



Egg-collar morphology and identity of nine species of Naticidae (Gastropoda) in Taiwan, with an assessment of their phylogenetic relationships

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ABSTRACT

The gross morphology of egg (sand) collars laid by nine naticid species in six genera from Taiwan are described and compared: *Paratectonatica tigrina*, *Notocochlis cernica*, *N. gualtieriana*, *N. sp. aff. antoni*, *Naticarius zonalis*, *Tectonatica bougei*, *Sinum haliotoideum* (= *planulatum*), *Mammilla melanostoma* and *M. melanostomoides*. Egg collars and adult animals were collected from Taiwan and its offshore islands, as well as from Four-Way Closure Ridge (1,648 m depth) in the South China Sea. Mitochondrial COI and 16 S rRNA sequences were obtained from both embryos and adults and the genetic distances of these sequences from maximum-likelihood trees were then compared to determine the identity of the egg collars. Of the egg collars of nine species identified using this procedure, seven are described here for the first time. Each species laid a consistent, distinctive egg collar that differed in the overall shape and size, number of coils, capsule size and packing density in different species. The largest collars, with basal diameters exceeding 8 cm, were laid by *M. melanostoma* and *S. haliotoideum*, while the smallest belonged to *Notocochlis* spp., with basal diameters as small as 1 cm. In the egg collars of all nine species examined, each embryo was enclosed within a single capsule. COI and 16 S sequences from egg collars were analysed together with published sequences from other studies. Seven groups, each with a unique egg-collar morphology, were defined, some of which were coincident with supported phylogenetic clades. These results represent only a small fraction of some 47 species of Naticidae recorded to date from Taiwan, but the use of a combination of morphological and molecular characters appears to be a viable method to identify egg collars. The egg-collar literature involving 52 naticid species worldwide is briefly reviewed in the light of our results.

INTRODUCTION

Egg (or sand) collars laid by naticids are often a conspicuous item on intertidal soft shores around the world where these snails are present. In these egg masses, egg capsules, sediment (chiefly sand, mud; occasionally faecal pellets) and adhesive are mixed together (Giglioli, 1955; Kingsley-Smith, 2003) to form a marvellously functional, but ephemeral structure. Ventilation, camouflage and protection (Aronowsky, 2003) are provided for the embryos for some weeks until they are ready to swim away as veligers or crawl away as juveniles. In addition, the characteristic form of the collar possibly helps keep it in position on the substratum when subjected to hydrodynamic forces (personal observation), while retaining its shape and form in a fluid environment. However, despite being easily observed in the field during low tide, the specific identities of the collars are difficult to ascertain. Spawning takes place under water (Giglioli, 1955), possibly rapidly, and the act of laying capsules is rarely observed in the field, although some species are able to produce egg collars in captivity (*Polinices lacteus*: Bandel, 1976; *Euspira alderi* [as *Polinices*]: Ansell, 1982; *Euspira fusca*: Ramón, 1994; *Laguncula pulchella* [as *Euspira fortunei*]: Okoshi & Sato-Okoshi, 2011).

The adults generally appear to abandon the sand collars after laying them.

In the tropics, where multiple naticid species can co-exist together on the shore, matching egg collar to species is a difficult task. While the process of identifying adult shells has benefited from recent taxonomic treatments of some fossil and living members (chiefly based on features of the shell, umbilicus and operculum; e.g. Marincovich, 1977; Majima, 1989), egg collar morphology is poorly elucidated in comparison. This is true for most naticid species living in the Indo-Pacific region, where diversity is highest with more than 200 species (Kabat, 1990). Some 47 species of Naticidae have been recorded from Taiwan (Yeh & Hsueh, 2009). Naticids continue to be economically important as food along the coastlines of the western Pacific including China (Zhang, 2016) and Southeast Asia (Poutiers, 1998). Recently, a number of authors notably Hülsken (2008) and Hülsken *et al.* (2008, 2011), working in the Mediterranean, southern Australia and the Caribbean using molecular techniques, have revealed that most species lay egg collars with species-specific morphologies, so that in some cases they have provided additional information to

clarify the taxonomy of disputed species complexes (Hülsken *et al.*, 2011). The sequences have also been useful in revealing phylogenetic structure in the Naticidae (Hülsken *et al.*, 2012), although there are still large gaps in our knowledge of generic relationships. Here we present the results of similar investigations carried out on common naticid species living on the shores of Taiwan and nearby islands, as well as on Dongsha (Pratas) Island atoll and Four-Way Closure Ridge (1,648 m depth) in the South China Sea.

The main objectives of our study were to (1) characterize egg collars of naticids obtained in the field using molecular sequences and morphology; (2) identify the egg collars by matching their sequences with those of adult specimens and (3) determine the phylogenetic positions of the identified species in relation to other naticids using available molecular sequences.

MATERIAL AND METHODS

Egg collars and adult animals were collected by hand on intertidal shores, by SCUBA diving in shallow water, or purchased from local fish markets, in Taiwan and adjacent islands including Penghu, Kinmen and Dongsha, between 2011 and 2015 (Kang, 2014; Fig. 1). In one case a museum specimen was used. Despite numerous visits to the field, we were unable to observe the deposition of egg collars by animals during low tide. Adults from a deep-sea trawl at Four-Way Closure Ridge (1,648 m depth) off the southern coast of Taiwan were also included in the analysis (Table 1). They were all either frozen at -20 °C or preserved in 95% ethanol.

Collar dimensions (Fig. 2) were measured in the laboratory following Amio (1955) and Giglioli (1955), with modifications. Collars were initially divided into 11 morphotypes based on their morphology (Fig. 3). Collar morphotype and locality were used to annotate each sequence obtained in the study and in the resulting molecular phylogenetic trees (Fig. 3). The shell heights (SH) of adult animals were measured, except for *Sinum*, where the shell length (SL) is provided. Maximum length (L) and width (W) of opercula were measured. Diameter (D) of egg capsules was recorded. Voucher specimens were deposited in the National Museum of Natural Science (NMNS), Taichung, Taiwan (Table 1).

Examination of morphological characteristics of naticid specimens and egg collars were made using stereo- and compound microscopes. As egg collars are flexible, measurements given are approximate, based on the shape assumed in seawater. Hand sections of living and preserved egg collars were made using a razor blade and the relative distribution of eggs with respect to sand grains was observed under the microscope. Where possible, mitochondrial COI and 16S rRNA from adults and collars were sequenced. These were then compared with sequences from Hülsken (2008). Classification of naticids used in this study broadly follows Kabat (1990), Hülsken (2008) and Torigoe & Inaba (2011).

Crude DNA was extracted with the Tissue & Cell Genomic DNA Purification Kit (GeneMark, DP021-150), following the manufacturer's instructions, with modifications. Part of the foot muscle of adults (1–25 mg) was put in extraction solution and ground with a tissue homogenizer. A piece of collar (10–40 mg)

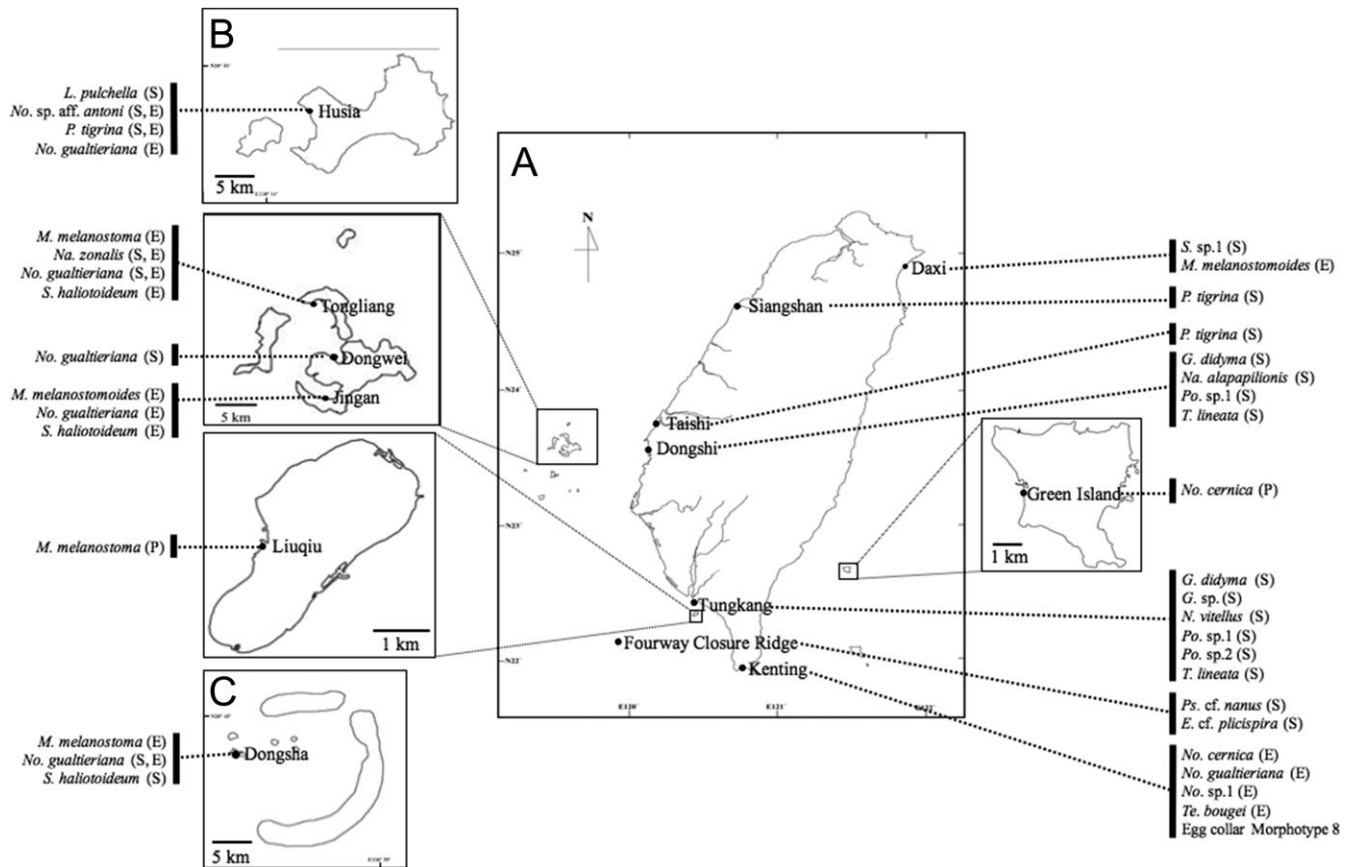


Figure 1. Collection localities of naticid egg collars and adults in Taiwan. **A.** Mainland Taiwan, Penghu (Pescadores Is.), Liuqiu I. and Green I. (see insets). **B.** Kinmen I. off Xiamen, China. **C.** Dongsha (Pratas Atoll), South China Sea. Each locality is provided with a list of species for which the adult snail (S) and/or egg collar (E) were either collected and sequenced, or photographed only (P). Generic abbreviations: *E.*, *Euspira*; *G.*, *Glossaulax*; *L.*, *Laguncula*; *M.*, *Mammilla*; *N.*, *Natica*; *Na.*, *Naticarius*; *No.*, *Notocochlis*; *P.*, *Paratetonatica*; *Po.*, *Polinices*; *Ps.*, *Pseudopolinices*; *S.*, *Sinum*; *T.*, *Tanea*; *Te.*, *Tectonatica*. Except at Four-Way Closure Ridge (depth 1,648 m), all specimens were collected either in the intertidal or shallow subtidal zones.

Table 1. Collection localities in Taiwan (see Fig. 1 for map) of sequenced specimens and egg collars, with museum accession numbers (NMNS-7708-0xx) in parentheses.

| Species | Adult animal | Egg collar | Habitat; remarks |
|--|--|--|--|
| <i>Paratectonatica tigrina</i> (Röding, 1798) | Taishi (04); Siang-shan (03); Kinmen (02) | Kinmen (31–33) | Intertidal |
| <i>Notocochlis cernica</i> (Jousseaume, 1874) | Not available | Kenting (49) | Subtidal; collar photographed in field only; COI and 16S sequences of adults from Hülsken (2008) |
| <i>Notocochlis gualtieriana</i> (Récluz, 1844) | Dongsha (19, 20); Penghu (21–24) | Dongsha (34,60); Penghu (35, 36, 40); Kenting (37–39); Kinmen (41) | Intertidal to subtidal |
| <i>Notocochlis</i> sp. aff. <i>antoni</i> | Kinmen (16–18) | Kinmen (55–57) | Intertidal |
| <i>Notocochlis</i> sp. 1 | Not available | Kenting (59) | Subtidal; COI sequences of adults from Hülsken (2008) |
| <i>Naticarius alapapilionis</i> (Röding, 1798) | Dongshi market (15) | Not available | Subtidal trawl |
| <i>Naticarius zonalis</i> (Récluz, 1850) | Penghu (14) | Penghu (50, 51) | Intertidal |
| <i>Natica vitellus</i> (L., 1758) | Tungkang market (01) | Not available | Subtidal trawl |
| <i>Tectonatica bougei</i> Sowerby, 1908 | Not available | Kenting (58) | Subtidal; egg collar photographed in field, not sequenced; 16S sequences of adults from Hülsken (2008) |
| <i>Sinum halioideum</i> (L., 1758) (= <i>planulatum</i> Récluz in Chenu, 1843) | Dongsha (museum spec. NMNS-007263-00015) | Penghu (42–46) | |
| <i>Sinum</i> sp. | Daxi market (05) | Not available | Deep-sea trawl |
| <i>Mammilla melanostoma</i> (Gmelin, 1791) | Not available | Penghu (48); Dongsha (47) | COI and 16S sequences of adults from Hülsken (2008) |
| <i>Mammilla melanostomoides</i> (Quoy & Gaimard, 1832) | Not available | Penghu (53); Daxi (52) | COI and 16S sequences of adults from Hülsken (2008) |
| <i>Polinices flemingianus</i> (Récluz, 1844) | Kenting (09) | Not available | Subtidal |
| <i>Polinices</i> sp. 1 | Dongshi (06) and Tungkang (07) markets | Not available | Commercial subtidal trawl |
| <i>Polinices</i> sp. 2 | Tungkang market (08) | Not available | Commercial subtidal trawl |
| <i>Glossaulax didyma</i> (Röding, 1798) | Tungkang (12) and Dongshi (11) markets | Not available | Commercial subtidal trawl |
| <i>Glossaulax</i> sp. | Tungkang market (10) | Not available | Commercial subtidal trawl |
| <i>Tanea lineata</i> (Röding, 1798) | Tungkang (27, 28) and Dongshi (29, 30) markets | Not available | Commercial subtidal trawl |
| <i>Euspira</i> cf. <i>placispira</i> (Kuroda, 1961) | 1648 m, Four Way Closure Ridge, 22° 5.01'N, 119° 48.04'E (25) | Not available | Research deep-sea trawl |
| <i>Pseudopolinices</i> cf. <i>nanus</i> (Møller, 1842) | 1,648 m, Four Way Closure Ridge, 22° 5.01'N, 119° 48.04'E (26) | Not available | Research deep-sea trawl |
| <i>Laguncula pulchella</i> Benson, 1842 | Husia, Kinmen (13) | Not available | Intertidal |
| undetermined species | Not available | Kenting (54) | Subtidal (SCUBA) |

was placed in extraction solution with 0.5 g of glass beads (Sigma G-9268, 425–600 µm) and homogenized with a benchtop Mini-BeadBeater (BioSpec 3110BX). Samples were then lysed and centrifuged several times to precipitate nuclei and debris. Finally, 50 µl double-distilled water was added to the resulting DNA pellets, which were stored at –20 °C for later use.

The primers used for PCR amplification of COI and 16S rRNA genes are listed in Table 2. Amplification was conducted in a thermal cycler (Applied Biosystems 2720). PCR conditions were those used by Hülsken (2008). The COI setting was as follows: 95 °C, 5 min (denaturation); 39.5 °C, 45 s (annealing) and 72 °C, 1 min (elongation), followed by another 38 cycles: 95 °C for 20 s (denaturation); 39.5 °C for 35 s (annealing) and 72 °C for 40 s

(elongation); after the last cycle, conditions were set to 95 °C for 10 s (denaturation); 39.5 °C for 10 s (annealing) and 72 °C for 2 min for final elongation. Conditions for 16S were as follows: 95 °C, 5 min (denaturation); 49 °C, 45 s (annealing) and 72 °C, 1 min (elongation), followed by another 38 cycles: 95 °C for 25 s (denaturation); 49 °C for 25 s (annealing) and 72 °C for 35 s (elongation); after the last cycle, conditions were set at 95 °C for 10 s (denaturation); 49 °C for 10 s (annealing); and 72 °C for 2 min for final elongation. The amplified DNA was directly sequenced on an automated DNA sequencer (Applied Biosystems 3730xl DNA Analyzer). Additional sequences from Hülsken (2008) were also used. Sequences of *Cypraea tigris* (Cypraeidae), *Planaxis sulcatus* (Planaxidae) and *Strombus luhuanus* (Strombidae)

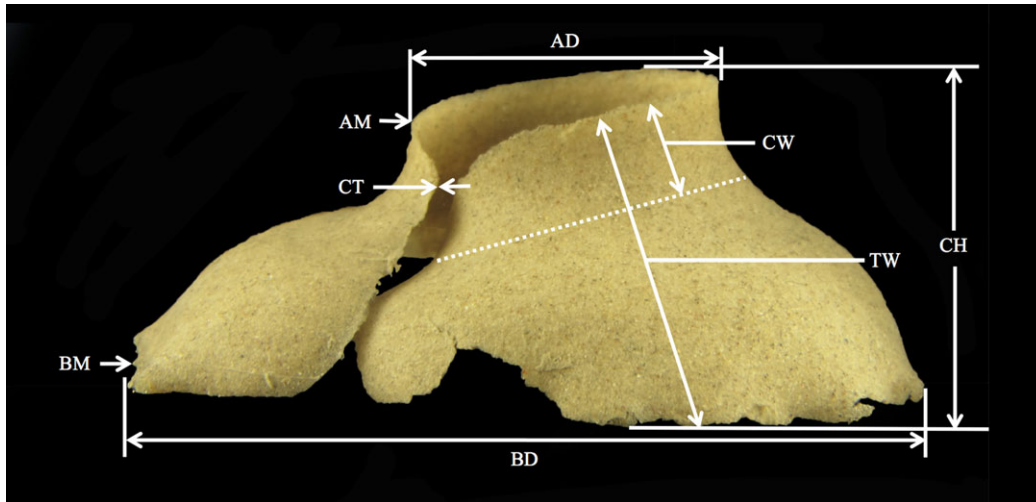


Figure 2. Egg collar of *Paratectonatica tigrina*, illustrating terms used and measurements made on egg collars. Abbreviations: AD, apical diameter; AM, apical margin; BD, basal diameter; BM, basal margin; CH, maximum collar height; CT, collar thickness; CW, crown width; TW, total width.

from Colgan *et al.* (2007) and Hülsken (2008) were used as out-group taxa.

The sequences were aligned with those of other naticid species from Hülsken (2008) (Table 1) using CLUSTAL W in MEGA v. 6 (Tamura *et al.*, 2013), using the Kimura 2-parameter model and maximum-likelihood (ML) method (Kimura, 1980). Bootstrap probability (BS) estimates (1,000 replicates) (Felsenstein, 1985) were also made to indicate robustness of nodes in neighbour-joining trees.

RESULTS

Molecular data analysis

For the COI gene, 52 sequences representing 21 species (Table 1, Fig. 1) were obtained from adults and egg collars. These were based on 29 adult animals and 23 collars, the latter representing eight naticid species, respectively. These sequences were analysed together with 51 naticid species sequenced by Hülsken (2008).

A total of 52 16 S sequences were examined, corresponding to 21 species (Table 1; Fig. 1). These sequences were based on 23 adult animals and 29 egg collars, of which collars represented ten naticid species. They were analysed together with the sequences of a further 40 naticid species from Hülsken (2008).

The resulting sequence lengths of COI and 16 S for naticid species were approximately 410 and 400 bp, respectively (Supplementary Material Tables S1, S2). In general, species sequence divergences of COI were greater than those of 16 S (see Table 3). For COI, the within-species ranges were between 0.000 and 0.035 for *Notocochlis gualtieriana* and between 0.014 and 0.028 for *N. sp. aff. antoni*. For 16 S, the within-species range was between 0.000 and 0.018 for *Sinum haliotoideum*, while *Paratectonatica tigrina*, *Naticarius zonalis* and *Mammilla melanostomoides* showed no variation in genetic distance across individuals. Within genera, sequence divergences ranged from 0.046–0.079 (*Mammilla*) to 0.053–0.222 (*Naticarius*) for COI, and 0.013–0.166 (*Naticarius*) to 0.063–0.093 (*Sinum*) for 16 S.

COI and 16 S sequences provided by Hülsken (2008) and Colgan *et al.* (2007) were analysed together with those obtained in this study. At the species level, COI and 16 S sequences of adults and egg collars of the same species from different localities always grouped together into the same clades with good BS support—see, for example, *M. melanostoma* and *N. zonalis* (Fig. 3; both COI and 16 S trees). However, there was one undetermined egg collar species (Morphotype 8 Kenting in Fig. 3), which clustered with the *Tanea* clade in the COI tree but grouped with *Euspira* in the 16 S

tree. The COI sequence of *Euspira cf. plicispira* obtained from Four-Way Closure Ridge in the South China Sea was consistent with those from the Philippines obtained by Hülsken (2008).

The COI analysis suggested that a cryptic species may be involved in *Notocochlis cernica*. Here, the sequence of an individual from the Philippines (sequence number 85211 of Hülsken, 2008) was assigned to *N. cernica s. s.* together with an egg collar from Kenting (Fig. 5B, C). This species was distinguished from another *Notocochlis* species, here assigned to *Notocochlis sp. 1*, based on sequences from Australia and Indonesia (85112 and 91111 of Hülsken, 2008), which clustered with an undetermined egg collar, also from Kenting.

Resolution at the generic level and below was poor in both trees. Only the genera *Naticarius*, *Tanea* and *Conuber* received significant BS support. Relationships between the genera were not resolved.

The deep-sea circumboreal naticid *Pseudopolinices cf. nanus* clustered with *Laguncula pulchella* (= *Euspira fortunei* of authors; it is disputed that *L. pulchella* may be a freshwater viviparid or assimineid) in the 16 S tree (BS = 85%; Fig. 3B). No COI sequence was available for *Pseudopolinices*.

Morphology

A total of nine egg collars were matched with the corresponding adult species based on genetic distances that fell within the intra-specific range assessed for adults (Table 3). These comprised six naticine, one sinine and two polinicine species in six genera. The six naticines were *Paratectonatica tigrina*, *Notocochlis cernica*, *N. gualtieriana*, *N. sp. aff. antoni*, *Naticarius zonalis*, and *Tectonatica bougei* (based on an undetermined collar from Kenting); the two polinicines were *Mammilla melanostoma* and *M. melanostomoides*, and the single sinine was *Sinum haliotoideum*. One egg collar was identified as *Notocochlis sp. 1* (based on an undetermined collar from Kenting; morphotype 9 in Fig. 3) and another as a possible *Euspira* or *Tanea* sp. (also based on an undetermined collar from Kenting; morphotype 8 in Fig. 3).

Descriptions of the adult shell, operculum, animal (where available) and egg collar (see Fig. 2 for terms and measurements used) for each species are provided below.

Paratectonatica tigrina (Röding, 1798)

(Fig. 4)

Shell (Fig. 4A, B): small, SH 21.5 mm; high-spired; suture narrow, not deep; periostracum thin, yellow brown with fine axial lines. Several rows of dark brown to black, sometimes overlapping

dashes over yellowish white background. Surface of last whorl smooth, with no axial undulations. Aperture wide, white; columella narrow; umbilicus open, funicle relatively small.

Operculum (Fig. 4D, E): calcareous, white, external surface slightly concave, with 2 narrow semicircular flattened ribs that terminate at inner edge adjacent to columella, where operculum is thickest (1.5 mm). Outer rib at edge of operculum, where it is thinnest, bears numerous fine, flattened granules along entire outer edge. Inner rib generally smooth, with some granules near edges of

operculum. The two ribs separated by a narrow groove. Internal surface smooth, greenish yellow, with thin corneous layer. L 13.0 mm, W 8.1 mm (for SH 21.5 mm).

Animal (Fig. 4C): foot uniformly translucent grey. Tentacles translucent grey, with anterior edges lined with black.

Egg collar (Fig. 4F–H; $n = 3$): 1–1.5 whorls, basal margin wavy in horizontal plane. Apical margin smooth, not thickened. BD 42–58 mm; AD 15–24 mm, about half BD; TW 17–23 mm; CT

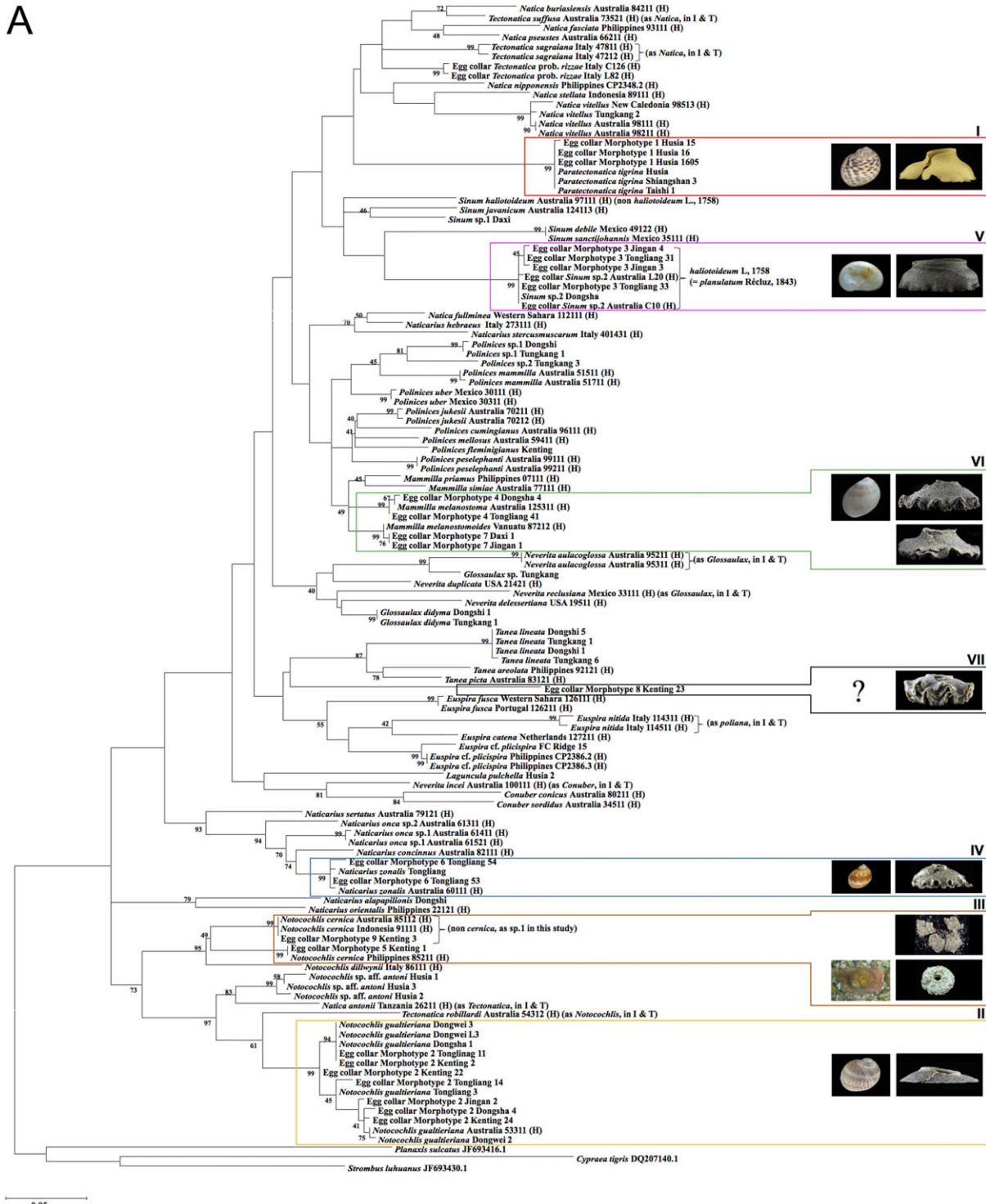


Figure 3. Continued on next page

B

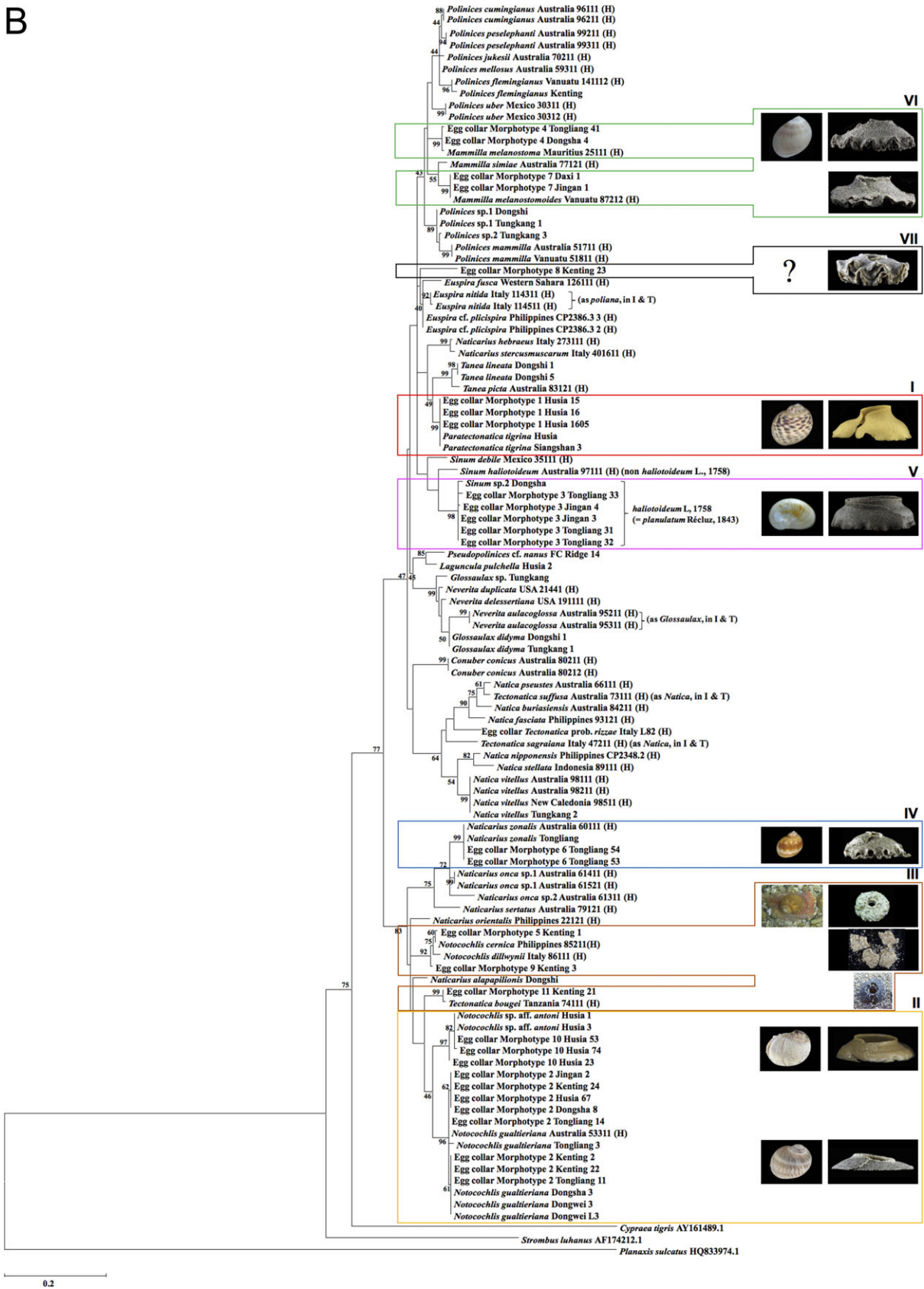


Figure 3. Maximum-likelihood trees based on mitochondrial COI and 16 S sequences obtained from egg collars and adult Naticidae in Taiwan, combined with additional data from Hülksen (2008). **A.** Mitochondrial COI tree. **B.** Mitochondrial 16 S rRNA tree. Roman numerals I–VII represent species groupings based on the suggested egg-collar classification (Table 4). Species sequenced by Hülksen are marked (H), together with localities and original reference numbers of Hülksen (2008: appendix 6.1). Egg collars sequenced in this study are labelled according to *a priori* Morphotypes 1–11, with collection localities in Taiwan; adults are labelled with collection localities only; reference numbers following localities correspond to voucher specimens deposited in National Museum of Natural Science, Taichung (see Table 1 for accession numbers).

Table 2. Forward (F) and reverse (R) PCR primers used for PCR amplification of COI and 16S rRNA genes, following Hülsken (2008).

| Gene | Name | Sequence 5' to 3' |
|------|----------|--------------------------------|
| COI | P388 (F) | GCTTTTGTATAATTTTYTT |
| COI | P390(R) | CGATCAGTTAAARTATWGTAAT |
| 16S | P744 (F) | ATARRGAGTCGGACCTGCCAGTGAT |
| 16S | P745(R) | AGAATTTTAAATGGTGAACAGACCAACCYT |

The IUB code for mixed base is used: N = G, A, T, C; V = G, A, C; D = G, A, T; B = G, T, C; H = A, T, C; W = A, T; M = A, C; R = A, G; K = G, T; S = G, C; Y = C, T.

0.6–1 mm; CH 18–23 mm; CW 4–9 mm, prominent, about 2/5 CH. Capsules medium-sized, diameter (D) 170–245 µm, arranged haphazardly within collar, density 2–3 capsules mm⁻²; each containing single embryo/larva.

Remarks: better known by its junior synonym *Natica maculosa* Lamarck, 1822 in older literature, it was placed in its own genus *Paratectonatica* by Azuma (1961) in view of its radula, where two subequal cusps flank the central cusp on either side, resembling the condition observed in members of the genus *Sinum*. Kabat (2000), however, assigned *tigrina* to *Notocochlis*, which Kabat (1991) considered as a possible senior synonym of *Paratectonatica*. The species has a wide geographical distribution, ranging from the Mascarene Islands in the Indian Ocean to Queensland, Australia (Poutiers, 1998).

***Notocochlis cernica* (Jousseume, 1874)** (Fig. 5)

Shell (based on illustration by Saito, 2000: 261, pl. 130, fig. 48 and unnumbered figure showing living animal; see also Kabat, 2000; Hülsken, 2008): small, SH 20 mm, high-spined; suture weak, shallow; surface with yellow-brown periostracum with 2 or 3 narrow light-coloured spiral bands connected by more numerous but thinner axial bands in shape of chevrons (Fig. 5A). Aperture wide, columella narrow, with open umbilicus; moderate-sized funicle partially occluding umbilicus.

Operculum: calcareous, white; external surface bears two grooves on outer margin (based on Hülsken, 2008).

Animal (Fig. 5A): foot translucent white with red spotting on dorsal surface (see also Saito, 2000).

Egg collar (Fig. 5B, C; $n = 1$): 2.5 whorls, basal margin slightly wavy along vertical axis. Apical margin well defined. BD 41 mm, AD 13.7 mm, about 1/3 BD; TW 16 mm, CT 2 mm. CH undetermined, CW 1.5 mm. Capsules small, D 140–155 µm, arranged haphazardly inside collar; density 3.4 capsules mm⁻², each containing single embryo/larva.

Remarks: adult shell resembles *N. gualtieriana* (see below) but the shell of *N. cernica* is thinner and sutures are weak (Torigoe & Inaba, 2011). The shell of *Naticarius zonalis* could be confused with *N. cernica*, but the operculum in *Naticarius* species bears 5–8 curved grooves along the outer edge, in contrast to only 1–2 curved opercular grooves in species of *Notocochlis* (see also Kabat, 2000). We have also distinguished *N. cernica* from a possibly cryptic *Notocochlis* species, based on their COI and 16S sequences (COI absolute genetic distance = 0.083 ± 0.000; 16S = 0.015 ± 0.003). The latter species is likely to be the *N. cernica* sequenced by Hülsken (2008) from Australia and Indonesia.

***Notocochlis gualtieriana* (Récluz, 1844)** (Fig. 6)

Shell (Fig. 6A–D): small, SH 23.3 mm; high-spined; suture narrow, not deep; surface with yellow-brown periostracum with fine axial

lines; shell colour varies between having numerous (about 15) discontinuous brown axial lines interrupted by two whitish spiral bands, to almost uniformly grey-brown with only faint evidence of axial lines. Anterior region of shell usually white, as is area just below suture defining the separation between penultimate and last whorls. Surface of last whorl with 18–20 narrow, raised axial undulations that become flattened towards base of shell. Aperture wide, white; columella narrow; umbilicus open with medium-sized funicle.

Operculum (Fig. 6E, F): calcareous, white, with greyish-brown concretion near anterior end. External surface slightly convex; single, narrow, peripheral flattened rib present along its outer edge corresponding to outer lip of shell. Operculum thickest (1.8 mm) along inner edge that is in contact with shell columella. Entire rib surface smooth, narrow, flat and devoid of granules. Internal surface smooth, greenish yellow, with thin corneous layer. L 14.3 mm, W 8.9 mm (for SH 23.3 mm).

Animal: foot translucent white, with very densely distributed brown to dark brown maculation on dorsal surface. Tentacles black-tipped, otherwise white.

Egg collar (Fig. 6G–L; $n = 9$): 1.5–3.5 whorls, basal margin slightly wavy or flat, entire collar flattened with low profile. Apical margin well defined, smooth. BD 10–44 mm, AD 6–20 mm, about half BD; TW 4–18 mm; CT 0.3–1.2 mm; CH 2.5–11 mm; CW 0.5–2.3 mm, narrow, about 1/5 CH. Capsules small, D 115–140 µm, arranged haphazardly inside collar, density 4–10 capsules mm⁻², each containing single embryo/larva.

Remarks: this and the next species are very similar in the morphology of their shells, opercula as well as foot pigmentation. The colour and pigmentation pattern of their shells appear to be highly variable, resulting in a long list of synonymies that have not been verified. The gross morphology of the egg collar agrees with the illustration provided by Kay (1979), p. 242, fig. 82B. *Notocochlis gualtieriana* has a wide, Indo-Pacific distribution ranging from East Africa to Hawaii (Poutiers, 1998).

***Notocochlis* sp. aff. *antoni* (Philippi, 1851)** (Fig. 7)

Shell (Fig. 7A, B): small, SH 15.8 mm; high-spined; suture narrow, not deep; periostracum yellow-brown with fine axial lines; shell colour almost uniformly grey-brown without markings. Anterior region of shell usually white, as is area just below suture defining the separation between penultimate and last whorls. Surface of last whorl has about 14 narrow axial raised undulations that become flattened towards base of shell. Aperture wide, white; columella narrow; umbilicus nearly closed by large funicle.

Operculum (Fig. 7C, D): calcareous, white, external surface slightly convex, with single, narrow peripheral flattened rib along outer edge, matching curvature of shell outer lip. Operculum thickest (1.1 mm) along inner edge making contact with shell columella. Entire rib surface smooth, narrow, flat, devoid of granules. Internal surface smooth, greenish yellow, with thin corneous layer and slightly protruding, brown nucleus. L 9.6 mm, W 6.0 mm (for SH 15.0 mm).

Animal: foot translucent white, with brown to dark brown spotting on dorsal surface. Tentacles black-tipped, otherwise white.

Egg collar (Fig. 7E–G; $n = 3$): 1–2 whorls, basal margin slightly wavy or flat. Apical margin smooth, slightly recurved. BD 31–47 mm; AD 14–20 mm, about half BD; TW 12–16 mm, CT 0.6–1.2 mm. CH 9–16 mm, CW 1.1–3.3 mm, 1/5 to 1/10 CH. Capsules small, D 90–130 µm, arranged haphazardly inside collar, density 9–13 capsules mm⁻²; each containing single embryo/larva.

Table 3. Absolute genetic distances (\pm SD, range in parentheses, and sample size) between egg-collar sequences and their respective species examined for COI and 16S genes according to the phylogenetic trees shown in Fig. 3. **A.** Within-species distances. **B.** Within-genera distances. ND, not determined.

| A | | | | | | |
|---|--|---|---|--|---|---|
| Species | COI | | | 16S | | |
| | Within species | Between egg collars | Between adults | Within species | Between egg collars | Between adults |
| <i>Paratectonatica tigrina</i> | 0.001 \pm 0.002 (0.000–0.003) (n = 6) | 0.002 \pm 0.002 (0.000–0.003) (n = 3) | 0.000 \pm 0.000 (0.000–0.000) (n = 3) | 0.000 \pm 0.000 (0.000–0.000) (n = 5) | 0.000 \pm 0.000 (0.000–0.000) (n = 3) | 0.000 (n = 2) |
| <i>Notocochlis cernica</i> | 0.000 (n = 2) | ND (n = 1) | ND (n = 1) | 0.004 (n = 2) | ND (n = 1) | ND (n = 1) |
| <i>Notocochlis gualtieriana</i> | 0.019 \pm 0.011 (0.000–0.035) (n = 13) | 0.022 \pm 0.010 (0.000–0.035) (n = 7) | 0.018 \pm 0.012 (0.000–0.035) (n = 6) | 0.006 \pm 0.004 (0.000–0.013) (n = 13) | 0.005 \pm 0.004 (0.000–0.009) (n = 8) | 0.006 \pm 0.006 (0.000–0.013) (n = 5) |
| <i>Notocochlis</i> sp. aff. <i>antoni</i> | 0.019 \pm 0.008 (0.014–0.028) (n = 3) | ND (n = 0) | 0.019 \pm 0.008 (0.014–0.028) (n = 3) | 0.005 \pm 0.005 (0.000–0.013) (n = 5) | 0.009 \pm 0.004 (0.004–0.013) (n = 3) | 0.000 (n = 2) |
| <i>Notocochlis</i> sp.1 | 0.000 \pm 0.000 (0.000–0.000) (n = 3) | ND (n = 1) | 0.000 (n = 2) | ND (n = 1) | ND (n = 1) | ND (n = 0) |
| <i>Naticarius zonalis</i> | 0.009 \pm 0.005 (0.003–0.014) (n = 4) | 0.010 (n = 2) | 0.007 (n = 2) | 0.000 \pm 0.000 (0.000–0.000) (n = 4) | 0.00 (n = 2) | 0.000 (n = 2) |
| <i>Tectonatica bougei</i> | ND (n = 0) | ND (n = 0) | ND (n = 0) | 0.004 (n = 2) | ND (n = 1) | ND (n = 1) |
| <i>Sinum halioideoideum</i> | 0.005 \pm 0.003 (0.000–0.010) (n = 5) | 0.006 \pm 0.003 (0.000–0.010) (n = 4) | ND (n = 1) | 0.007 \pm 0.005 (0.000–0.018) (n = 6) | 0.005 \pm 0.005 (0.000–0.013) (n = 5) | ND (n = 1) |
| <i>Mammilla melanostoma</i> | 0.005 \pm 0.002 (0.003–0.007) (n = 3) | 0.007 (n = 2) | ND (n = 1) | 0.006 \pm 0.003 (0.004–0.009) (n = 3) | 0.004 (n = 2) | N.D (n = 1) |
| <i>Mammilla melanostomoides</i> | 0.002 \pm 0.002 (0.000–0.003) (n = 3) | 0.000 (n = 2) | ND (n = 1) | 0.000 \pm 0.000 (0.000–0.000) (n = 3) | 0.000 (n = 2) | ND (n = 1) |

| B | | |
|--------------------|--|--|
| Genus | COI | 16S |
| <i>Notocochlis</i> | 0.128 \pm 0.025 (0.072–0.198) (n = 24) | 0.063 \pm 0.013 (0.013–0.098) (n = 22) |
| <i>Naticarius</i> | 0.152 \pm 0.043 (0.053–0.222) (n = 13) | 0.099 \pm 0.047 (0.013–0.166) (n = 12) |
| <i>Mammilla</i> | 0.059 \pm 0.010 (0.046–0.079) (n = 8) | 0.049 \pm 0.008 (0.036–0.055) (n = 7) |
| <i>Sinum</i> | 0.133 \pm 0.012 (0.091–0.164) (n = 12) | 0.073 \pm 0.008 (0.064–0.084) (n = 8) |

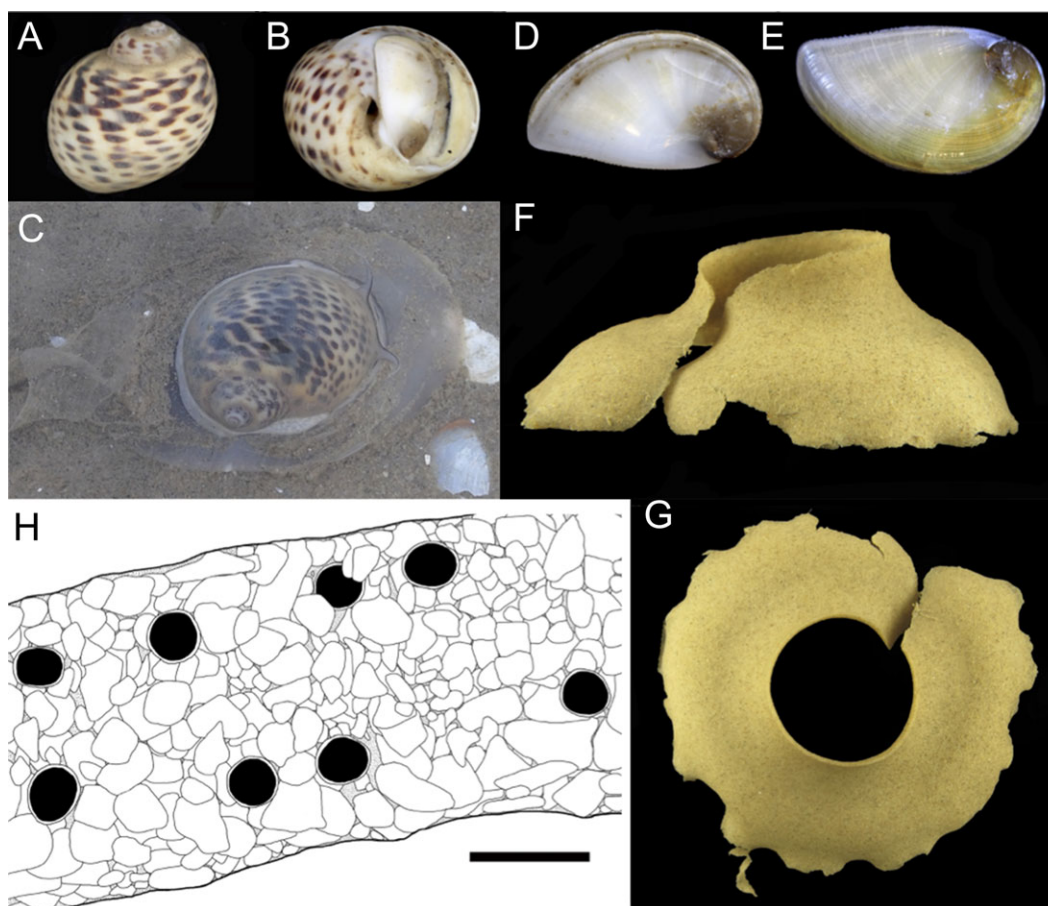


Figure 4. *Paratectonatica tigrina* (Röding, 1798), Husia, Kinmen. **A, B.** Shell; SH 21.5 mm. **C.** Living animal. **D, E.** Operculum; L 13.5 mm. **D.** External surface. **E.** Internal surface. **F–H.** Egg collar. **F.** Side view; CH 20 mm. **G.** Top view; BD 55 mm. **H.** Cross-section showing egg capsules (black spheres) among sand grains; scale bar = 1 mm.

Remarks: our Taiwan specimens strongly resemble the shells of *Natica* ‘*lurida*’ illustrated by Philippi (1852: pl. 3, figs 12, 13), although the origin of these shells is unknown. In the same monograph, three other shells (plate 12, figs 2–4) were labelled as follows: fig. 2: *N. lurida* from Havana; fig. 3: *N. lurida* from Sandwich Islands (Hawai’i); fig. 4: *N. lurida* from China (although it is stated as ‘Lieukieusinseln’, i.e. Ryukyu Islands, in the text; Ryukyu at that time could have included Taiwan). Except for plate 12: fig. 2, all the other illustrated shells also bear a strong resemblance to our specimens collected in Taiwan. Philippi (1836) first referred to *N. lurida* in his treatment of naticids from Sicily, when providing a correction to a species he described earlier, named *Natica intermedia*. In the corrigendum, he referred *intermedia* to *marochiensis* Gmelin in Lamarck, but noted that the shells which Chemnitz figured in plate 188: figs 1907 and 1908 were similar to but not *marochiensis*, and hence named them as *luridum*. Chemnitz’s figures are now referable to *marochiensis* Gmelin, 1791. Later, Philippi (1852) synonymized *luridum* and *marochiensis* under ‘*maroccana* Chemnitz’, which is *marochiensis* Gmelin (Coan & Kabat, 2017), a tropical Atlantic species (see also Table 5). To add to the confusion, *lurida* is a name that has been synonymized with *N. gualtieriana* and to a lesser extent, *N. cernica* (see e.g. Torigoe & Inaba, 2011), although they are clearly different as shown in our study.

We have instead referred our specimens to another closely related species *Notocochlis antoni* Philippi, 1851 (also often synonymized with *N. gualtieriana*; see e.g. Kilburn, 1976; Kabat, 2000; Torigoe & Inaba, 2011) originally described from the Ryukyu Islands, despite their differences: (1) *N. antoni* has a shiny, smooth shell surface,

as opposed to the rather rough surface (due to the axial undulations present) that is consistent across all specimens observed in this study; (2) the umbilicus of the shell of *N. antoni* is covered by a callus, but in all of our specimens, a narrow but open umbilicus is present; (3) the COI sequence of *N. antoni* (as identified by Hülsken, 2008) appears to be different from our specimens from Taiwan (see Fig. 3A). We are currently unable to confirm the taxonomic relationship between our specimens and *N. antoni*.

Naticarius zonalis (Récluz, 1850) (Fig. 8)

Shell (Fig. 8A, B): small, SH 14.4 mm; high-spined; suture deep; periostracum yellow brown with fine axial lines; a white spiral band lies between two dark brown bands that are unequal in width; broad darker brown spiral band about twice width of the narrow dark brown band that lies anteriormost. Anterior to this narrow brown band are about 10 brown dashes and, posterior to the broad dark brown band, there are larger irregular blotches of white and brown. Surface of last whorl has about 13 narrow raised axial undulations that become flattened towards base of shell. Aperture wide, white; columella narrow; umbilicus open, funicle relatively small.

Operculum (Fig. 8C, D): calcareous, white, external surface generally flat, bearing 8 prominent semicircular ribs that terminate at inner edge adjacent to columella, forming 8 low teeth where operculum is thickest (1.2 mm). Outermost rib at edge of operculum where it is thinnest bears numerous (>70) fine granules arranged in single

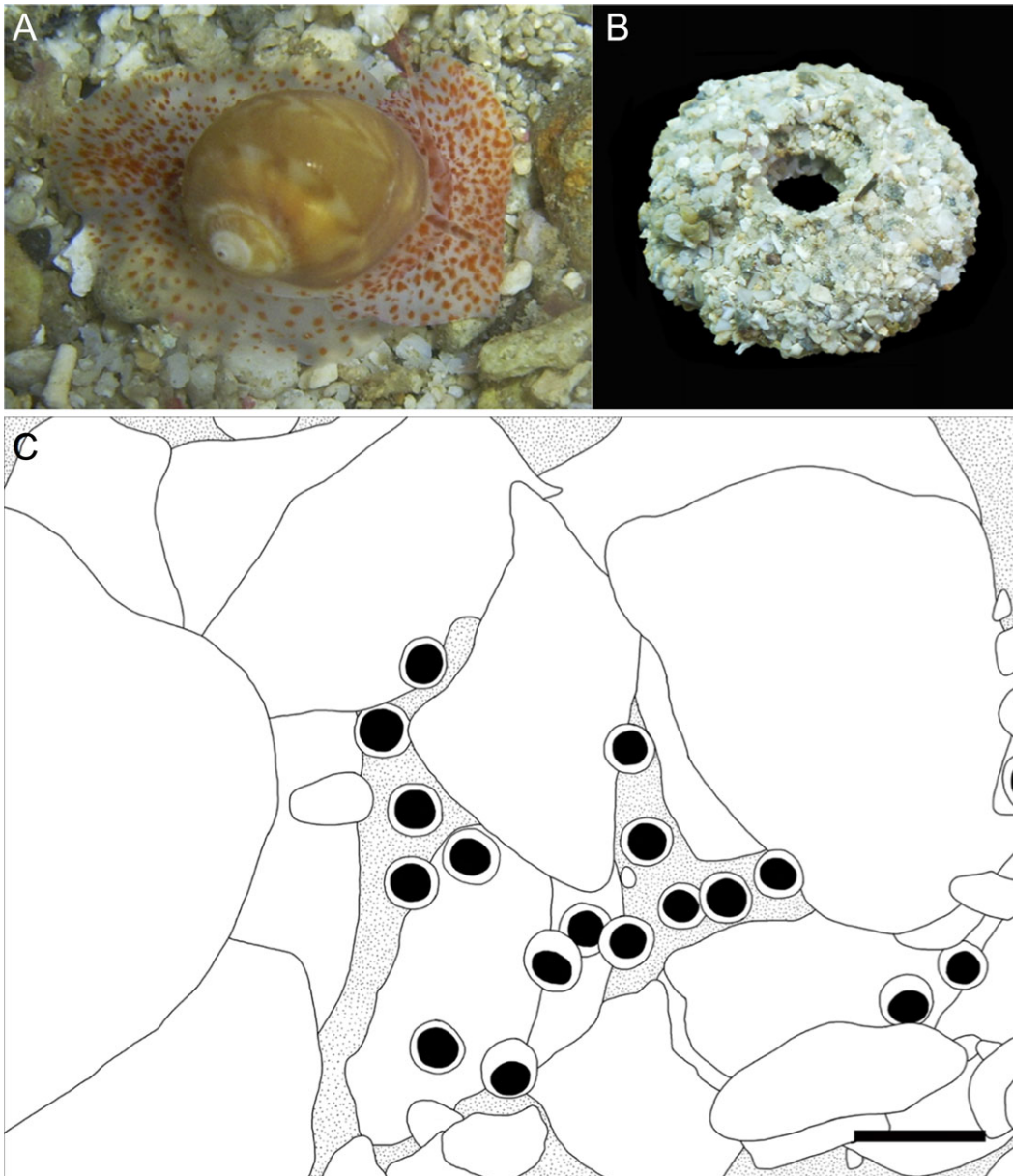


Figure 5. *Notocochlis cernica* (Jousseaume, 1874). **A.** Living animal (SH 18 mm), Green I., Taiwan. **B.** Egg collar (BD 41 mm), Kenting. **C.** Cross-section of egg collar showing egg capsules (black spheres) among sand grains; scale bar = 1 mm.

row. Ribs separated by deep grooves about as wide to half width of the ribs. Grey concretion present near anterior region (orientation when animal is withdrawn). Internal surface smooth, greenish yellow, with thin corneous layer. L 7.9 mm, W 4.7 mm (for SH 14.4 mm).

Animal: foot translucent white with densely distributed pink or light red dashes on dorsal surface.

Egg collar (Fig. 8E–G; $n = 2$): 2–3.5 whorls, basal margin wavy along vertical axis; the waves traced by successive whorls are out of phase with each other. BD 25–36 mm, AD 6–8 mm, about 1/5 BD; TW 12–15 mm; CT 0.9–1.5 mm; CH 8–11.6 mm; CW 1–2 mm, narrow, about 1/11 CH. Capsules large, D 470–550 μm , arranged in single layer inside collar; density 0.5–1.1 capsules mm^{-2} , each containing single embryo/larva.

Remarks: this species was synonymized with *Naticarius sertatus* (Menke, 1843) by Torigoe & Inaba (2011), but the two species

are clearly distinguished based on COI, 16S, 18S and H3 sequences by Hülksen (2008). The shells of *N. concinnus* (Dunker, 1860) and *N. manceli* (Jousseaume, 1874) also resemble *N. zonalis* to different degrees. In the case of *N. concinnus*, the COI sequences from Hülksen (2008) for this species were sufficiently different from those we obtained from adults and egg masses in Taiwan (Fig. 3) to distinguish the two species, although their egg masses are strikingly similar. As for *N. manceli*, there were no sequences available for this species, but here we regard it sufficiently different conchologically from *N. zonalis*.

***Tectonatica bougei* Sowerby, 1908**

(Fig. 9)

Shell: small, SH 4.5 mm; medium-spined; suture shallow; surface with thin periostracum. Shell generally white with dark- or reddish-brown irregular markings. Protoconch region also reddish

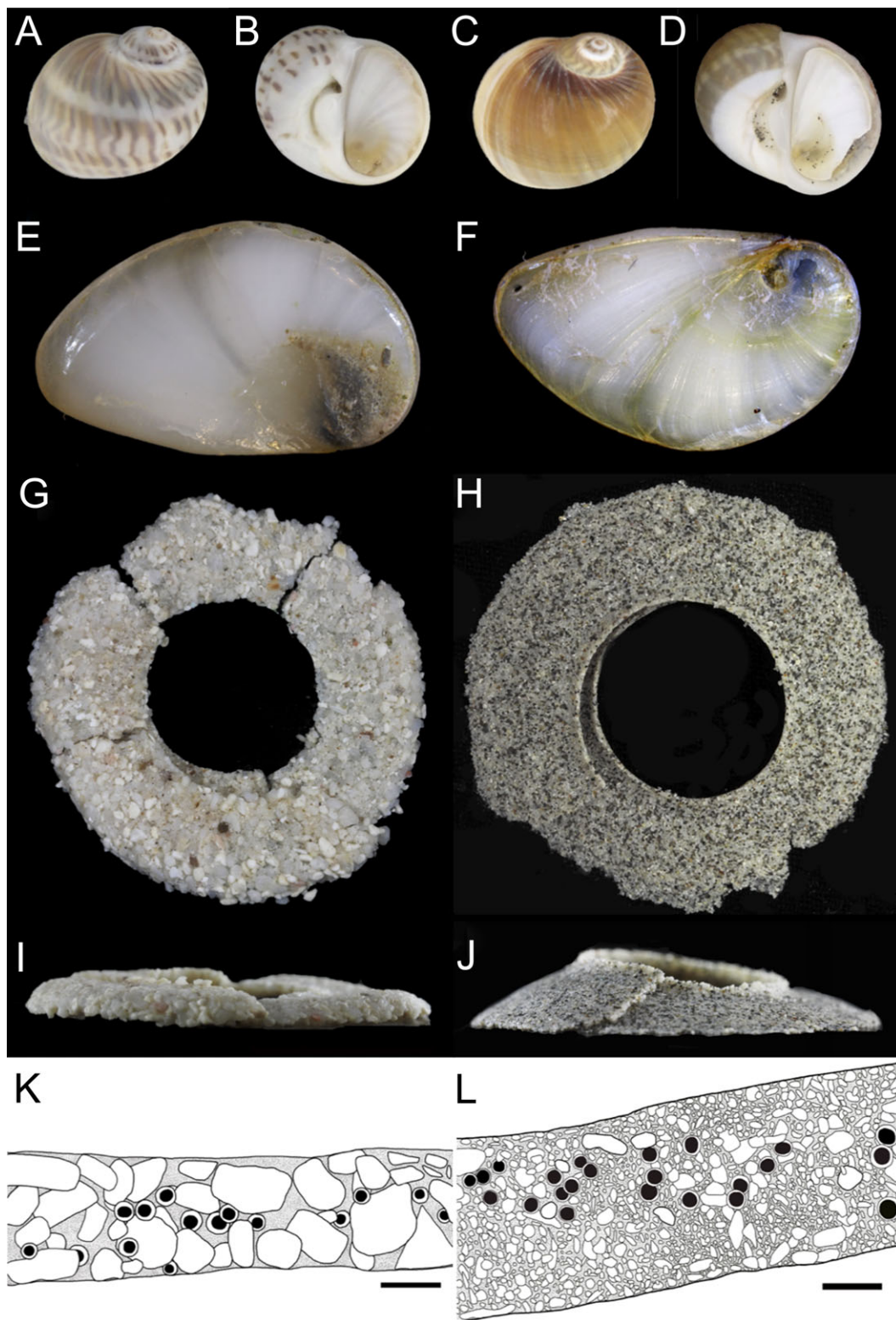


Figure 6. *Notocochlis gualtieriana* (Récluz, 1844). **A–D.** Shell. **A.** Dongsha; SH 15.6 mm. **B.** Dongsha, ventral view with operculum. **C.** Dongwei, dorsal view; SH 16.5 mm. **D.** Dongwei, ventral view with operculum. **E, F.** Operculum, Tongliang; L 10.0 mm. **E.** External surface. **F.** Internal surface. **G–L.** Egg collars. **G, I, K.** Dongsha, top, side view and cross section; BD 32 mm; CH 3 mm. **H, J.** Jingan, top and side view; BD 31 mm; CH 5 mm; **L.** Dongwei, cross-section. Scale bars **K, L** = 1 mm.

brown. Aperture wide, white, with moderately broad columella and closed umbilicus with large funicle (based on Hülsken, 2008: fig. A.27).

Operculum: calcareous, white, external surface generally flat with single, narrow peripheral flattened rib along outer edge, corresponding to outer lip of shell (based on Hülsken, 2008: fig. A.27).

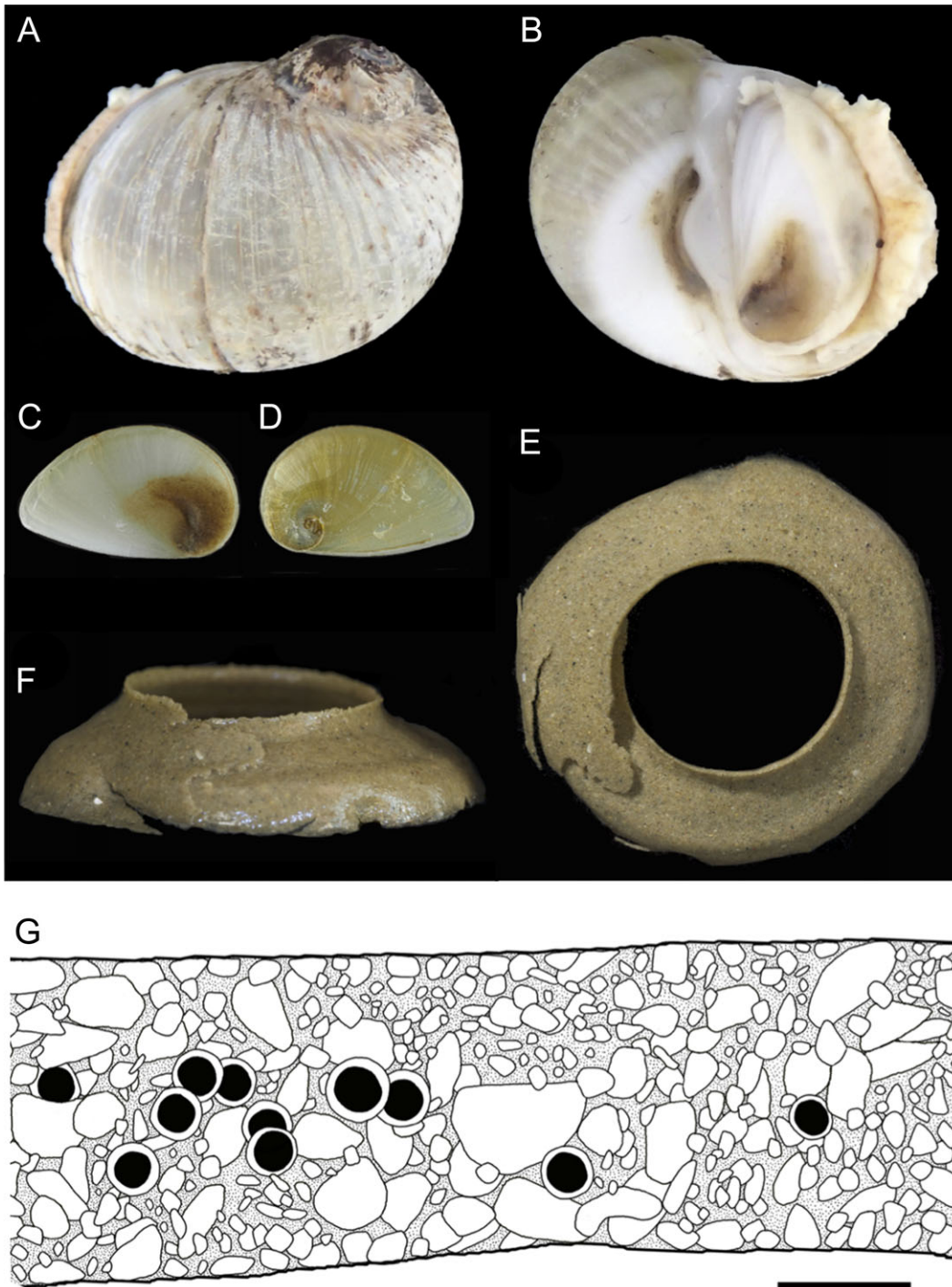


Figure 7. *Notocochlis* sp. aff. *antoni*, Husia. **A, B.** Shell; SH 15.8 mm. **C, D.** Operculum, external and internal surfaces; L 10.0 mm. **E–G.** Egg collar, top, side view and cross-section; BD 42 mm; CH 10 mm. Scale bar **G** = 1 mm.

Animal: foot translucent white, with brown spots dashes on dorsal surface of the frontal lobe (after Hülksen, 2008).

Egg collar (Fig. 9A, B; $n = 1$): 3 whorls, basal margin smooth along vertical axis. Apical margin distinct, slightly recurved. BD 8 mm, AD 2 mm, about $\frac{1}{4}$ BD; CW 3 mm, CT 0.5 mm; CH 3 mm, CW not measured. Capsules large, diameter 93–105 μm , arranged in a single layer inside collar, density 0.02 capsule mm^{-2} , each containing single embryo/larva.

Remarks: this species was considered a synonym of *Tectonatica venustula* (Philippi, 1851) by Torigoe & Inaba (2011). Based on the

holotype of *T. bougei* examined by Hülksen (2008), *bougei* has a thick shell and closed umbilicus, as opposed to the thin shell and partially open umbilicus of *venustula*. Saito (2000, 2017) also showed that the umbilicus of *T. bougei* (as *Natica bougei*) was almost completely covered by callus. However, Kabat (2000) identified a specimen from the Cook Islands showing an open umbilicus as *T. bougei*. The taxonomic significance of the state of the umbilicus appears to be played down by Torigoe & Inaba (2011). This may have led them to synonymize the two species, as well as confounding *Notocochlis gualtieriana*, whose shell has an open umbilicus, with *N.* sp. aff. *antoni*, which has a closed umbilicus. The latter two

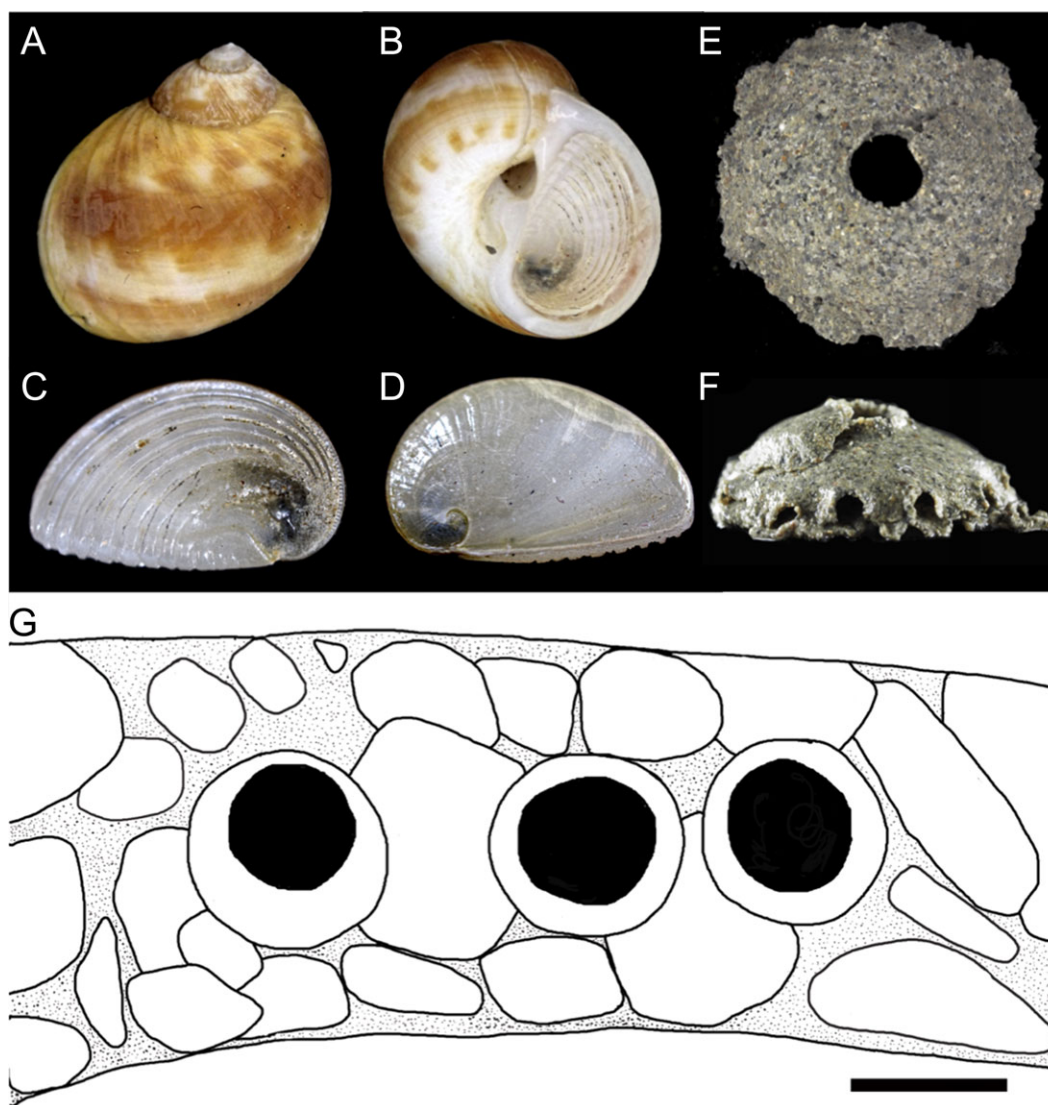


Figure 8. *Naticarius zonalis* (Récluz, 1850), Tongliang. **A, B.** Shell; SH 14.4 mm. **C, D.** Operculum, external and internal surfaces; L 7.9 mm. **E–G.** Egg collar, top, side view and cross-section; BD 28 mm; CH 11 mm. Scale bar **G** 1 mm.

species are clearly different based on our current study, reiterating the importance of the umbilicus as a taxonomic character at the species level. Its significance at the genus level may be less certain, given that species assigned to *Tectonatica* (all of which are characterized by a closed umbilicus) are generally grouped with other genera (e.g. *Natica*, *Notocochlis*) having an open or narrow umbilicus in both COI and 16S trees (Fig. 3).

***Sinum haliotoideum* (Linnaeus, 1758)**

(Fig. 10)

Shell (Fig. 10A, B): medium-sized, SL = 20–34 mm; low-spined and flattened dorsoventrally. Suture narrow, not deep. Shell surface with thin, yellow-brown periostracum with fine axial shell growth lines visible beneath it; spiral lines on shell are not visible. Shell colour almost uniformly white. Aperture wide, white, with narrow columella; umbilicus small, shallow.

Operculum: small, triangular, corneous, thin and translucent; normally buried inside foot and not visible on living animal (Saito, 2000).

Animal: Living specimen not observed. Foot large, white in preserved specimens (L 70 mm, W 20 mm, for SL 34 mm)

Egg collar (Fig. 10C–E; $n = 5$): 1–2.5 whorls, basal margin wavy along horizontal axis, and in some parts the margin is folded slightly inwards so that it is not visible from above. Apical margin smooth, upright. BD 62–87 mm, AD 33–47 mm, about half BD; CW 26–43 mm, CT 0.7–0.9 mm; CH 24–39 mm, CW 4.6–10.6 mm, about 1/4 to 1/5 CH. Capsules medium-sized, diameter (D) 170–210 μm , arranged haphazardly within collar, density 6–10 capsules mm^{-2} ; each containing single embryo/larva.

Remarks: the species names *planatum* Récluz in Chenu, 1843 and *planulatum* Récluz, 1843 have been used for this species but according to Kabat (1990), the name *haliotoideum* Linnaeus, 1758 has priority, and the lectotype chosen by Kabat is closest to the species examined in this study. Members of the subgenus *Sinum* have shells with prominent sutures and ribs in contrast to those of *Ectosinum* (Iredale, 1931), which are lacking in spiral sculpture. Based on the sequence analyses of mt COI and 16S rRNA (Fig. 3), Hülsken's (2008) '*haliotoideum*' may be another species of *Sinum*.

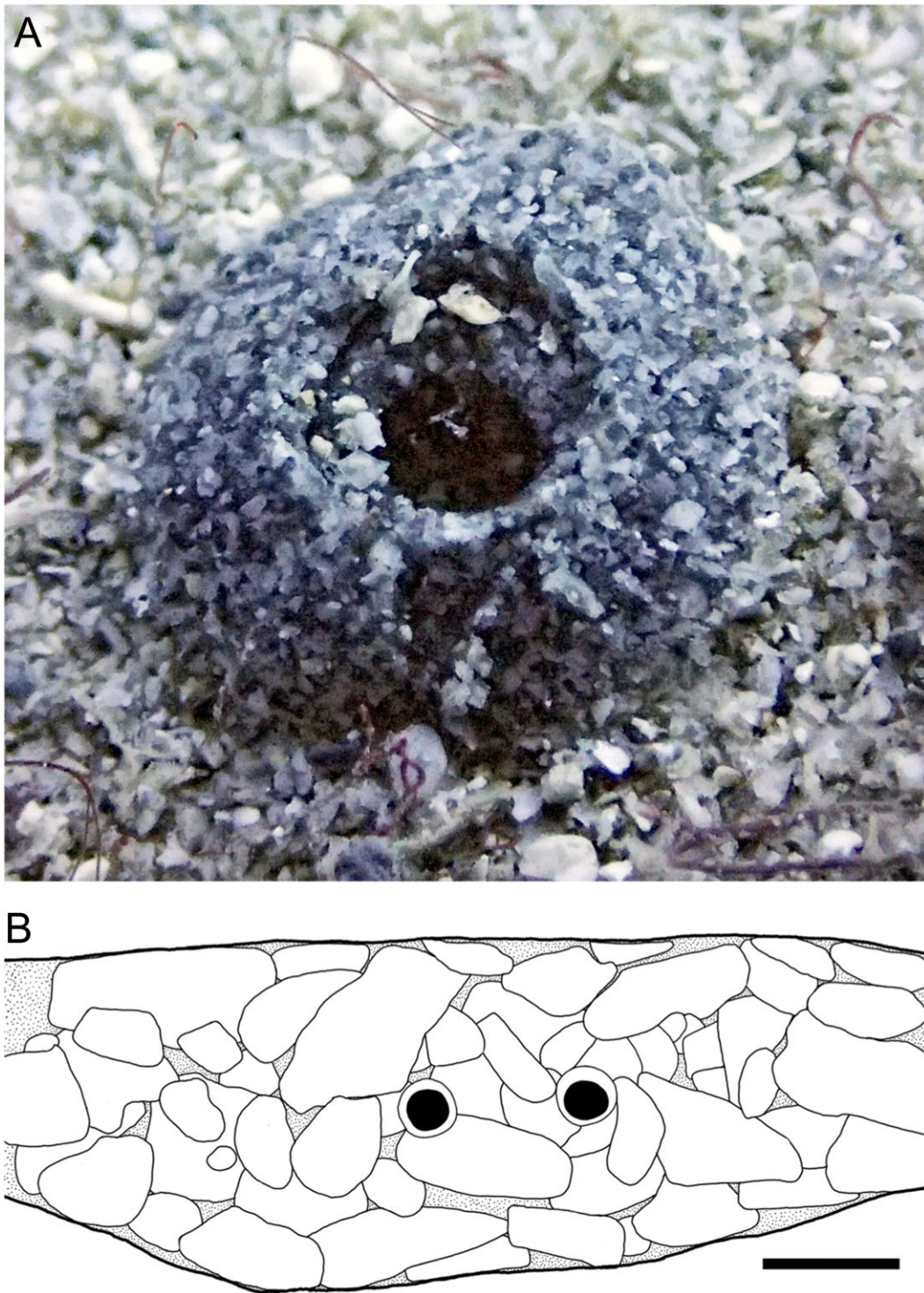


Figure 9. *Tectonatica bougei* (Sowerby, 1908), Kenting, egg collar. **A.** Field photograph; BD 8 mm. **B.** Cross-section. Scale bar **B** 1 mm.

***Mammilla melanostoma* (Gmelin, 1791)**
(Fig. 11)

Shell (Fig. 11A, B): large, SH 29 mm, high spired; suture shallow; external surface mostly white with faint brown spiral bands of different widths and fine axial lines. Spiral sculpture absent. Aperture wide, white, with narrow columella; umbilicus nearly

closed by swollen columella. Funicle absent. Both columella and umbilicus stained dark brown.

Operculum (Fig. 11C): corneous, rusty brown. L 22 mm, W 10 mm (for SH 29.0 mm); size of operculum similar to shell aperture.

Animal: foot large, white, no surface pigmentation.

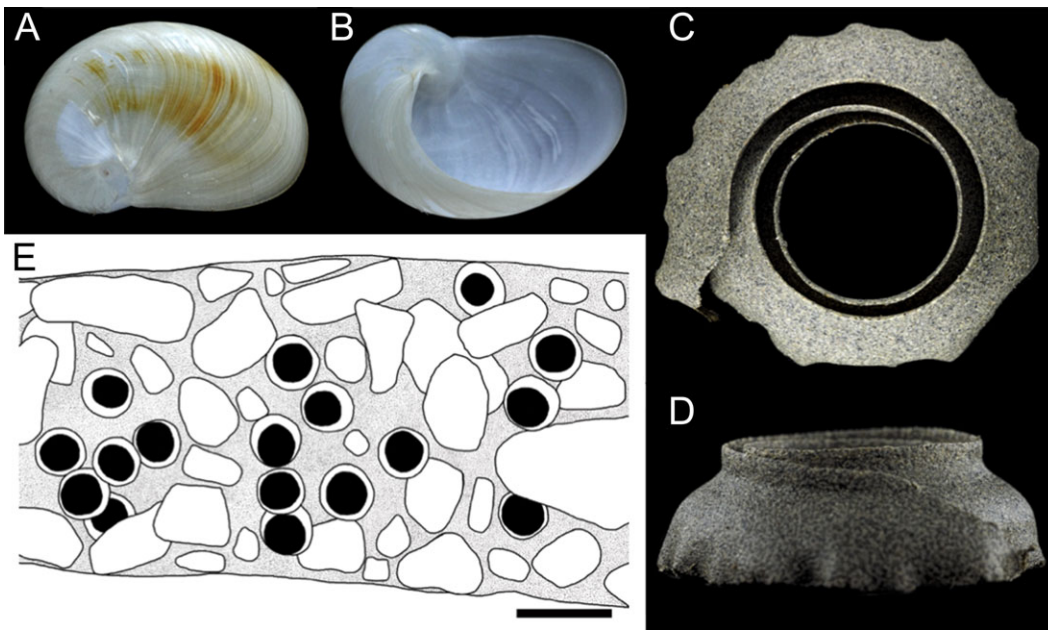


Figure 10. *Sinum haliotoideum* (Linnaeus, 1758). **A, B.** Shell, dorsal and ventral views, Penghu (NMNS 003750-00030); SL 22.0 mm. **C–E.** Egg collar, Tongliang, top, side view and cross-section; BD 74 mm; CH 25 mm. Scale bar **E** = 1 mm.

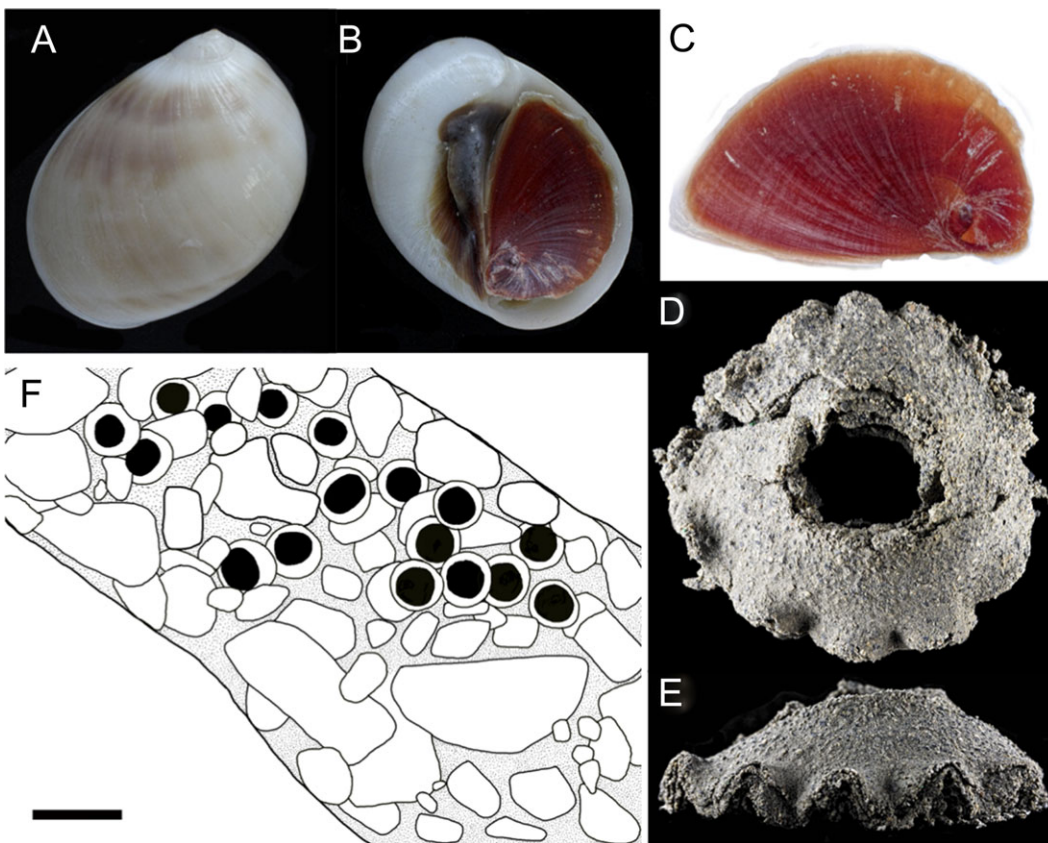


Figure 11. *Mammilla melanostoma* (Gmelin, 1791). **A, B.** Shell, Liufu (NMNS 003232-00039); SH 29 mm. **C.** Operculum, external surface; L 22 mm. **D–F.** Egg collar, Tongliang, Penghu, top, side view and cross-section; BD 89 mm; CH 18 mm. Scale bar **F** = 1 mm.

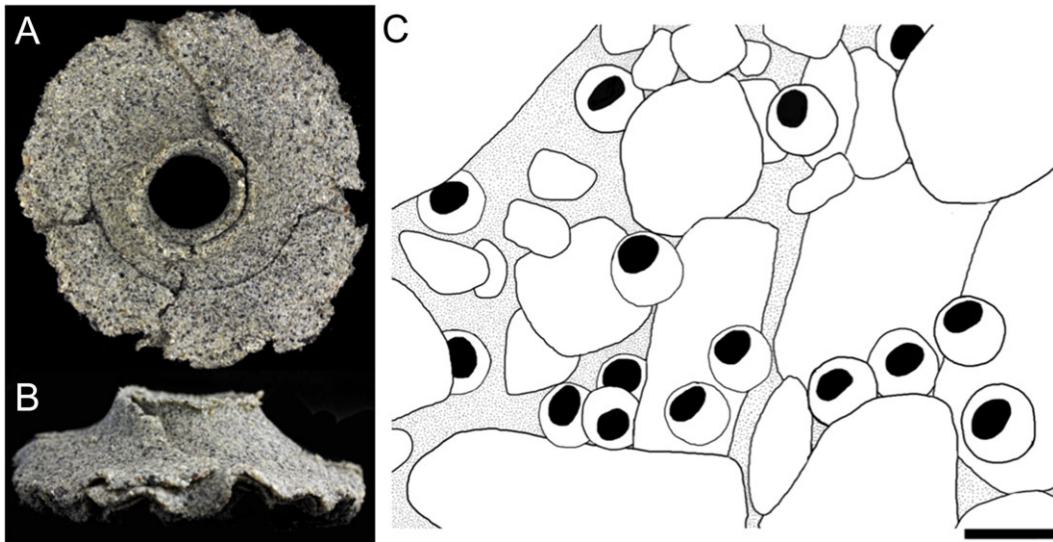


Figure 12. *Mammilla melanostomoides* (Quoy & Gaimard, 1832), egg collar. **A, B.** Jingan, Penghu, top and side view; BD 48 mm; CH 14 mm. **C.** Daxi. Scale bar **C** = 1 mm.

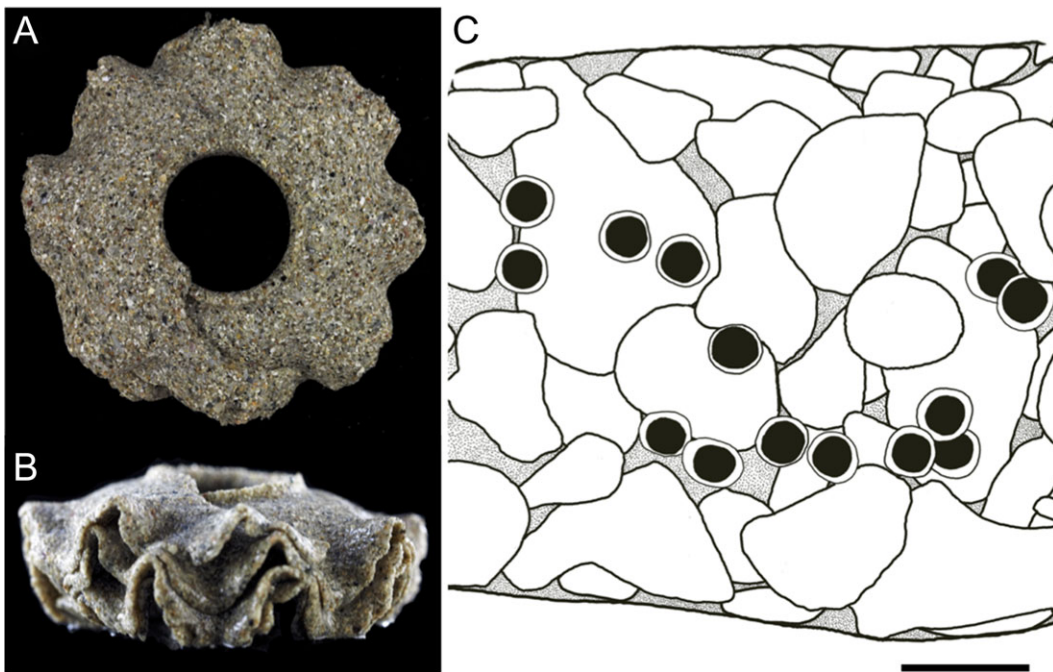


Figure 13. Egg collar of an undetermined naticid (possibly *Tanea* sp. or *Euspira* sp.), Kenting. **A, B.** Top and side view; BD 48 mm; CH 18 mm. **C.** Cross-section. Scale bar **C** = 1 mm.

Egg collar (Fig. 11D–F; $n = 2$): 4 whorls, basal margin prominently sinuous in vertical plane, the waves traced by successive whorls are in phase with each other. BD 89 mm, AD 25 mm; CW 33 mm, CT 1.4 mm. CH 18 mm, crown absent. Capsules medium-sized, D 205–230 μm , arranged haphazardly within collar, density 3–5 capsules mm^{-2} ; each containing single embryo/larva.

Remarks: This is a widespread and well known species in the Indo-West Pacific (Poutiers, 1998). The living animal and egg collar are illustrated in Chiu, Huang & Su (2011).

***Mammilla melanostomoides* (Quoy & Gaimard, 1832)**
(Fig. 12)

Shell: large, SH 30 mm, high spired; suture shallow; external surface mostly white with irregular brown spots. Spiral sculpture absent. Aperture wide, white, with very narrow, concave columella, umbilicus nearly closed by swollen columella. Funicle absent. Both columella and umbilicus stained dark brown.

Operculum: corneous, rusty brown, substantially smaller than shell aperture.

Animal: unknown.

Egg collar (Fig. 12A–C; $n = 2$): 2 and 4.5 whorls; basal margin wavy in vertical plane. BD 48 and 58 mm, AD 10 and 23 mm, CW 21 mm, CT 1 and 2 mm; BD about three times AD; TW 14–22 mm, CW 1.9–2.6 mm. Crown is 1/8 height of upright egg mass. Capsules medium-sized, D 220–260 μm , arranged sparsely within collar, density 3–6 capsules mm^{-2} . Each capsule contains single embryo/larva.

Remarks: this and the preceding species have similar shells and egg collars, but differ sufficiently in detail to be regarded as distinct species.

Undetermined sp.

(Fig. 13)

Shell, operculum and animal: unknown.

Egg collar (Fig. 13A–C; $n = 1$): about 4 whorls; basal margin wavy in vertical and horizontal planes. Apical margin smooth, slightly recurved. BD 50 mm, AD 18 mm, about 1/3 BD; TW 16 mm, CT 4 mm; CW 2 mm, about 1/8 CH. Capsules large, D 300–400 μm , arranged sparsely within collar, density 2–4 capsules mm^{-2} , each containing single embryo/larva.

Remarks: the COI sequence obtained from this egg collar appeared near *Tanea* spp. and *Euspira* spp. (Fig. 3), but without bootstrap support. Unfortunately, none of the egg collars of *Tanea* species has been characterized to date (Table 5) and none of the known egg collars of *Euspira* have a similar morphology to our specimen described above.

Egg-collar morphology and molecular phylogeny

We examined the morphology of the egg collars in relation to the phylogenetic trees (Fig. 3) obtained from sequence data and classified the 11 different egg collars into seven groups (I–VII; Table 4). While these bore some relationship to the molecular trees, not all

were supported as monophyletic. The following groups were discernible, here listed together with traditional taxonomic characters of the shell and operculum:

Group I: collars with tall crown and single whorl; medium-sized shell with distinct spire and open umbilicus; calcareous operculum with two ribs (e.g. *Paratectonica tigrina*; Fig. 4).

Group II: collars with moderate AD; small shell with distinct spire and either open or nearly closed umbilicus; calcareous operculum with single rib (e.g. *Notocochlis gualtieriana* and *N. sp. aff. antoni*; Figs 6, 7).

Group III: collars with a small apical diameter, small shell with distinct spire and open umbilicus, calcareous operculum with two ribs (e.g. other *Notocochlis* spp.; Fig. 5).

Group IV: small, pyramidal collars with very small apical diameter; small shell with distinct spire and open umbilicus; calcareous operculum with multiple ribs (e.g. *Naticarius* spp.; Fig. 8).

Group V: collars with nearly perpendicular sides; shell with low, indistinct spire and small, shallow umbilicus; small, corneous operculum (e.g. *Sinum* spp.; Fig. 10).

Group VI: many-whorled collars with basal margin wavy in vertical plane; shell with distinct spire and almost closed umbilicus; large, corneous operculum (e.g. *Mammilla* spp.; Figs 11, 12).

Group VII: many-whorled, flattened collars with extremely wavy basal margin; shell and opercular characters not determined (Fig. 13; possibly *Tanea* or *Euspira* spp.).

DISCUSSION

Molecular analyses

Molecular tools applied to resolve phylogenies of various gastropod groups have achieved varying degrees of success (see reviews

Table 4. Proposed classification of Taiwanese egg collars. A total of seven groups (I–VII) were recognized during this study based on their morphological attributes.

| Group | Egg collar | Shell | Umbilicus | Operculum/number of ribs on surface | Typical species |
|-------|--|--|-----------------------|-------------------------------------|--|
| I | Medium-sized, with tall crown; single whorl; basal diameter 2–3 times apical diameter | Medium-sized, distinct spire | Open | C/2 | <i>Paratectonica tigrina</i> |
| II | Small to medium-sized, low crown, basal diameter twice apical diameter; 1.5–3.5 whorls; | Small-sized, distinct spire | Open or nearly closed | C/1 | <i>Notocochlis gualtieriana</i> , <i>N. sp. aff. antoni</i> |
| III | Small, with low crown; basal diameter 4–5 times apical diameter; 1.5–2 whorls | Small-sized, distinct spire | Open | C/2 | <i>Notocochlis</i> spp. and <i>Tectonatica bougei</i> |
| IV | Small pyramidal collars with very small apical diameter; crown indistinct; multiple whorls | Small-sized, distinct spire | Open | C/8 | <i>Naticarius zonalis</i> |
| V | Generally large; high crown, basal diameter <1.5 times apical diameter; 1–2.5 whorls | Medium-sized, low spire | Shallow | NC, small | <i>Sinum halioideum</i> |
| VI | Generally large; low or absent crown; multiple whorled collars with wavy margin along vertical axis; basal diameter >2 times apical diameter | Medium-sized, distinct spire | Nearly closed | NC, large | <i>Mammilla</i> spp. |
| VII | Generally large, low crown; multiple whorled flattened collars with extremely wavy basal margin; basal diameter >3 times apical diameter | Medium- to large sized, distinct spire | ? | ? | Unknown |

Shell and opercular characters corresponding to the groups are also provided.

Abbreviations: C, calcareous; NC, noncalcareous (i.e. corneous).

by Colgan *et al.*, 2007; Aktipis *et al.*, 2008; Ponder *et al.*, 2008; Zapata *et al.*, 2014). Attempts to resolve genus-level relationships amongst the caenogastropods have also been somewhat uneven. Hülksen *et al.* (2008) using sequences based on H3, COI, 16 S and 18 S genes, provided a first molecular phylogenetic tree for the Naticidae. The results, although based on a limited number of taxa, recalled uncertainties raised by earlier researchers (e.g. Powell, 1933; Marincovich, 1977; Golikov & Sirenko, 1988; Majima, 1989; Bandel, 1999) who observed inconsistencies in morphological characters such as the operculum and shell umbilicus used to delineate naticid subfamilies and genera.

In our study of Taiwanese Naticidae, we combined our new COI and 16 S sequences with those from Hülksen *et al.* (2008). The resulting dataset is still lacking some critical taxa (e.g. *Globisnum*, *Amauropsis* and deep-sea species) and the poorly supported basal clades in the phylogenetic trees reflect the very limited number of taxa examined in this study. While we did not set out to examine the detailed relationships between naticid genera, our trees do not contradict the topologies of those obtained by of the Hülksen *et al.* (2008), which seem to suggest that the currently recognized Naticinae (i.e. taxa bearing calcareous opercula) are not a monophyletic clade. On the other hand, our results were unable to corroborate the subsequent findings of Hülksen *et al.* (2012), which showed that species of *Euspira*, *Mammilla* and *Polinices* formed a clade, i.e. that the Polinicinae are a monophyletic group. In both the COI and 16 S rRNA trees obtained here, the relationships between *Euspira*, *Mammilla* and *Polinices* were equivocal. Clearly there is a need for future work involving more taxa, to clarify and stabilize the phylogenetic relationships between naticid genera.

Egg collars: identification, classification and review

Egg collars were generally distinct among the nine species examined, differing in their overall shape, number of whorls, capsule size and arrangement of capsules within the collar, as previously detailed for other species (Thorson, 1940; Amio, 1955; Giglioli, 1955; Bandel, 1976; Baxter, 1983; Table 5). Our findings support the studies by Hülksen (2008) and Hülksen *et al.* (2008, 2011), showing that molecular analysis of egg masses allows the confirmation of the identity of naticid species without having access to adult specimens, if suitable reference sequences from reliably identified adults are available.

Among the six naticine species bearing calcareous opercula examined in this study, the small, tightly coiled egg collar of *Naticarius zonalis* with a diminutive apical opening (Group IV; Fig. 8E, F) appears to be similar to those of two congeners described by Hülksen *et al.* (2008, 2011; *N. concinnus* and *N. onca*; Table 5). The egg collars of these three species all possess multiple whorls that are wound at an acute angle, such that the low-profile collars have a small apical diameter relative to the base. In the COI and 16 S trees (Fig. 3A, B), *zonalis* and *onca* belong to a clade of at least four *Naticarius* species. In contrast, two other larger-shelled congeners, *canrenus* (see Bandel, 1976) and *cruentatus* (as *hebraeus* in Hülksen *et al.*, 2008), lay collars with less than two whorls and the apical diameters are wider. Members of the genus *Naticarius* possess calcareous opercula whose external surface bears several sulci and spiral ridges or ribs (Fig. 8C, D; Cernohorsky, 1971; Kilburn, 1976; Kabat, 2000; Zhang, 2016). However, monophyly of the genus, as traditionally defined by shell and opercular characters, was not supported by our molecular analyses.

Three species of the genus *Notocochlis* also lay egg collars with multiple whorls (Groups II and III; Table 4, Figs 5B, 6G–J, 7E, F). However, the apical diameter of their collars is considerably wider than in *Naticarius*. The collars of *Notocochlis cernica*, *N. gualtieriana* and *N. sp. aff. antoni* are consistent with those of *N. isabelleana* from South America (Pastorino, Averbuj & Penchaszadeh, 2009).

Members of this genus have calcareous opercula that bear only one or two peripheral ribs on their external surface (Kabat, 2000; Figs 6E, F, 7C, D). In Group II, members of which have one peripheral rib on their operculum and lay collars with a moderate apical diameter, *N. gualtieriana* (type species of *Notocochlis*) has very similar egg collar features to those of *N. sp. aff. antoni*. These two species were synonymized by Kay (1979) and Torigoe & Inaba (2011), but are considered distinct species here, based on their genetic distances. Members of Group III, which form a well supported clade distinct from Group II (not monophyletic in either tree), have an operculum with two peripheral ribs and lay collars with a relatively small apical diameter. This suggests that further analysis could support the assignment of members of Group III to a different genus.

Egg collars with multiple whorls were also observed among members of the subfamily Polinicinae, which is characterized by a corneous operculum (Cernohorsky, 1971; Kilburn, 1976; Kabat, 2000; Hülksen *et al.*, 2012). Both *Mammilla melanostoma* and *M. melanostomoides* lay distinctive collars having up to 4.5 whorls that are thrown into sinuous folds in both the vertical and horizontal planes (Group VI; Table 4, Figs 11D, E, 12A, B). These folds probably help to stabilize the collars on the substratum in moving water, while allowing oxygenated water to pass under and over the multilayered collar walls. This collar morphology is also shared by the conchologically similar Indo-Pacific *Polinices mammilla* (see Gohar & Eisawy, 1967) and the Caribbean *P. lacteus* (see Bandel, 1976). However, most other polinicine species whose collars have been described produce single-whorled collars (Table 5), which can also be sinuous along the basal edge. As noted above, our molecular results provided no support for the traditional Polinicinae.

We also obtained an undetermined egg collar with multiple whorls that was distinctly flattened, with sinuous folds, which we assigned as Group VII (Table 4; Figs 3, 13). Despite successfully obtaining both COI and 16 S sequences from the egg collar, its identity remains unclear. In both trees the sequence grouped near *Tanea* and *Euspira*, but without statistical support.

A number of unrelated species lay egg collars with a distinct crown. The naticine *Paratectonatica tigrina* lays a distinctive, single-whorled egg collar that has a tall crown (Group I; Fig. 4F, G). This monotypic genus is otherwise distinguished by their unusual rachidian radula teeth, which resemble those observed in *Sinum* species. The egg collar of *Natica marochiensis* similarly has a tall crown (Knudsen, 1950), as do those of the polinicines *Glossaulax didyma*, *G. vesicalis* and *G. reiniana* (Amio, 1955; Kim *et al.*, 2007). Most other naticid species appear to produce collars with a short crown (e.g. *Notocochlis*, *Naticarius* and *Sinum*; Figs 6–8, 10), or a crown may be absent altogether (*M. melanostoma*; Fig. 11D). Unusually, the apical margin of the collars of *N. sp. aff. antoni* and *M. melanostomoides* (Fig. 12A, B) is slightly but distinctly flared outwards (recurved).

To date, the egg collars of only three species of the small subfamily Sininae have been described (Table 5). Its members are characterized by reduced opercula and thin shells that are dorso-ventrally flattened, with large apertures. Their egg collars have up to 2.5 whorls (Group V; Table 4, Fig. 10C, D). *Sinum japonicum* is the only one of the three sinines with large egg capsules about 1 mm in diameter, each containing 10–12 larvae (Knudsen, 1994). The others have only a single larva in each capsule, which is 170–290 µm in diameter. The egg collar of *S. halioideum* is distinct in having its apical and basal diameters of comparable size (Fig. 10C, D), the walls having a nearly vertical orientation. This is similar in shape to the egg collar identified as the same species by Hülksen (2008). However, the shell shown by Hülksen (2008; fig A80A) is beige with stronger spiral striae, differing from the white shell with very weak striae that is the lectotype of *S. halioideum*. Both COI and 16 S genetic distances between our *Sinum* sp. and Hülksen's *S. halioideum* suggest that they are not conspecific, but share a similar egg collar morphology.

Table 5. Egg collar characteristics in the Naticidae, based on this study and available literature. Adult sizes, classification of subfamilies and genera, and geographical distributions of species follow [Torigoe & Inaba \(2011\)](#), unless otherwise stated.

| Species (subfamily) (sample size) | Adult shell height (mm) | No. of whorls | Presence of crown; relative height | Basal diameter (mm) | Apical diameter, or length × width (mm) | Basal margin folds / direction of fold | Capsule size (µm) | Capsule arrangement; density (mm ⁻²) | No. of embryos in capsule | Distribution; reference |
|---|----------------------------|------------------|---------------------------------------|---------------------------|---|---|-----------------------|---|---|---|
| <i>Paratectonatica tigrina</i> (Naticinae) (n = 9) | 30 | 1–1.5 | Yes; high | 42–58 | 15–24 | Sinuuous / horizontal | 170–245; | Irregular; 2–3; | 1 | Indo-West Pacific; this study; |
| | | 1 | Yes; high | 37–76 | 14–33 | Sinuuous / horizontal | 220–300 | Irregular; 3–5 | | Japan; Amio (1955) ; as <i>Natica maculosa</i>); |
| | | 1.5 | Yes; high | 56–79 | ? | Smooth or folded | 251–284 | Double layer | 1 | India; Natarajan (1957) ; as <i>Natica</i>) |
| <i>Notocochlis cernica</i> (Naticinae) (n = 1) | 20 | 2.5 | Yes; low | 41 | 14 | Slightly sinuous / vertical | 140–155 | 3.4 | 1 | W Pacific; this study |
| <i>Notocochlis dillwyni</i> (Payraudeau, 1826) (Naticinae) (n = 6) | 12 | 3–5 | Yes; low | 20–40 | 7–9 | Flat or slightly sinuous | ? | ? | ? | Mediterranean to W. Africa and Caribbean; Hülsken et al. (2008) |
| <i>Notocochlis gualtieriana</i> (Naticinae) (n = 9) | 20 | 1.5–3.5 | Yes; low | 10–44 | 6–20 | Flat or slightly sinuous / vertical | 115–140 | 4–10 | 1 | Indo-West Pacific; this study (see also Kay, 1979 : fig. 82B) |
| | | 15–27 | 1.5–2 | Yes; low | 35–50 | ? | Slightly sinuous | 133 | Single layer; 3–7 capsules in spherical egg space 183–367 µm in diameter | 1 |
| <i>Notocochlis isabelleana</i> (d'Orbigny, 1840) (Naticinae) (n = 23) | 15 | 1–1.5 | Yes; low | 35–67 | 14–28 | Sinuuous / horizontal | 154–235 | 14–16 | 1 | Brazil to Argentina; Pastorino et al. (2009) |
| <i>Notocochlis</i> sp. aff. <i>antoni</i> (Naticinae) (n = 14) | 20 | 1–2 | Yes; low | 31–47 | 14–20 | Flat or slightly sinuous | 90–130 | 9–13 | 1 | Taiwan; this study |
| <i>Naticarius canrenus</i> (L., 1758) (Naticinae) | 67 | 1–1.5 | Yes; low | 80–120 | 40–45 | Slightly sinuous / horizontal | 350–500 | Single layer or double layer; 1 | 1 | Caribbean; Bandel (1976) |
| <i>Naticarius concinnus</i> (Dunker, 1860) (Naticinae) (n = 1) | 20 | 3 | ?yes; low | 25 | 2 | Flat or slightly sinuous | ? | ? | ? | Japan–Australia; Hülsken et al. (2011) |
| <i>Naticarius hebraeus</i> Martyn, 1784 (Naticinae) (n = 1) | 30–40 | 1.25 | Yes; low | 75 | 40 | Flat | ? | ? | ? | Mediterranean; Hülsken et al. (2008) |
| <i>Naticarius onca</i> (Röding, 1798) (Naticinae) (n = 8) | 25–30 | 3 | Yes; low | 30 | 0–5 | Flat or slightly sinuous | ? | ? | ? | Indo-West Pacific; Hülsken et al. (2011) |
| <i>Naticarius zonalis</i> (Naticinae) (n = 7) | 20 | 2–3.5 | Yes; low | 25–36 | 6–8 | Sinuuous / vertical | 470–550 | 0.5–1.1 | 1 | Indo-West Pacific; this study (= <i>sertatus</i> Menke, 1843 according to Torigoe & Inaba, 2011) |
| <i>Natica livida</i> Pfeiffer, 1840 (Naticinae) | 7–15 | 1.5 | Yes; low | 15–17 | 6–7 | Slightly sinuous / horizontal | 150 | Irregular, generally single layer; 3 | 2–5 | Caribbean; Bandel (1976) |
| | | 40 | <1 | Yes; low | 70 | 28 | Sinuuous / horizontal | 1,000 | Single layer; 1 | 1 |

| | | | | | | | | | | | |
|---|-------|-----------|----------------------------|--------|-----------------|--|-------------|---|-------|--|--|
| <i>Natica vitellus</i> (L., 1758) (Naticinae) | | | | | | | | | | | Indo-West Pacific; Thorson (1940) ; as <i>Natica rufa</i> |
| <i>Natica marochiensis</i> (Gmelin, 1791) (Naticinae) (<i>n</i> = 1) | 15–27 | 1 | Yes; high | 38 | 21 | Sinuuous / horizontal; egg mass made of faecal pellets | 500 | Single layer; 20–25 embryos in each capsule | 20–25 | | W Africa; Knudsen (1950) |
| <i>Natica (Tectonatica)? rizzae</i> (Philippi, 1844) (Naticinae) (<i>n</i> = 4) | 14 | 1.25 | Yes; low | 37–48 | 15 | Flat | ? | ? | ? | | Mediterranean Sea; Hülsken et al. (2008) ; as <i>Tectonatica</i> |
| <i>Natica rubromaculata</i> Smith, 1871 (Naticinae) | 20 | ? | ? (fragment only observed) | ? | ? | Slightly sinuous | 750 | Single layer; 1 | 1 | | W Africa; Knudsen (1950) |
| <i>Natica sagraiana</i> (d'Orbigny, 1842) (Naticinae) (<i>n</i> = 8) | 10 | 1 | Yes; low | 24–40 | 20 | Flat | ?400 | ? | 1 | | Mediterranean Sea; Hülsken et al. (2008) ; as <i>Tectonatica</i> |
| <i>Natica (Tectonatica) venustula</i> Philippi, 1851 (Naticinae) (<i>n</i> = 1) | 10 | 3 | Yes; low | 8 | 2 | Flat | 93–105 | Single layer; 0.02 | 1 | | Tropical Pacific; this study |
| <i>Natica (Tectonatica) tecta</i> Anton, 1839 (Naticinae) | 20–41 | leaf-like | NA | NA | 30 (L) × 10 (W) | Stalked base attached to hard substratum | ? | ? | ? | | South Africa; Kilburn & Rippey (1982) |
| <i>Cryptonatica adamsiana</i> (Dunker, 1860) (Naticinae) | 30 | 1.5 | ? | 32–56 | 18–31 | ? | 290–340 | Single layer; 1 | 12–13 | | Japan; Amio (1955) ; as <i>Natica</i> |
| <i>Cryptonatica clausa</i> (Broderip & Sowerby, 1829) (Naticinae) | 60 | 1 | No | 40 | 20 | Flat | 2,000–2,250 | Single layer; 1 | 1 | | Arctic Ocean; Thorson (1935) |
| <i>Cryptonatica janthostoma</i> (Deshayes, 1839) (Naticinae) | 50 | 1.2 | Yes; low | 88 | 37 | Flat | 770 | Single layer; 1 | 18–26 | | Kamchatka to Korea; Kulikova, Kolbin, and Kolotukhina (2007) |
| <i>Cryptonatica janthostomoides</i> (Kuroda & Habe, 1949) (Naticinae) | 40 | 1 | Yes; low | 73–105 | 30–46 | ? | 290–340 | Single layer; 1 | 14–17 | | Japan; Amio (1955) ; as <i>Natica</i> |
| <i>Sinum japonicum</i> (Lischke, 1872) (Sininae) (<i>n</i> = 1) | 15 | 1.2 | Yes; low | 60 | 25 | Slightly sinuous | 1,000 | Single layer; 1 | 10–12 | | China and Japan; Knudsen (1994) |
| <i>Sinum halotoideum</i> (Sininae) (<i>n</i> = 4) | 20 | 1–2.5 | Yes; low | 62–87 | 33–47 | Sinuuous / vertical and horizontal | 170–210 | Irregular; 6–10 | 1 | | Indo-West Pacific; this study |
| <i>Eunaticina papilla</i> (Gmelin, 1791) (Sininae) | 20 | 1.5 | Yes; high | 38–86 | 33–38 | Flat or slightly sinuous | 200–290 | Irregular; 4–6 | 1 | | Africa to E Asia; Amio (1955) ; as <i>Sinum</i> |
| <i>Conuber conicum</i> (Lamarck, 1822) (Polinicinae) | 40 | 1 | No | 90 | ? | None | 300 | Diffuse in gelatinous mass; no sand grains | 1–3 | | S Australia; Murray (1962) |
| | 20–30 | <1 | Yes? | ?40 | ? | None | 350 | | 1 | | S Australia; Murray (1966) |

Continued

Table 5. Continued

| Species (subfamily) (sample size) | Adult shell height (mm) | No. of whorls | Presence of crown; relative height | Basal diameter (mm) | Apical diameter, or length × width (mm) | Basal margin folds / direction of fold | Capsule size (µm) | Capsule arrangement; density (mm ⁻²) | No. of embryos in capsule | Distribution; reference |
|--|----------------------------|------------------|---------------------------------------|---------------------------|---|---|----------------------|---|------------------------------|---|
| <i>Conuber incei</i> (Philippi, 1853) (Polinicinae) | | | | | | | | Diffuse in gelatinous mass; no sand grains | | |
| <i>Conuber sordidum</i> (Swainson, 1821) (Polinicinae) | 40–50 | <1 | No | 70–100 | 10–20 | None | 625 | Within 3 mm of outer surface in gelatinous mass; no sand grains | 1–3 | S Australia: Murray (1962); Booth (1995) |
| <i>Mammilla melanostoma</i> (Polinicinae) (n = 1) | 40 | 4 | No | 89 | 25 | Prominently sinuous / vertical | 205–230 | Irregular; 3–5 | 1 | Indo-West Pacific; this study |
| | ? | 1 | Yes; low | 69 | 33 | Flat | 300 | Double layer; 3–5 | 1 | Indo-West Pacific: Gohar & Eisawy (1967) |
| | 23 | 1 | Yes; low | 60 | 12 | Flat | 300? | Double layer; 3–5 | 1 | Hong Kong: Knudsen (1992); as <i>Polinices</i>) |
| <i>Mammilla melanostomoides</i> (Polinicinae) (n = 2) | 40 | 2, 4.5 | Yes; medium | 48, 58 | 10, 23 | Sinuous | 220–260 | Irregular; 3–6 | 1 | Indo-West Pacific; this study |
| <i>Polinices lacteus</i> (Guilding, 1834) (Polinicinae) | 25 | 2.5–5.5 | Yes; low | 23–43 | 7–10 | Sinuous / horizontal | 200 | Irregular; 10 | 1 | Caribbean and W Africa; Bandel (1976) |
| <i>Polinices hepaticus</i> (Röding, 1798) (Polinicinae) | 50 | 0.75–1.5 | Yes; low | 40–45 | 20–23 | Slightly sinuous / horizontal | 300 | Irregular; 5 | 1 | Caribbean; Bandel (1976) |
| <i>Polinices mammilla</i> L., 1758 (Polinicinae) | 30–40 | 2–5 | Yes; low | 36–80 | 12–32 | Sinuous / horizontal | 135 | Irregular; 25 | 1 | Indo-West Pacific; Gohar & Eisawy (1967) |
| | to 58 | up to 5 | Yes; low | 30 | 17 | Sinuous / horizontal? | ? | ? | ? | Kilburn & Rippey (1982; as <i>tumidus</i> Swainson, 1840) |
| <i>Neverita josephinia</i> (Risso, 1826) (Polinicinae) (n = 2) | 40 | 1 | Yes; low | 51–59 | 38 | Sinuous / horizontal | 1,000 | Single layer; 1 | 1 | Mediterranean Sea; Giglioli (1955); Hülsken et al. (2008) |
| <i>Amauropsis islandica</i> (Gmelin, 1791) (Polinicinae) | 20–30 | ? | No | ? | ? | Sinuous / horizontal | 1,500–1,750 | Single layer; 1 | 1 | N Atlantic; Thorson (1935); Giglioli (1955) |
| <i>Glossaulax reiniana</i> (Dunker, 1877) (Polinicinae) | 40 | <1 | Yes; high | 52–64 | 21–27 | Sinuous / horizontal | 350–410 | Irregular; 8–10 | 1 | East China Sea to Japan; Amio (1955; as <i>Neverita</i>) |
| <i>Glossaulax vesicalis</i> (Philippi, 1849) (Polinicinae) | 80 | 1 | Yes; high | 29–64 | 16–35 | Sinuous / horizontal | 1,300–1,450 | Single layer; 1 | 1 | Amio (1955; as <i>Neverita</i>) |
| <i>Glossaulax didyma</i> (Röding, 1798) (Polinicinae) | 40–90 | 1 | Yes; high | 80–95 | 60 | Sinuous / horizontal | 1,000 | Single layer; 1 | 1 | Indo-West Pacific; Thorson (1950; as <i>Natica ampla</i>) |
| | | 1 | Yes; high | 64–130 | 33–65 | Sinuous / horizontal | 520–580 | Double layer; 2 | 1–3 | Japan; Amio (1955; as <i>Neverita</i>) |
| | | 1 | Yes; low | 63–160 | 40–50 | Sinuous / horizontal | 240–260 | ? | 1 | |

| | | | | | | | | | | |
|--|--------|----------|-----------|--------|-----------------------|-----------------------|---------------------|-------------------------------------|--------------------------------------|---|
| | | 1.2 | Yes; low | 90 | 60 | Flat | 240–300 | ? | 1 | Monora I., Pakistan; Tirmizi & Zehra (1983) ; as <i>Neverita</i> |
| | | 1 | Yes; high | 66 | 34 | Flat | 300 | Double layer; 2 | 1 | China; Liu & Sun (2008) ; as <i>Neverita</i> |
| <i>Laguncula pulchella</i> Benson, 1842 (Polinicinae) | 25–45 | 1 | Yes; high | ? | ? | Sinous / horizontal | 530–570 | Irregular; | 1 | Korea; Kim et al. (2007) |
| | <1 | Yes; low | 69–96 | 27–43 | Sinuuous / horizontal | ? | ? | 3–5 (about 100 nurse cells present) | 1 | China, Korea, Japan; Tomiyama (2013) ; as <i>Euspira fortunei</i> |
| | ? | 1 | Yes; low | 50–120 | 40 | Sinuuous / horizontal | 1,200–3,400 | Single layer | 2–8 (36–93 nurse cells) | Miyagi Pref., Japan; Sakai & Suto (2005) ; as <i>Neverita didyma</i> |
| <i>Euspira catena</i> (da Costa, 1778) (Polinicinae) | 30 | 1 | Yes; low | 73 | 47 | Flat | 1,425×1,925 spheres | Single layer; 1 | 1–19 (up to 180 nurse cells present) | North Sea and Mediterranean; Ankel (1930) ; Hertling (1932) ; as <i>Lunatia</i> ; Giglioli (1949) ; Fretter & Graham (1981) |
| <i>Euspira fusca</i> (Blainville, 1825) (Polinicinae) | 30 | <1 | No | 120 | 50 | Flat | 492×468 | Irregular; 1 | 1 | Mediterranean Sea; Ramón (1994) ; as <i>Euspira</i> |
| <i>Euspira montagui</i> (Forbes, 1838) (Polinicinae) | 10 | 1.2 | No | 40 | 10–13 | Flat | 230 | ? | 'numerous' (?nurse eggs) | Fretter & Graham (1981) |
| <i>Euspira heros</i> (Say, 1822) (Polinicinae) | 50–100 | 1.2 | Yes; low | 50–60 | to 40 | Flat | 630×850 spheres | Single layer; 1 | 4–84 | W Atlantic; Giglioli (1955) |
| <i>Euspira lewisi</i> (Gould, 1847) (Polinicinae) | to 125 | 1 | Yes; low | 120 | 50 | Flat | 200×250 spheres | Irregular; 4–5 | 1 | E Pacific; Giglioli (1955) |
| <i>Euspira nitida</i> (Donovan, 1804) (Polinicinae) | 10–20 | 1–3.5 | No | 17–40 | 8–18 | Flat | 208–254 | Irregular; | 1 | North Sea; Ziegelmeier (1961) ; as <i>Lunatia</i> ; Hülsken et al. (2008) ; as <i>Euspira</i> |
| <i>Euspira pila</i> (Pilsbry, 1911) | 20–30 | ? | ? | 79 | 38 | ? | 770 | Single layer; 1 | 1 | Yakovlev & Kolotukhina (1996) |
| <i>Euspira triseriata</i> (Say, 1826) (Polinicinae) | 10 | 1.2 | No | 40 | 15 | Flat | 800×1,150 spheres | Single layer; 1 | 1–3 | W Atlantic; Giglioli (1955) |
| <i>Globisium drewi</i> (Murdoch, 1899) (Globisininae) | 30 | 1.5 | ? | 100 | 45 | Flat | 6,500 | Single layer; <1 | ? | New Zealand; Dell (1956) |
| <i>Falsilunatia carcellesi</i> (Dell, 1990) (? Globisininae) | 25 | ? | ? | ? | ? | Flat | 8,780–14,140 | Single row; single layer, <1 | 1 | Argentina, 200–2000 m; Penchaszadeh et al. (2016) , as <i>Bulbus carcellesi</i> |

The largest egg collar observed in this study measured up to 90 mm in basal diameter, belonging to *Mammilla melanostoma* (Group VI; Fig. 11D–F), which has an adult shell height of about 40 mm. The egg collar of the same species in Hong Kong reported by Knudsen (1992: pl. 4D) measured 60 mm in diameter. However, those of *Glossaulax didyma* (Indo-Pacific), *Euspira fusca* (Mediterranean) and *E. lewisi* (East Pacific) can be in excess of 120 mm (Amio, 1955; Giglioli, 1955; Ramón, 1994). The egg collar of the deep-sea *Globisium dreavi* was recorded by Dell (1956) to be about 100 mm in diameter.

All egg collars examined in this study incorporated a single embryo in each capsule, but there are a few species occurring elsewhere whose capsules contain more than one embryo, including *Cryptonatica adamsiana* and *S. japonicum* that have more than 10 eggs in each capsule (Amio, 1955; Knudsen, 1994). Knudsen (1950) observed that each capsule in the egg collar of *Natica marochiensis* from West Africa contained between 20 and 25 eggs, while those of *Euspira heros* from the Western Atlantic have up to 84 eggs in a single capsule (Giglioli, 1955). Capsule sizes vary considerably between species. The largest capsules recorded so far are those of *Falsilunatia carcellesi* (Table 5; Penchaszadeh et al., 2016) with diameters of 8.8–14.1 mm. Each capsule accommodates a single larva that undergoes direct development. The only globisinine whose egg capsule has been described is *Globisium dreavi* from New Zealand, which has a capsule diameter of 6.5 mm (Dell, 1956). Most species with planktotrophic larvae have capsule sizes ranging between 100 and 300 µm, while those with larvae that undergo some form of direct development have larger capsules, typically 500–3,000 µm, in which some of the multiple eggs may act as nurse cells (e.g. *Laguncula pulchella*, *Euspira catena* and *E. montagui*; Table 5). The size and arrangement of the capsules affect the external appearance of the egg collar as well as its consistency. Collars with large capsules feel more rigid than those incorporating small capsules. Small capsules are usually arranged haphazardly in the sand matrix, although it is often difficult to see the capsules from the surface even with the aid of a stereomicroscope. In contrast, collars incorporating large capsules are at once recognizable due to the bulging collar surfaces created by the capsules within (e.g. *Cryptonatica clausa*, *E. catena*, *E. pallida*, *E. heros* and *E. triseriata*; e.g. Thorson, 1935; Giglioli, 1955; Table 5).

Not all naticids lay egg collars. The naticine *Natica tecta* lays a series of flattened leaflets made of sand, each attached to the hard substratum by a stalk (Kilburn & Rippey, 1982: fig. 26). Members of the polinicine genus *Conuber* lay gelatinous egg masses resembling thick sausages that are free of sand (Murray, 1962, 1966; Booth, 1995; Table 5).

The egg masses of some 52 species of Naticidae have been described (Table 5), since the first published description of an egg collar, that of *Euspira catena*, by Ankel (1930). This is less than 20% of the world's extant naticids, estimated at between 260 and 300 species (Kabat, 1996; Torigoe & Inaba, 2011). Based on the data in Table 5, egg collars of some 23 species of Naticinae, 24 of Polincinae, three of Sininae and two of Gobisininae have been documented. The compilation has revealed inconsistencies in the identities of at least two species based on their egg collar and capsule dimensions. Among the Naticinae, the egg collar of *Natica marochiensis* described from West Africa by Knudsen (1950) differs from those observed by Natarajan (1957) from India, particularly in capsule size, as well as the number of embryos in each capsule (Table 5). It seems likely that Natarajan (1957) has misidentified the adult shell, which was probably *Notocochlis gualtieriana*, based on the similarities of the egg collar to those observed in our study. Similarly, there appear to be three distinct forms of egg collar described for the economically important polinicine *Glossaulax didyma* from the Persian Gulf, Japan/Korea and China (Thorson, 1950; Amio, 1955; Kim et al., 2007; Liu & Sun, 1983; Table 5), suggesting that 'didyma' of authors may comprise more than one species. This is also reflected in the complex synonymy (reviewed

by Majima, 1989), differences in shell shape (Sun et al., 2012) and molecular diversity (Zhao et al., 2017).

As discussed above, we found some correspondence between molecular phylogeny and egg-collar morphology, but generally poor support for the monophyly of traditional genera. Genus-level taxonomy is currently strongly dependent upon umbilical and opercular characteristics (Kabat, 2000), but our results hint that egg-collar morphology may also prove to be a useful character indicating phylogenetic affinity. As the identities of more egg collars are revealed, the combination of morphological and molecular characters should result in a more natural and stable classification of the Naticidae.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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