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On some Vetigastropoda (Mollusca, Gastropoda) from the Plio-Pleistocene of the Philippines with descriptions of three new species

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Abstract

We studied representatives of seven vetigastropod families in an extremely well-preserved Plio-Pleistocene mollusc fauna found in relatively deep water sediments (c. 200–300 m paleodepth) from the north-western Philippines. The fauna is systematically described and its paleoenvironmental and paleobiogeographical character is explored. Twenty-six species of gastropods were studied, three of which are described as new: *Halystina conoidea* **n. sp.**, *Calliotropis arenosa* **n. sp.** and *Ethminolia wareni* **n. sp.** Four new combinations are proposed: *Pseudotalopia taiwanensis* (Chen, 2006), *Solariella segersi* (Poppe, Tagaro & Dekker, 2006), *Zetela tabakotanii* (Poppe, Tagaro & Dekker, 2006) and *Ilanga konos* (Vilvens, 2009). Fourteen species are known living. Most extant species nowadays occur around the Philippines. Two of the species also occur in Neogene deposits from western Pacific islands. The new fauna offers insights into the character of relatively deep water Indo-West Pacific mollusc faunas prior to the onset of the late Quaternary ice ages.

Key words: taxonomy, new species, gastropod, mollusk, fossil, deep water, Indo-West Pacific

Introduction

Our understanding of the biodiversity and phylogenetics of Vetigastropoda has increased rapidly over the last years. This is especially true for the Indo-West Pacific vetigastropods, which are the focus of publications by Poppe, Tagaro & Dekker (2006), Vilvens (2006; 2007; 2009), Kano (2008), Geiger (2012), Williams (2012) and Williams *et al.* (2008; 2013). Studies on fossil vetigastropods from the same region have lagged behind, even though fossils contain valuable information, e.g. for understanding taxonomy, dating molecular phylogenies and for understanding the history of the Indo-West Pacific marine biodiversity hotspot.

During an expedition to northwestern Philippines in 1999 John de Vos (Naturalis) collected a few sediment samples in shore outcrops on the island of Cabarruyan that contained a very well preserved diverse mollusk fauna, including pelagic groups such as pteropod and heteropod snails. These samples were initially studied by Arie W. Janssen (Naturalis), who participated in a second visit to the island localities in 2001. During this second visit two cliff sections were sampled and an additional road section in the same deposits on the neighboring mainland of Luzon was studied as well. The material contained the most diverse fossil pteropod and heteropod gastropod fauna found globally to date (Janssen 2007). The material also yielded a very diverse benthic fauna, comprising several hundreds of species. The deep-water character of the fauna (c 200–300 m paleo-water depth; Janssen 2007) makes this one of the very rarely well-preserved fossil deep-water faunas.

Several of the benthic mollusk groups are currently under investigation. The new material contains new species but also taxa that hitherto have only been known from Recent material. Vetigastropods occur from intertidal to abyssal or even hadal environments, but in the newly studied material we almost exclusively encountered subtidal taxa of considerable depths (c. 100–1000 m). The group is representative for the deep-water character of the newly studied fauna. Representatives of seven vetigastropod families were investigated; other families, such as Fissurellidae, Scissurellidae, Anatomidae, Lepetellidae, Lepetodrilidae and Skeneidae, are the subject of ongoing study. This study aims at a taxonomic characterization of the fauna, a reconstruction of depositional environments

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and an assessment of the biogeographic signature. The fauna predates the major glaciations of the Middle and Late Pleistocene and thus offers a unique opportunity to assess the character and diversity of an Indo-West Pacific deep-water fauna prior to that time.

The fossil fauna treated in this paper derives from bioturbated carbonate-bearing siltstones of the Santa Cruz Formation (see Wani *et al.* (2008) for a discussion on the formation names). The studied localities are located in close proximity on the main island of Luzon (Tiep) or on Cabarruyan Island (Roxas, Anda) (Janssen 2007). Both at the Tiep locality (an 80 m section) and at Roxas, interbedded harder and softer claystones and marly siltstones are exposed. At Anda no bedding could be observed in the grey to yellow-brown marly siltstone and the total height of the section is possibly a few meters only. Contacts with overlying formations are obscured by dense vegetation.

The stratigraphic age of the three localities studied is currently the subject of debate. Based on holoplanktonic mollusks, Janssen (2007) proposed a Late Pliocene (Piacenzian) age. His stratigraphic distribution ranges of pteropod and heteropod species from the Santa Cruz Formation includes one species with a last occurrence date (LOD) of Early Pliocene (Zanclean), various species with LOD or even exclusive occurrence in the Piacenzian and several species with a first occurrence date (FOD) in the Early Pleistocene (Gelasian) or later. The Pliocene age estimate was backed up by additional foraminiferal analyses that gave an age estimate of approximately 3.1–3.3 Ma. The Anda localities and four other localities nearby were also investigated by Wani *et al.* (2008) for planktonic Foraminifera and nannoplankton. These authors found that their localities were mostly of a Gelasian age based on LOD of two planktonic foraminiferan species and FOD of two nannoplankton species. The Anda localities were the basal localities in the Wani *et al.* (2008) study, one of which containing *Globigerinoides fistulosus* Schubert, 1910 (=*G. sacculifer* var. *fistulosa* (Schubert, 1910)) with a LOD of older than 1.77 Ma. The exact stratigraphic age of the localities, therefore, must still be considered uncertain but is Late Pliocene (Piacenzian) or Early Pleistocene (Gelasian).

Material and methods

All localities are listed in Table 1 and some localities are shown in figure 1.

Sample treatment has been described in Janssen (2007); we used the benthic mollusks from the same samples. Numbers of specimens studied are indicated in parentheses after the locality information. Characterizations are based on the studied material only.

FIGURE 1. Locality map. For additional Anda localities and details of locality Tiep see Janssen (2007).

Abbreviations used:

AA	apical angle
DN	diameter of the nucleus (initial globular portion of the protoconch)
H	height
Hap	height of the aperture
MSA	mean spire angle
NW	number of whorls
P/T	protoconch/teleoconch (boundary)
P1	protoconch 1
P2	protoconch 2
W	width
*	estimate

Shells were studied, photographed and measured using a Leica M165C motorized microscope system. All shell measurements were taken using the measuring mode of the Leica Application System (LAS software version 3.8), along, parallel or perpendicular to the longitudinal axis. Height, width, height of the aperture, mean spire angle and apical angle were measured in the apertural view, while diameter of the nucleus and number of whorls were measured and counted in the apical view. Number of whorls is counted by starting at the semicircular nucleus, which is counted as 0.5 whorls (Figure 2a). The mean spire angle is the angle between two straight lines from the apex to the sutures of the body whorl on opposite sides of the shell axis (Figure 2b). Apical angle is the angle between two straight lines that touch adjacent whorls on opposite sides. Measurements are in line with those proposed by the Conchological Society of Great Britain and Ireland (2012). All measurements are given in Table 2. Height and width measurements of the largest specimen measured are given in the characterizations, as well as ranges of the nucleus diameter, based on all nucleus diameter measurements. We have indicated material with well developed terminal apertural characters that are in the size range of extant adults of the same genus as "adults", despite the lack of direct indications of sexual maturity. All descriptions below are based on the newly collected fossil material.

TABLE 1. Locality data (adapted from Janssen, 2007).

Sample	Coordinates	Collector & date
AndaClif1	16°17′24.8″N 119°56′11.8″E	W. Renema 23.11.1999
AndaClif3	16°17′24.8″N 119°56′11.8″E	W. Renema 23.11.1999
AndaDeVos	16°17′24.8″N 119°56′11.8″E	J. de Vos 04.2000
Anda1–6	16°17′24.8″N 119°56′11.8″E	A.W. Janssen 28.04–09.2001
Roxas	16°16′11.5″N 119°56′52.9″E	A.W. Janssen 06.05.2001
Tiep1	16°13′48.6″N 119°51′32.9″E	W. Renema 28.04.2001
Tiep2	16°13′54.3″N 119°51′36.2″E	W. Renema & A.W. Janssen 28.04.2001
Tiep3	16°14′0″N 119°51′33.7″E	W. Renema 28.04.2001
Tiep4	16°14′3.2″N 119°51′36.2″E	W. Renema 28.04.2001
Tiep5	16°13′54.3″N 119°51′36.2″E	W. Renema 28.04.2001

Systematic Palaeontology

Superfamily Phasianelloidea Swainson, 1840

Family Colloniidae Cossmann, 1917

Remarks. The Colloniidae were formerly regarded as a subfamily of Turbinidae by Hickman & McLean (1990), but molecular evidence suggests that they form a family within the superfamily Phasianelloidea instead (Williams *et al.* 2008).

TABLE 2. Measurements. Height, width, height of the aperture and diameter of the nucleus are given in millimeters. RGM number refers to the registration number of the measured specimen.

Species	RGM number	Height	Width	Height of the aperture	Diameter of the nucleus	Number of whorls	Mean spire angle	Apical angle
Homalopoma tosaense Habe, 1953	608.201	3.6	3.8	2.0	0.17	3.9	110°	122°
	608.202	1.6	2.0	1.2	0.15	2.9	114°	119°
	608.204	1.3*	3.2*	*	0.16	3.8	118°	119°
Seguenzia cf. *keikoae* Poppe, Tagaro & Dekker, 2006	608.208	1.8	1.6	0.9	0.12	5.5	80°	87°
	608.207	1.9	1.7	1.0	0.12	5.5	77°	94°
Seguenzia donaldi Ladd, 1982	608.217	1.7	1.6	0.8	0.11	5.2	84°	101°
	608.216	1.8	1.7	1.0	0.12	5.5	80°	85°
	608.215	1.9	1.9	1.0	0.14	5.5	80°	92°
Seguenzia cf. *elegantissima* Poppe, Tagaro & Dekker, 2006	608.221	2.3	1.9*	1.0	0.11	6.2	69°	81°
	608.222	1.9	1.4*	1.0*	0.14	5.3	74°	77°
Halystina conoidea nov. spec.	608.230	1.6	1.4	0.9	0.11	4.9	78°	83°
	608.232	0.9	0.9	0.5	0.12	3.9	86°	103°
	608.229	2.1	1.7	1.1	0.13	5.6	69°	89°
	608.233	0.7	0.8	0.3	0.12	4.0	81°	101°
Fluxinella membranacea Marshall, 1991	608.239	0.9	2.1	0.6	0.10	4.4	123°	147°
Calliobasis lapulapui Poppe, Tagaro & Dekker, 2006	608.251	2.5	2.6	0.9	0.12	7.0	69°	81°
Thelyssina? spec. 1	608.263	0.8	0.7	0.3	0.08	4.3	58°	80°
Thelyssina? spec. 2	608.268	0.8	0.7	0.4	0.11	3.8	87°	120°
Calliotropis arenosa nov. spec.	608.272	3.4	2.7	1.3	0.19	6.1	63°	90°
	608.273	1.3	1.2	0.6	0.19	4.0	77°	90°
Calliotropis cf. *pyramoeides* Vilvens, 2007	608.281	2.8	2.9	1.1	0.18	6.2	68°	66°
	608.282	1.2	1.0	0.5	0.17	3.8	65°	64°
Calliotropis limbifera (Schepman, 1908)	608.292	3.1*	5.0*	1.6*	0.25	5.6*	94°	88°
Calliotropis spec. 1	608.296	0.7	0.8	0.4	0.22	2.4	101°	103°

……continued on the next page

TABLE 2. (Continued)

Species	RGM number	Height	Width	Height of the aperture	Diameter of the nucleus	Number of whorls	Mean spire angle	Apical angle
Calliotropis spec. 2	608.301	2.0	2.8	1.2	0.18	4.9	93°	112°
Calliostoma spec. 1	608.304	1.9	1.8	0.7	0.21	4.0	64°	71°
Calliostoma spec. 2	608.306	0.8	0.8	0.4	0.18	2.3	76°	78°
	608.305	1.6	1.4	0.7	0.20	3.7	62°	61°
Pseudotalopia taiwanensis Habe, 1961	608.316	1.5	2.0	0.8	0.09	3.4	95°	106°
	608.317	1.9*	*	*	0.08	*	100°	100°
	608.318	5.9*	7.3	4.0	*	3.3*	85°*	89°*
Conotalopia musiva (Gould, 1861)	608.319	0.7	0.7	0.3	0.09	3.8	93°	117°
Ethminolia wareni nov. spec.	608.321	3.0	4.4	1.8	0.12	5.3	107°	127°
	608.322	0.9	1.2	0.6	0.10	3.4	111°	124°
Solariella chodon Vilvens, 2009	608.338	1.7*	2.0	0.6*	0.15	4.3	86°	99°
	608.339	2.8	3.0	1.2	0.13	5.3	74°	101°
Solariella cf. *segersi* (Poppe, Tagaro & Dekker, 2006)	608.348	3.5*	3.1	1.2	0.31*	4.8*	72°*	88°
	608.349	3.2*	3.4	1.3	*	3.5*	82°*	74°
Spectamen spec. 1	608.353	0.7	1.0	0.5	0.15	2.6	116°	121°
Archiminolia spec. 1	608.352	1.8*	3.2*	1.2*	0.17	4.2*	111°*	111°
Zetela tabakotanii (Poppe, Tagaro & Dekker, 2006)	608.355	1.9	1.7	0.9	0.11	4.3	69°	110°
	608.356	2.1	1.8	1.0	0.10	4.3	70°	125°
Ilanga konos (Vilvens, 2009)	608.366	1.2	1.8	0.8*	0.15	2.9	121°	142°
	608.367	1.3	2.1	0.9	0.16	3.4	126°	141°
	608.369	1.3	1.8	0.9*	0.13	3.4	132°	138°
Guildfordia yoka Jousseaume, 1888	608.376	0.8	2.2	0.7	0.23	2.4	154°	146°
	608.377	5.9	15.7*	3.9	*	4.4*	122°	136°
	608.379	2.4	7.4*	1.8	0.16	4.2	134°	134°

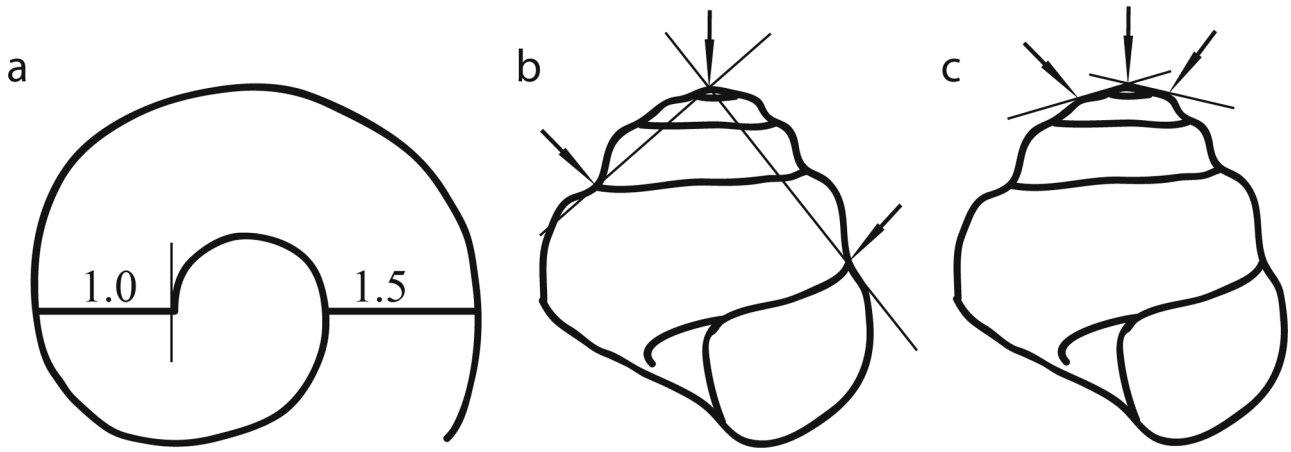


FIGURE 2. Methods of counting whorls and determination of a shell angles; a. Schematic representation of a gastropod apex, displaying the method of whorl counting used here; b. Determination of mean spire angle; c. Determination of apical angle.

Subfamily Colloniinae Cossmann, 1917

Genus *Homalopoma* Carpenter, 1864

Type species. *Turbo sanguineus* Linnaeus, 1758 (by monotypy); Recent, North Atlantic.

***Homalopoma tosaense* Habe, 1953**
(Figures 3–5)

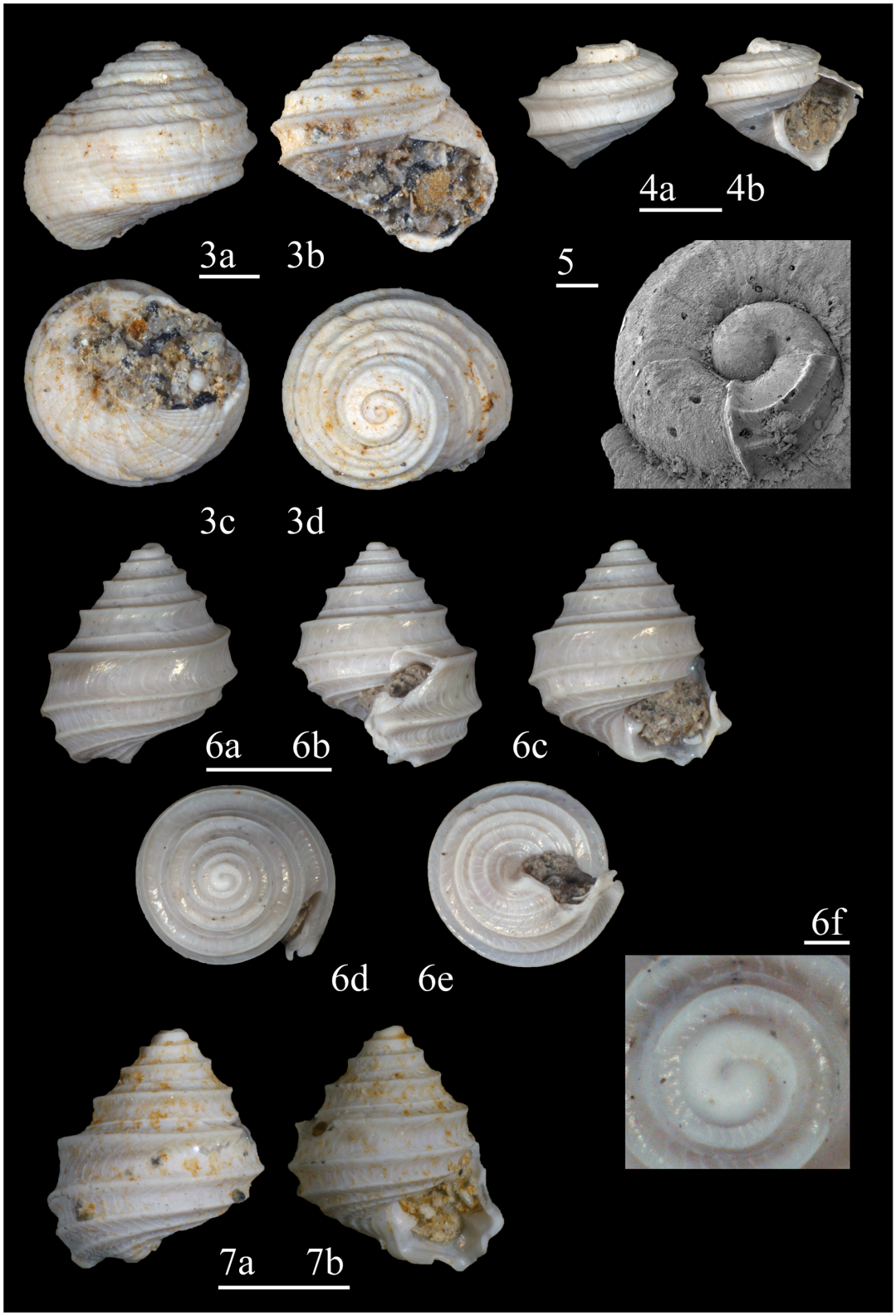
1982 *Homalopoma druidi* nov. spec.—Ladd: p. 27–28, pl. 36, figs 5–8.
1999 *Homalopoma tosaensis* (Habe, 1953)—Higo *et al.*: p. 46.
2001 *Leptothyra tosaensis* (Habe, 1953)—Higo *et al.*: p. 17, fig. G198.
2013 *Leptothyra tosaensis* (Habe, 1953)—Poppe & Poppe: http://www.conchology.be/?t=27&family=COLLONIIDAE&species=Leptothyra%20tosaensis
2013 *Homalopoma tosaense* Habe, 1953—Rosenberg: http://marinespecies.org/aphia.php?p=taxdetails&id=737892

Material. Anda 2 (1); Anda 6 (1); AndaDeVos (4).

Characterization. Shell turbiniform, robust, H 3.6 mm, W 3.8 mm; P1 smooth, 1.0 whorls, DN 0.15–0.17 mm; P2, 0.3 whorls, with two robust spiral ribs on median-upper part and third basal spiral rib; P/T boundary distinct terminal varix at 1.3 whorls; T sculpture of spiral ribs; additional spiral ribs between uppermost spiral and suture; spiral and axial lirae in interspaces; umbilicus narrow.

Distribution. Apart from the studied material, this species is known from Tosa Bay and southern Kyushu (Japan), East China Sea (Higo *et al.* 1999), as well as Pliocene deposits of Viti Levu, Fiji (Ladd 1982).

Remarks. *Homalopoma druidi* (Ladd, 1982) is synonymized here with *Homalopoma tosaense* Habe, 1953 and *Leptothyra tosaensis* (Habe, 1953), because of its overall similar conchology. Although the holotype of *Homalopoma druidi* (Ladd, 1982) has a rather high spire when compared to the holotype of *Leptothyra tosaensis* (Habe, 1953), its spire height falls well within the range of intraspecific variation observed on the website: http://www.conchology.be/?t=27&family=COLLONIIDAE&species=Leptothyra%20tosaensis. It remains unclear whether the species should be assigned to *Leptothyra* or *Homalopoma*, as these genera are not well delimited.



FIGURES 3–5. Colloniidae. **3.** *Homalopoma tosaense* Habe, 1953. RGM 608.201. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. For this and remaining figures all material derives from the Piacenzian or Gelasian Santa Cruz Formation of Cabarruyan Island and nearby Luzon island, Philippines. Locality data in Table 1. Scale bars shells = 1 mm, scale bars SEM =100 µm. **4.** *Homalopoma tosaense* Habe, 1953. RGM 608.202. Locality Anda2. (a) rear view, (b) apertural view. **5.** *Homalopoma tosaense* Habe, 1953. RGM 608.203. Locality AndaDeVos, SEM detail of protoconch. **FIGURES 6–7.** Seguenziidae. **6.** *Seguenzia* cf. *keikoae* Poppe, Tagaro & Dekker, 2006. RGM 608.207. Locality Roxas. (a) rear view, (b) side view, (c) apertural view, (d) basal view, (e) apical view, (f) detail of protoconch, scale bar 100 µm. **7.** *Seguenzia* cf. *keikoae* Poppe, Tagaro & Dekker, 2006. RGM 608.208. Locality Anda3. (a) rear view, (b) apertural view.

Superfamily Seguenzioidea Verrill, 1884

Family Seguenziidae Verrill, 1884

Remarks. Protoconchs were examined across a range of *Seguenzia* material. Apart from *S.* cf. *elegantissima* Poppe, Tagaro & Dekker, 2006, protoconchs were invariably deeply corroded and are not illustrated here.

Subfamily Seguenziinae Verrill, 1884

Genus *Seguenzia* Jeffreys, 1876

Type species. *Seguenzia formosa* Jeffreys, 1876 (by monotypy); Recent, North Atlantic.

Seguenzia cf. *keikoae* Poppe, Tagaro & Dekker, 2006
(Figures 6–7)

cf. 2006 *Seguenzia keikoae* nov. spec.—Poppe, Tagaro & Dekker: p. 27, pl. 5, fig. 3.
cf. 2008a *Seguenzia keikoae*—Poppe & Tagaro: p. 162, pl. 26, fig. 3.

Material. Anda 2 (1); Anda 3 (1); Anda 4 (1); Anda 6 (1); AndaDeVos (2); AndaClif3 (1); Roxas (6).

Characterization. *Seguenzia* with numerous low, thin more or less regularly spaced sigmoid axial lirae; H 1.9 mm, W 1.7 mm; DN 0.12 mm; two strong spiral ribs on shoulder, five on base; columella denticulate; adult shell with closed umbilicus.

Distribution. Apart from the studied material, *Seguenzia keikoae* Poppe, Tagaro & Dekker, 2006 has been reported from Bohol, off Pamilacan Island, Philippines, in a sample from between 196–216 m water depth.

Remarks. The attribution to *S. keikoae* is uncertain despite the overall similar shell morphology because the adult specimens in our material have a closed umbilicus. Specimens shown by Poppe *et al.* (2006) have a slit-like umbilicus, but the latter specimens might be juveniles.

Seguenzia donaldi Ladd, 1982
(Figures 8–9)

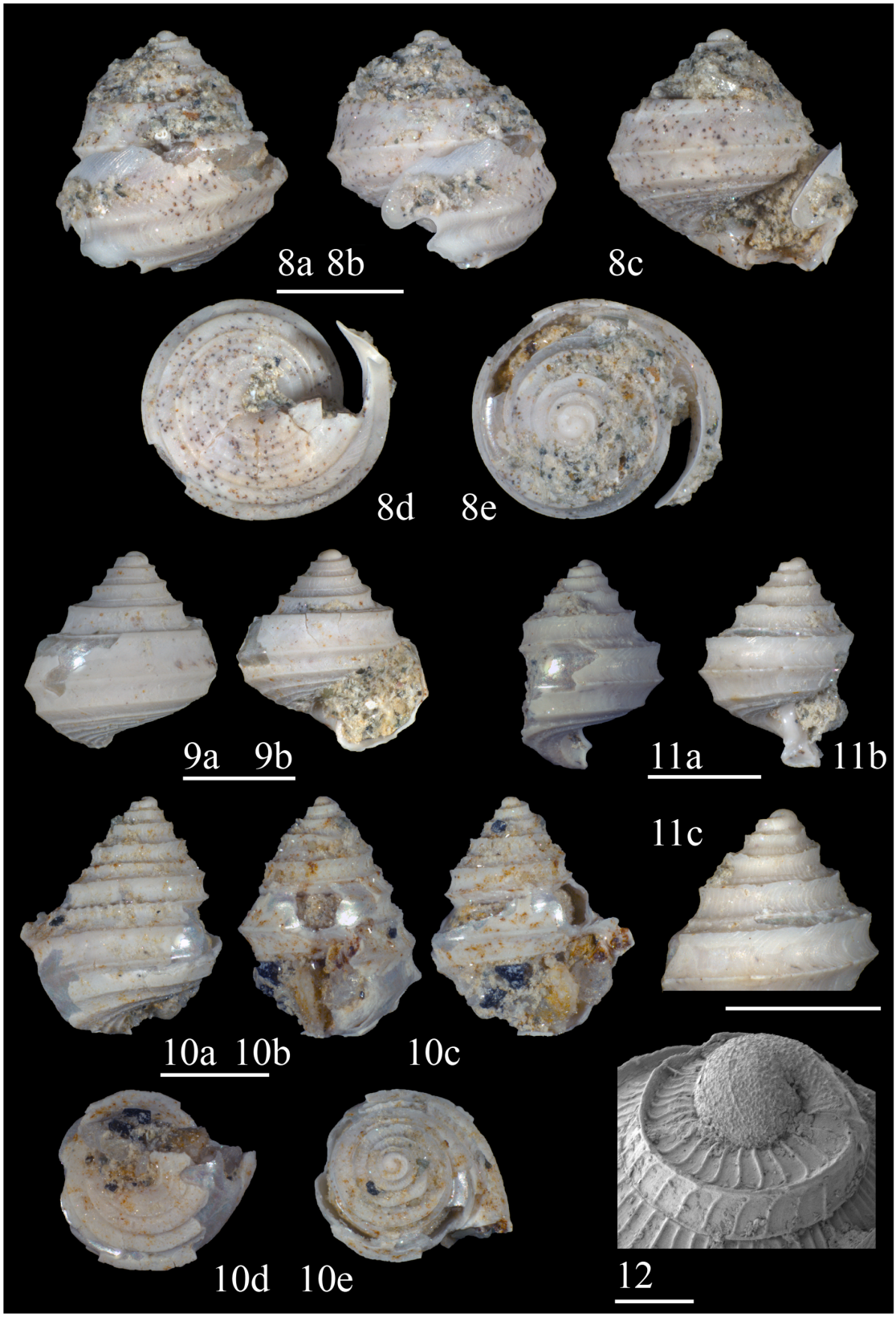
1982 *Seguenzia donaldi* nov. spec.—Ladd: p. 32–33, pl. 35, figs 9–15.

Material. Anda 6 (6); AndaDeVos (29); AndaClif3 (10).

Characterization. Shell relatively broad conical to trochiform, H 1.9 mm, W 1.9 mm; P small, 1.1 whorls; nucleus weakly inclined, DN 0.11–0.14 mm; P/T boundary weak; T with numerous sigmoid axial lirae fading on later T whorls; relatively wide body whorl with three peripheral spiral ribs and five to seven basal spiral ribs; upper apertural retraction deep, upper projection strongly expanding forwards; basal columellar fold or tooth present; umbilicus narrow.

Distribution. Apart from the studied material, this species is known from Pleistocene deposits of Vanuatu (Ladd 1982).

Differentiation. This species is rather similar to *S. trochiformis* Poppe, Tagaro & Dekker, 2006, in having a strong tooth on the columella and an aperture with projections and retractions. However, *S. trochiformis* has a higher spire (H/W ratio of holotype Poppe *et al.*, 2006: 1.10; H/W ratio of *S. donaldi* 1.02-1.07 (table 2)) and a less swollen body whorl. *Seguenzia donaldi* differs from *S.* cf. *keikoae* by its wider whorls. The keel in *S. donaldi* is stronger, its axial lirae are weaker, the protoconch less inclined, the base of the body whorl flatter and the umbilicus wider.



FIGURES 8–12. Seguenziidae. **8.** *Seguenzia donaldi* Ladd, 1982. RGM 608.215. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) side view, (d) basal view, (e) apical view. **9.** *Seguenzia donaldi* Ladd, 1982. RGM 608.216. Locality Anda3. (a) rear view, (b) apertural view. **10.** *Seguenzia* cf. *elegantissima* Poppe, Tagaro & Dekker, 2006. RGM 608.221. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) side view, (d) basal view, (e) apical view. **11.** *Seguenzia* cf. *elegantissima* Poppe, Tagaro & Dekker, 2006. RGM 608.222. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) spire. **12.** *Seguenzia* cf. *elegantissima* Poppe, Tagaro & Dekker, 2006. RGM 608.223. Locality AndaDeVos. SEM detail of protoconch.

Seguenzia cf. *elegantissima* Poppe, Tagaro & Dekker, 2006
(Figures 10–12)

2006 *Seguenzia elegantissima* nov. spec.—Poppe, Tagaro & Dekker: p. 26, pl. 3, fig. 2.
2008a *Seguenzia elegantissima*—Poppe & Tagaro: p. 162, pl. 26, fig. 4.

Material. Anda 6 (6); AndaDeVos (18); AndaClif3 (7); Tiep 1 (1).

Characterization. High spired, H 2.3 mm, W 1.9 mm; P 1.1 whorls, with erect nucleus and two discontinuous spiral ribs, DN 0.11–0.14 mm; T with fine but regular and well developed axial lirae on early whorls, fading on later whorls; slightly erect upper keel; markedly beaded subsutural cord on later T whorls; body whorl with three peripheral spiral ribs and four basal spiral ribs; columellar lip with low basal fold or broadly folded; upper apertural sinus pronounced and thickened.

Distribution. Apart from the studied material, this species is known only from the type locality in the Bohol Sea, Philippines, from 679–740 m water depth (Poppe *et al.* 2006).

Remarks. The elongate shape, thin and regular axials, the beaded suprasutural ridge and the folded columellar lip distinguish this species from the two species treated above. The assignment of the present material to *S. elegantissima* is uncertain, because the outer lip is severely damaged in all specimens, making a complete comparison with the material described by Poppe *et al.* (2006) impossible. Furthermore the subsutural spiral ridge appears to be smooth to marginally knobby in the recent species, whereas it is distinctly beaded in the fossil material studied here. *Seguenzia praeceps* Marshall, 1991, *S. fulgida* Marshall, 1983 and *S. serrata* Marshall, 1983 are quite similar in shape, but their subsutural ridge is not as strongly crenulated as in the studied material.

Genus *Halystina* Marshall, 1991

Type species. *Halystina caledonica* Marshall, 1991 (by original designation); Recent, New Caledonia.

Halystina conoidea nov. spec.
(Figures 13–15)

Type material. Holotype RGM 608.229. Paratype RGM 608.230 (Anda 6); 7 paratypes RGM 608.235 (AndaDeVos).

Type locality. AndaDeVos, Bolinao, Philippines, Santa Cruz Formation, Pliocene or Early Pleistocene.

Derivatio nominis. Named after the conical outline of this species. Adjective.

Other material. Anda 5 (1); Anda 6 (2); AndaDeVos (7); AndaClif3 (4); Tiep 1 (1).

Diagnosis. Shell conoid, H 2.1 mm, W 1.7 mm, DN 0.11–0.13 mm, low spiral ribs, thin axial lirae; axial lirae gradually disappearing; two slightly thicker but low spiral ribs at middle of whorl, just above suture; after second teleoconch whorl, third spiral rib appears just below suture; body whorl with additional rib on periphery; 11 spiral ribs on the convex base; base of aperture with broad short siphonal canal.

Description. The protoconch is paucispiral and has rounded whorls and a relatively dull white surface. The protoconch surface in the studied specimens is corroded, but two spiral ribs appear to be present. The nucleus is slightly inclined. The P/T boundary is located at about 1.1 whorls. The teleoconch ornamentation starts with thin axial riblets that are low and narrow but well delimited. They have a reverse sigmoid shape and are most pronounced at the upper quarter of the whorl. Within 0.2 whorls from the P/T boundary, a very low and rounded spiral rib develops at half the height of the whorl that subsequently moves to two-thirds of the whorl height within half a whorl. This poorly defined rib delimits a low shoulder on the first and second teleoconch whorl. Already on the first teleoconch whorl, a second spiral develops at approximately one quarter of the whorl height. On the second teleoconch whorl, a narrow subsutural ridge develops that forces the suture into a narrow and shallow depression. The whorl profile becomes gradually flatter with the initial spiral rib becoming even lower and located at 0.6 of the whorl height and the basal rib at 0.2. In between the spiral ribs, the profile is straight or slightly concave. The axials (approximately 55–60 on the second teleoconch whorl) gradually disappear over most parts of the whorls, but can remain visible at the top of the whorls. The suprasutural spiral forms a low and broad median

keel on the body whorl, together with a spiral rib on the periphery. At the slightly convex base of the body whorl, 11 more or less regularly spaced low spiral ribs occur, whose interspaces are about twice as wide as the ribs. The aperture is damaged and/or partially covered in all specimens, but is subtrapezoidal in juveniles and subquadrate in adults, where the outer lip is expanded basally. The outer lip also has a retraction in the upper part, between the suture and the periphery. The columellar lip is barely thickened, appears slightly twisted and grades into a broad and shallow basal sinus. A single specimen contains a very subtle columellar fold on the base of the columella. The umbilicus is rimate.

Differentiation. *Halystina conoidea* differs from *H. vaubani* Marshall, 1991 and *H. caledonica* Marshall, 1991, both Recent species from New Caledonia, in having axial ribs that become obsolete instead of being well developed throughout the teleoconch. It differs from *H. carinata* Marshall, 1991, also from New Caledonia, and *H. simplex* (Barnard, 1963) from South Africa by a more subtle shoulder. It resembles most closely *H. globulus* Poppe, Tagaro & Dekker, 2006, from the Philippines, but differs in the almost entirely closed umbilicus (instead of open). *Halystina conoidea* differs from *H. edax* Bertolaso & Palazzi, 1999, from the Pliocene of Italy, and *H. siberutensis* (Thiele, 1925), a Recent species from Indonesia, in having an angular periphery.

Genus *Fluxinella* Marshall, 1983

Type species. *Fluxinella lepida* Marshall, 1983 (by original designation); Recent, New Zealand.

Fluxinella membranacea Marshall, 1991
(Figures 16–17)

1991 *Fluxinella membranacea* sp. nov.—Marshall, 1991: p. 68, figs 91, 93, 94.
2006 *Fluxinella membranacea*—Poppe *et al.*: p. 23, pl. 2, fig. 4.
2008a *Fluxinella membranacea*—Poppe & Tagaro: p. 160, pl. 25, fig. 4.

Material. Anda 1 (28); Anda 2 (41); Anda 3 (26); Anda 4 (37); Anda 5 (2); Anda 6 (5); AndaDeVos (15); AndaClif1 (1); AndaClif3 (2); Roxas (3).

Characterization. Shell very low domed, H 0.9 mm, W 2.1 mm, disk-shaped, smooth and shiny; P small, smooth, 1.1 whorls, DN 0.10 mm; T growth lines very fine, sigmoid; prominent keel on periphery; umbilicus wide.

Distribution. Shells of *Fluxinella membranacea* have been reported from off southern New Caledonia, 250–440 m depth (Marshall 1991) and from Balicasag Island, Philippines, from 242–400 m depth (Poppe *et al.* 2006).

Remarks. The specimen shown by Marshall (1991) is similar to the shells in the studied material. The specimen shown by Poppe *et al.* (2006, pl. 2, fig. 4) has a more pronounced folded columellar lip, a more pronounced shoulder and median keel than the fossil material as well as the material shown by Marshall (1991). More material is required to investigate whether these differences represent intraspecific variation.

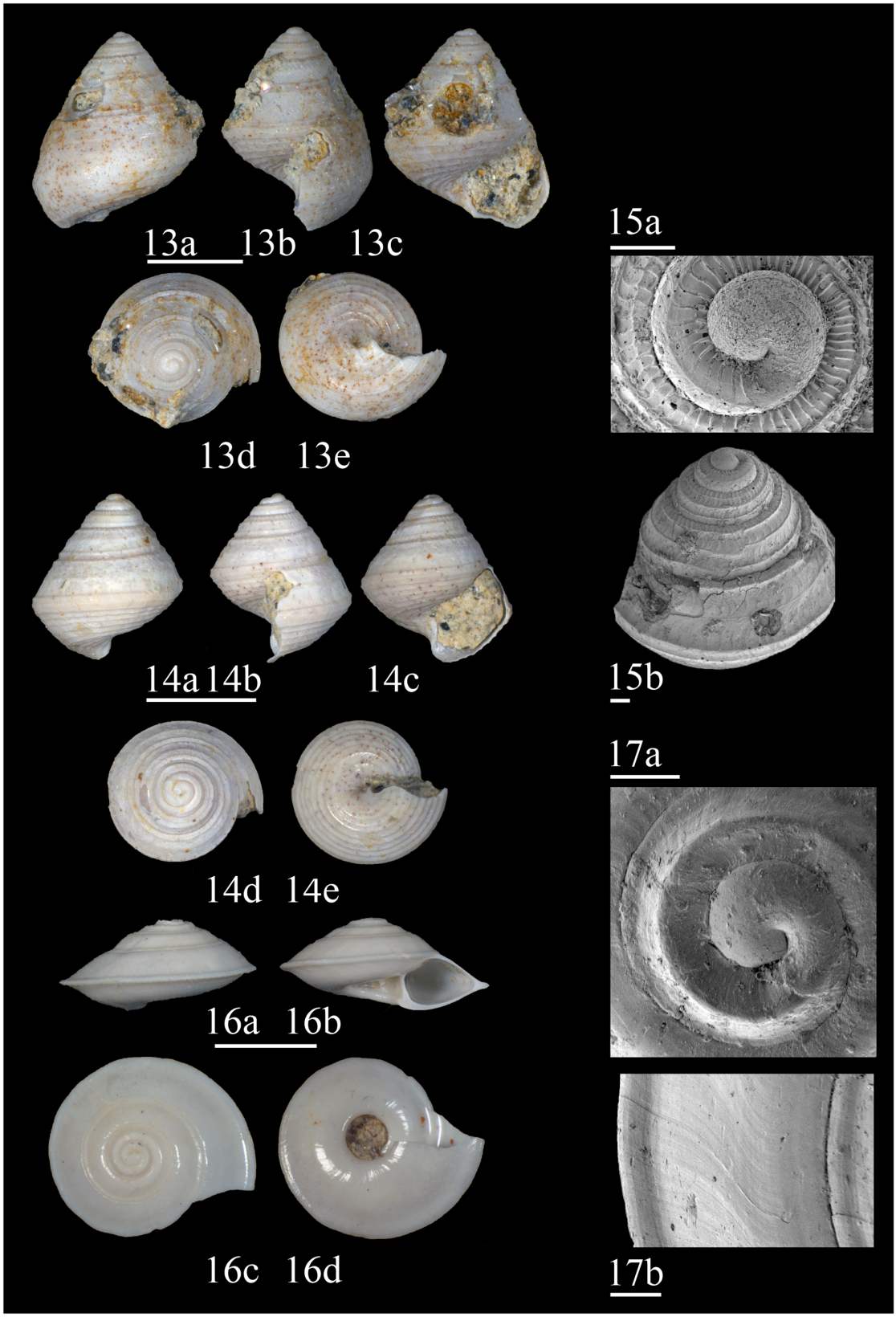
Genus *Calliobasis* Marshall, 1983

Type species. *Basilissa bombax* Cotton & Godfrey, 1938 (by original designation); Recent, southern Australia.

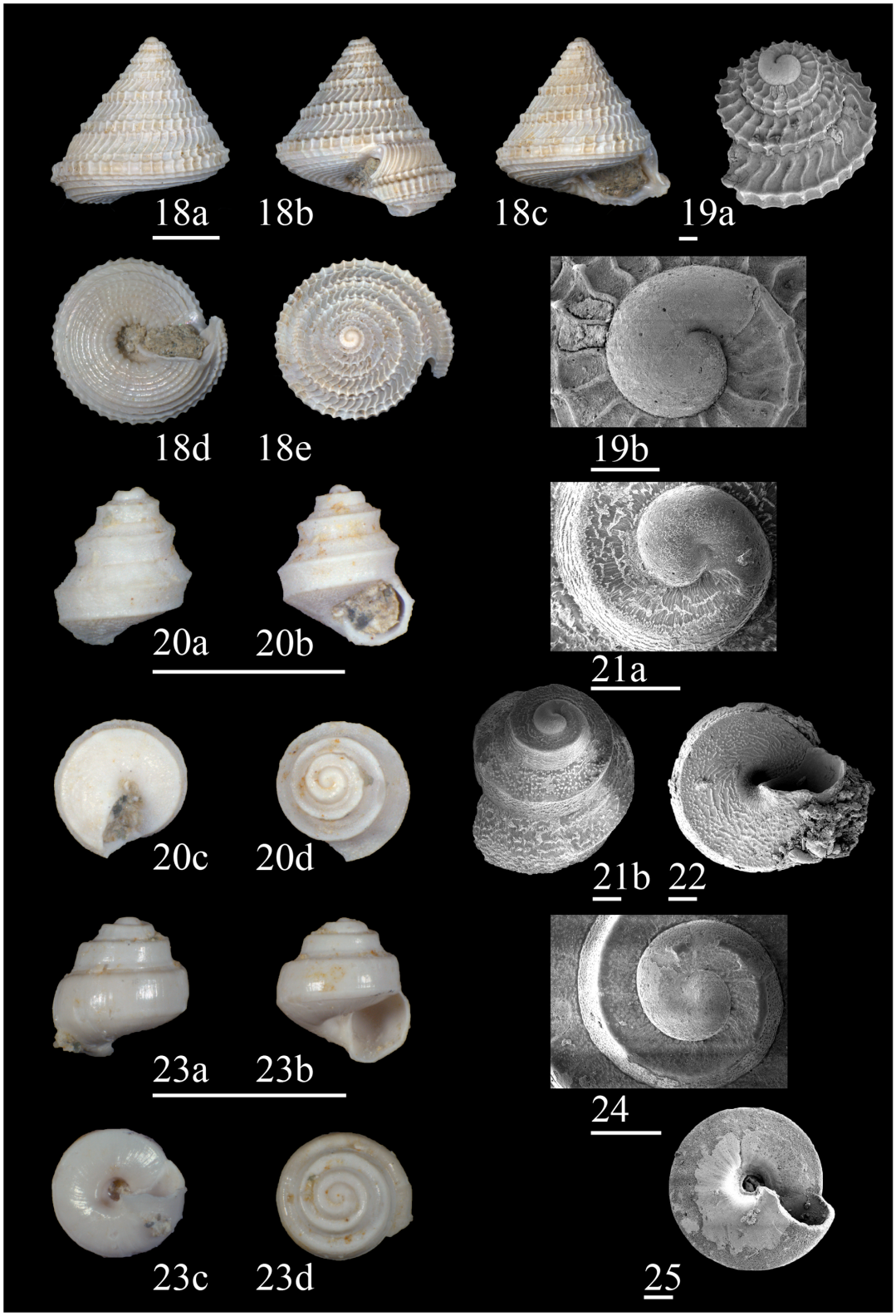
Calliobasis lapulapui Poppe, Tagaro & Dekker, 2006
(Figures 18–19)

2006 *Calliobasis lapulapui* nov. spec.—Poppe *et al.*: p. 21, pl. 1, fig. 2.
2008a *Calliobasis lapulapui*—Poppe & Tagaro: p. 160, pl. 25, fig. 1.

Material. Anda 1 (72); Anda 2 (81); Anda 3 (44); Anda 4 (83); Anda 5 (1); Anda 6 (2); AndaDeVos (3); Roxas (1); Tiep 3 (3); Tiep 5 (5).



FIGURES 13–17. Seguenziidae. **13.** *Halystina conoidea* nov. spec. RGM 608.229 (holotype). Locality AndaDeVos. (a) rear view, (b) apertural view, (c) side view, (d) basal view, (e) apical view. **14.** *Halystina conoidea* nov. spec. RGM 608.230 (paratype). Locality Anda6. (a) rear view, (b) apertural view, (c) side view, (d) basal view, (e) apical view. **15.** *Halystina conoidea* nov. spec. RGM 608.231 (paratype). Locality AndaDeVos. SEM detail of protoconch. **16.** *Fluxinella membranacea* Marshall, 1991. RGM 608.239. Locality Anda1. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **17**. *Fluxinella membranacea* Marshall, 1991. RGM 608.240. Locality Anda1. (a) apical view, (b) SEM detail of surface sculpture.



FIGURES 18–25. Seguenziidae. **18.** *Calliobasis lapulapui* Poppe, Tagaro & Dekker, 2006. RGM 608.251. Locality Anda1. (a) rear view, (b) apertural view, (c) side view, (d) basal view, (e) apical view. **19.** *Calliobasis lapulapui* Poppe, Tagaro & Dekker, 2006. RGM 608.252. Locality Anda3. (a) SEM, side view, (b) SEM detail of protoconch. **20.** *Thelyssina?* spec.1. RGM 608.263. Locality Anda2. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **21.** *Thelyssina?* spec.1. RGM 608.264. Locality Anda2. (a) SEM detail of protoconch, (b) SEM, side view. **22.** *Thelyssina?* spec.1. RGM 608.265. Locality Anda2. SEM, basal view. **23.** *Thelyssina?* spec.2. RGM 608.268. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **24.** *Thelyssina?* spec.2. RGM 608.269. Locality AndaDeVos. SEM detail of protoconch. **25.** *Thelyssina?* spec.2. RGM 608.270 Locality AndaDeVos. SEM, basal view.

Characterization. Conical shell with regularly-spaced, well-defined erect sigmoid axial ribs, H 2.5 mm, W 2.6 mm; P globular, 1.1 whorls, DN 0.10 mm; one or two spiral ribs on lower T whorls; body whorl with strong keel; base with nine spiral ribs; plane of aperture tilted downwards; outer lip with strong upper and lower retractions.

Distribution. Apart from the studied material, *Calliobasis lapulapui* has been reported from the Dipolog Bay, Mindanao Island, Philippines, 172–175 m depth (Poppe *et al.* 2006).

Remarks. The specimen shown in Poppe *et al.* (2006) does not have the elaborate outer lip organisation, but is likely not fully grown. It is smaller than the fossil material studied here (H 2.2 mm versus H 2.53 mm). The shape of the shell and the ornamentation are the same as in the fossils studied here.

Subfamily Asthelysinae Marshall, 1991

Genus *Thelyssina* Marshall, 1983

Type species. *Thelyssina sterrha* Marshall, 1983 (by original designation); Recent, New Zealand.

Thelyssina? spec. 1

(Figures 20–22)

Material. Anda 2 (5); AndaDeVos (2).

Characterization. Shell minute, H 0.8 mm, W 0.7 mm; P 1.1 whorls, with fine anastomosing sculpture, DN 0.08 mm; P/T boundary rounded varix; second varix at 1.6 whorls; T whorls with a sharp keel; microsculpture granulate; body whorl with two sharp spiral ribs; aperture rounded; umbilicus narrow; umbilical ridge weak.

Remarks. This seguenzioid skeneimorph species is provisionally placed in *Thelyssina*, based on the presence of dendritic teleoconch sculpture and a keeled shoulder. At the highest magnifications available, we observed very brilliantly shiny shell material at the inner side of the outer lip that we interpret as nacre. The small protoconch is also similar to the protoconch of the type species for the genus, *T. sterrha* Marshall, 1983, in the anastomosing sculpture and characteristic shape. However, this assignment is uncertain, because the fossil species is relatively tall and more strongly granulate and keeled. *Thelyssina?* spec. 1 also resembles *Conotalopia minima* (Golikov, 1967), a Recent trochid species from Japan, in general shape, but it has a smaller protoconch relative to the first teleoconch whorl, a dendritic granulate sculpture on the teleoconch and a narrower umbilicus.

Thelyssina? spec. 2

(Figures 23–25)

Material. AndaDeVos (10).

Characterization. Shell minute, H 0.8 mm, W 0.7 mm, trochiform, turreted; DN 0.11 mm; P/T boundary thin varix at 1.1 whorls; second varix at 1.6 whorls; T whorls shouldered, with axial lirae and minute pits; body whorl with rounded shoulder and low spiral rib; aperture subquadrate; very thin nacre observed at the damaged outer lip of one specimen; umbilicus narrow, with spiral rib inside.

Remarks. This seguenzioid skeneimorph species is also provisionally placed in *Thelyssina*, based on the presence of minute pits, a well defined angular shoulder, a basal spiral rib, an umbilical spiral rib and a small protoconch with anastomosing sculpture and a shape similar to the protoconch of the type species for the genus. However, this assignment is open to further scrutiny as *Thelyssina?* spec. 2 is relatively tall and lacks dendritic sculpture.

Family Calliotropidae Hickman & McLean, 1990

Remarks. Calliotropidae were previously regarded as a subfamily of Chilodontidae by Bouchet *et al.* (2005). However, Kano *et al.* (2009) regarded the Calliotropidae as an independent family within the Seguenzioidea.

Genus *Calliotropis* Seguenza, 1903

Type species. *Trochus ottoi* Philippi, 1844 (by original designation); Pleistocene, Mediterranean.

Calliotropis arenosa nov. spec.

(Figures 26–29)

Type material. holotype RGM 608.272. Paratype RGM 608.273 and RGM 608.275 (type locality); paratype RGM 608.274 (Anda 3).

Type locality. AndaDeVos, Bolinao province, Philippines, Santa Cruz Formation, Pliocene or Early Pleistocene.

Derivatio nominis. Named after the sediment covering adult shells.

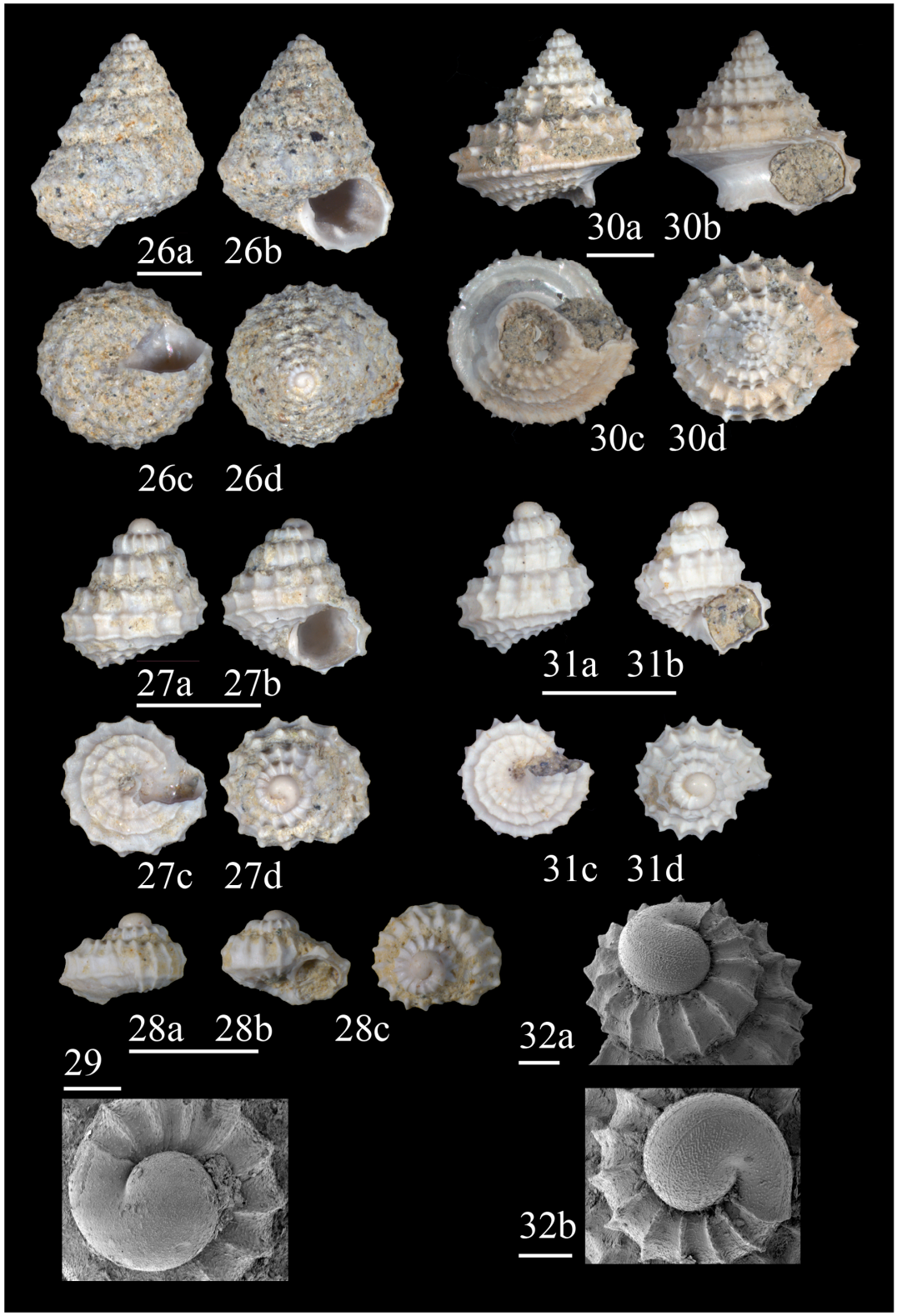
Other material. Anda 2 (1); Anda 5 (1); Anda 6 (49); AndaDeVos (102); AndaClif3 (18).

Diagnosis. Shell conical, covered in sediment, H 3.4 mm, W 2.7 mm; P large, DN 0.19 mm); T sculpture of multiple axial ribs and two spiral ribs, with granules at intersections; suture canaliculate; aperture with three lamellae and a columellar denticle; umbilicus narrow.

Description. This species has a conical-shaped shell that is covered with a thin, even layer of fine sand from the early teleoconch onwards. This sand is most likely agglutinated by the live animal. The protoconch has a large, globose nucleus (DN 185–192 µm) and it is finely granular and consists of 1.0 whorls. The P/T boundary is marked by a thin varix. The teleoconch bears microscopic pustules. The first teleoconch whorl is sculpted with 15 axial ribs. Their interspaces are about three times as wide as their width. Sediment cover develops within the first 0.5 teleoconch whorl. Two spiral ribs appear on the second teleoconch whorl. The axial ribs develop granules at intersections with these spiral ribs. The whorl profile changes from round to angular as the spiral ribs become more pronounced. The area between the spiral ribs becomes slightly concave. The suture is canaliculate. The body whorl bears four additional spiral ribs. The area between the middle rib and basal rib is also slightly concave. The three basal ribs are slightly weaker than the three ribs on the preceding whorls. The base is slightly convex. The aperture is weakly nacreous and subcircular to subquadrate. The parietal margin is slightly convex and contains a thin callus and a weak knob on its upper part. The general shape of the outer lip is rounded, but the spiral ribs produce local angulations. The inner side of the outer lip contains two weak lamellae and a stronger basal lamella. The columellar lip is also rounded but the columella is nearly straight. A weak denticle is present at midpoint of columella in holotype, but absent in most other specimens. The umbilicus is narrow.

Differentiation. *Calliotropis arenosa* is most similar to the slightly taller *C. acherontis* Marshall, 1979 (Recent, southwest-Pacific), but the latter species does not agglutinate sand to the shell. Furthermore, the specimens figured by Marshall (1979) and Vilvens (2007) do not appear to have lamellae or a denticle in the aperture, while the larger specimens in the studied material, in which the aperture is not filled with sediment, always have lamellae and sometimes also have a denticle.

Remarks. The layer of sediment on the adults of this species is considered here as a characteristic of the species, because it is present in all adult material and its appearance, thickness and evenness is constant and similar in all adults. Furthermore, such a characteristic layer is not present in any other species of shells in the studied material. The origin of this layer of sediment remains speculative, but is perhaps facilitated by periostracal fluids, as it is in the Caenogastropod genus *Scaliola* Adams, 1860 (Healy & Wells 1998). One specimen in the studied material has grown wider whorls after a break in the shell, so injuries to snails of this species may sometimes alter shell development.



FIGURES 26–32. Calliotropidae. **26.** *Calliotropis arenosa* nov. spec. RGM 608.272 (holotype). Locality AndaDeVos. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **27.** *Calliotropis arenosa* nov. spec. RGM 608.273 (paratype). Locality AndaDeVos. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **28.** *Calliotropis arenosa* nov. spec. RGM 608.274 (paratype). Locality Anda3. (a) rear view, (b) apertural view, (c) apical view. **29.** *Calliotropis arenosa* nov. spec. RGM 608.275 (paratype). Locality AndaDeVos. SEM detail of protoconch. **30.** *Calliotropis* cf. *pyramoeides* Vilvens, 2007. RGM 608.281. Locality Anda2. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **31.** *Calliotropis* cf. *pyramoeides* Vilvens, 2007. RGM 608.282. Locality Anda2. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **32.** *Calliotropis* cf. *pyramoeides* Vilvens, 2007. RGM 608.283. Locality Anda1. (a) SEM, side view, (b) SEM detail of protoconch.

Calliotropis cf. *pyramoeides* Vilvens, 2007
(Figures 30–32)

cf. 2007 *Calliotropis pyramoeides* nov. spec.—Vilvens: p. 36, figs 112–115.

Material. Anda 1 (20); Anda 2 (19); Anda 3 (11); Anda 5 (4); Anda 6 (5); AndaDeVos (4); AndaClif3 (3); Tiep 1 (1).

Characterization. Shell broadly conical, H 2.8 mm, W 2.9 mm; P globular, finely granulate, with four discontinuous spiral ribs and zigzag patterns, 1.1 whorls, DN 0.17–0.18 mm; P/T boundary thin rib; T ornamented with spiral and axial ribs with spines at intersections; spines lower on whorl develop into C-shaped lamellae; umbilicus broad, encircled by rib, with spiral and axial ribs inside.

Distribution. South-western Pacific (New Caledonia area), alive at 200 m depth, empty shells at 250–350 m depth (Vilvens 2007), apart from the studied material.

Remarks. The base of our shells appears to be taller than those figured in Vilvens (2007).

Calliotropis limbifera (Schepman, 1908)
(Figures 33–34)

1908 *Solariellopsis limbifera* nov. spec.—Schepman: p. 54–55, pl. IV, fig. 3.
1979 *Calliotropis limbifera*—Marshall: p. 526.
2007 *Calliotropis limbifera* —Vilvens: p. 50, figs 172–175.

Material. AndaDeVos (1 adult, damaged; 1 juvenile, damaged); AndaClif3 (1 juvenile, damaged).

Characterization. Shell broadly conical, keeled, H 3.1 mm, W 5.0 mm; P large, bulbous, weakly granulate, 1.1 whorls, DN 0.25 mm; P/T boundary weak rib; T microsculpture of discontinuous axial threads; reticulate ornamentation on first 2.5 T whorls; ornamentation changes to rows of knobs, rows of scales with axial lirae in between and a keel ornamented with axial ribs.

Distribution. Apart from the studied material the species is known from the Sulu Archipelago, Philippines, 522 m depth (Schepman 1908) and the south-western Pacific, 315–415 m depth (Vilvens 2007).

Calliotropis spec. 1
(Figures 35–36)

Material. Anda 1 (1); Anda 2 (2); Anda 4 (2).

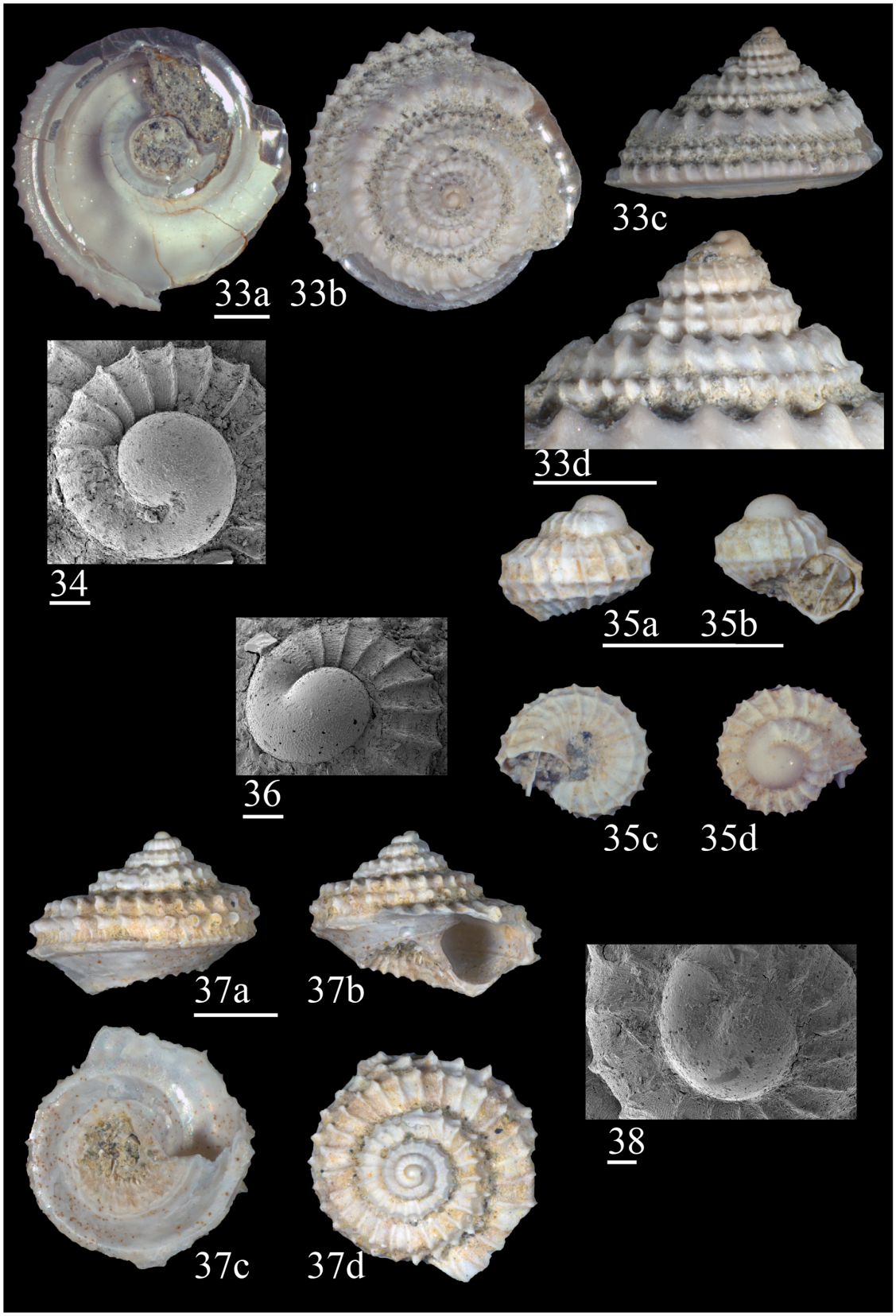
Characterization. Shell with rounded whorls, H 0.7 mm, W 0.8 mm; P large, bulbous, granulate, 1.1 whorls, DN 0.22 mm; P/T boundary distinct rib; T with reticulate ornamentation; weak spines on intersections of spiral and axial ribs; microsculpture of discontinuous granulate spiral threads; body whorl with four spiral ribs; aperture rounded; umbilicus moderately wide.

Remarks. These shells are probably all juveniles of a single species that could not be matched with any of the other *Calliotropis* species in the studied material. It is most similar to *C. limbifera* (Schepman, 1908), but the spiral ribs are placed lower on the whorls in these specimens than in *C. limbifera* (Schepman, 1908), the microscopic threads are spirally instead of axially arranged and the protoconch is less inclined.

Calliotropis spec. 2
(Figures 37–38)

Material. Anda 1 (1); Anda 2 (1); Anda 3 (1).

Characterization. Shell low trochiform, H 2.0 mm, W 2.8 mm; P globular, slightly elevated, 1.2 whorls, DN 0.18; P/T boundary weak rib; sculpture of axial ribs and two weak spiral ribs, with spines at intersections which become stronger and hollow; upper spiral rib becomes acute; many small axial ribs below lower spiral rib; umbilicus wide, with distinct umbilical ridge, axial ribs with small spines inside.



FIGURES 33–38. Calliotropidae. **33.** *Calliotropis limbifera* (Schepman, 1908). RGM 608.292. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) apical view, (d) spire detail. **34.** *Calliotropis limbifera* (Schepman, 1908). RGM 608.293. Locality AndaDeVos. SEM detail of protoconch. **35.** *Calliotropis* spec.1. RGM 608.296. Locality Anda2. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **36.** *Calliotropis* spec.1. RGM 608.297. Locality Anda4. SEM detail of protoconch. **37.** *Calliotropis* spec.2. RGM 608.301. Locality Anda2. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **38.** *Calliotropis* spec.2. RGM 608.302. Locality Anda3. SEM detail of protoconch.

Remarks. The studied specimens differ from *C. bucina* Vilvens, 2006 (Reunion Island and Mayotte Island) and *C. sagarinoi* Poppe, Tagaro & Dekker, 2006 (Philippines) by having a more angular keel and higher whorls.

Superfamily Trochoidea Rafinesque, 1815

Family Calliostomatidae Thiele, 1924

Remarks. Most calliostomatid species have a characteristic protoconch showing a honeycomb pattern.

Genus *Calliostoma* Swainson, 1840

Type species. *Trochus zizyphinus* Linnaeus, 1758 (by monotypy); Recent, Europe.

***Calliostoma* spec. 1**
(Figure 39)

Material. Anda 4 (1).

Characterization. Shell conical, H 1.9 mm, W 1.8 mm; DN 0.21; P/T boundary at 1.0 whorls characterized by sudden onset of teleoconch ornamentation of axial and radial ribs with knobs at intersections; base of body whorl with spiral ribs; umbilicus apparently closed.

***Calliostoma* spec. 2**
(Figures 40–44)

Material. Anda 2 (2 juveniles and 2 partially preserved subadults); Anda 3 (2 juveniles); Anda 4 (1 subadult partially preserved); Anda 6 (2 juveniles); AndaDeVos (2 juveniles); AndaClif3 (1 juvenile).

Characterization. Shell conical, H 1.6 mm, W 1.4 mm; DN 0.18–0.20 mm; distinct terminal varix marks P/T boundary at 1.1 whorls; spiral and axial sculpture with spines at intersections; lower primary rib develops into peripheral row of spines; sutural ramp progressively concave; base of studied material damaged; umbilicus probably open, encircled by two rows of granules.

Family Trochidae Rafinesque, 1815

Subfamily Cantharidinae Gray, 1857

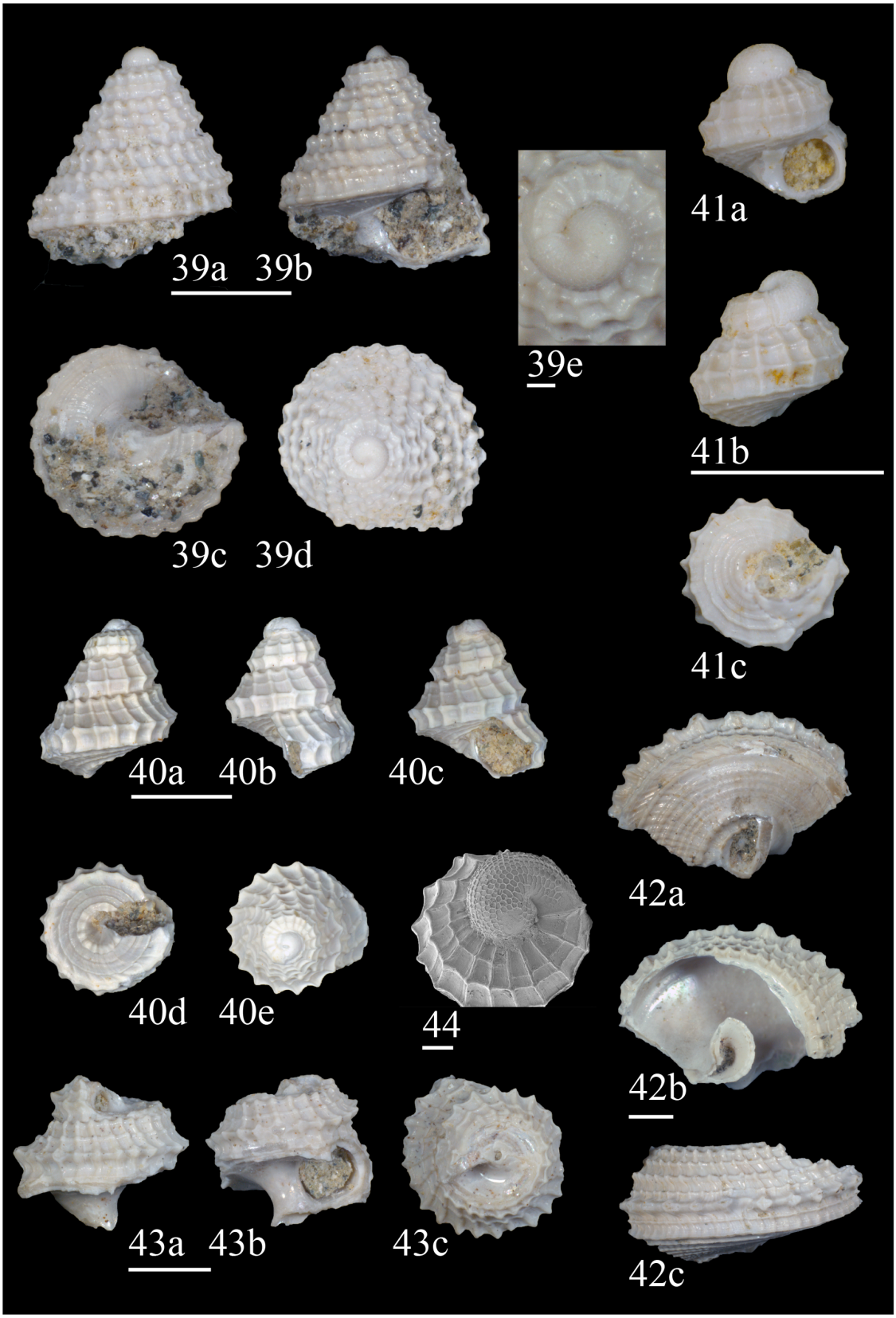
Genus *Pseudotalopia* Habe, 1961

Type species. *Pseudotalopia sakuraii* Habe, 1961 (by monotypy); Recent, Indo-Pacific.

***Pseudotalopia taiwanensis* (Chen, 2006) nov. comb.**
(Figures 45–47)

2006 *Gibbula taiwanensis* nov. spec.—Chen: p. 21, fig. 1.
2007 *Gibbula taiwanensis*—Chen & Fu: p. 67, fig. 2.

Material. Anda 3 (1 adult); Tiep 2 (1 damaged specimen); Tiep 3 (1 juvenile).



FIGURES 39–44. Calliostomatidae. **39.** *Calliostoma* spec.1. RGM 608.304. Locality Anda4. (a) rear view, (b) apertural view, (c) basal view, (d) apical view, (e) detail protoconch. **40.** *Calliostoma* spec.2. RGM 608.305. Locality Anda3. (a) rear view, (b) apertural view, (c) side view, (d) basal view, (e) apical view. **41.** *Calliostoma* spec.2. RGM 608.306. Locality Anda6. (a) rear view, (b) apertural view, (c) basal view. **42.** *Calliostoma* spec.2. RGM 608.307. Locality Anda2. (a) basal view, (b) apical view, (c) rear view. **43.** *Calliostoma* spec.2. RGM 608.308. Locality Anda2. (a) rear view, (b) apertural view, (c) apical view. **44.** *Calliostoma* spec.2. RGM 608.309. Locality Anda3. SEM detail of protoconch.

Characterization. Domed, thick trochiform shell with narrow spiral ribs, a well-developed basal keel and color blotches on a pinkish background color, H 5.9 mm, W 7.3 mm; protoconch glossy white, DN 0.08–0.09 mm; P/T boundary poorly defined at 1.2 whorls; inner lip white, glossy, columellar lip twisted; deep, narrow umbilicus with spiral cord and weak lamellae.

Distribution. Hitherto the species has only been reported from waters off Taiwan, on sandy bottoms, 150–200 m depth (Chen 2006).

Remarks. Chen (2006) found a specimen of this species inside the stomach of a starfish, so apparently this species is predated on by starfishes. The deep-water Indo-West Pacific species currently assigned to *Gibbula* are likely unrelated to that European genus of intertidal species (STW unpub. genetic data). We tentatively assign '*Gibbula' taiwanensis* to the deep-sea genus *Pseudotalopia* based on preliminary genetic data (STW). Molecular data show that *Pseudotalopia* should be assigned to the trochid subfamily Cantharidinae (Williams 2012).

Subfamily Umboniinae H. Adams & A. Adams, 1854

Genus *Conotalopia* Iredale, 1929

Type species. *Minolia henniana* Melvill, 1891 (by original designation); Recent, Australia.

Conotalopia musiva (Gould, 1861)

(Figures 48–49)

1861 *Margarita musiva* nov. spec.—Gould: p. 15.
1989 *Minolia holdsworthana* (G. & H. Nevill, 1871)—Herbert: p. 370, fig. 1h.
1999 *Conotalopia musiva*—Higo *et al.*: p. 67.
2006 *Pseudominolia musiva*—Poppe *et al.*: p. 109, pl. 58, fig. 3.
2008c *Pseudominolia musiva*—Poppe & Tagaro: p. 200, pl. 45, fig. 2.

Material. AndaDeVos (2).

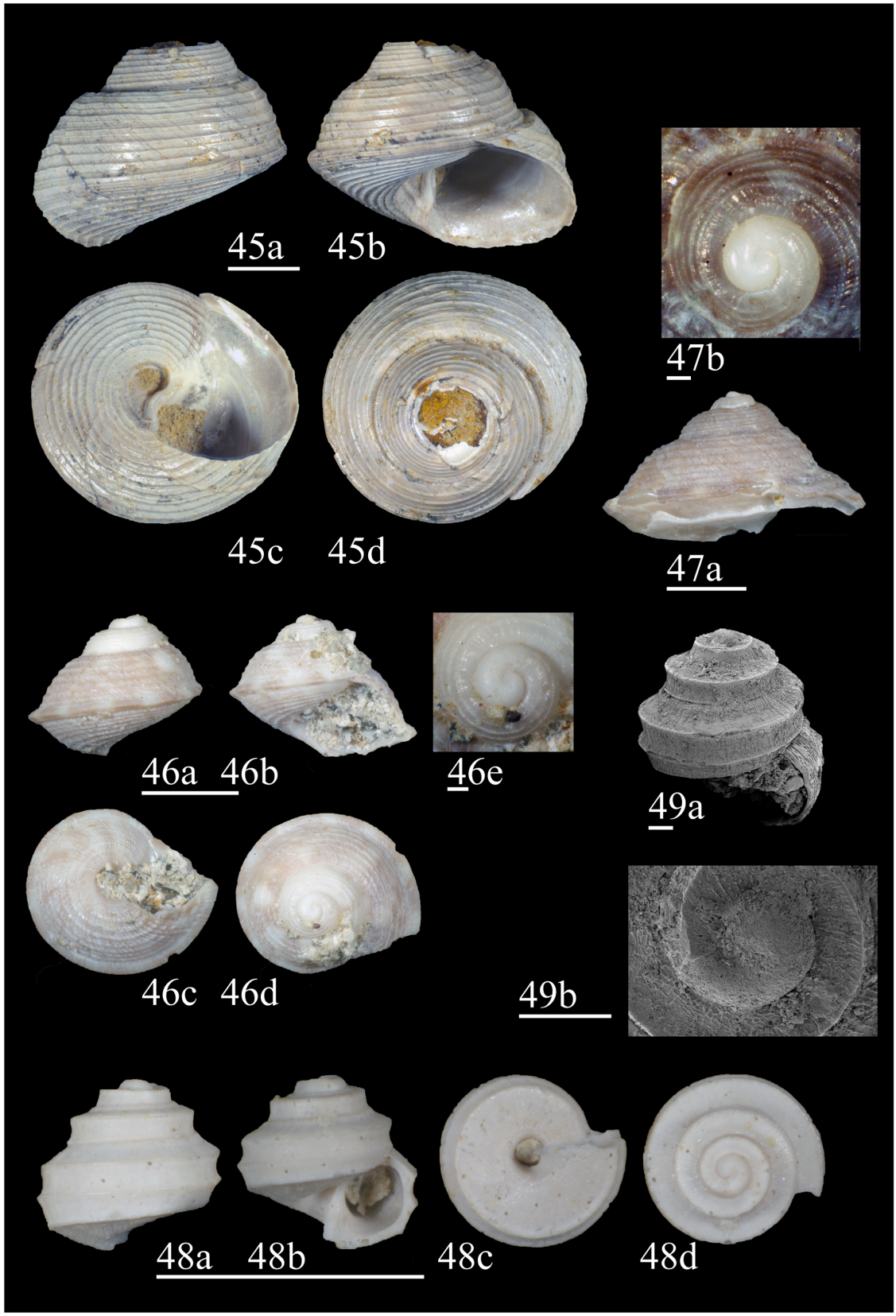
Characterization. Shell minute, H 0.7 mm, W 0.7 mm; DN 0.09 mm; P terminated by well defined, rounded varix at 1.1. whorls; T whorls with a sharp keel and covered by fine, axially arranged granules; body whorl with 3 sharp spiral ribs; base broad and flat; umbilicus narrow, umbilical ridge weakly granulated.

Distribution. Reported from Bohol, Philippines, 38 m depth, Wakasa Bay, Japan, 40–161 m depth (Higo *et al.* 1999), and Hong Kong, Pakistan, Sri Lanka, Malaysia and Thailand (Poppe *et al.* 2006).

Remarks. *Minolia holdsworthana* (G. & H. Nevill, 1871) was synonymized with *M. charmosyne* Melvill, 1918 by Herbert (1989). These two species were synonymized with *Margarita musiva* Gould, 1861 and attributed to *Pseudominolia* by Poppe *et al.* (2006). The synonymy is considered here to be justified, based on the strong conchological similarity, but the allocation to *Pseudominolia* by Poppe *et al.* (2006) is superfluous, because the species is already allocated to *Conotalopia*, according to Higo *et al.* (1999). The allocation to *Conotalopia* is also preferred here, because *C. musiva* shares similarities with other species of *Conotalopia*, such as a relatively high spire and strong spiral ribs. Furthermore, the apical beak of the protoconch, which is a diagnostic feature for *Pseudominolia* (Herbert 1992), is very poorly developed in the studied material. Unfortunately, there are no SEM pictures of the protoconch of type material of *Pseudominolia musiva* (Gould, 1861) or the synonymized taxa available to verify the absence of the apical beak in the species.

Genus *Ethminolia* Iredale, 1924

Type species. *Ethminolia probabilis* Iredale, 1924 (by monotypy); Recent, Indo-Pacific.



FIGURES 45–52. Trochidae. **45.** *Pseudotalopia taiwanensis* Chen, 2006. RGM 608.316. Locality Anda3. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **46.** *Pseudotalopia taiwanensis* Chen, 2006. RGM 608.317. Locality Tiep3. (a) rear view, (b) apertural view, (c) basal view, (d) apical view, (e) detail protoconch. **47.** *Pseudotalopia taiwanensis* Chen, 2006. RGM 608.318. Locality Tiep2. (a) rear view, (b) detail protoconch. **48.** *Conotalopia musiva* (Gould, 1861). RGM 608.319. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **49.** *Conotalopia musiva* (Gould, 1861). RGM 608.320. Locality AndaDeVos. (a) SEM, side view, (b) SEM detail of protoconch.

***Ethminolia wareni* nov. spec.**
(Figures 50–52)

Type material. Holotype RGM 608.321, paratypes RGM 608.322 and RGM 608.323 (Anda 4).

Type locality. Anda 2, Bolinao, Philippines, Santa Cruz Formation, Pliocene or Early Pleistocene.

Derivatio nominis. Named after Anders Warén (Swedish Museum of Natural History), a prominent deep-water malacologist.

Other material. Anda 1 (74); Anda 2 (66); Anda 3 (28); Anda 4 (42); Anda 5 (3); Anda 6 (11); AndaDeVos (27); AndaClif 1 (1); AndaClif 3 (4); Roxas (3); Tiep 1 (1); Tiep 3 (18); Tiep 4 (2); Tiep 5 (27).

Diagnosis. Shell low conical, H 3.0 mm, W 4.4 mm; DN 0.10–0.12 mm; early teleoconch whorls angular; later whorls with subsutural row of knobs; two peripheral ribs; many weak ribs on base; open umbilicus with furrowed umbilical ridge.

Description. This shell is conical with a low spire (H/W ratio 0.67). Larger specimens are covered with brownish blotches and a nacreous shine. The protoconch is small, smooth and consists of 1.1 whorls. The P/T boundary is marked by an adnate varix. After the boundary, three spiral cords are present. The upper rib becomes more prominent and shouldered, while the lower ribs gradually disappear after two whorls. On the third whorl, a spiral row of knobs is gradually formed directly below the suture. The rib and the shoulder it delimits gradually disappear on the fourth whorl. Growth lines are microscopic. The body whorl has two spiral ribs on the periphery and many weak spiral ribs on the base. The aperture is broken in all specimens, but it appears to be subquadrate, with a straight columellar lip. The umbilicus is deep and staircase-like, because of the straight angle of the columella and the base. The edge of the umbilicus has many narrow furrows.

Differentiation. This species differs from *E. nektonica* (Okutani, 1961) by the lack of spiral ribs on the upper side of the later whorls, while *E. nektonica* (Okutani, 1961) has rather strong spiral ribs on the apical side of these whorls. The subsutural row of knobs is more pronounced in *E. wareni*.

Family Solariellidae Powell, 1951

Remarks. This family was considered a subfamily of Trochidae (Bouchet *et al.* 2005), but has since then been raised to family level (Williams *et al.* 2008).

Genus *Solariella* Wood, 1842

Type species. *Solariella maculata* Wood, 1842 (by monotypy); Pliocene, England.

***Solariella chodon* Vilvens, 2009**
(Figures 53–55)

2009 *Solariella chodon* nov. spec.—Vilvens: p. 74–75, figs 11–16.

Material. Anda 1 (19); Anda 2 (13); Anda 3 (7); Anda 4 (2); AndaClif 1 (1); Roxas (1); Tiep 1 (1).

Characterization. Shell thin, cyrtoconoid, glossy, H 2.8 mm, W 3.0 mm; whorls shouldered and keeled; protoconch with six spiral ribs, DN 0.13–0.15 mm; terminal varix very fine at 1.0 whorls; axials and spirals on first two T whorls with microscopic granules in between; later whorls with distinctly beaded subsutural ridge and strong beaded basal spiral rib, shell smooth in between; strong sutural depression; base of body whorl almost smooth; five narrow spiral chords with low spines in umbilicus that is encircled by beads.

Distribution. Apart from the studied material, known only from the type locality, the Kai Islands in Indonesia, from 181–184 m depth (Vilvens 2009).

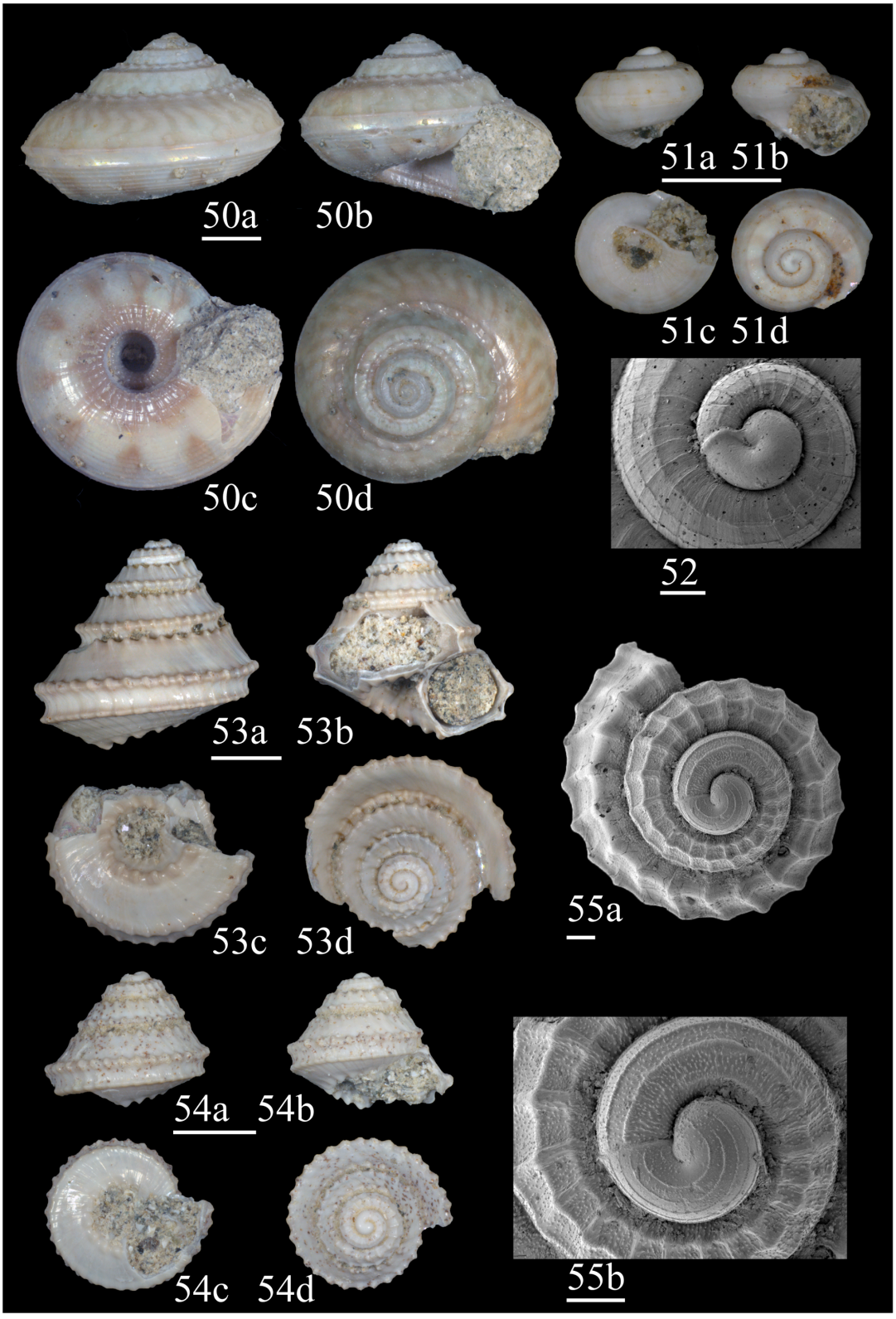


FIGURE 50–52. Trochidae. **50.** *Ethiminolia wareni* nov. spec. RGM 608.321 (holotype). Locality Anda2. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **51.** *Ethiminolia wareni* nov. spec. RGM 608.322 (paratype). Locality Anda4. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **52.** *Ethiminolia wareni* nov. spec. RGM 608.323 (paratype). Locality Anda4. SEM detail of protoconch. **FIGURES 53–55.** Solariellidae. **53.** *Solariella chodon* Vilvens, 2009. RGM 608.338. Locality Anda1. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **54.** *Solariella chodon* Vilvens, 2009. RGM 608.339. Locality Anda1. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **55.** *Solariella chodon* Vilvens, 2009. RGM 608.340. Locality Anda2. (a) SEM, apical view, (b) SEM detail of protoconch.

***Solariella* cf. *segersi* (Poppe, Tagaro & Dekker, 2006) nov. comb.**
(Figures 56–57)

cf. 2006 *Minolia segersi* nov. spec.—Poppe *et al.*: p. 132–133, pl. 72, figs 1–3.
cf. 2009 *Minolia segersi*—Vilvens: p. 94, figs 93–100.

Material. Anda 5 (2).

Characterization. Shell conical, thick-walled, H 3.5 mm, W 3.1 mm; protoconch damaged or missing in studied material; sculpture of spiral and axial ribs with low knobs; deep sutural depression; base of body whorl with spiral ribs; umbilicus open, encircled by grooves and with axial and spiral chords.

Distribution. Apart from the studied material, *Solariella segersi* has been found in the Philippines between 100–224 m depth and has been reported from the East China Sea at 200 m depth (Poppe *et al.* 2006) as well as from Eastern Indonesia from 186–291 m depth (Vilvens 2009).

Remarks. The species has been assigned to *Solariella* on the basis of its moderately tall spire, turriculate outline, spiral sculpture, deep umbilicus and complete peristome, as well as genetic data (Williams *et al.* 2013). The shells in the studied material do resemble *Solariella segersi*, but the vertical arrangement of the spiral ribs is slightly different: the lower spiral rib is situated slightly lower in the fossil material so that it becomes visible only on the body whorl.

Genus *Spectamen* Iredale, 1924

Type species. *Trochus philippensis* Watson, 1880 (by original designation); Recent, Indo-Pacific.

***Spectamen* spec. 1**
(Figure 58)

Material. AndaDeVos (1); Tiep 3 (1).

Characterization. Material probably consists of juveniles; shell low, H 0.7 mm, W 1.0 mm; P of 1.1 whorls with 3 spiral ribs, DN 0.15 mm; P/T boundary thin slightly raised axial rib; T with 6 primary low rounded spiral ribs; body whorl with 3 keels; aperture trapezoid; umbilical ridge beaded; umbilicus wide.

Genus *Archiminolia* Iredale, 1929

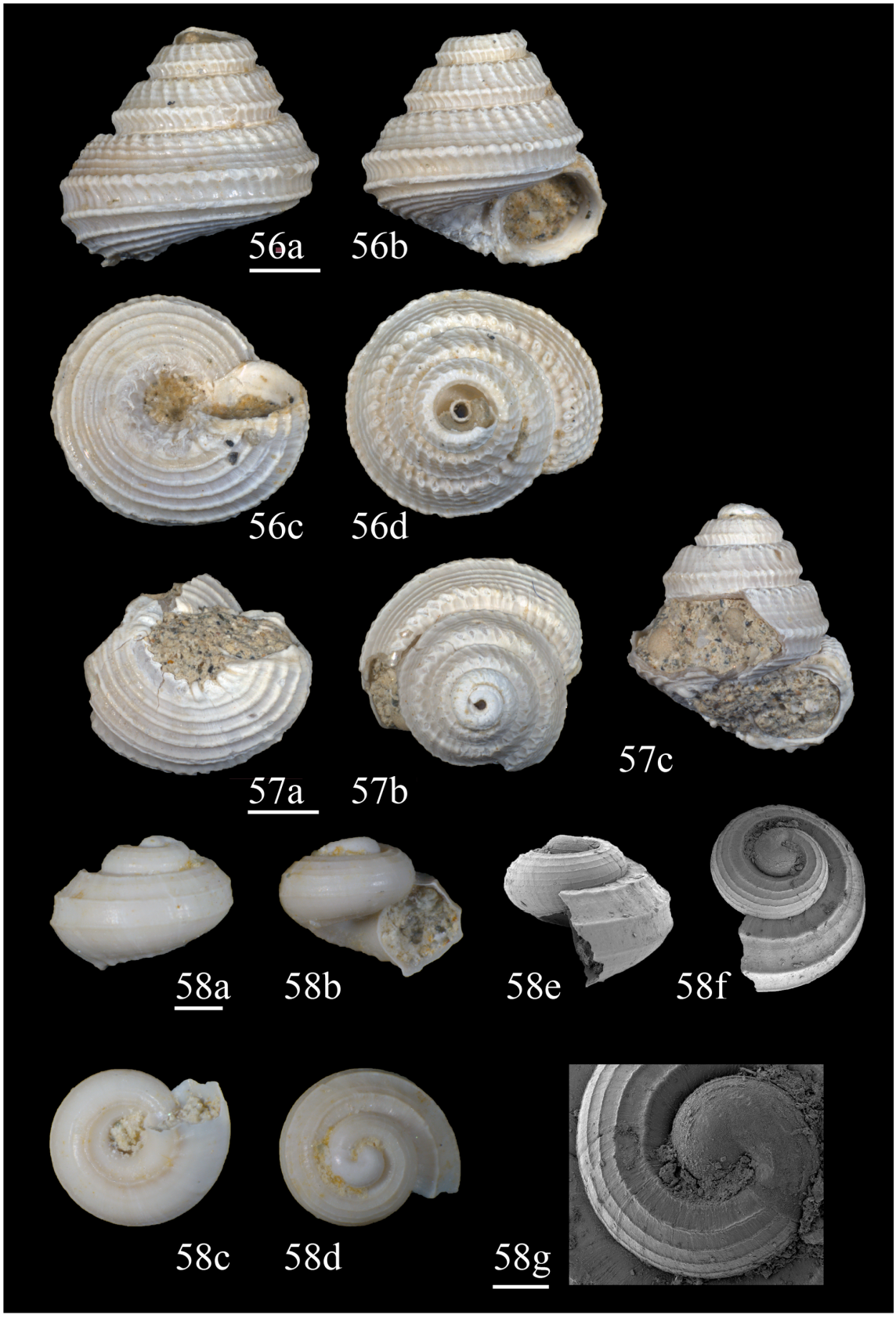
Type species. *Monilea oleacea* Hedley & Petterd, 1906 (by original designation); Recent, Indo-Pacific.

***Archiminolia* spec. 1**
(Figures 59–60)

Material. AndaDeVos (4).

Characterization. Shell low, H 1.8 mm, W 3.2 mm; P 1.1 whorls, with two spiral ribs, DN 0.17 mm; P/T boundary thin, slightly raised varix; first three T whorls with low spiral and axial ribs and axially arranged microscopic granules; fourth whorl smooth, coronate.

Remarks. This species is tentatively assigned to the genus *Archiminolia* on the basis of its similarity to the early whorls of an undescribed *Archiminolia* species collected from the Solomon Islands in the MNHN collection (STW, pers. obs.).



FIGURES 56–58. Solariellidae. **56.** *Solariella* cf. *segersi* (Poppe, Tagaro & Dekker, 2006). RGM 608.348. Locality Anda5. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **57.** *Solariella* cf. *segersi* (Poppe, Tagaro & Dekker, 2006). RGM 608.349. Locality Anda5. (a) apertural view, (b) basal view, (c) apical view. **58.** *Spectamen* spec.1. RGM 608.350. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) basal view, (d) apical view, (e) SEM, side view, (f) SEM, oblique view, scale bar in a–f 500 µm, (g) SEM detail of protoconch.

Genus *Zetela* Finlay, 1926

Type species. *Minolia textilis* Murdoch & Suter, 1906 (by original designation); Recent, New Zealand.

Zetela tabakotanii (Poppe, Tagaro & Dekker, 2006) nov. comb.

(Figures 61–63)

2006 *Minolia tabakotanii* nov. spec.—Poppe *et al.*: p. 133, pl. 68, fig. 1.
2008d *Minolia tabakotanii*—Poppe & Tagaro: p. 224, pl. 57, fig. 2.

Material. Anda 1 (12); Anda 2 (14); Anda 3 (7); Anda 4 (26); Anda 5 (3); Anda 6 (2); AndaDeVos (4); AndaClif1 (3).

Characterization. Small turbiniform shell with rounded whorls, H 2.1 mm, W 1.8 mm); P smooth, globular, DN 0.10–0.11; P/T boundary at 1.2 whorls marked by indistinct rib; T reticulate ornamentation with axial lamellae and microscopic granules in interspaces; aperture circular; narrow umbilicus.

Distribution. Apart from the studied material, known only from the type locality offshore Mactan Island, Philippines from 200 m depth (Poppe *et al.* 2006; Poppe & Tagaro 2008d).

Remarks. This species is assigned to *Zetela* on the basis of the similarity of its sculpture to that of the type species *Z. textilis* (Murdoch & Suter, 1906). It differs from that species by having a much smaller umbilicus and a more continuous peristome.

Genus *Ilanga* Herbert, 1987

Type species. *Trochus laevissimus* von Martens, 1881 (by original desination); Recent, South Africa.

Ilanga konos (Vilvens, 2009) nov. comb.

(Figures 64–68)

2009 *Microgaza konos* nov. spec.—Vilvens: p. 88, figs 64–66.

Material. Anda 1 (5); Anda 2 (2); Anda 6 (1); AndaDeVos (9); Tiep 2 (3).

Characterization. Shell broad and umbilicate H 1.3 mm, W 2.1 mm; P with distinct spiral ribs and axially arranged granulate microsculpture, DN 0.13–0.16 mm; P/T boundary sharp at 1.1 whorls; four spiral ribs on early T whorls, later whorls smooth; pinkish blotches; umbilical ridge narrow, four spiral ribs or more in umbilicus.

Distribution. Apart from the studied material, *Ilanga konos* is known only from the type locality Bashi channel, south Taiwan, from a depth of 305 m (Vilvens 2009).

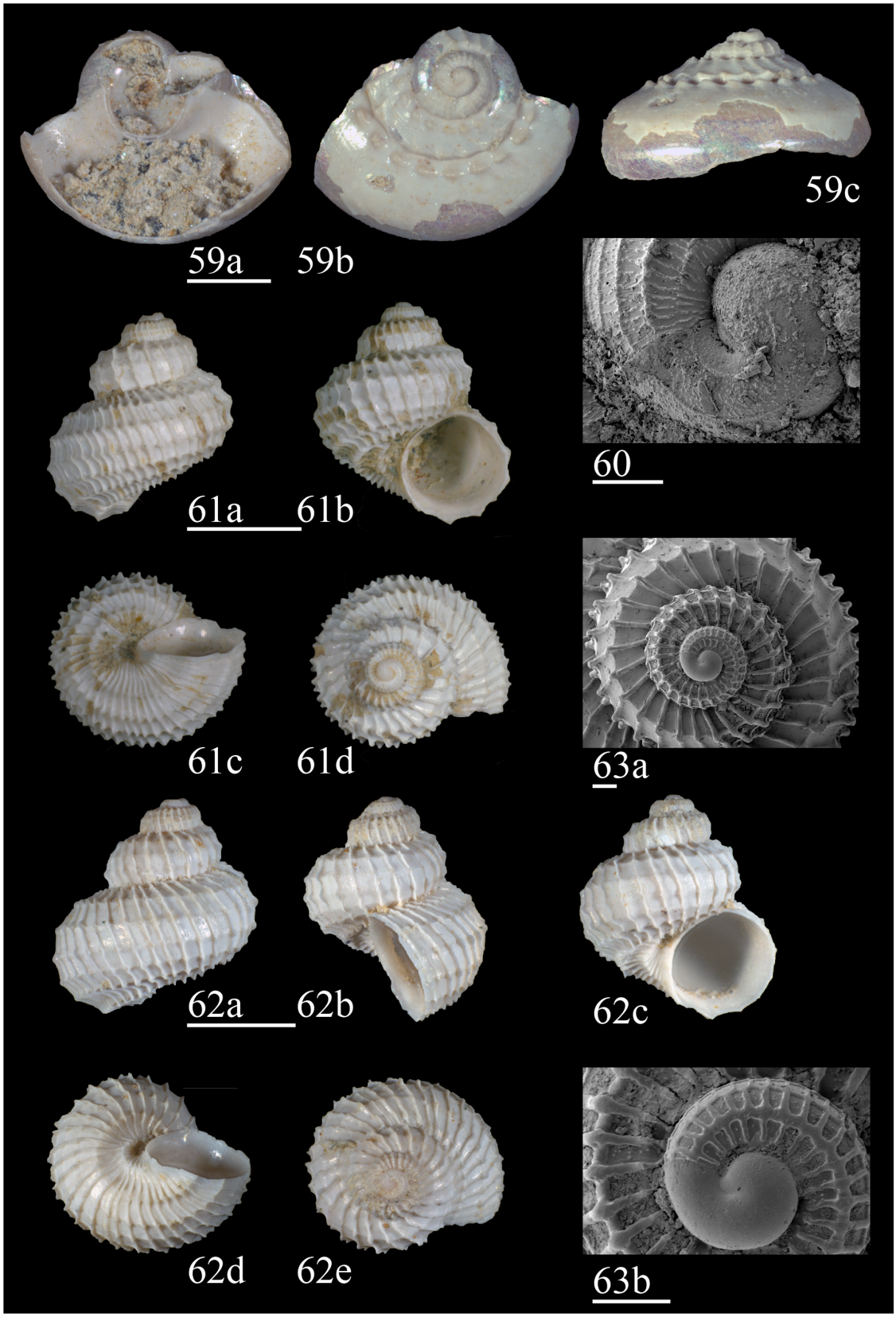
Remarks. This species has been reassigned to *Ilanga* on the basis of genetic data that shows that all western Pacific and Indian Ocean '*Microgaza'* like species, such as *Microgaza konos*, fall into a clade with the type species of *Ilanga* (Williams *et al.* 2013). Both Herbert (1987) and Marshall (1999) recognize *Ilanga* and *Microgaza* as distinct genera, but additional genetic studies are needed to confirm the delimitation of each.

Family Turbinidae Rafinesque, 1815

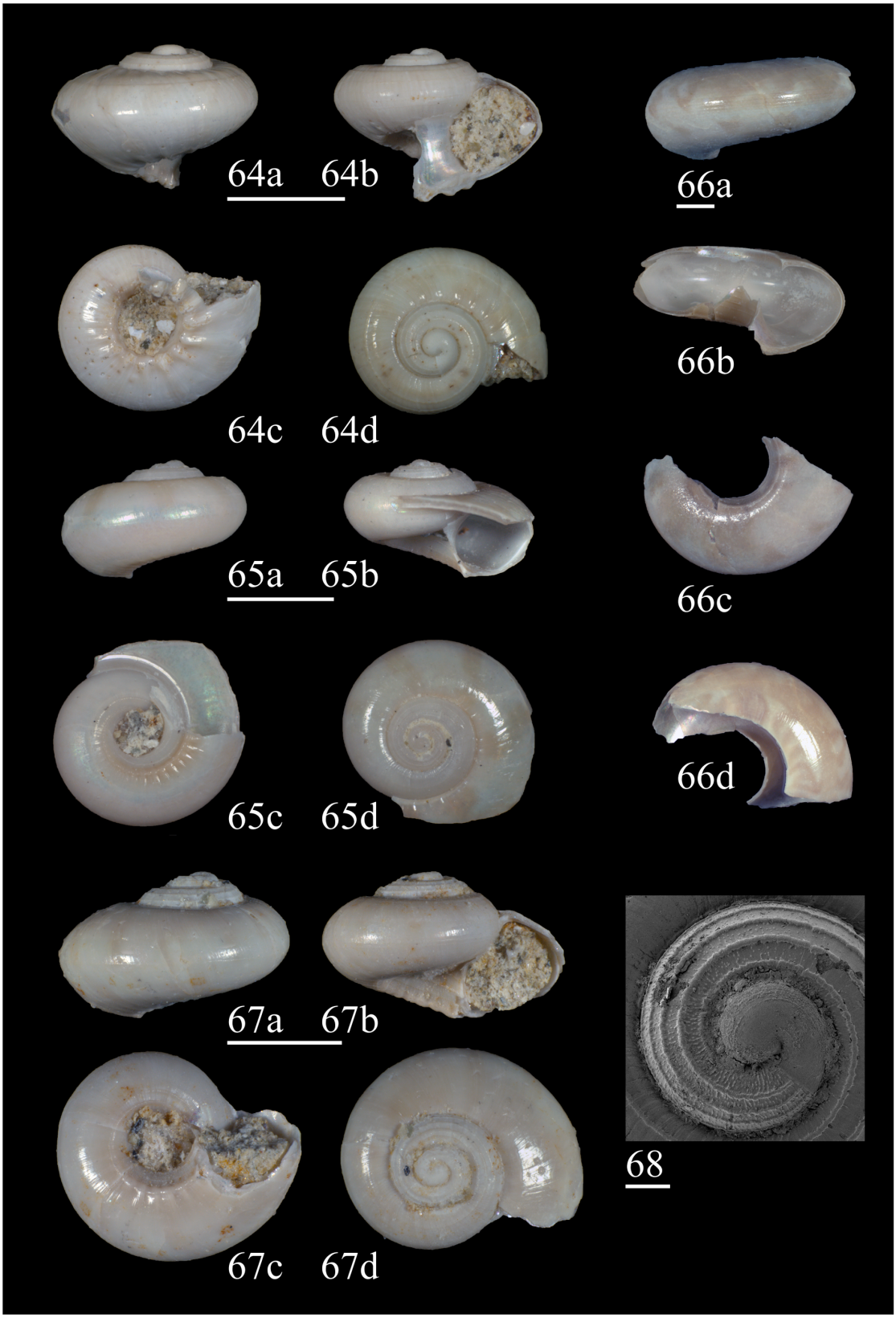
Subfamily Turbininae Rafinesque, 1815

Genus *Guildfordia* Gray, 1850

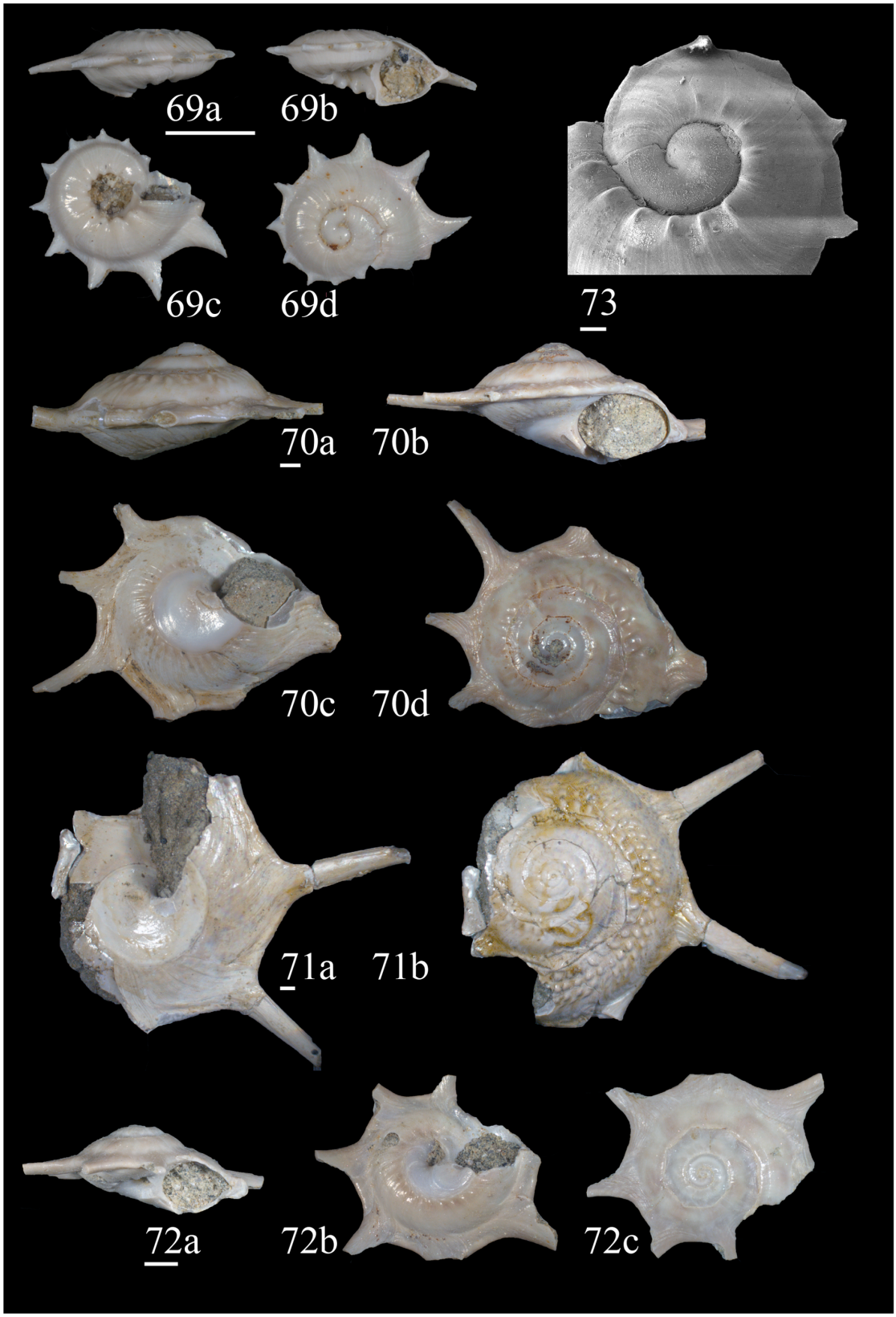
Type species. *Trochus triumphans* Philippi, 1841 (by subsequent designation); Recent, Indo-Pacific.



FIGURES 59–63. Solariellidae. **59.** *Archiminolia* spec.1. RGM 608.352. Locality AndaDeVos. (a) rear view, (b) basal view, (c) apical view. **60.** *Archiminolia* spec.1. RGM 608.353. Locality AndaDeVos. SEM detail of protoconch. **61.** *Zetela tabakotanii* (Poppe, Tagaro & Dekker, 2006). RGM 608.355. Locality Anda1. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **62.** *Zetela tabakotanii* (Poppe, Tagaro & Dekker, 2006). RGM 608.356. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) side view, (d) basal view, (e) apical view. **63.** *Zetela tabakotanii* (Poppe, Tagaro & Dekker, 2006). RGM 608.357. Locality Anda1. (a) SEM, apical view, (b) SEM detail of protoconch.



FIGURES 64–68. Solariellidae. **64.** *Ilanga konos* (Vilvens, 2009). RGM 608.366. Locality Anda1. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **65.** *Ilanga konos* (Vilvens, 2009). RGM 608.367. Locality Tiep2. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **66.** *Ilanga konos* (Vilvens, 2009). RGM 608.368. Locality Tiep2. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **67.** *Ilanga konos* (Vilvens, 2009). RGM 608.369. Locality AndaDeVos. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **68.** *Ilanga konos* (Vilvens, 2009). RGM 608.370. Locality Anda1. SEM detail of protoconch.



FIGURES 69–73. Turbinidae. **69.** *Guildfordia yoka* Jousseaume, 1888. RGM 608.376. Locality Anda1. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **70.** *Guildfordia yoka* Jousseaume, 1888. RGM 608.377. Locality Anda1. (a) rear view, (b) apertural view, (c) basal view, (d) apical view. **71.** *Guildfordia yoka* Jousseaume, 1888. RGM 608.378. Locality Anda2. (a) basal view, (b) apical view. **72.** *Guildfordia yoka* Jousseaume, 1888. RGM 608.379. Locality Anda1. (a) apertural view, (b) basal view, (c) apical view. **73.** *Guildfordia yoka* Jousseaume, 1888. RGM 608.380. Locality Anda3. (a) SEM detail of protoconch.

***Guildfordia yoka* Jousseaume, 1888**
(Figures 69–73)

2000 *Guildfordia yoka* Jousseaume, 1888—Sasaki: p. 101, fig. 51.
2008 *Guildfordia yoka delicata* Habe & Okutani, 1983—Kreipl & Alf: p. 250, pl. 70, fig, 5.

Material. Anda 1 (42); Anda 2 (38); Anda 3 (24); Anda 4 (18); Anda 6 (4); AndaDeVos (4); AndaClif1 (1); AndaClif3 (4); Roxas (1).

Characterization. Shell almost planispiral, with reddish surface, H 5.9 mm, W 15.7 mm; P planispiral, 1.1 whorls, two discontinuous spiral ribs and granulate surface in between, DN 0.16–0.23 mm; slightly elevated terminal varix; T 7–9 long spines per whorl, initially triangular, thin hollow, on later whorls elongate and massive; rows of knobs below the suture; umbilicus covered with white, shiny callus.

Distribution. Today the species occurs in Central southern Japan and southward to Indo-West Pacific, at 200–500 m depth on sand bottom (Sasaki 2000). It has also been reported from the Philippines, Aliguay Island, from 50–150 m depth (Kreipl & Alf 2008).

Discussion

This paper reports 26 vetigastropod species from the Late Pliocene or Early Pleistocene of the Philippines. Fourteen species have been previously described from Recent material, two have been described from Pliocene deposits, three are described as new and eight unidentified vetigastropod species are present. One species of Trochidae and four species of Solariellidae previously described are transferred to other genera.

Assessing depth ranges of Recent species found in the Cabarruyan fauna shows a maximum overlap between c. 150–400 m water depth. This is comparable to the estimated depth range (200–300 m) given by Janssen (2007) in his study of the holoplanktonic mollusks of the same fauna.

The Calliotropidae and Solariellidae, comprising 11 of the 26 species, are considered to be deposit feeders (Hickman 1998a, 1998b and Marshall 1999 respectively). The eight species of Seguenziidae are inferred to feed on foraminifera (Marshall 1983), which may be considered as selective deposit feeding. The Colloniidae, non-umboniine Trochidae and Turbinidae, represented by three species, are reported to be grazers (Hickman & McLean 1990). The two species of Calliostomatidae are carnivorous predators, feeding on sessile invertebrates, such as cnidarians (Marshall 1995). The two umboniine Trochidae may be deposit feeders, filter feeders or both (Hickman 1998b). The fauna is thus dominated by deposit feeders, which is to be expected in a fauna occurring at a depth of 200–300 m. Organisms living below the photic zone rely on the deposition of organic matter produced higher in the water column and closer to the shore (with the exception of vent and seep communities). Even below 250 m water depth, however, light penetration may still be sufficient for the occurrence of algae (Littler *et al.*, 1986), which could explain the presence of grazers.

The known substrate preferences for the taxa present in this fauna all include sand and mud (Hickman & McLean 1990, Poppe & Tagaro 2008a–b, Chen 2006, Hickman 1998a, 1998b, Marshall 1999 and Kreipl & Alf, 2008). For instance, the Trochidae and Turbinidae, species of which are often common on rocky shores, are represented in this fauna only by species with a preference for soft sediments, such as *Pseudotalopia taiwanensis* (Chen, 2006) and *Guildfordia yoka* Jousseaume, 1888. Solariellid snails are reported to be proficient burrowers and occur on unconsolidated sediment (Herbert 1987, Marshall 1999).

The known distributions of the Recent species give some crude insights into the biogeographic affinity of the fauna. Of the 14 species, seven (50 %) have a relatively broad distribution including the Philippines, four (29 %) are exclusively known from the Philippines and three (21 %) are not known from the Philippines, but only from their type localities in Indonesia, Taiwan or New Caledonia. Although the very incomplete knowledge of distribution ranges of modern species makes a biogeographic assignment of the fauna difficult it seems to show a biogeographic affinity with the modern Philippine fauna, albeit that that fauna is also among the best studied deep water faunas of the Indo-Pacific region.

On the contrary, the occurrence of *Homalopoma tosaense* Habe, 1953, which is known from the Pliocene of Viti Levu, Fiji as *Homalopoma druidi* Ladd, 1982 and *Seguenzia donaldi* Ladd, 1982, which was described from the Pleistocene of Santo, Vanuatu, in the studied Philippine fauna demonstrates that at least some deep water

mollusk species have had a very broad distribution. Additionally, the extensive work of Geiger (2012) on modern scissurellid snails shows no biogeographic differentiation within the western tropical Pacific (including New Zealand, New Caledonia and the Philippine area). More data on the taxonomy and species distribution ranges (including depth ranges) for the groups treated in this paper is needed to establish whether deep water gastropod provinces in the Indo-Pacific do exist at all.

Scanning electron microscope (SEM) micrographs proved to be essential in the documentation of morphological characters. Protoconch, teleoconch and umbilicus often bear intricate microsculpture that can only be studied using SEM. For many of the modern taxa such images and data are still lacking, making comparisons difficult. The extremely well preserved state of the studied material is also illustrated by the SEM micrographs, as most specimens showed hardly any sign of corrosion. The material in some samples, notably Anda 5 and Tiep 1, is partially decalcified and a substantial part of the material consists of broken shells, but there are also many undamaged specimens of a wide variety of species present in the material. Well preserved fossil deep water mollusk faunas from the Indo-Pacific are rare, making this exquisitely preserved, diverse fauna very valuable.

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