Babylonia spirata</i>	1111120110	1130001101	2210		Herein
<i>Leucozonia nassa</i>	0101220121	0000200001	0211		MARCUS & MARCUS, 1962a + unpublished observations
<i>Melongena melongena</i>	0101220111	0010200001	2212		Unpublished observations
<i>Columbella mercatoria</i>	0101220132	0001200011	0210		MARCUS & MARCUS, 1962b
<i>Ilyanassa obsoleta</i>	1101220121	0010200211	121?		BROWN, 1969
<i>Buccinum undatum</i>	0101220121	0000210200	0212		DAKIN, 1912 + unpublished observations
<i>Chlaniidota densesculpta</i>	0101220121	0001200001	0212		HARASEWYCH & KANTOR, 1999
<i>Neptunea antiqua</i>	0101220121	0010200200	0212		GORYACHEV & KANTOR, 1983 + SMITH, 1967
<i>Latitromita cryptodon</i>	0000110100	00100001??	0001		BOUCHET & KANTOR, 2000
<i>Oliva oliva</i>	0101111100	0010000200	2010		KANTOR & TURSCH, 1998
<i>Vasum muricatum</i>	0101210111	0000200101	0000		MEDISKAYA ET AL. 1996
<i>Vexillum luculentum</i>	0001010101	0000100101	1010		PONDER, 1972
<i>Alciithoe arabica</i>	0101011240	0020000001	2010		PONDER, 1970
<i>Xymenopsis muriciformis</i>	0101010101	0000000201	1011		PASTORINO & HARASEWYCH, 2000

#### Morphological Characters and Character States:

1. Posterior pedal tentacle: (0) Absent; (1) Present.
2. Buccal mass: (0) at base of proboscis; (1) at distal end of proboscis.
3. Radular diverticulum: (0) < 1/3 of retracted proboscis length; (1) > 1/3 of retracted proboscis length.
4. Radular retractor muscles: (0) passing through nerve ring, attached to the columellar muscle; (1) not passing through the nerve ring, attached to the proboscis walls.
5. Accessory salivary glands: (0) paired; (2) single, not embedded in primary salivary gland; (3) absent.
6. Ducts of the primary salivary glands: (0) free, entering the walls of the buccal cavity; (1) entering the walls of oesophagus just anterior to valve of Leiblein, embedded in the walls of the oesophagus along; (2) free along most of the length, entering oesophagus walls posterior to buccal cavity.
7. Primary salivary glands: (0) Acinous; (1) Ramified tubular.
8. Number of radular teeth in a transverse row: (0) 5; (1) 3; (2) 1.
9. Lateral teeth: (0) Unicuspid; (1) Bicuspid; (2) 3 or more cusps; (3) Multicuspid with narrow base; (4) absent.
10. Cusps of the rachidian teeth: (0) Emanating from the anterior edge of the basal plate; (1) Emanating from mid-portion or posterior edge of the basal plate; (2) Absent.
11. Cusp at lateral edge of rachidian: (0) Absent; (1) Present.
12. Valve of Leiblein: (0) Present; (1) Absent.
13. Gland of Leiblein: (0) Large; (1) Reduced; (2) Tubular, convoluted; (3) Absent.
14. Posterior esophagus: (0) Not glandular; (1) Glandular.
15. Dorsal glandular folds of the oesophagus: (0) Present; (1) Present, stripped from the oesophagus; (2) Absent.
16. Oesophageal caecum: (0) Absent; (1) Present.
17. Stomach: (0) Not covered by nephridium; (1) Covered by nephridium.
18. Posterior mixing area (caecum): (0) Absent; (1) Present, small; (2) Present, large.
19. Gastric shield: (0) Absent; (1) Present.
20. Posterior sorting area in stomach: (0) Present; (1) Absent.
21. Ducts of the digestive system: (0) Paired, broadly separated; (1) Paired, closely spaced; (2) Fused into single duct prior to entering stomach.
22. Rectal gland: (0) Present, opening into rectum; (1) Present, opening into mantle cavity; (2) Absent.
23. Seminal duct: (0) Open; (1) Closed.
24. Penis with terminal papilla: (0) Absent; (1) Present, simple, tubular; (2) Present, surrounded by circular fold at its base.





Stomach very small (Fig. 3), simple, U-shaped, with very short caecum (= posterior mixing area) (Fig. 3A,C, pma), mostly or completely covered by nephridium (Fig. 3D). Transition of posterior oesophagus into stomach marked by changes in epithelium color, presence of the powerful sphincter (Fig. 3C, sph). Walls of caecum much thicker, more muscular than remaining regions of stomach, dark pink in living animals, suggesting that caecum is capable of contracting and mechanically processing food. Epithelial folds of caecum mostly transverse. Single, thick digestive gland duct (Fig. 3A, ddg) opens into stomach in deep pouch (Fig. 3C, dp), giving rise to pronounced, raised fold (Fig. 3C, lf) along floor of stomach that becomes progressively thicker in posterior part of stomach, terminating abruptly at transition to intestine. Several smaller longitudinal folds are present along stomach floor, but no separation into dorsal and ventral channels is evident in stomach. Examination of ciliary currents in living animals revealed strongest currents to run along longitudinal fold (Fig. 3C, arrows; arrow size corresponds to current strength), with slight, turbulent ciliary currents in area of duct pouch, and slight flow of particles out of digestive gland duct into stomach. Duct of digestive gland bifurcates at some distance from stomach, each branch leading to lobe of digestive gland. Lobes of digestive gland fused, without clear demarcation.

### *Babylonia papillaris* (Sowerby, 1825)

Figures 1B, 5E-H, 6A-I

**Material examined:** NM V7705. Jeffrey's Bay, Cape of Good Hope, South Africa, dredged in 70 m. col. W. Immelman, January 2000, 1 shell + 1 animal without shell, now in ZMMU Lc-25250.

**External anatomy:** (Fig. 6A). Soft tissues comprise approximately 3 whorls. Mantle cavity spans ~ 1/2 whorl. Mantle edge thin, does not cover head. Nephridium wide, covering ~ 1/3 whorl (Fig. 6B, nep). Foot moderately large, elongate, oval ( $L/W \approx 1.5$ ), terminating posteriorly in distinct pedal tentacle (Fig. 6A, ped.t). Base color of preserved specimen light cream, with dorsal-lateral surfaces of foot, tentacles, siphon mottled with pale red-orange. Head with long conical, tapering tentacles (Fig. 6A, cep.t) with large black eyes at their bases. Operculum leaf-shaped, yellow, transparent, with terminal nucleus.

**Mantle cavity:** Mantle thin, translucent. Mantle edge slightly thickened, smooth. Length of mantle cavity equals width. Siphon long, muscular, thick-walled, extending substantially beyond mantle edge, slightly pigmented dorsally with pale orange spots. Osphradium small bipectinate, slightly asymmet-

Table 2. Taxa, collection localities, voucher material and GenBank accession numbers for Cytochrome *c* oxidase I sequences used in this study.

#### CONOIDEA

<i>Conus jaspideus</i> Gabb, 1868	ex HARASEWYCH ET AL. 1997b	U86337
<i>Hastula cinerea</i> (Born, 1778)	ex HARASEWYCH ET AL. 1997b	U86336

#### BUCCINOIDEA

<i>Fasciolaria tulipa</i> (Linné, 1785)	Berry Islands, Bahamas USNM 894804	AF373884
<i>Pleuroploca gigantea</i> (Kiener, 1840)	Ft. Pierce, Florida USNM 894805	AF373885
<i>Buccinum oedematum</i> Dall, 1907	ex HARASEWYCH ET AL. 1997b	U86327
<i>Neptunea antiqua</i> (Linné, 1758)	Millport, Scotland USNM 894806	AF373886
<i>Neptunea polycostata</i> Scarlatto, 1952	ex HARASEWYCH ET AL. 1997b	U86326
<i>Busyconotus canaliculatus</i> (Linné, 1758)	ex HARASEWYCH ET AL. 1997b	U86325
<i>Busycon carica</i> (Gmelin, 1791)	ex HARASEWYCH ET AL. 1997b	U86323
<i>Busycon sinistrum</i> Hollister, 1958	ex HARASEWYCH ET AL. 1997b	U86324
<i>Busycon perversum</i> (Linné, 1758)	Celestun, Mexico USNM 894807	AF373887

#### "VOLUTOIDEA"

<i>Turbinella angulata</i> (Lightfoot, 1786)	ex HARASEWYCH ET AL. 1997b	U86332
<i>Oliva sayana</i> Ravenel, 1834	ex HARASEWYCH ET AL. 1997b	U86333
<i>Babylonia japonica</i> (Reeve, 1842)	Osaka, Japan USNM 894808	AF373888
<i>Arctomelon stearnsii</i> (Dall, 1872)	ex HARASEWYCH ET AL. 1997b	U86334
<i>Scaphella junonia</i> (Lamarck, 1804)	ex HARASEWYCH ET AL. 1997b	U86335

#### MURICOIDEA

<i>Coralliophila abbreviata</i> (Lamarck, 1816)	ex HARASEWYCH ET AL. 1997b	U86331
<i>Thais haemastoma canaliculata</i> (Gray, 1839)	ex HARASEWYCH ET AL. 1997b	U86330
<i>Phyllonotus pomum</i> (Gmelin, 1791)	ex HARASEWYCH ET AL. 1997b	U86328
<i>Murex troscheli</i> Lischke, 1868	ex HARASEWYCH ET AL. 1997b	U86329



rical (dorsal lamellae slightly wider than ventral lamellae), with very narrow axis, spanning  $\sim 0.45$  mantle cavity length, slightly  $< \frac{1}{2}$  ctenidium length. Ctenidium (Fig. 6B, ct) large, very broad, spanning  $> 0.8$  mantle cavity length, three times as wide as osphradium. Ctenidial lamellae low, subtriangular, similar in shape throughout ctenidium length. Hypobranchial gland weakly differentiated, lacking distinct folds. Rectum broad, thin-walled, transparent, free at its terminal end. Anal opening round, with slightly thickened reflected edge. Capsule gland broad, rounded in transverse section (Fig. 6B, cg). Bursa copulatrix large, swollen. Ingesting gland (Fig. 6B, ig) at posterior portion of capsule gland very large, dark. Rectal gland absent.

*Alimentary system:* (Figs. 5C-I). Mouth opening in form of triangular slit. Partially extended proboscis 16 mm long, with slightly folded walls. Proboscis wall  $\sim 1.6$  mm thick at distal-most margin (Fig. 6G), becoming thinner ( $\sim 0.25$  mm) posterior to buccal cavity, sharply decreasing in thickness in middle part and gradually thickening in the posteriormost limit, reaching  $\sim 0.4$  mm. Proboscis retractors (Figs. 5C-E, prr) numerous, arranged in two bundles, attached to mid-lateral sides of the rhynchodaeum (Figs. 5D-E, prr). Anterior oesophagus narrow, flattened dorso-ventrally, constricted before passing through nerve ring, sharply expanded posterior to ring. Epithelium in expanded region slightly darker than in rest of oesophagus.

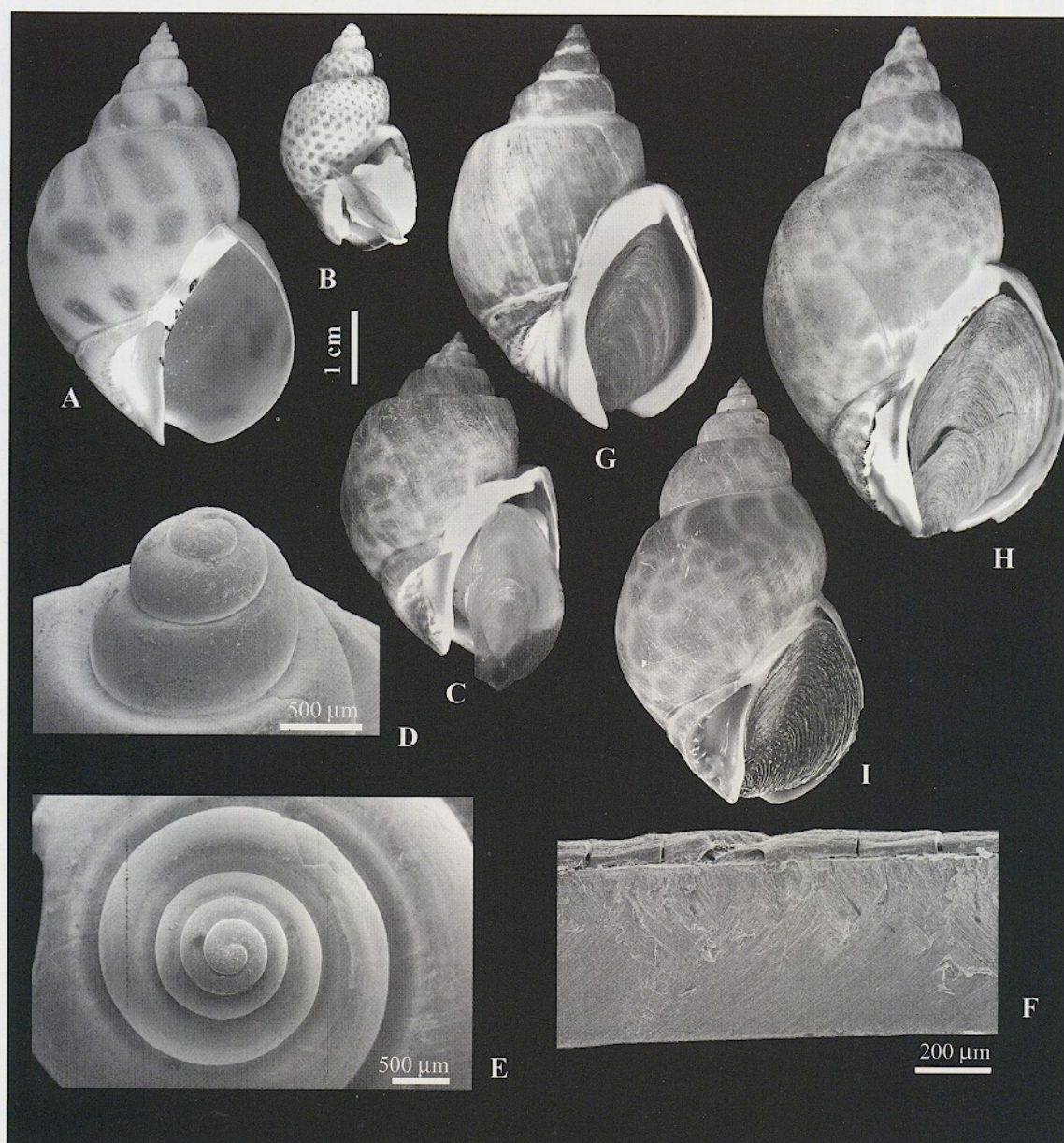


Figure 1. Shells of the species of *Babylonia* examined in this study. A — *Babylonia areolata* (Link, 1807), Hua Him, Thailand, USNM 679439. B — *B. papillaris* (Sowerby, 1825), South Africa, Cape of Good Hope, Jeffrey's Bay, NM V7705 (now in ZMMU). C — *B. spirata* (Linnaeus, 1758), South India, off Tuticorin. D-E — lateral and apical view of protoconch of juvenile of *B. spirata*, USNM 443286, Back Bay, Bombay. F — shell ultrastructure of *B. spirata* (middle portion of outer lip), South India, off Rameswaram. G — *B. lutosa* (Lamarck, 1822), Borneo, USNM 31342. H — *B. japonica* (Reeve, 1842), Hashimoto, Japan, USNM 665016. I — *B. zeylanica* (Bruguière, 1789) South India, off Tuticorin, ZMMU Lc-25173.



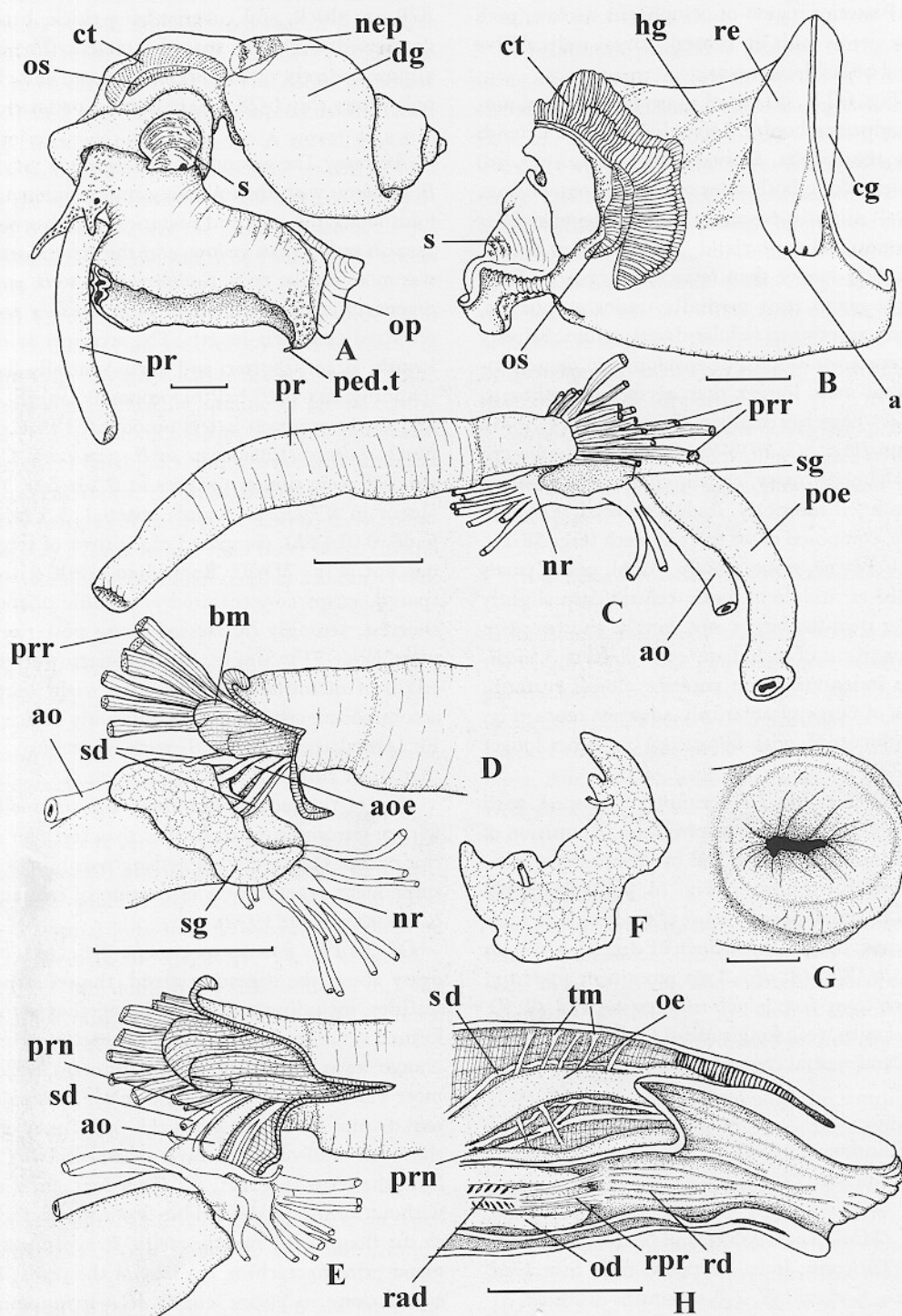


Figure 2. Anatomy of *Babylonia areolata* (Link, 1807). A — Lateral view of animal removed from the shell. B — Mantle cavity organs of ♀ specimen. C — Left lateral view of anterior alimentary system. D — Right lateral view of the posterior part of the proboscis (oesophagus turned clockwise to show salivary gland). E — Right lateral view of the posterior part of the proboscis (salivary gland removed to show the circumoesophageal nerve ring, oesophagus turned clockwise, proboscis opened laterally). F — Dorsal view of the salivary gland. G — Anterior view of the proboscis tip. H — Anterior part of the proboscis opened laterally from the right side. Scale bars = 5 mm for A-F, H; 1 mm for G.

Abbreviations: ao, anterior aorta; bm, buccal mass; cg, capsule gland; ct, ctenidium; dg, digestive gland; hg, hypobranchial gland; nep, nephridium; nr, circumoesophageal nerve ring; od, odontophore; oe, oesophagus; op, operculum; os, osphradium; ped.t, pedal tentacle; poe, posterior oesophagus; pr, proboscis; prr, proboscis retractor muscles; rad, radula; rd, radular diverticulum; re, rectum; rpr, radular protractors; s, siphon; sd, salivary duct; sg, salivary gland; tm, tensor muscles.





Folds on dorsal wall of oesophagus enlarged, seemingly glandular (Fig. 6H, dgf). Posterior region of oesophagus narrow, with dorsal folds of same size as folds on ventral, lateral walls. Valve of Leiblein and gland of Leiblein absent.

Salivary glands (Fig. 6C-F, sg) dorsal to nerve ring, medium-sized, fused, with indistinct border. Left salivary gland extends further posteriorly than right. Salivary ducts (Fig. 6G, sd) coiled, running loosely along both sides of anterior oesophagus, entering into its wall slightly posterior to opening of radular diverticulum. Accessory salivary gland (Fig. 6G, asg) single, narrow, tubular, slightly longer than retracted proboscis. Duct of accessory salivary gland runs medially under esophagus, entering buccal cavity anterior to radular diverticulum. Salivary glands, nerve ring, posterior esophagus enveloped in dense connective tissue. Buccal mass longer than retracted proboscis, extending beyond its posterior margin (Figs. 6C-E, G, bm). Radular diverticulum (Fig. 6G, rd)  $\sim 1/2$  of retracted proboscis. Odontophore  $\sim 2/3$  of buccal mass length, composed of paired subradular cartilages fused anteriorly. Radula triserial, 9.45 mm long, 1.27 mm wide, composed of 46 rows of teeth (Fig. 5E-H). Rachidian teeth with 3 large, stout, closely spaced, nearly parallel cusps concentrated at middle of tooth, central cusp slightly longer, much broader than flanking cusps. Single, shorter cusps present near lateral margins of rachidian tooth. Each of 3 median cusps with deep indentations on anterior, dorsal surfaces, accommodating tips of cusps of anteriorly adjacent tooth (Fig. 5G-F). Lateral teeth bicuspid, with outer cusp  $> 2$  times longer than inner cusp.

Stomach very small (Fig. 6B, I st), simple, U-shaped, with very short caecum, mostly covered by nephridium. Transition of posterior oesophagus into stomach marked by changes in epithelium, presence of powerful sphincter (Fig. 6I, sph). Epithelial folds of caecum (Fig. 6I, pma) positioned at obtuse angle to folds of posterior oesophagus. Single thick duct of digestive system opens into deep pouch (Fig. 6I, dp). Two prominent folds run along floor of stomach from deep pouch to intestine (Fig. 6I, lf). Rest of stomach lined with weak longitudinal folds. Stomach not separated into dorsal and ventral channels.

### *Babylonia spirata* (Linnaeus, 1758)

Figures 1C-F, 4D, 7D-F, 8A-B

**Material examined:** ZMMU Lc-24965, Tamil Nadu, in vicinities of Rameswaram and Tuticorin, India. Obtained from fishermen. October 2000, coll. Yu. Kantor. 1 ♀ 2 ♂ specimens dissected.

**Protoconch:** The protoconch of *B. spirata* (Fig. 1 D,E) is smooth, paucispiral and conical, with an initial diameter of about 170  $\mu\text{m}$ . The transition from protoconch to teleoconch could not be unambiguously distinguished in any of the ten specimens with an uneroded protoconch that we examined. The sutural canal first appears at about  $1\frac{1}{4}$  whorls (diameter of about 670  $\mu\text{m}$ ), suggesting that the larvae may hatch at this size. The color of the protoconch is dark reddish brown, gradually fading to ivory between the second and fourth whorl.

**Shell ultrastructure:** (Fig. 1 F). The shell of *B. spirata* is about 470  $\mu\text{m}$  thick, and covered by a thick, brown, periostracum composed of closely spaced lamellae. The shell is composed almost entirely of comarginal crossed-lamellar crystals, with only a very thin ( $\approx 28 \mu\text{m}$ ) outermost prismatic layer.

**Anatomy:** The anatomy of *B. spirata* is very similar to that of *B. areolata*, with the following minor differences. The glandular folds along the mid and posterior oesophagus of *B. spirata* were grayish rather than yellow, and the general arrangement of folds was more similar to *B. papillaris* than to *B. areolata*. The radular diverticulum is shorter than in *B. areolata* and occupies  $\sim 1/3$  of retracted proboscis length. The accessory salivary gland is yellowish, larger, shorter, and dorso-ventrally flattened (Fig. 4D), spanning less than half of proboscis length. The longitudinal fold in the stomach is less pronounced than in *B. areolata*, but much more distinct than in *B. papillaris*. Ciliary currents in stomach were similar to those in *B. areolata*. The rectal gland is absent in *B. spirata*. Radula triserial, 5.5 mm long, 0.72 mm wide (0.014 SL), composed of 29 rows of teeth, of which 3 are nascent (Fig. 7D-F). Rachidian teeth with 3 long, closely spaced, cusps concentrated at middle of tooth, central cusp shortest, strongly buttressed along posterior margin of basal plate (Fig. 7F). Single, shorter, narrower cusps along outer edges of rachidian. Median cusp with sharp indentation to accommodate central cusp of anteriorly adjacent tooth (Fig. 7E-F). Lateral teeth bicuspid, with outer cusp  $> 2$  times longer than inner cusp.

One of the radulae examined was unusually short, minute, with anteriormost teeth smaller than teeth on central and posterior portions of radula, suggesting possibility of amputation and subsequent regeneration of portion of buccal mass and radula (CARRIKER ET AL. 1972).

Of the two female specimens dissected, one had a fecund ovary above the digestive gland, the other possessed imposex features, including a short penis together with an incompletely formed *vas deferens*. A mature male specimen had a large yellow-orange testis that spanned the posterior surfaces of the uppermost 1.5 whorls of the visceral mass. A seminal duct (Fig. 8A, sem.d) runs anteriorly from the upper part of the testis along the inner wall of the visceral mass, receiving 7-8 coiled ducts from the testis (Fig. 8A, td). This duct enters the mantle cavity without forming a discernible seminal vesicle. After descending to the floor of the mantle cavity, it expands to form a prostate gland prior to reaching the base of the penis. The duct remains closed along its entire length. In a living animal, the penis is long, thin, tapering, flagellum-like, lacking a papilla. When this animal was preserved, the penis (Fig. 8B, p) contracted to become short, stout, and conical.

### *Babylonia lutosa* (Lamarck, 1822)

Figure 1G, 9A-B

**Material examined:** ZMMU Lc-25237, Mirs Bay, Hong Kong, coll. J.D. Taylor.

1 ♂ + 1 ♀ specimen dissected.





Anatomy of *B. lutososa* is, in all respects, very similar to that of *B. areolata*. Alimentary system differed from that of *B. areolata* only in that oesophagus broadened not immediately posterior to nerve ring, but at some distance from it. The dorsal glandular folds in this broadened region of the oesophagus are fused together, forming thick glandular lining. A rectal gland is absent. Gross morphology of the reproductive system as of a fecund female was the same as those of *B. areolata* and *B. papillaris*. Male reproductive system was the same as that of *B. spiralis*, except for the absence of the multiple coiled ducts entering the seminal duct.

Radula triserial, 12 mm long, 1.33 mm wide (0.022 SL) (female with SL ~ 60 mm), composed of 45 rows of teeth, of which 3 are nascent (Fig. 9A-B). Rachidian teeth with 3 long, closely spaced, cusps concentrated at middle of tooth, central cusp slightly shorter than flanking cusps, strongly buttressed along posterior margin of basal plate, indented to accommodate central cusp of adjacent tooth. Additional shorter, narrower, single cusps at outer margins of basal plate. Lateral teeth bicuspid, with outer cusp > 2 times longer than inner cusp. Central cusp broken on 7 consequent rachidian teeth at bending plane of radula.

#### *Babylonia japonica* (Reeve, 1842)

Figure 1D, 7A-C, 8C-D

*Material examined:* USNM 905325, Seafood market, Osaka, Japan. 1 ♂ + 1 ♀ specimen dissected.

Anatomy of *B. japonica* is very similar to that of *B. areolata*. Rectal gland present, small, grayish, opens directly in mantle cavity outside rectum. Male reproductive system characterized by presence of normal long *vesicula seminalis*, situated on the border between testis and digestive gland (Fig. 8C). Radula triserial, 11.7 mm long, 1.84 mm wide (0.027 SL) (female with SL 68.0 mm), composed of 42 rows of teeth (Fig. 7A-C).

Rachidian and lateral teeth similar to those of *B. lutososa*.

#### *Babylonia zeylanica* (Bruguère, 1789)

Figure 1I, 9C-D

*Material examined:* ZMMU Lc-25173, South India, off Tuticorin, from fishermen, 1 ♀ specimen (SL 60.7 mm), radula examined.

The preservation of the single specimen available was poor. Gross external anatomy was identical to that of other *Babylonia*, and is figured by Riedel (2000). We were not able to determine if this species has a rectal gland or accessory salivary gland based on the specimen available to us.

Radula triserial, 10.9 mm long, 1.49 mm wide (0.025 SL), composed of 37 transverse rows of teeth, of which 3 nascent (Fig. 9C-D). Rachidian teeth similar to those of *B. lutososa*, but basal plate slightly narrower, with outermost cusps closer to central group of 3 cusps. Lateral teeth also similar to those of *B. lutososa*, but outer cusps slightly shorter and broader.

### Phylogenetic Analyses Of Morphological Data

A maximum parsimony analysis of the morphological data using the Exhaustive Search Option of PAUP 4.02b (Acctran character optimization) yielded a single most parsimonious tree [L = 62, Consistency index (CI) = 0.613, Retention Index (RI) = 0.671] shown in Figure 10A. When the analysis was repeated using Deltran character optimization, a single tree was produced with identical topology, length and indices, but differing slightly in the character optimization and branch lengths within the non-buccinoidean clade. Only the node uniting the two representative species of *Babylonia* enjoyed significant bootstrap or jackknife support. The remaining nodes uniting rachiglossan neogastropods had Bremer support values of 1 and lacked bootstrap or jackknife support.

Of the 24 anatomical characters (comprising 62 states) used in this study, 15 exhibited some degree of homoplasy, and 2 of the remaining 9 were autapomorphic and therefore parsimony uninformative.

### Phylogenetic Analyses Of Molecular Data

Maximum parsimony analysis [Branch and Bound Search] of the aligned 591 base pair sequences resulted in a single most parsimonious tree [L = 1065, CI = 0.409, RI = 0.383] shown in figure 10B. There was significant bootstrap and jackknife support only for the monophyly of *Busycon*, *Busyconinae*, *Nepitunea*, *Fascioliidae* and *Muricidae*. Of the 591 characters, 224 were parsimony-informative.

### DISCUSSION

The genus *Babylonia* has traditionally been attributed to the family Buccinidae, primarily on the basis of its "bucciniform" shell shape with very short anterior canal, supplemented by the inferences of similarity in external anatomy (see REEVE, 1849) and radular morphology (based on line drawings of radulae produced using light microscopy).

The Buccinoidea, comprising the families Buccinidae, Fascioliidae, Melongenidae, Nassariidae, Columbellidae and Colubrariidae, is generally regarded as a morphologically cohesive, monophyletic group within Neogastropoda (e.g., PONDER, 1974; PONDER & WARÉN, 1988; KANTOR, 1996; HARASEWYCH ET AL., 1997b). Although there is little agreement as to the rank or inter-relationships of its constituent higher taxa (e.g. THIELE, 1929; WENZ, 1938; PONDER & WARÉN, 1988; KANTOR, 1996), buccinoideans share a number of anatomical features, among them: a long proboscis with a terminal buccal mass; a short radular diverticulum with the odontophore protruding into the buccal cavity; a radula with bicuspid to multicuspid lateral teeth and with rachidian teeth composed of a flattened basal plate without cusps or with cusps emanating at an acute angle from its mid- to posterior region; the absence of accessory salivary glands; and the absence of a rectal gland. Most Buccinoidea have a well-developed valve of Leiblein and large gland of Leiblein, although one or both of these structures have been lost



in some taxa [e.g. in the subfamily Volutopsiinae (KANTOR, 1990) and the genus *Melongenina* (PONDER, 1974)]. The buccinoidean mid-esophagus lacks glandular dorsal folds, although it may become secondarily glandular in Colubrariidae (PONDER, 1968). The buccinoidean stomach is extremely variable. A posterior mixing area can be present (sometimes very large and long, as in Nassariidae), or absent. A gastric shield is developed in some Nassariidae, Columbelloidae and Buccinidae, but is absent in most genera. Ducts of digestive gland can be paired and broadly separated, closely spaced, or fused into a single duct prior to entering the stomach.

The gross morphology of the animal, mantle cavity, and radula of species of *Babylonia* have led several authors to infer or accept the affinities of this genus to Buccinidae (KIENER, 1835; ADAMS & REEVE, 1848; EYDOUX & SOULEYET, 1852; SOWERBY, 1902; ALTENA & GITTENBURGER, 1983; RIEDEL, 2000). However, our more detailed examination of the anatomy of the digestive system of *Babylonia* revealed it to differ substantially from

that of all buccinoideans studied to date. All species of *Babylonia* have a single, unpaired accessory salivary gland with typical neogastropod histology (Fig. 4D), consisting of two layers of epithelium (Fig. 4D, oel, iel) separated by a layer of circular muscle fibers (Fig. 4D, cml). Both the valve of Leiblein and the gland of Leiblein are absent in all species of *Babylonia* studied. Posterior to the nerve ring, the oesophagus abruptly expands, its dorsal wall occupied by enlarged, conspicuously glandular folds (Fig. 6H). The salivary glands, nerve ring, and posterior esophagus are enveloped in dense connective tissue, a feature not known in any buccinoidean.

Scanning electron micrographs reveal the radula of *Babylonia* to differ consistently from the radulae of Buccinoidea. While the lateral teeth of *Babylonia* are very similar in shape to those of some Buccinidae and Melongenidae, the rachidian teeth are of fundamentally different design. In *Babylonia*, the bases of the three central cusps emanate from the anterior edge of the basal plate and are strongly buttressed (see Fig. 7F), being similar in this respect to the rachidian teeth of *Oliva*, Muricidae, and some

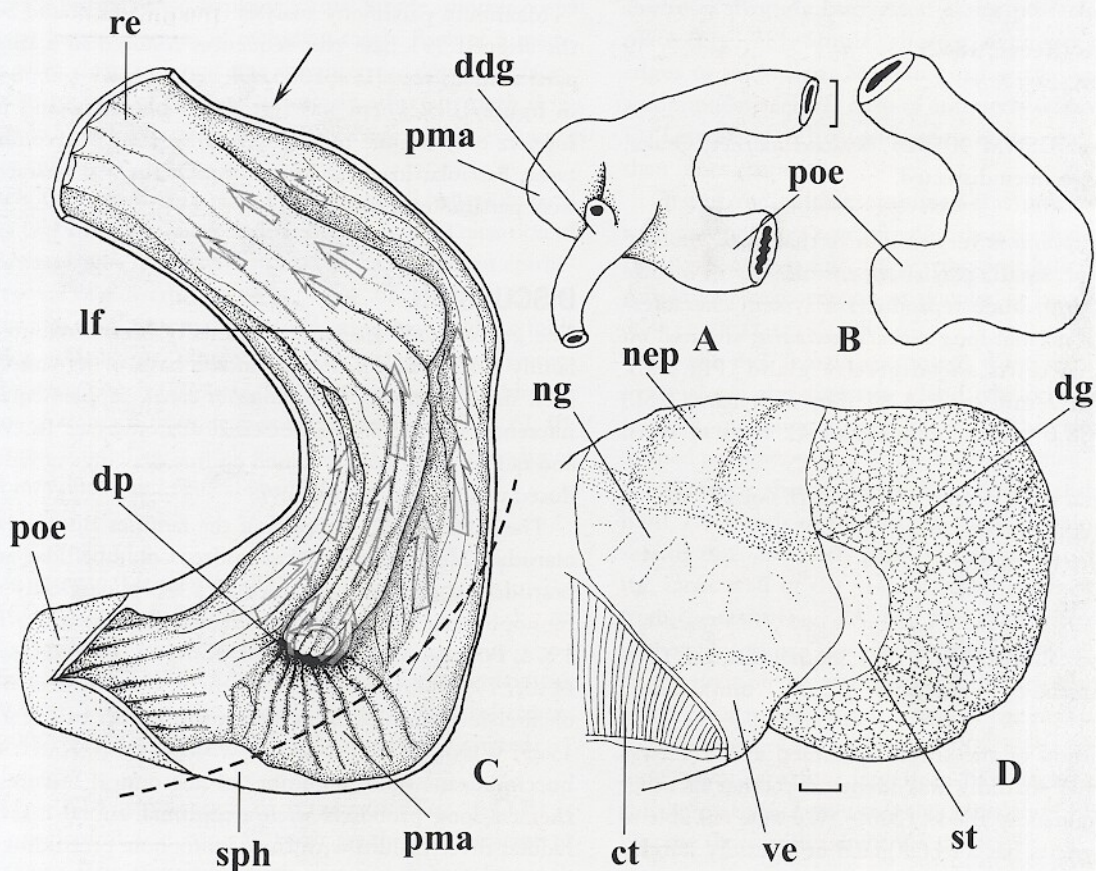


Figure 3. Anatomy of the stomach of *Babylonia areolata* (Link, 1807). A—Dorsal and B—ventral views of the stomach. C—Stomach opened along dorsal midline. Open arrows indicate ciliary currents. The dashed line represents the edge of the nephridium and nephridial gland, while the black arrow demarcates the posterior limit of the mantle cavity. D—View of the visceral mass showing the stomach nearly completely covered by the nephridium. Scale bars = 1 mm.

Abbreviations: ct, ctenidium; ddg, duct of the digestive gland; dg, digestive gland; dp, pouch of the duct to the digestive gland; lf, longitudinal fold of the stomach; nep, nephridium; ng, nephridial gland; pma, posterior mixing area; poe, posterior oesophagus; re, rectum; sph, sphincter between the posterior oesophagus and stomach; st, stomach; ve, ventricle.



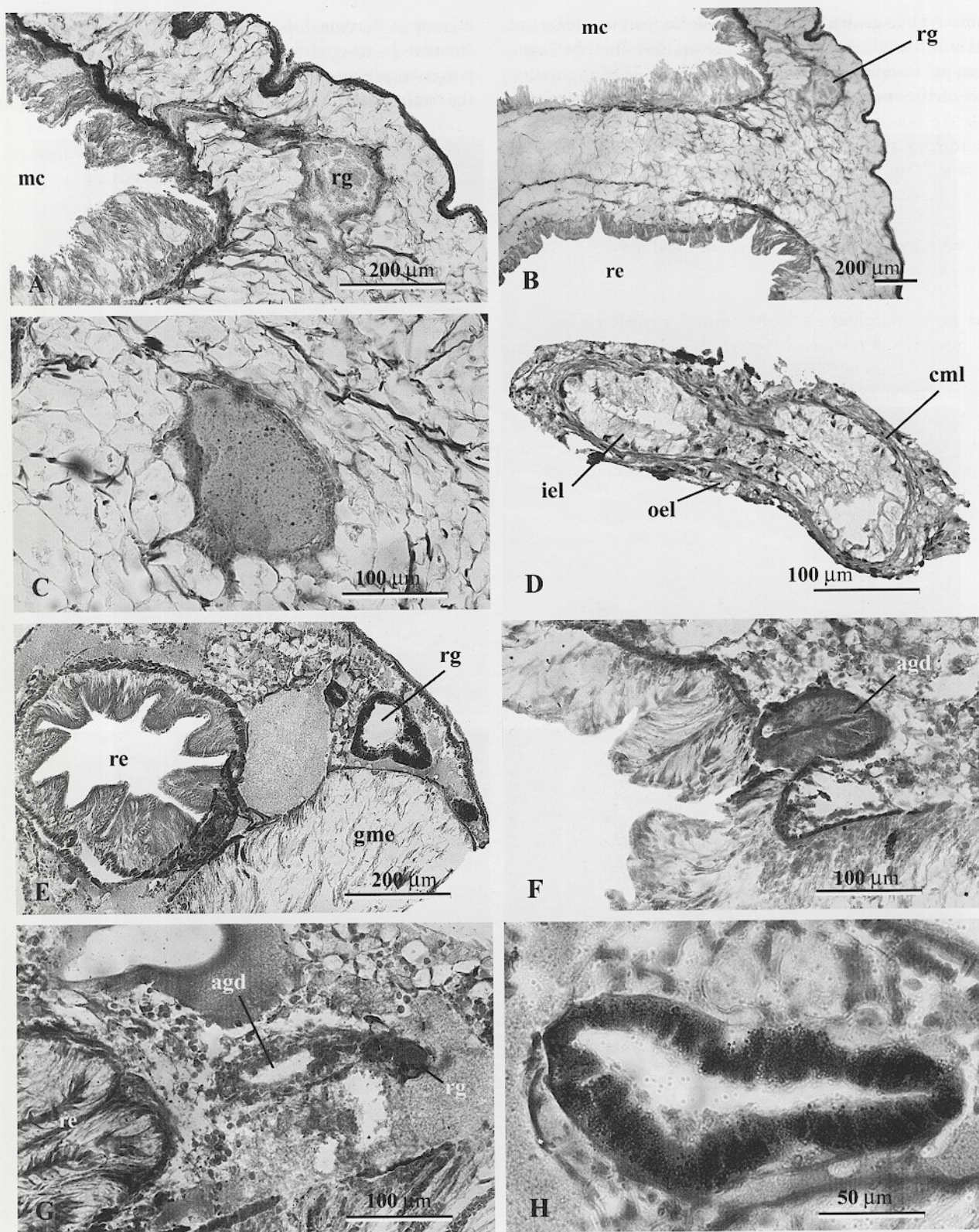


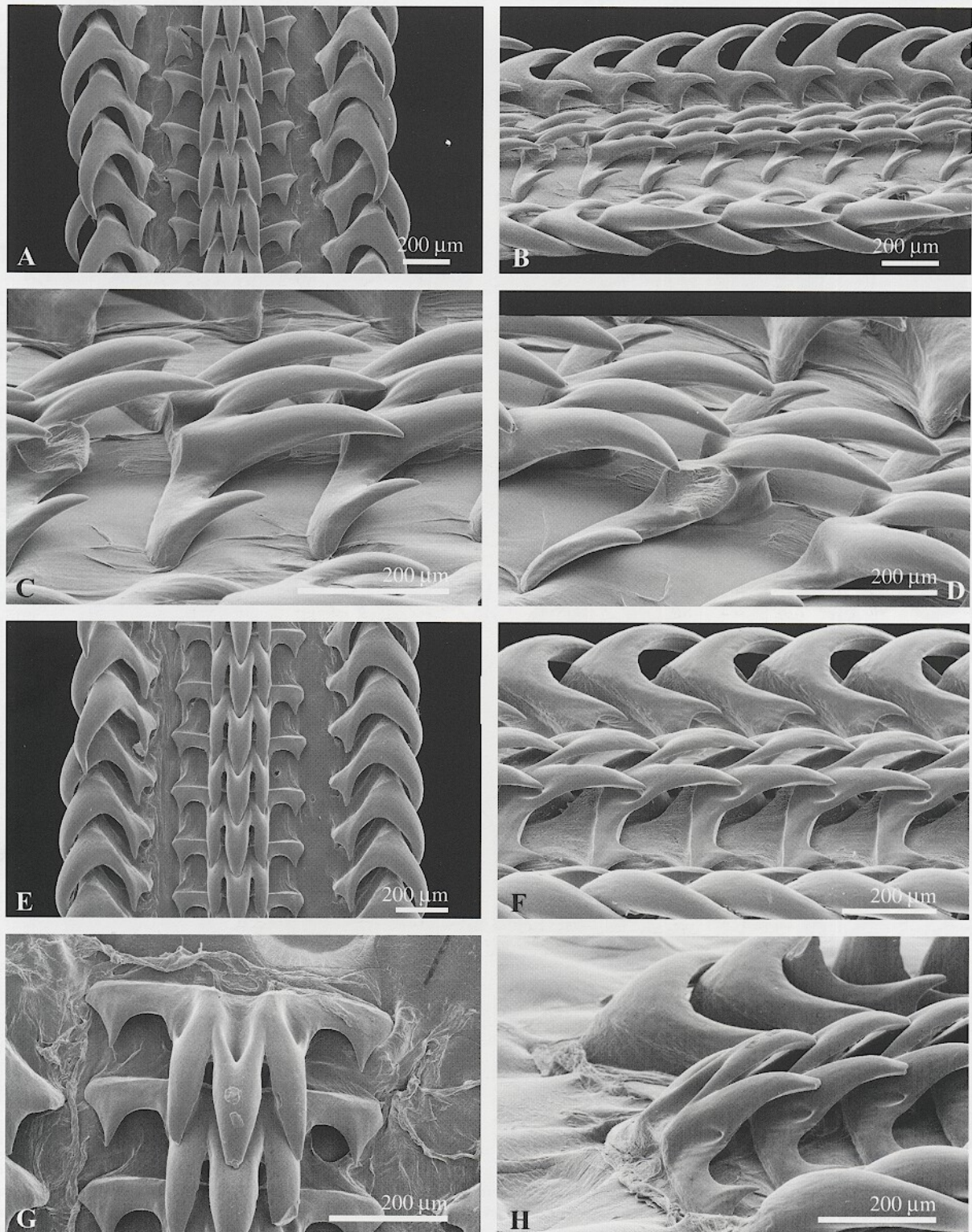
Figure 4. Histology of rectal gland and accessory salivary gland. A — Transverse section through posterior part of mantle of *B. areolata*, showing rectal gland opening into the mantle cavity. B — Same, at lower magnification, showing position of rectum. C — Transverse section through rectal gland of *B. areolata* at midlength. D — Transverse section through accessory salivary gland of *B. spirata*. E-H — Rectal gland of the conoidean *Horpospira maculosa*. E — transverse section through posterior part of mantle to show the rectal gland and rectum. F — Opening of the rectal gland duct into the mantle cavity. G — Transverse section through the rectal gland at the transition of the gland into the duct (explanation in the text). H — transverse section of the rectal gland. Abbreviations: cml, circular muscle layer; gme, glandular mantle epithelium; iel, inner epithelial layer; mc, mantle cavity; oel, outer epithelial layer; re, rectum; rg, rectal gland; rgd, duct of the rectal gland.



Volutidae. The smaller, flatter cusps along the outer edges of the rachidian teeth of *Babylonia* somewhat resemble the "marginal cusps" found in some muricids (see KOOL, 1987).

One of the most prominent characters of *Babylonia* is an

extremely shortened digestive system. The stomach is nearly completely covered by the nephridium and only part of the posterior mixing area is visible beyond the posterior margin of the nephridium. The stomach is greatly simplified and small,



**Figure 5.** Radulae of *Babylonia areolata* (A-D) (SL 38.0 mm) and *Babylonia papillaris* (E-H) (SL unknown). A, E — Dorsal and B-E — left lateral (45°) views of central portion of radular ribbon. C,D — left lateral (45°) views of rachidian to show indentation (C) and buttress of central cusp (D). G,H — dorsal and left lateral views of posteriormost rachidian teeth to show 3 indentations.





with a very short, muscular caecum. The juncture of the posterior oesophagus and stomach is marked by large and powerful sphincter, which is bright red in living specimens. The stomach is not divided into dorsal and ventral channels, and may

have either a strong longitudinal fold (*B. areolata*, *B. spirata*) or smaller longitudinal folds (*B. papillaris*). The intestine is indistinguishable anatomically, and the stomach appears to open directly into the rectum. The ducts of the digestive

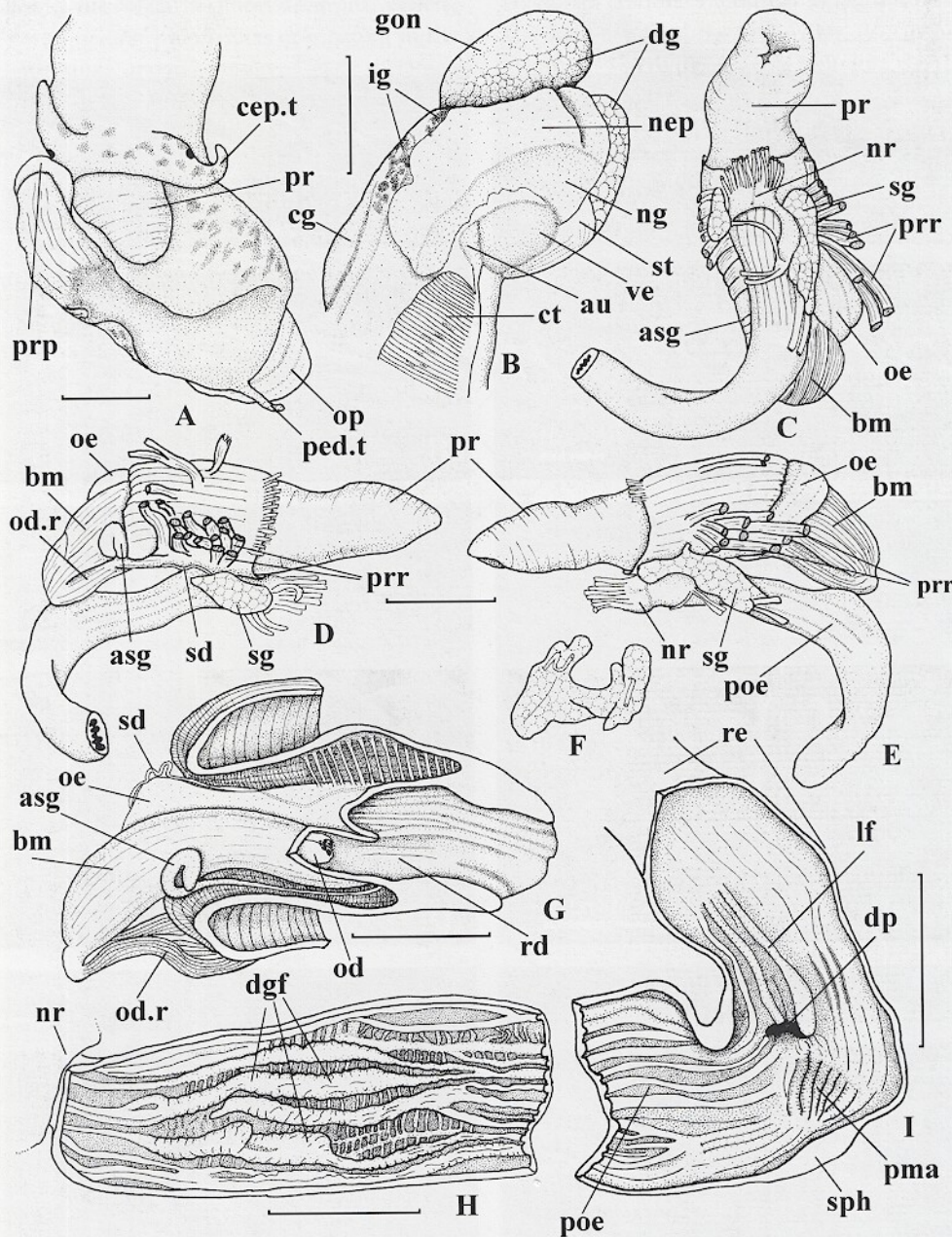


Figure 6. Anatomy of *Babylonia papillaris* (Sowerby, 1825). A — Head-foot of animal removed from the shell. B — View of the visceral mass to show the stomach, nearly completely covered by nephridium. C — Ventral, D — right lateral, and E — left lateral views of anterior alimentary system. F — Dorsal view of the salivary gland. G — Proboscis opened from the right side. H — Mid-posterior oesophagus, opened ventrally to show the dorsal glandular folds. I — Stomach opened along midline of the dorsal wall. Scale bars = 5 mm.

Abbreviations: asg, accessory salivary gland; au, auricle; bm, buccal mass; cep.t, cephalic tentacle; cg, capsule gland; ct, ctenidium; dg, digestive gland; dgf, dorsal glandular folds of the oesophagus; dp, pouch of the duct of digestive gland; ig, ingestive gland; gon, gonad; lf, longitudinal fold of the stomach; nep, nephridium; ng, nephridial gland; nr, circumoesophageal nerve ring; od, odontophore; od.r, odontophore retractor; oe, oesophagus; op, operculum; ped.t, pedal tentacle; pma, posterior mixing area; poe, posterior oesophagus; pr, proboscis; prp, propodium; prr, proboscis retractor muscles; rd, radular diverticulum; re, rectum; sd, salivary duct; sg, salivary gland; sph, sphincter between the posterior oesophagus and stomach; st, stomach; ve, ventricle.



gland join prior to entering the stomach via a single opening.

The tubular rectal gland, found in *Babylonia areolata* and *B. japonica*, runs along the rectum but opens into the mantle cavity (Fig. 4B) rather than into rectum, as in other neogastropods. This gland can be distinguished from the surrounding tissues by its darker coloration, but its epithelium is low and poor in melanin granules, unlike that of *Nucella lapillus*, the only species for which the rectal gland has been examined histologi-

cally (FRETTER & GRAHAM, 1962; ANDREWS, 1992). The differences between the rectal gland of *Babylonia* and those of most other neogastropods raise questions as to the homology of these structures. The rectal gland of *Hormospira maculosa* (Pseudomelatomidae, Conoidea) is intermediate in morphology between *Babylonia* and *Nucella* in that it opens into the mantle cavity very near the anus (KANTOR, 1988) (Fig. 4F, agd). In this species, the posterior portion of the gland is lined with tall

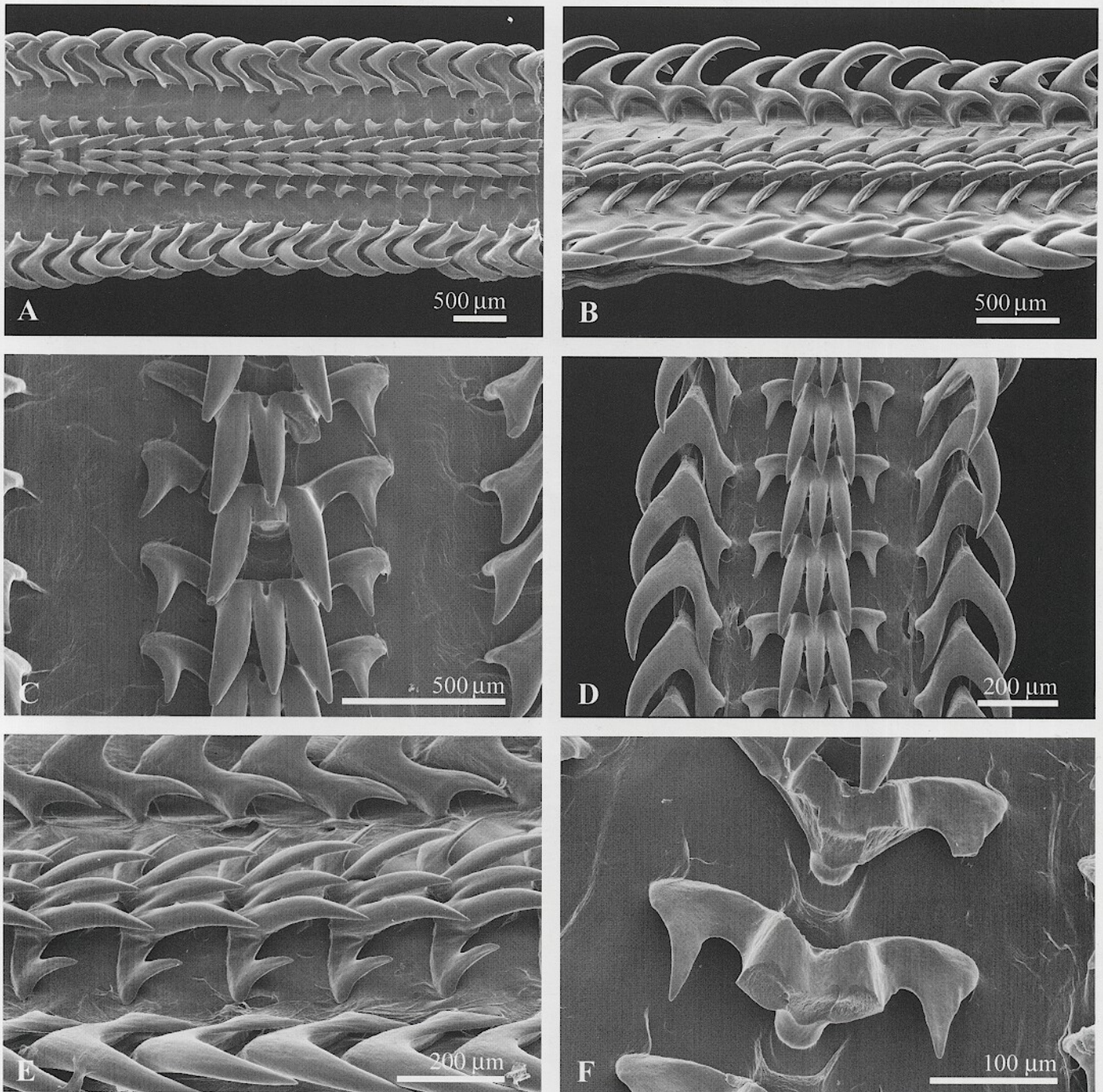


Figure 7. Radulae of *Babylonia japonica* (A-C) (SL 68.0 mm) and *B. spirata* (D-F) (SL 53.0 mm). A, D — Dorsal and B-E — left lateral (45°) views of central portion of radular ribbon. C — dorsal enlarged view of rachidian teeth to show the indentation at base of median cusp. F — dorsal enlarged view of damaged rachidian teeth from bending plane to show indentation and buttress of central cusp.





epithelial cells containing melanin granules (Fig. 4H, similar to *Nucella*), while the anterior region forms a duct (Fig. 4G, agd) lined with lower epithelial cells containing reduced quantities of melanin granules. The epithelium in the anterior region of the rectal gland of *Hormospira* is similar to, and likely homologous with, the rectal gland of *Babylonia* (Fig. 4C).

Dissection of a single male specimen of *Babylonia spirata* revealed that the seminal duct does not form a seminal vesicle, but rather is joined by numerous, coiled ducts originating in the testis (Fig. 8A, td). The single, poorly preserved male specimen of *B. lutosa* available for study lacked these ducts as well as a seminal vesicle. In male specimens of *B. japonica*, the seminal duct does form a well-defined seminal vesicle (Fig. 8C, vs).

Phylogenetic analyses of morphological (Fig. 10A) as well as molecular (Fig. 10B) data sets reveal *Babylonia* to be more closely

related to volutoidean families such as Volutidae, Turbinellidae and Olividae than to any member of the Buccinoidea. The high incidence of homoplasy in morphological characters that has long confounded attempts to resolve phylogenetic relationships within Neogastropoda (e.g., PONDER, 1974; KANTOR, 1996) is also apparent in this study. While the morphological tree is fully resolved, only the node uniting species of *Babylonia* has significant bootstrap, jackknife or Bremer support. Moving the two species of *Babylonia* to a basal position within Buccinoidea increased the tree length by 4 steps (6%), while including *Babylonia* at various nodes within Buccinoidea increased tree length by as little as 2 steps (3%) (sister taxon to *Melongena*) to as many as 5 steps (8%) (sister taxon to either *Buccinum*, *Neptunea* or *Chlanidota*).

Portions of the phylogeny based on partial sequences of the cytochrome c oxidase subunit I mitochondrial gene are slightly

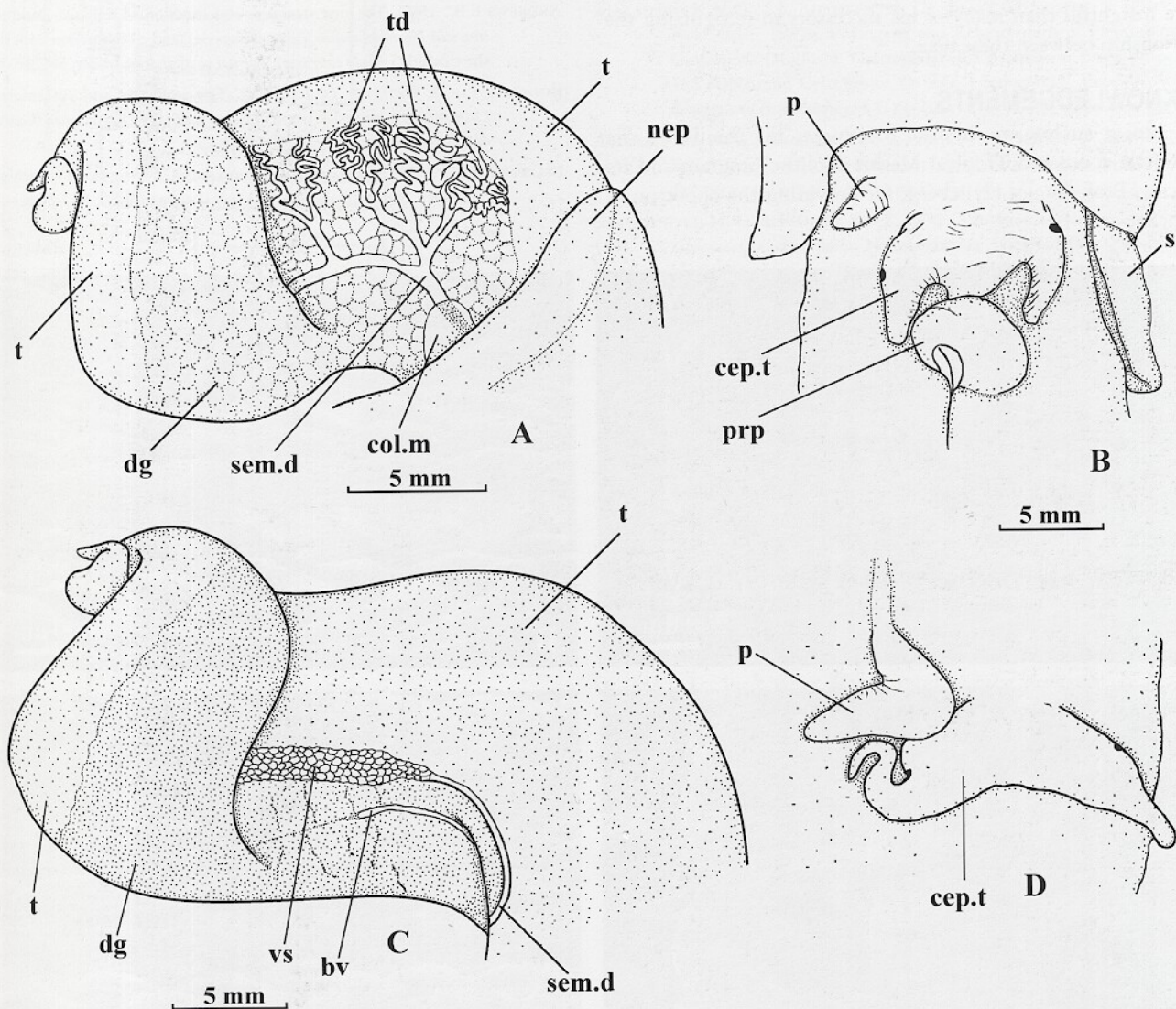


Figure 8. Male reproductive system of *Babylonia*. A-B. *Babylonia spirata*. C-D. *Babylonia japonica* (Reeve, 1842). A, C — view of internal part of the whorls of visceral mass to show position of seminal duct and vesicula seminalis (C). B, D — anterior views of foot-head to show penis.

Abbreviations: bv, blood vessel; cep.t, cephalic tentacles; col.m, columellar muscle; dg, digestive gland; nep, nephridium; p, penis; prp, propodium; s, siphon; sem.d, seminal duct; t, testis; td, ducts from testis to seminal duct; vs, vesicula seminalis.



more robust, in that there is significant support for the monophyly of the families Fasciolaridae, Muricidae and the subfamily Busyconinae. Thirteen additional steps (6% of phylogenetically informative characters) are required to shift *Babylonia* to the base of Buccinoidea, while placing the genus within Buccinoidea requires 19-31 additional steps (9-14% of phylogenetically informative characters). Although neither morphological nor molecular data provide robust support for the monophyly of Buccinoidea, both data sets exclude *Babylonia* from the Buccinoidea, indicating instead affinities with the "volutoid" families Volutidae, Turbinellidae and Olividae. As our analyses contain a small proportion of the families historically attributed to "Volutoidae" [show to be grade rather than a clade by HARASEWYCH ET AL., 1997b], identification of the sister group of *Babylonia* must await further study. While we are not suggesting that species of *Babylonia* are congeneric with the olivid genus *Eburna*, it appears that LAMARCK (1822) was perhaps more insightful than many of his successors in recognizing the relationship between these taxa.

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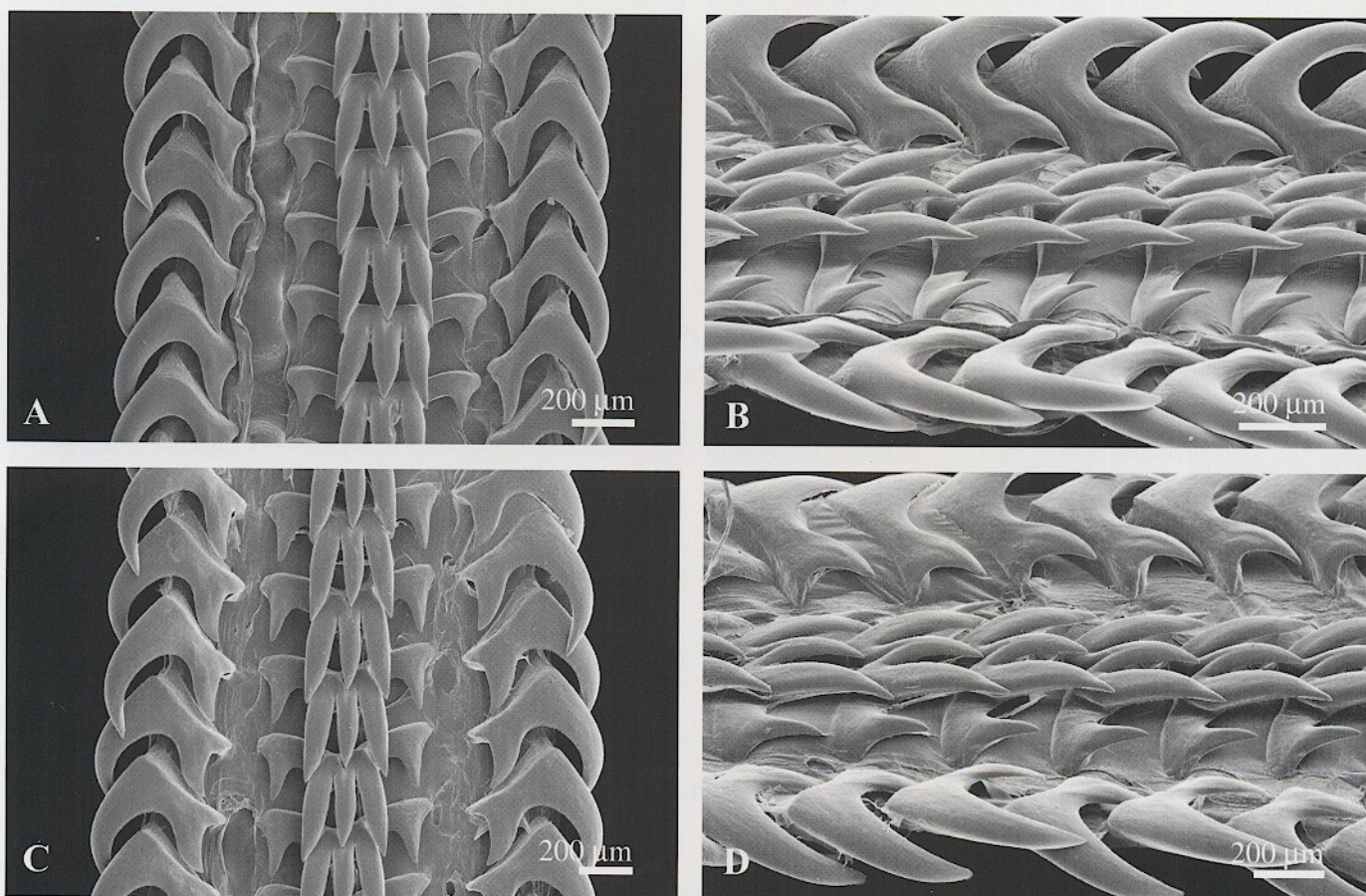


Figure 9. Radulae of *Babylonia lutosa* (A-B) (SL ~60 mm) and *B. zeylanica* (C-D) (SL 60.7 mm). A, C — Dorsal and B-D — left lateral (45°) views of central portion of radular ribbon.





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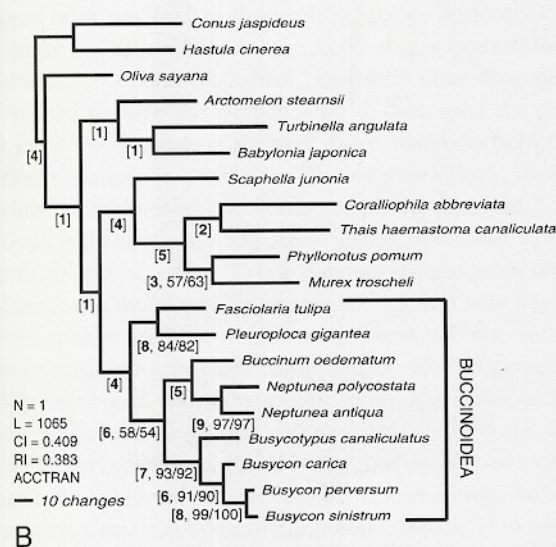
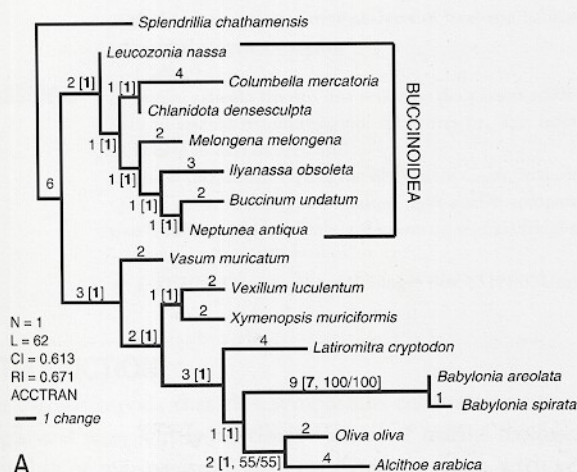


Figure 10. Phylogenetic relationships of *Babylonia* to rachiglossan Neogastropoda. A — The single most parsimonious tree resulting from a maximum parsimony analysis (branch and bound search, ACCTRAN character transformation) of the anatomical data matrix (Table 1). Branch lengths are shown on all nodes. Square brackets [ ] enclose Bremer support indices (bold) followed by bootstrap / jackknife proportions in percent, for the nodes for which support exceeded 50%. B — The single most parsimonious tree derived from a maximum parsimony analysis (branch and bound search) of partial cytochrome c oxidase I sequences (591 bp) of taxa in Table 2. Square brackets [ ] enclose Bremer support indices (bold) followed by bootstrap / jackknife proportions in percent, for the nodes for which support exceeded 50%.

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