

**The systematic position of *Tritonidea dentata* Schepman, 1911
(Gastropoda, Prosobranchia: Buccinidae)**

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Tritonidea dentata Schepman, 1911, is characterized by the presence of a basal labral tooth and by a deeply recessed ridge bearing elongate denticles on the adaxial (inner) side of the outer lip. This central Indo-West Pacific species is here recognized as a Recent member of *Preangeria* Martin, 1921, a genus previously known only from the Miocene of southeast Asia. *Taurasia* Bellardi, 1882 (Muricidae: Rapaninae), in which species of *Preangeria* had been included by several earlier authors, differs from *Preangeria* by lacking a labral tooth and by having a lateral rather than terminal opercular nucleus. Comparisons with other genera suggest that *Preangeria* belongs to the buccinid subfamily Pisaninae.

Key words: Gastropoda, Prosobranchia, Buccinidae, Pisaninae, *Tritonidea*, *Preangeria*, *Taurasia*, Indian Ocean, Java, Miocene.

INTRODUCTION

Many neogastropods have a shell in which the outer lip bears a blunt or sharp, downwardly projecting tooth on its abapical part. This so-called labral tooth has evolved many times independently. In an effort to understand when, where, and in which clades the evolution of labral teeth has taken place, I have been conducting studies of the taxonomy, relationships, and distribution of living and fossil species of gastropod in which a labral tooth is present. Here I report on the previously unsuspected relationship between two taxa with a well-developed labral tooth, the Recent *Tritonidea dentata* Schepman, 1911, and the Miocene species from Indonesia that have variously been treated as members of the genera *Acanthina*, *Preangeria*, *Acantinella*, and *Taurasia*. I shall argue that this group comprises a single, distinctive, early Miocene to Recent clade, for which the generic name *Preangeria* Martin, 1921, is available.

MATERIALS AND METHODS

This study was based on my examination of *Tritonidea dentata* Schepman, 1911; *Acanthina javana* Martin, 1899; and *Preangeria angsanana* Martin, 1921. In addition, I have examined (table 1) species of *Buccinulum*, *Cymia*, *Eosipho*, *Janiopsis*, and *Pisania*, genera which are either related to the three species named above or which were linked to these species by previous authors.

- Acanthina javana* Martin, 1899: RGM 9755, Selacau, Java
Buccinum l. lineum (Martyn, 1784): Leigh, New Zealand (GJV)
B. vittatum littorinoides (Reeve, 1846): Dunedin, New Zealand (GJV)
Cymia tecta (Wood, 1828): Paitilla, Panama (GJV)
Eosipho smithi Schepman, 1911: Philippines (MNHN)
Janiopsis angulosa (Brocchi, 1814): Montegibbio, Italy (MNHN); Orciano, Italy (IRSNB)
J. maxillosa (Bonelli in Bellardi & Michelotti, 1840): Lapugy, Rumania (NHMW)
J. parisiensis (Deshayes, 1835): Chaussy, France (MNHN, GJV)
Pisania pusio (Linnaeus, 1758): Fernando de Noronha, Brazil (GJV); Garden Key, Florida Keys, Florida (USNM 890264)
P. striata (Gmelin, 1791): Mediterranean coast, Israel (two lots, GJV)
Preangeria angsanana Martin, 1921: Ci Angsana, Java (RGM 9753)
Taurasia pleurotoma (Grateloup, 1832): Saint-Paul-les-Dax, France, and Leognan, France (MNHN)
T. striata (Quoy & Gaimard, 1833): Puerto Galera, Philippines (GJV)
Tritonidea dentata Schepman, 1911: Kuandang Bay, Indonesia; ZMA MOLL 3.11.032; Philippines (MNHN)

Table 1. Material examined.

Abbreviations: ANSP — Academy of Natural Sciences, Philadelphia; GJV — Vermeij collection; IRSNB — Institut Royal des Sciences Naturelles de Belgique, Brussels; MNHN — Museum National d'Histoire Naturelle, Paris; NHMW — Naturhistorisches Museum, Wien; RGM — Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum voor Geologie en Mineralogie); USNM — United States National Museum of Natural History, Washington; ZMA — Zoölogisch Museum, Amsterdam.

SYSTEMATICS

Family Buccinidae Rafinesque, 1815

Subfamily Pisaniinae Gray, 1857

Genus *Preangeria* Martin, 1921

Type species. — Designation by Wenz (1943, p. 1356), *Preangeria angsanana* Martin, 1921.

Synonym. — *Acantinella* Shuto, 1969 (p. 109); type species by original designation, *Acanthina javana* Martin, 1899.

Revised description. — Shell up to 31 mm high, elongate-ovate, consisting of a protoconch of about two smooth whorls and of a teleoconch of four to six whorls separated by an impressed suture; last whorl of teleoconch rounded or weakly shouldered above, little or not constricted below; spire moderately high, comprising 35 to 44% of total shell height; spiral sculpture consisting of well-defined cords; axial sculpture present as riblets on early whorls, often obsolete on last one or two whorls; aperture elongate-ovate; outer lip indeterminate, its adaxial side bearing a deeply recessed ridge with nine to twelve elongate denticles; abapical end of outer lip bearing sharp labral tooth, situated at apertural end of external groove; columella with one or two central folds and up to four superficial abapical riblets; adapical end of inner lip with weak or no parietal tooth; outer lip without adapical notch; siphonal fasciole present; siphonal canal short, broadly open; periostracum thick, hairy.

Included species. — *P. angsanana* Martin, 1921; *P. dentata* (Schepman, 1911); *P. javana* (Martin, 1899); *P. sundaica* (Oostingh, 1935).

Geographical and stratigraphic distribution. — Early Miocene to Recent, central Indo-West Pacific.

Preangeria dentata (Schepman, 1911), fig. 1

Tritonidea dentata Schepman, 1911: 303, pl. 19, fig. 8.

Axymene philippinensis Petuch, 1979: 8, figs. 14-15.

Eosipho dentatus (Schepman, 1911): Bouchet & Warén, 1986: 470, figs. 17, 58-61.

Revised description of shell. — Shell ovate, consisting of one and a half to two protoconch whorls and five teleoconch whorls; maximum height 30.0 mm; last whorl comprising 56 to 62% of total shell height; suture deeply impressed; last whorl weakly shouldered above periphery, weakly constricted; spiral sculpture consisting of ten to fifteen cords on last whorl, and five cords on penultimate whorl; secondary spiral sculpture absent; axial sculpture consisting of twenty-one to twenty-five very fine riblets on penultimate whorl, absent on last whorl; basal external groove, situated below all other external shell sculpture, ends in sharp, abapically directed tooth at edge of outer lip; this labral tooth separated from adapical sector of outer lip by shallow sinus; outer lip weakly convex, crenulated at edge; adapical sinus on outer lip very weak or absent; adaxial side of outer lip with deeply recessed ridge, on which are situated nine to twelve denticles; columella straight, bearing one or two central folds; parietal rib at adapical end of inner lip absent; inner lip adherent; low siphonal fasciole present; siphonal canal short, broadly open; umbilicus absent; aperture elongate-ovate, height:breadth ratio 2.4 to 2.8.

Discussion. Previous assignments of *Tritonidea dentata*. — Schepman (1911: 303, pl. 19 fig. 8) described and illustrated *Tritonidea dentata* on the basis of a very fresh, empty shell from a depth of 72 m in the Bay of Kuandang in the Celebes Sea in Indonesia. Since its original description, the species has been found at various localities in the Celebes and Sulu Seas and near New Caledonia at depths of 72 to 700 m. Authors of the three previous discussions of *T. dentata* compared the species only to other Recent forms, and assigned it to three genera in two families. Placement in the Buccinidae, broadly defined, is amply justified on the basis of the radula (Bouchet & Warén, 1986). According to Bouchet & Warén (1986), the radula has a square central tooth with larger outer and smaller inner cusp. This radular type resembles that in the buccinid genera *Eosipho* Thiele, 1929, and *Manaria* Smith, 1906, both of which contain generalized, deep-water, tropical buccinids with many plesiomorphic features (see Bouchet & Warén, 1986; Harasewych, 1990).

With considerable hesitation, Schepman (1911) assigned his new species to *Tritonidea* Swainson, 1840, an objective junior synonym of *Pollicia* Gray in Sowerby, 1834 (type species: *Buccinum undosum* Linnaeus, 1758). As restricted by Vermeij & Bouchet (in preparation), this early Miocene to Recent pisaniine buccinid genus is characterized by a fusiform, weakly basally constricted shell with an externally thickened, adapically extended, terminal varix, a shallow adapical sinus on the outer lip, and a parietal tooth at the adapical end of the inner lip. All species have rounded axial ribs on at least the early teleoconch whorls, although in the type species and in several other members of the genus the ribs are reduced or lost on the last two or more whorls of the adult shell. Most individuals of most species have the central crenulation on the sharp edge of the

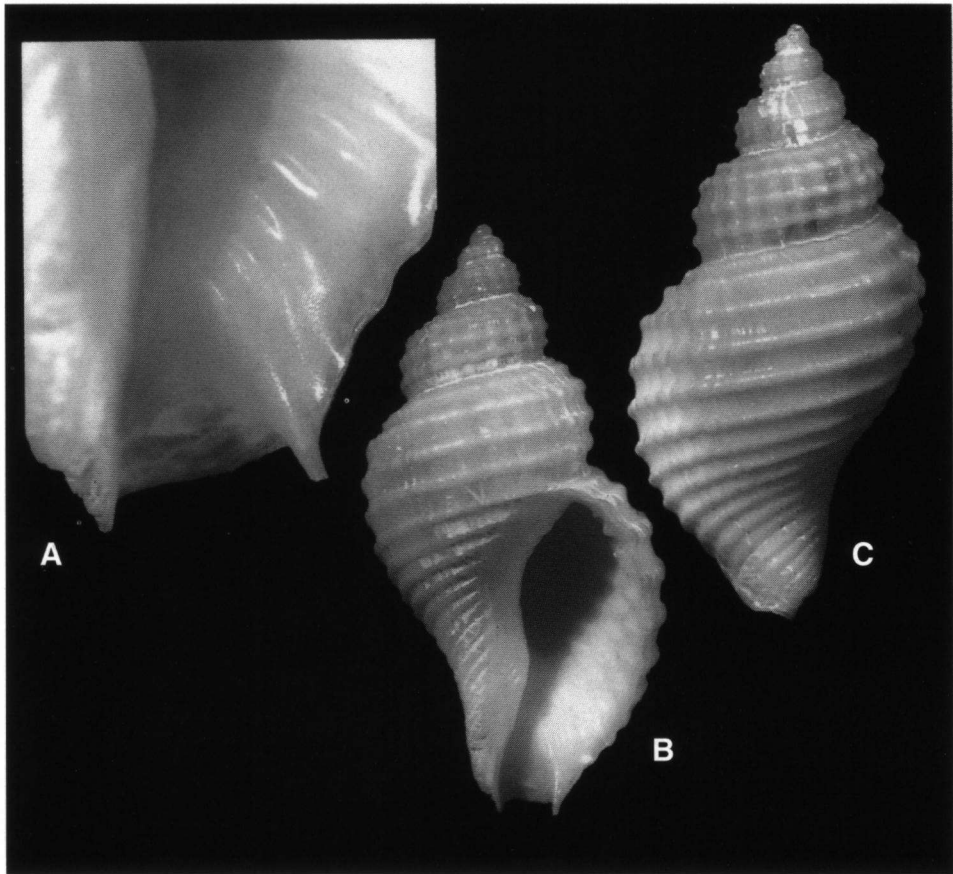


Fig. 1. *Preangeria dentata* (Schepman, 1911), Panglao, Bohol, Philippines; height, 22.2 mm. A, outer lip with labral spine; B, apertural view; C, dorsal view.

outer lip enlarged and slightly ventrally projecting beyond the other crenulations. This labral tooth lies near the middle of the outer lip. In the related genus *Cantharus* Röding, 1798 (type species: *Buccinum tranquebaricum* Gmelin, 1791), the labral tooth is usually better developed and is situated on the lower third of the outer-lip margin. Compared to *Pollia*, *Cantharus* has a relatively broader aperture and a less well-developed parietal tooth. The axial sculpture continues to the last whorl, and the outer lip of *Cantharus* remains thin and therefore does not become a terminal, externally roundly thickened, adapically extended varix as it does in *Pollia*. Both genera are characterized by a thick, hairy periostracum.

Tritonidea dentata differs from *Pollia* and *Cantharus* by having a deeply recessed ridge on the adaxial side of the outer lip, a large labral tooth situated at the abapical end of the outer lip below all elements of external sculpture instead of on its lower or middle third, and by lacking an adapical sinus on the outer lip, central folds on the columella,

and a parietal rib on the adapical end of the inner lip. The outer lip is not externally thickened or adapically extended as it is in *Polia*.

Bouchet & Warén (1986) assigned *Tritonidea dentata* with some doubt to *Eosipho* Thiele, 1929 [type species: *Chrysodomus (Sipho) smithi* Schepman, 1911]. They cited similarities in the radula to other species of *Eosipho*, and pointed out that *T. dentata* has many shell features in common with *Cantharus aldermenensis* Powell, 1971, and *Eosipho thorybopus* Bouchet & Warén, 1986, species without a labral tooth that Bouchet & Warén (1986) likewise assigned to *Eosipho*. *E. smithi*, the type of *Eosipho*, resembles *T. dentata* in having little or no axial sculpture, in the absence of a parietal rib or tooth, and in lacking an adapical notch or sinus on the outer lip. It differs, however, in having a smooth instead of plicate columella, and in lacking a labral tooth and a deeply recessed, tooth-bearing ridge on the adaxial side of the outer lip. *Cantharus aldermenensis* and *Eosipho thorybopus* have a thin outer lip with lirae (spiral ridges) on its adaxial side, a smooth columella, and axial sculpture on the spire whorls (Bouchet & Warén, 1986). Like *E. smithi*, these species lack a parietal tooth. Shell characters including the adaxially thickened outer lip, plicate columella, and labral tooth set *Tritonidea dentata* apart from other species assigned by Bouchet & Warén (1986) to *Eosipho*.

Muricid affinities of *Tritonidea dentata* were postulated by Petuch (1979), who described this species under the name *Axymene philippinensis*. Finlay (1927, p. 424) proposed *Axymene* for a New Zealand trophonine muricid (*Axymene turbator* Finlay, 1927, = *Trophon aucklandicus* Smith, 1902) in which the axial sculpture is obsolete. Powell (1979) synonymized *Axymene* with *Xymene* Iredale, 1915 (type species: *Fusus plebejus* Hutton, 1873). Like *Tritonidea dentata*, species of *Xymene* have a deeply recessed, denticulate ridge on the adaxial side of the planar outer lip. This feature occurs commonly among muricids, especially among members of the Ocenebrinae and some Rapaninae (see Vermeij & Kool, 1994; Vermeij, 1995; Vermeij & Carlson, in review). *Xymene* and other trophonine muricids, however, lack the periostracum and the labral tooth present in *Tritonidea dentata*.

Assignment of *Tritonidea dentata* to *Preangeria*. — Authors who treated *Tritonidea dentata* were evidently unaware of several closely similar fossil species from Indonesia and the Philippines that were revised by Beets (1984). These species, which have been assigned variously to genera in the Muricidae and Cancellariidae, were reassigned by Beets (1984) to *Taurasia* Bellardi, 1882 (type species: *Purpura subfusiformis* d'Orbigny, 1852, = *Purpura pleurotoma* Grateloup, 1832; see Cossmann & Peyrot, 1924). Beets placed this genus in the muricid subfamily Drupinae (= Rapaninae in the sense of Kool, 1993).

Martin (1899: 137, pl. 21 fig. 315) described and illustrated the first of these species as *Acanthina javana*. Shuto (1969: 109) later made this species the type of his new genus *Acantinella*. Martin's species is remarkably like *Tritonidea dentata* in shell characters. The holotype (RGM 9755) from the Selacau beds (late Miocene) of Jawa is like *T. dentata* in having an ovate outline without basal constriction, one central and four abapical columellar folds, fine axial riblets on early whorls, fine cords persisting to the aperture, a long labral tooth at the abapical end of the outer lip, a deeply recessed ridge bearing ten lira-like denticles on the adaxial side of the outer lip, and a deeply impressed suture, and by lacking an adapical notch on the outer lip. It differs from *T. dentata* by being slightly higher-spined (last whorl comprising 65% instead of 58-62% of total shell height), by having the cords more numerous and of alternating instead of uniform size, a slightly narrower aperture (height-to-breadth ratio 3.0 instead of 2.4 to 2.8), and by having a very weak parietal tooth. The height of the holotype (30.4 mm) is very similar to that of the largest *T. dentata* (30.0 mm).

Beets (1984) recognized that three other species are very closely related to *Acanthina javana*. Two of these, *Preangeria angsanana* Martin, 1921, and *P. talahabensis* Martin, 1921, were described as members of *Preangeria* Martin, 1921, for which Wenz (1943: 1356) designated *P. angsanana* as type species. Martin (1921: 450) originally proposed *Preangeria* as a member of the Cancellariidae because of the presence of columellar folds. Recognizing that such folds also occur in various muricid groups, Martin (1928: 124) later transferred *Preangeria* to the Purpuridae (= Rapaninae in the sense of Kool, 1993). He did not realize that these species possess a labral tooth, and therefore did not perceive the connection between them and *Acanthina javana*. The trajectory of the growth lines near the base of the shell led Beets (1984) to infer the presence of a tooth in *Preangeria* and to link *Acanthina javana* with the two species of *Preangeria*. He also placed *Nucella (Acanthinucella) sundaica* Oostingh, 1935, from the Bojongmanik beds (Preangerian, late Miocene) of Java in this group, and assigned all four species, together with several others without a labral tooth, to *Taurasia*.

The type species of *Taurasia* (*Purpura subfusiformis* d'Orbigny, 1852) is a Miocene fossil considered by Cossmann & Peyrot (1924) to represent a relatively weakly sculptured form of the variable early Miocene (Aquitanian and Burdigalian) southern European species *Purpura pleurotoma* Grateloup, 1832. This species is characterized by an elongate-ovate, basally very weakly constricted shell whose planar, crenulated outer lip bears a deeply recessed axial ridge adorned with six to ten denticles that continue into the aperture as lirae. A distinct parietal tooth and one or two central columellar folds are present on the inner lip. Spiral sculpture consists of several sizes of cords, which are scaly by virtue of lamellose incremental lines. Axial sculpture is variably expressed. In some forms of *Taurasia pleurotoma*, they may form a row of prominent nodes, whereas in others the axial ribs are low. In the Recent fauna, *Taurasia* is represented by a single species, *Purpura striata* Quoy & Gaimard, 1833 (better known as *Purpura buccinea* Deshayes, 1844; see Houart, 1996), distributed from the Solomon Islands to New Guinea, the Philippines, and eastern Indonesia. In this species, axial sculpture consists of eight broadly rounded ribs that on the last whorl become obsolete toward the base. The abapical sector of the outer lip is slightly concave when viewed from the apertural side. The adapical sector of the outer lip forms a shallow subsutural sinus. The lip joins the penultimate whorl at a low angle, and with the parietal tooth at the adapical end of the inner lip forms a narrow, very short adapical apertural channel. A periostracum is absent. *T. niasensis* Beets, 1984, from the Plio-Pleistocene of Nias (west of Sumatra) is a somewhat more strongly sculptured species that is evidently very close to *T. striata*.

Although *Taurasia* as circumscribed above is morphologically very similar to the labral-tooth-bearing group, the available evidence leads me to regard the two groups as representing two taxonomically distant genera. For the group with a labral tooth, the earliest available name is *Preangeria* Martin, 1921, of which *Acanthinella* Shuto, 1969, is a junior subjective synonym. It differs from *Taurasia* by the presence of a labral tooth, by having the axial sculpture more or less confined to the spire whorls, by lacking the adapical apertural channel, by the absence of squamose growth increments, and (in the living species) by the presence of a well-developed periostracum.

Beets (1984) discussed two additional species from southeast Asia as probable members of *Taurasia*. These are *T. pendopoensis* Beets, 1984, from beds of probable late Miocene (Preangerian) age at Palembang, Sumatra, and *Tritonidea praeundosa* Vredenburg, 1923, from the Kama beds (Miocene) of Burma. These species, which may prove to be synonyms (Beets, 1984), apparently lack axial sculpture as well as a labral tooth. The presence of columellar folds in *T. pendopoensis*, together with other features of the

shell, implies that this species, and the less well-preserved *T. praeundosa*, are related to *Preangeria*. The two species may belong to *Eosipho* in the broad sense as used by Bouchet and Warén (1986).

Evolutionary trends in *Preangeria*. — Comparisons among the five species of *Preangeria* reveal a consistent evolutionary trend toward a reduction in axial sculpture. The two earliest species, *P. angsanana* and *P. talahabensis* (both from the early Miocene Nyalindung beds of Jawa), have axial ribs persisting to the aperture of the last whorl. In the late Miocene *P. javana* from Java and the Philippines, and the less slender *P. sundaica*, axial sculpture occurs only on the spire whorls. The Recent *P. dentata* usually lacks axial sculpture altogether, or has it expressed as fine riblets on the spire whorls. *P. dentata* also shows a reduction in the parietal tooth and a broader aperture relative to the earlier species. These trends are possibly related to an increasing depth of habitat of the species of *Preangeria* over time. At the depths of 72 to 700 m in which the Recent *P. dentata* lives, predation and therefore selection in favour of antipredatory reinforcing sculpture and a narrow aperture may be less intense than in the shallower-water habitats inferred for the Miocene representatives of the genus.

Taxonomic position of *Preangeria*. — As indicated above, evidence from the radula implies that *Preangeria* belongs to the Buccinidae, broadly defined. Shell characters are not inconsistent with this assignment. Several shell characters of *Preangeria*, however, are somewhat unusual for members of this large group. Below I review briefly some other genera with features in common with *Preangeria*, and make some tentative suggestions about the position of *Preangeria* within the Buccinidae.

Preangeria has several shell characters in common with some members of a group of genera including *Buccinulum* Deshayes, 1830 (early Miocene to Recent, New Zealand and Australia; see Ponder, 1971); *Euthria* J. E. Gray in M. E. Gray, 1850 (middle Eocene to Recent, Europe); *Samudra* Beets, 1986 (middle Eocene to middle Miocene, Indonesia); and *Siphonofusus* Kuroda & Habe, 1952 (Oligocene to Recent, Europe and Indo-West Pacific). The characters and systematics of these genera have been reviewed by Ponder (1971), Shuto (1978), and Beets (1986). Many members of this group, especially species of *Buccinulum* and *Euthria*, are characterized by having the axial sculpture confined to the early teleoconch whorls, by the absence of an abapical sinus on the outer lip, and by having a deeply recessed ridge bearing elongate denticles or lirae on the adaxial side of the outer lip. The genera of the *Buccinulum* group, which have been assigned to the Buccinulinae or Pisaniinae (Powell, 1951; Cernohorsky, 1971), differ from *Preangeria* by lacking the central columellar fold and labral tooth.

Representatives of several other genera of buccinids also have a deeply recessed adaxial ridge on the outer lip. These include *Pisania* Bivona-Bernardi, 1832 (Middle Eocene to Recent, Europe; Recent, Indo-West Pacific and western Atlantic); *Janiopsis* Rovereto, 1899 (Middle Eocene to ?Recent, Europe and Indo-West Pacific); and *Austriumphis* Vermeij, 1997 (Pliocene, South Africa). Axial sculpture is reduced or absent on the adult teleoconch whorls of *Pisania* and *Austriumphis*. An abapical sinus on the outer lip is lacking in *Pisania* and *Janiopsis* but is present in *Austriumphis*. *Pisania* and *Janiopsis* are usually considered to be members of the buccinid subfamily Pisaniinae (see e.g. Peyrot, 1927; Cernohorsky, 1971; Givens & Kennedy, 1976), whereas *Austriumphis* was tentatively assigned to the Photinae because of the presence of an abapical sinus (Vermeij, 1997). The only genus of this group with one or two central columellar folds as seen in *Preangeria* is *Janiopsis*. Shells of *Janiopsis* differ from *Preangeria* by having strong,

persistent axial sculpture, and in characters of the outer lip. The type species, *J. angulosa* (Brocchi, 1814) from the middle Miocene (Langhian) to the Pliocene of southern Europe, has a distinct, blunt, labral tooth situated at the end of a groove just below the midpoint of the convex, externally thickened, and adapically extended terminal varix. Other species of *Janiopsis* I have examined, including the middle Eocene (Lutetian) *J. parisiensis* (Deshayes, 1835) from the Paris Basin of France and the middle Miocene (Langhian) *J. maxillosa* (Bonelli in Bellardi & Michelotti, 1840) from the Vienna Basin of Austria, lack a labral tooth, as do species of *Pisania* and *Austriumphis*.

In the light of this discussion, I tentatively assign *Preangeria* to the subfamily Pisaniinae, broadly defined. This assignment may have to be revised as anatomical and other data become available for *Preangeria*, and as phylogenetic relationships within the Buccinidae as a whole become better understood.

Taxonomic position of *Taurasia*. — In view of the striking similarities in shell form between *Taurasia* and *Preangeria*, the question of where to assign *Taurasia* is worth considering. Bellardi (1882, p. 194) introduced *Taurasia* as a genus in the Purpuridae (= Rapaninae in the sense of Kool, 1993). This assignment was followed by most later authors (Cossmann, 1901; Cossmann & Peyrot, 1924; Wenz, 1938-1944; Beets, 1984; Vermeij & Kool, 1994). Placement near *Pisania* in the buccinid subfamily Pisaniinae was advocated by Fischer (1884).

Unfortunately, nothing is known about the anatomy or radula of the living species, *T. striata*. Shell characters, though not definitive, point toward an assignment in the Rapaninae. These include the more or less planar, crenate outer lip, small but distinct adapical apertural channel, squamose growth increments, and absence of a periostracum (see Vermeij & Kool, 1994; Vermeij, 1995, for characterization of Rapaninae). At my request, G. Rosenberg has examined the operculum of *T. striata* (ANSP 206569, under the name *Cronia buccinea*), which he reports has a lateral nucleus. Opercula with a lateral nucleus are the rule in the Rapaninae, whereas weakly spiral opercula or those with a terminal nucleus are typical of Buccinidae (Powell, 1951; Bouchet & Warén, 1985; Ponder & Lindberg, 1997). Only *Buccinum* Linnaeus, 1758, and its allies in the Buccininae have a concentric operculum. *Taurasia* therefore appears to belong to the muricid subfamily Rapaninae.

The presence of one of two central columellar folds in *Taurasia* could imply a relationship between *Taurasia* and such other rapanine genera as *Acanthais* Vermeij & Kool, 1994 (Recent, eastern Pacific); *Cymia* Mörch, 1860 (Oligocene to Recent, eastern Pacific; Oligocene to Miocene, Europe; Miocene to Pliocene, western Atlantic); *Habromorula* Houart, 1994 (Recent, Indo-West Pacific); *Morula* Schumacher, 1817 (Miocene to Recent, Indo-West Pacific); *Drupa* Röding, 1798 (Recent, Indo-West Pacific); and *Ricinella* Schumacher, 1817 (Recent, Indo-West Pacific), and *Thalessa* H. & A. Adams, 1853 (Recent, Indo-West Pacific). Cladistic analysis based on shell characters (Vermeij & Carlson, in review) places *Taurasia* near *Morula* and several other genera that comprise the so-called ergalataxine subclade. The conspicuous lirae on the adaxial side of the outer lip of *Taurasia* and the presence of a shallow subsutural sinus on the outer lip indicate a relationship with *Cymia*, which differs from *Taurasia* mainly by having a deep adapical outer-lip notch instead of a shallow sinus. *Taurasia* may therefore represent a relatively early lineage in the ergalataxine subclade, which could have diverged from a *Cymia*-like ancestor. In any case, the similarities between *Taurasia* and *Preangeria* in shell form appear to result from convergence rather than from shared ancestry.

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