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# Miocene Vetigastropoda and Neritimorpha (Mollusca, Gastropoda) of central Chile

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**Abstract**

Species of Vetigastropoda (Fissurellidae, Turbinidae, Trochidae) and one species of Neritimorpha (Neritidae) from the Navidad area, south of Valparaíso, and the Arauco Peninsula, south of Concepción, are described. Among these, the Fissurellidae comprise *Diodora fragilis* n. sp., *Diodora pupuyana* n. sp., two additional unnamed species of *Diodora*, and a species resembling *Fissurellidea*. Turbinidae are represented by *Cantrainea* sp., and Trochidae include *Tegula (Chlorostoma) austropacifica* n. sp., *Tegula (Chlorostoma) chilena* n. sp., *Tegula (Chlorostoma) matanzensis* n. sp., *Tegula (Agathistoma) antiqua* n. sp., *Bathybembix mcleani* n. sp., *Gibbula poeppigii* [Philippi, 1887] n. comb., *Diloma miocenica* n. sp., *Fagnastesia venefica* [Philippi, 1887] n. gen. n. comb., *Fagnastesia matanzana* n. gen. n. sp., *Calliostoma mapucherum* n. sp., *Calliostoma kleppi* n. sp., *Calliostoma covacevichi* n. sp., *Astele laevis* [Sowerby, 1846] n. comb., and *Monilea riorapelensis* n. sp. The Neritidae are represented by *Nerita (Heminerita) chilensis* [Philippi, 1887]. The new genus *Fagnastesia* is introduced to represent low-spired trochoideans with a sculpture of nodes below the suture, angulated whorls, and a wide umbilicus. This Miocene Chilean fauna includes genera that have lived at the coast and in shallow, relatively warm water or deeper, much cooler water. This composition therefore suggests that many of the Miocene formations along the central Chilean coast consist of displaced sediments. A comparison with different fossil and Recent faunas from around the Pacific and South America indicates that the vetigastropod and neritid fauna from the Miocene of Chile has only minor affinities with taxa living near New Zealand, Argentina, and the tropical eastern Pacific at that time.


*Keywords:* *Astele*; *Bathybembix*; *Calliostoma*; *Cantrainea*; Chile; *Diloma*; *Diodora*; *Fagnastesia*; Gastropoda; *Gibbula*; Miocene; *Monilea*; *Nerita*; *Tegula*

## 1. Introduction

The Miocene of the Pacific margin of South America has been described as a transgressive sequence from 19 to 10 Ma B.P. (Martínez-Pardo, 1990). However, DeVries (1998) showed that the Cenozoic history in Peru is more complex. A similarly complex history might be assumed for Chile, but too few localities have been sufficiently dated to provide a detailed age determination. Martínez-Pardo (1990) recognized only the Navidad Formation described by Darwin (1846), the type area of which is on the Pacific coast near Santiago. The sedimentology and fauna indeed are strikingly homogeneous, at least from Navidad to the island of Chiloé in southern Chile (Fig. 1), but there are several local stratigraphic names for geographically distant, well-defined, isolated areas. In the context of this work, we use the name Navidad Formation in a strict sense to refer to the type area around Navidad. We use the name Ranquil Formation provisionally for all sediments of the Miocene from Arauco Peninsula, even though there appear to be two lithologically distinguishable units. Although this situation is not satisfying, it is not the aim of this paper to clarify the stratigraphy of Arauco. In addition, the age is only given broadly as Miocene because there are no reliable data from Arauco, and the available data from the Navidad region are contradictory.

The Miocene deposits consist of clastic sediments ranging from conglomerate to mudstone. They reflect all environments, from the shore to shallow marine to outer shelf. The lithology of the Navidad area has been described by Tavera (1979) and is representative for most of the Chilean Miocene. A more detailed analysis of the depositional environment

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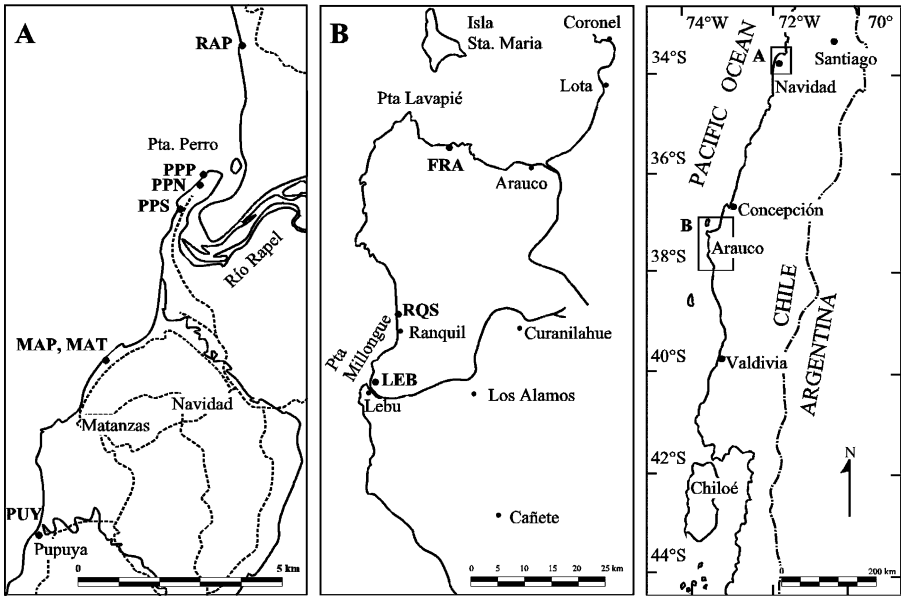



Fig. 1. Fossil localities of Archaeogastropoda in Central Chile. (A) Navidad area, (B) Peninsula Arauco. FRA, Punta El Fraile; LEB, Lebu; MAP, MAT, Matanzas; PPN, PPP, PPS, Punta Perro; PUY, Pupuya; RAP, north of Río Rapel; and RQS, Ranquil, coarse gray sand.

of these strata is in preparation (Encinas, 2002; Encinas et al., 2003).

Within the gastropod fauna of the Miocene deposits of Chile, only a few trochids have been described (Sowerby, 1846; Philippi, 1887; Tavera, 1979), some of which are redescribed here. *Trochus araucanus* Philippi, 1887 is regarded as a *nomen dubium* because the type material is lost and the type locality is unknown. The holotype of *Trochus macsporrani* Philippi, 1887 from Isla Santa Maria is an unidentifiable internal mold. *Trochus rapeleanus* Tavera, 1979 is regarded as *nomen nudum* because Tavera (1979) did not provide a diagnosis to distinguish his species from other taxa and did not figure his specimen. Consequently, the name is considered unavailable under ICZN, Article 13.1.1.

## 2. Description of fossil localities

### 2.1. Navidad area

Several classical localities in the Navidad area (Fig. 1A) have yielded a diverse gastropod fauna. Most localities have been discussed in detail by Tavera (1979). At Pupuya (PUY), just above the southern end of the beach sand barrier that produces a pond, a coarse sandstone yields a sparse fauna of coastal species. Another locality, approximately 1 km north of Matanzas, has been described by Frassinetti and Covacevich (1993), who sampled the modern tidal flat (MAP), next to which a similar fauna appears approximately 2 m higher in the cliff (MAT). Several samples come from Punta Perro (PPN), where the modern intertidal platform (PPP) and a coarse sand lens in the cliff (PPS) have been sampled. North of the Río Rapel (RAP), where the cliffs are too steep for climbing and collecting, a block fall has been sampled without regard to the former position of different blocks to one another. Few localities have been dated, and the results obtained from PPP range from Early (Dremel in Herm, 1969; Tavera, 1979; Frassinetti and Covacevich, 1993) to Late (Tsuchi et al., 1990; Ibaraki, 1992) Miocene. New data on Foraminifera collected at our localities agree with Ibaraki (1992), indicating a Late Miocene age (Finger et al., 2003).

### 2.2. Arauco

Two lithological units can be distinguished at Punta El Fraile (Fig. 1B). One is a brown sandstone typical of the Ranquil Formation (FRA); the other is a gray siltstone comparable to the siltstones of the Navidad area. A concordant boundary between the two units has been observed, and the fauna indicates a Miocene age for the gray siltstone (FRM of Finger et al., 2003).

On the modern intertidal flat near Ranquil, near-shore sandy sediments are exposed and show several intercalated layers of coarse sandstone rich in glauconite. Coarse gray sandstones with as yet unclear stratigraphical relationships are exposed a little to the north (RQS), where the siltstones also are present in boulders.

Immediately north of Lebu, on the Arauco Peninsula, a crevice in Eocene sandstone is filled with Miocene deposits (LEB). This outcrop represents a rare case of deposits from the former rocky shore. Foraminifera from FRA and LEB indicate a Late Miocene age (Finger et al., 2003).

## 3. Material and methods

Larger fossils and sediment samples have been collected in the field. Sediment samples were processed with a 5–10% hydrogen peroxide solution and separated with sieves of different sizes (1.0, 0.5, 0.2 mm). Small fossils were picked under a microscope, ultrasonically cleaned, mounted on stubs, sputtered with gold, and photographed with a scanning electron microscope.

Materials are deposited in the Museo Nacional de Historia Natural, Santiago, Chile (SGO.PI) and the Senckenberg Museum Frankfurt, Germany (SMF). The holotype of *Trochus laevis* remains in the Natural History Museum, London, Great Britain (NHM, formerly BMNH). The type locality for each species is the respective locality where the holotype has been found.

## 4. Systematic paleontology

We use the general classification adopted by Sasaki (1998), though the broader term Neritimorpha is used here rather than Neritopsina. Vetigastropoda and Neritimorpha are easily distinguished from each other by their different protoconchs, as has been shown by Bandel (1982, 1997). To classify Trochoidea, we follow Hickman and McLean (1990), though Calliostomatinae have been recognized at the family level by several authors (e.g. Marshall, 1995a,b).

*Class Gastropoda Cuvier, 1795*

Order Vetigastropoda Salvini-Plawen, 1980
Superfamily Fissurelloidea Fleming, 1822
Family Fissurellidae Fleming, 1822
Subfamily Emarginulinae Gray, 1834
Genus *Diodora* Gray, 1821

*Type species*. *Patella graeca* Linnaeus, 1758; Recent, Europe.

*Diodora fragilis new species (Figs. 2–6)*

*Diagnosis*. Shell conical, lateral slopes straight, anterior and posterior slopes slightly concave. Foramen slightly constricted. Sculpture of approximately 28 fine radial primary ribs and as many secondary ribs.

*Description*. This species of *Diodora* has an average-sized, conical shell with an oval outline. The anterior end is narrower than the posterior end. The shell profile has straight sides with slightly concave anterior and posterior ends. Callus surrounding the slightly constricted foramen is truncated posteriorly. Sculpture consists of approximately 28 primary and 28 secondary radial ribs (holotype), with primary ribs more prominent. Dimensions: length 15 mm, width 8.5 mm, height 4 mm (holotype); length 11 mm, width 7 mm, height 3 mm (paratype).

*Etymology*. After the small fragile shell.

*Type material*. Holotype SGO.PI.5994 (PPN), paratype SMF 323621 (PUY). Two additional fragments (PUY) remain with the paratype.

*Occurrence*. PPN, PUY; Miocene, Navidad Formation, central Chile.

*Remarks*. The type material represents juvenile specimens, as indicated by the size of an additional fragment that indicates a specimen of approximately twice the size. *D. fragilis* resembles the recent *D. codoceoae* McLean and Andrade, 1982 from the Chilean coast in its general shell shape but has fewer, coarser ribs and a thicker shell. *D. fragilis* is also similar to the Recent Caribbean *D. cayenensis* (Lamarck, 1822) and *D. dysoni* (Reeve, 1850), but those have tertiary ribs that are not present in *D. fragilis*.

*Diodora pupuyana new species (Figs. 7 and 8)*

*Diagnosis*. Shell conical, slopes straight. Sculpture of coarse radial ribs crossed by raised growth lamellae to produce a beaded appearance.

*Description*. A species of *Diodora* with a high-conical shell. Outline is oval with straight sides. Foramen is situated anteriorly. Radial sculpture consists of 22 primary ribs (holotype) with intercalated secondaries. Raised growth lamellae, together with ribs, produce a beaded appearance. Callus surrounding the foramen is truncated at its posterior end. Dimensions: length 9 mm, width 5.7 mm, height 3.3 mm (holotype).

*Etymology*. After the type locality near the village Pupuya, central Chile.

*Type material*. Holotype SGO.PI.5995 (PUY), paratype SMF 323622 (PUY).

*Occurrence*. PUY; Miocene, Navidad Formation, central Chile.

*Remarks*. The holotype is a juvenile specimen. The paratype shows that adult specimens are at least twice the size of the holotype. *Diodora pupuyana* has a relatively higher shell, coarser sculpture, and fewer ribs than *D. fragilis*.

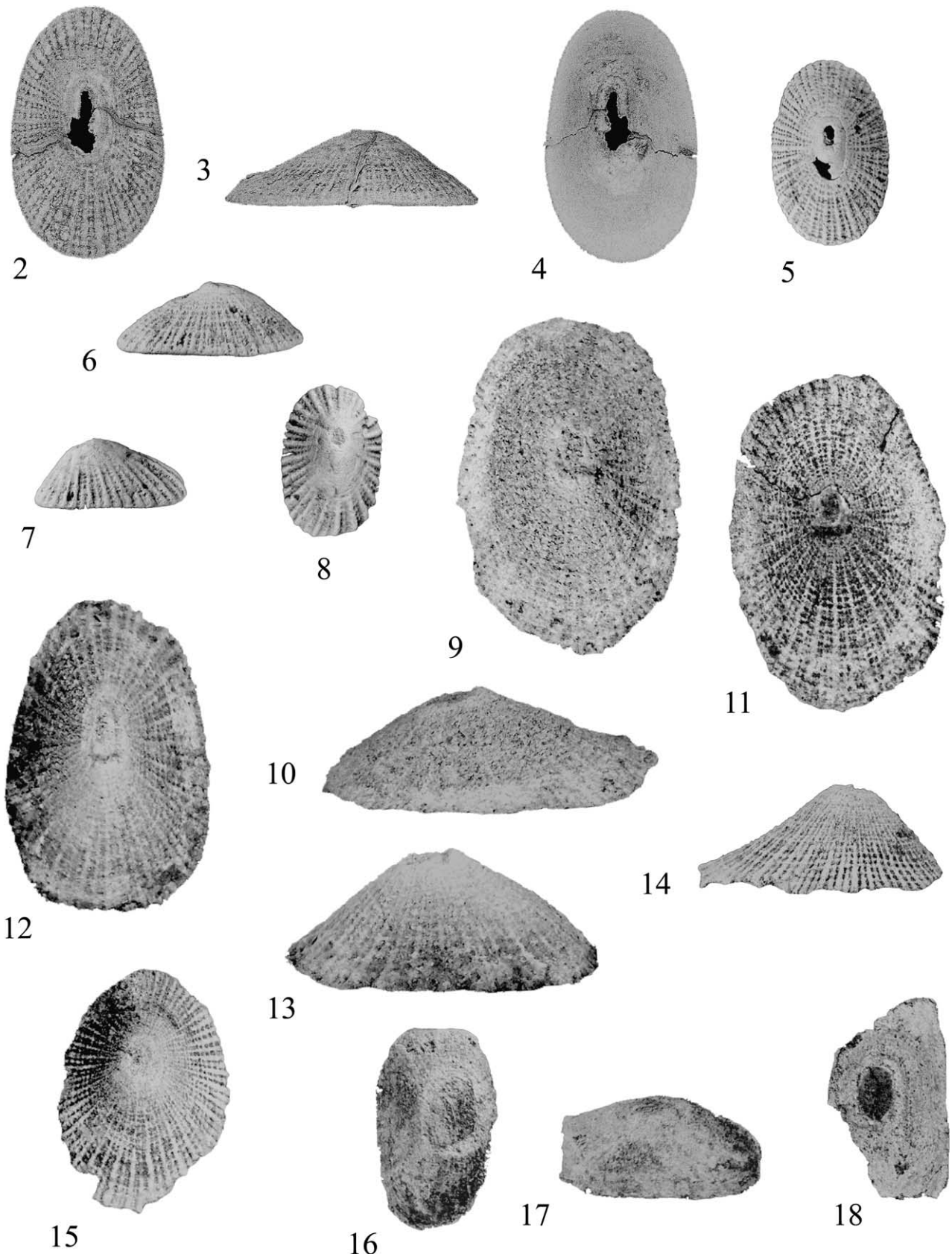
*Diodora sp. 1 (Figs. 9–11)*

*Description*. The shell is of average size, with a sculpture of approximately 20 fine radial ribs. The foramen is elongated and tripartite, and the callus surrounding the foramen is truncated at its posterior end. Dimensions: length 20 mm, width 12 mm, height 5 mm.

*Material*. Two specimens; SGO.PI.5996 (LEB), SMF 323623 (LEB).

*Occurrence*. LEB; Miocene, Ranquil Formation, south central Chile.

*Remarks*. This *Diodora* resembles the Recent Caribbean *D. listeri* d'Orbigny, 1842 in shell shape and number of ribs. Because no other features are available due to bad preservation of the fossils, we refrain from placing it in this Caribbean species and do not attribute it to any species.




Figs. 2–18. Fissurellidae. 2–6. *Diodora fragilis* n. sp., 2–4. Holotype SGO.PI.5994, 5–6. Paratype SMF 323621. 7–8. *Diodora pupuyana* n. sp., holotype SGO.PI.5995. 9–11. *Diodora* sp. 1, SGO.PI.5996. 12–15. *Diodora* sp. 2, 12–13. SGO.PI.5997, 14–15. SMF 323624. 16–18. Fissurellidae indet., SGO.PI.5998.

*Diodora sp. 2 (Figs. 12–15)*

*Description*. Small, relatively high shell with oval basal outline. Sculpture consists of fine radial ribs. The foramen is elongate and tripartite, and the surrounding callus is truncated at its posterior end. Dimensions: length 18.5 mm, width 11.5 mm, height 7 mm.

*Material*. Two specimens; SGO.PI.5997 (LEB), SMF 323624 (LEB).

*Occurrence*. LEB; Miocene, Ranquil Formation, south central Chile.

*Remarks*. This species differs from *Diodora* sp. 1 by its considerably higher shell. Due to bad preservation, distinguishing features are too few for an acceptable diagnosis.

*Fissurellidae indet.*

*Description*. The shell is elongate oval, with steeply sloping sides and unknown ends. The anterior slope is longer than the posterior. The foramen is 3 mm long. Dimensions: length 12 mm, width 7.5 mm, height 3.3 mm (Figs. 16–18).

*Material*. Two specimens, each represented by an interior and exterior mold: SGO.PI.5998 (LEB), SMF 323625 (LEB).

*Occurrence*. LEB; Miocene, Ranquil Formation, south central Chile.

*Remarks*. The foramen of this species is relatively large, bringing to mind genera included in the Fissurellidini (Pilsbry, 1890) (sensu McLean, 1984) or other genera that share this character, such as *Megathura* Pilsbry, 1890, *Cosmetalepas* Iredale, 1924, *Monodilepas* Finlay, 1926, and *Amblychilepas* Pilsbry, 1890 but that were placed outside this group by McLean (1984). Considering the Recent occurrences of *Fissurellidea* d'Orbigny, 1841 and *Pupillaea* Sowerby, 1835 (see McLean, 1984) and the missing fossil record before the Pliocene (*Fissurellidea megatrema* d'Orbigny, 1841), this specimen might represent a transitional form between *Diodora* and the Fissurellidini.

*Superfamily Trochoidea Rafinesque, 1815*

Family Turbinidae Rafinesque, 1815

Subfamily Colloniinae Cossmann, 1916

Genus *Cantrainea* Jeffreys, 1883

*Type species*. *Trochus peloritanus* Cantraine, 1835; Recent, Mediterranean.

*Cantrainea* sp. (Figs. 19–21).

*Description*. The figured specimen has a diameter of 1.3 mm. Other than three keels, which give the shell its characteristic appearance, there is no sculpture present. The first prominent keel starts immediately after the embryonic shell and forms a distinct peripheral shoulder. The second keel appears at the suture of the following whorl, and the third keel is situated closely below the second one. The protoconch has a wrinkled surface and consists of 0.75 whorls. There is no umbilicus developed, and the aperture is unknown.

*Material examined*. SGO.PI.5999 (RAP).

*Occurrence*. RAP; Miocene, Navidad Formation, central Chile.

*Remarks*. Most species of *Cantrainea* show four or more keels and are therefore easily distinguished from *Cantrainea* sp. *Cantrainea panamensis* Dall, 1908 is similar to *Cantrainea* sp. but the interspaces between its keels are approximately equal, whereas in *Cantrainea* sp., the second keel is close to the third. Because the protoconches of *C. panamensis* and the Atlantic *C. mcleani* Warén and Bouchet, 1993 are still unknown, a direct comparison with *Cantrainea* sp. is not possible. However, the available material does not permit naming of a new species. *Cantrainea* is regarded as a deep-water genus by Hickman and McLean (1990).

*Family Trochidae Rafinesque, 1815*

Subfamily Tegulinae Kuroda, Habe and Oyama, 1971

Genus *Tegula* Lesson, 1835

*Type species*. *Tegula elegans* Lesson, 1835 ( = *Trochus pellisserpentis* Wood, 1828); Recent, Pacific Central America.

Subgenus *Chlorostoma* Swainson, 1840

*Type species*. *Trochus argyrostomus* Gmelin, 1791; Recent, Japan.

*Tegula (Chlorostoma) austropacifica new species (Figs. 22–24)*

*Diagnosis*. Shell small, conical, almost straight-sided. Sculpture of six spiral cords, base with numerous spiral cords. Small umbilicus. Aperture oblique, columella slightly concave. Denticle at base of columella.

*Description*. The small shell is conical with an oblique aperture, a denticle at the base of the columella, and a small umbilicus. Its sculpture consists of six spiral cords on the whorls, and the base has numerous fine spiral cords that are strongest near the umbilicus. There is no axial sculpture present. The protoconch is unknown. Dimensions: height 2.7 mm, diameter 2.5 mm (holotype).

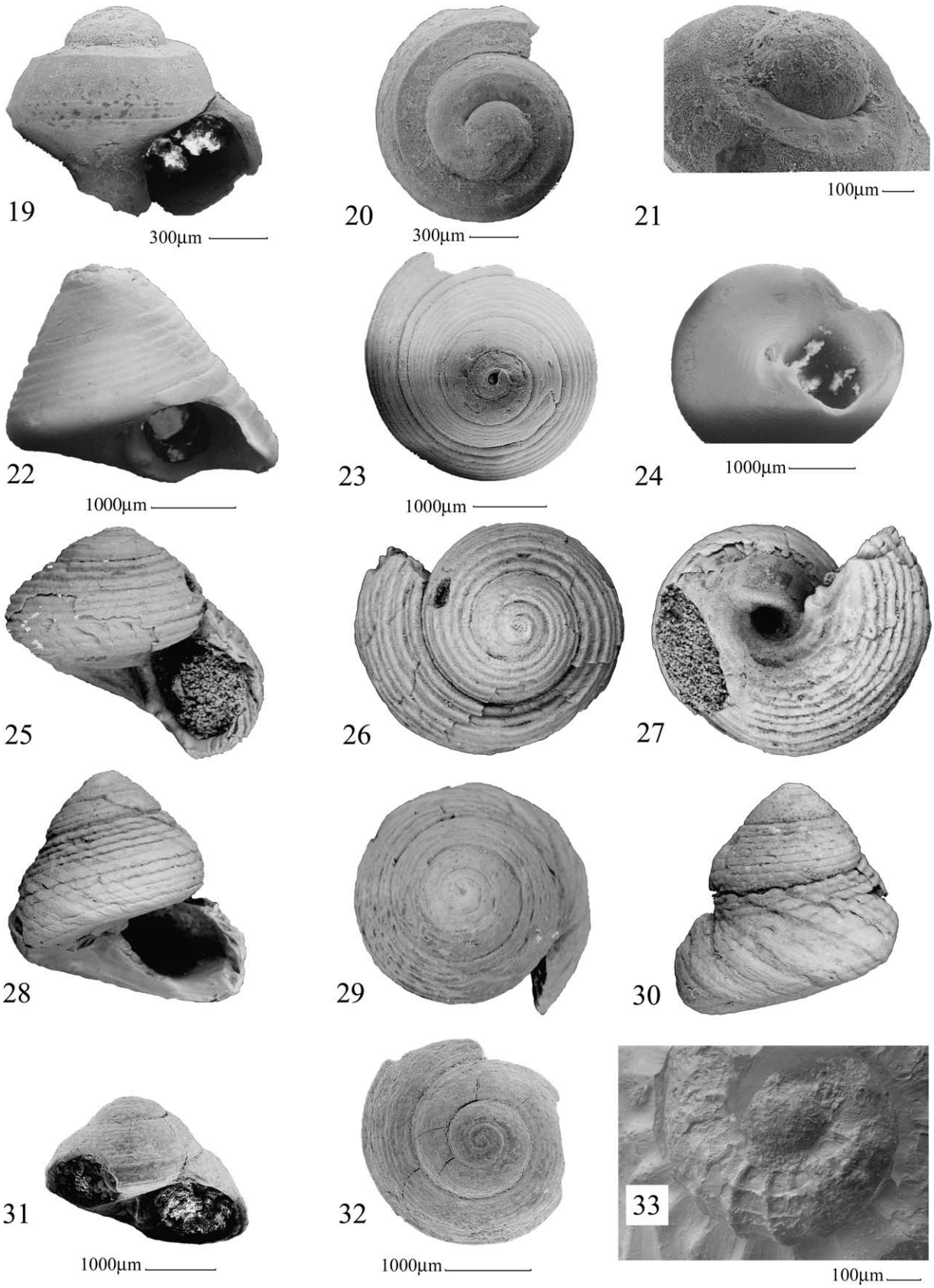
*Etymology*. This species comes from the southern (austral) Pacific.

*Type material*. Holotype SGO.PI.6001 (RAP).

*Occurrence*. RAP; Miocene, Navidad Formation, central Chile.

*Remarks*. *Chlorostoma* is considered the oldest subgenus of *Tegula*, known from the Miocene of Japan and western North America (Hickman and McLean, 1990). Its occurrence in the Miocene of South America extends its distribution into the South Pacific. However, it is absent from New Zealand (see Beu and Maxwell, 1990) and Australia (Beu, pers. comm.).

*Tegula (Chlorostoma) chilena new species (Figs. 25–27)*




Figs. 19–34. Turbinidae and Trochidae, Tegulinae. 19–21. *Cantrainea* sp., SGO.PI.5999. 22–24. *Tegula (Chlorostoma) austropacifica* n. sp., holotype SGO.PI.6001. 25–27. *Tegula (Chlorostoma) chilena* n. sp., holotype SGO.PI.4967. 28–30. *Tegula (Chlorostoma) matanzensis* n. sp., holotype SGO.PI.4969. 31–33. *Tegula (Agathistoma) antiqua* n. sp., holotype SGO.PI.6000. 34. *Bathybembix mcleani* n. sp., holotype, detail of protoconch.

*Diagnosis*. Shell medium, globose. Aperture oblique, with two denticles on base of columella. Umbilicus small and open. Sculpture of about 10 strong spiral cords on whorl and additional 7 on base. Two spiral cords on umbilical callus terminate at denticles.

*Description*. The shell is medium-sized, globose, and low-conical. It has an oblique aperture, shows two denticles at the base of the columella, and has a narrow, open umbilicus. The sculpture consists of strong primary and secondary spiral cords, 10 on the spire whorls and 7 on the base of the last whorl. Spiral sculpture is fused toward the umbilicus and creates a smooth area on which spiral sculpture is obsolete. At the edge of the umbilicus, two prominent spiral cords are present, which terminate in the two denticles at the base of the columella. The inner shell layer is nacreous, and the protoconch is unknown. Dimensions: height 14.4 mm, diameter 17 mm (holotype).

*Etymology*. A Chilean species of *Tegula*.

*Type material*. Holotype SGO.PI.4967 (MAP).

*Occurrence*. MAP; Navidad Formation, Miocene, central Chile.

*Remarks*. The presence of two denticles is characteristic of *Tegula* species but also of many other trochids (Hickman and McLean, 1990). *Tegula (Chlorostoma) chilena* differs from *T. (C.) austropacifica* mainly due to its more globose shell. It can easily be separated from *Tegula (C.) matanzensis* by the presence of an open umbilicus. Most recent species such as *T. (C.) brunnea* (Philippi, 1849) or *T. (C.) funebralis* (Adams, 1855) have a less coarse sculpture.

*Tegula (Chlorostoma) matanzensis new species (Figs. 28–30)*

*Diagnosis*. Shell medium-sized, high-conical. Whorls convex. Aperture oblique, with one denticle at base of columella. No umbilicus. Spiral sculpture of 10 coarse cords on spire, 3–4 spiral cords on base.

*Description*. The shell is medium-sized and high-conical and has convex whorls. The aperture is oblique, and there is no umbilicus present. A denticle is present at the base of the columella, though part of the columella is broken, so it is unknown if a second denticle was present. The outer lip is unknown. Axial sculpture is not developed; only growth lines are sometimes prominent. Ten coarse spiral cords are present on the spire, with three to four more on the base. An umbilicus is not present, but there is a low depression on the umbilical callus. The inner shell layer is nacreous, and the protoconch is unknown. Dimensions: height 20.5 mm, diameter 18 mm (holotype).

*Etymology*. After the type locality near the village Matanzas.

*Type material*. Holotype SGO.PI.4969 (MAP).

*Occurrence*. MAP; Navidad Formation, Miocene, central Chile.

*Remarks*. *Tegula (Chlorostoma) matanzensis* resembles *T. (C.) funebralis* Adams, 1855 from Baja California, Mexico. The latter has a straight-sided spire, not, as in *T. (C.) matanzensis*, an incised suture and clearly convex whorls.

*Subgenus Agathistoma Olsson and Harbison, 1953*

*Type species*. *Trochus viridulus* Gmelin, 1791; Recent, northern South America to eastern Brazil.

*Tegula (Agathistoma) antiqua* new species (Figs. 31 and 32).

*Diagnosis*. Shell is small and globose. Whorls convex. Sculpture of low beaded cords. Flat base with weak spiral cords. Umbilicus small. Aperture circular with denticle on base of columella.

*Description*. This *Tegula* has a small globose shell with convex whorls. Its shell surface is sculptured by numerous fine spiral cords, and additional cords are present on the flat base. The aperture is circular and shows the typical denticle on the base of the columella. A small umbilicus is present in juveniles. The protoconch is unknown. Dimensions: height 2.2 mm, diameter 2.6 mm (holotype).

*Etymology*. Antiqua (Latin) = old. This species is among the earliest representatives of *Agathistoma* described so far.

*Type material*. Holotype SGO.PI.6000 (RAP).

*Occurrence*. RAP; Miocene, Navidad Formation, central Chile.

*Remarks*. *Tegula (Agathistoma) antiqua* is similar to *T. (A.) mariana* Dall, 1919 but has less angulated whorls. The Recent Atlantic-South American species *T. (A.) patagonica* d'Orbigny, 1835 ( = *T. dorbignyana* (Pilsbry, 1900)) has a similar sculpture but is much higher with a more prominent suture (Pastorino, 1994) and has been reported from the Miocene of Argentina (e.g. del Río, 1998). *Tegula (A.) cooksoni* Smith, 1877, on the Galapagos Islands, has a lower spire and more angulated whorls and thus is not as globulous as *T. (A.) antiqua*.

Hickman and McLean (1990, p. 70) state that "*Agathistoma* first appears in the Pliocene of the western Atlantic, where it underwent an exclusively tropical and incompletely documented radiation." *Agathistoma antiqua* extends the fossil record of the subgenus into the Miocene of the Pacific and could indicate a Pacific origin for the group. It therefore closes the geographical gap in the assumed origin of the antitropical *Chlorostoma*, which is also known from the Miocene Pacific.

*Subfamily Eucyclinae Koken, 1897*

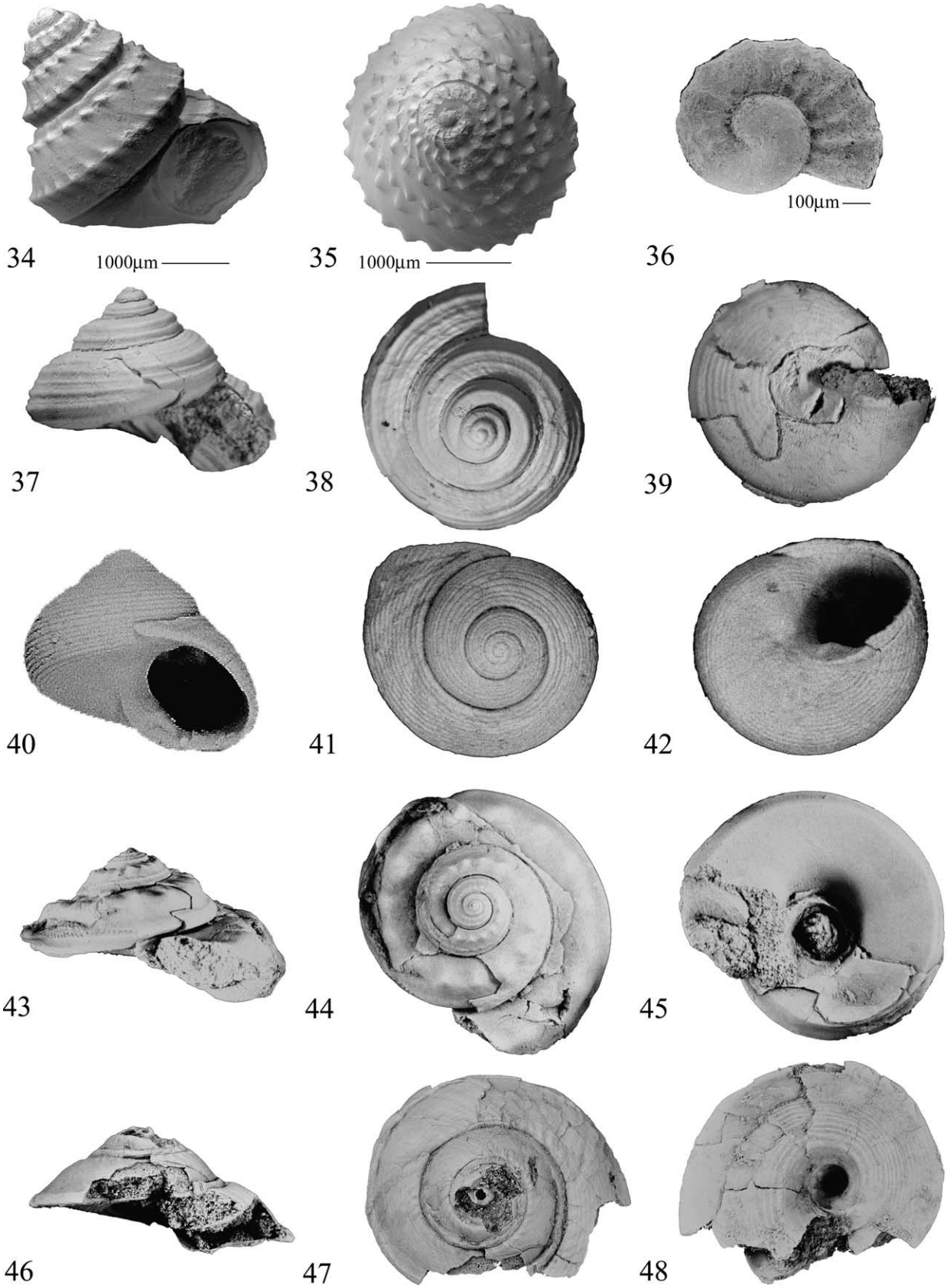
Tribe Calliotropini Hickman and McLean, 1990.

Genus *Bathybembix* Crosse, 1893

*Type species*. *Bembix aeola* Watson, 1879; Recent, Japan.

*Bathybembix mcleani* new species (Figs. 33–36).

*Diagnosis*. Shell thin and high spired. Whorls strongly carinate. Protoconch smooth, diameter 280 μm. Early whorls strongly keeled. Spiral sculpture of two cords per




Figs. 34–48. Trochidae, Eucyclinae, and Trochinae. 34–36. *Bathybembix mcleani* n. sp, 34–35. Holotype SGO.PI.6002, 36. Paratype SGO.PI.6003. 37–39. *Gibbula poeppigii* (Philippi, 1887) lectotype SGO.PI.815. 40–42. *Diloma miocenica* n. sp., holotype SGO.PI.6016. 43–45. *Fagnastesia venefica* (Philippi, 1887), lectotype SGO.PI.817. 46–48. *Fagnastesia matanzana* n. sp., holotype SGO.PI.6004.

whorl with projecting spines. Base with prominent spiral cords.

*Description*. The high-spired shell of this *Bathybembix* is small. The protoconch is smooth, and the early adult shell shows spiral cords and axial ribs, which create a beaded appearance. In later whorls, the axial sculpture is lacking except for fine growth striae. Spiral sculpture on the adult shell consists of two cords per whorl, a prominent projecting peripheral cord with short projecting spines, and a weaker cord with fewer projecting spines just below the suture. The base shows prominent spiral cords. The outer lip is thin with a nacreous interior. Dimensions: height 4.4 mm, diameter 3.3 mm (holotype).

*Etymology*. After our colleague James H. McLean, who made significant contributions to the Recent gastropod fauna of Chile.

*Type material*. Holotype SGO.PI.6002 (FRA), Paratype SGO.PI.6003 (FRA).

*Occurrence*. FRA; Miocene, Ranquil Formation, south central Chile.

*Remarks*. Recent species of *Bathybembix* from Chile have been described by McLean and Andrade (1982); of these, *B. macdonaldi* Dall, 1890 strongly resembles *B. mcleani*. Unfortunately, the specimens of the two Recent *Bathybembix* species from Chile in the collection of the Los Angeles County Museum do not have preserved protoconchs (McLean, pers. comm.). However, *B. mcleani* appears to have a stronger subsutural spiral cord. Species of this genus usually have large shells, so the specimens described here probably represent juveniles. Hickman and McLean (1990) regarded *Bathybembix* as a cold-water genus.

*Subfamily Trochinae Rafinesque, 1815*

Tribe Gibbulini Stoliczka, 1868

Genus *Gibbula* Risso, 1826

*Type species*. *Trochus magus* Linnaeus, 1758; Recent, Mediterranean.

*Gibbula poeppigii* (Philippi, 1887) new combination (Figs. 37–39).

*Trochus poeppigii* Philippi, 1887; p. 102, pl. 11, Fig. 20.

*Trochus poeppigii* Philippi, Frassinetti, 2001; p. 79

*Original diagnosis*. *Testa parva, conica, imperforata, altitudine diametrum subaequante; anfractus sex, modice convexi, paullo pone medium subangulati, ultimus basi biangulatus; cingula plura, laevigata, unum majus, anfractus ornantia, basis sulcata*.

*Diagnosis*. Shell small, low-conical, whorls convex. No umbilicus. Sculpture of six prominent spiral cords.

*Description*. The shell is low-conical and similar in width and height. Whorls are convex. The sculpture consists of six prominent spiral cords, of which the second and fifth from the suture form weak peripheral angulations. Numerous weak spiral cords sculpture the base. There is no umbilicus, and the aperture is subquadrate. Dimensions: height 5 mm, diameter 7 mm.

*Type material*. Philippi (1887, p. 96) reported four specimens, three from Navidad and one from Matanzas. In his collection, only two syntypes are present. Syntype SGO.PI.815 (Matanzas) agrees with the original figure; the other is SGO.PI.811 (Navidad).

*Occurrence*. Miocene, Navidad Formation, central Chile to Stokes Island, southern Chile (Frassinetti, 2001).

*Remarks*. Assignment to *Gibbula* is tentative and based on the general shell shape and its markedly stepped profile. *G. poeppigii* also resembles the Recent *Calliostoma nudiusculum* Martens, 1881 from Argentina, but until the protoconch is known, it might be better placed in *Gibbula*. *Gibbulla poeppigii* differs from *G. magus*, type species of *Gibbula*, by the absence of tubercles below the suture and absence of an umbilicus.

*Genus Diloma Philippi, 1845*

*Type species*. *Turbo nigerrima* Gmelin, 1791; Recent, New Zealand, Chile, and South Africa.

*Diloma miocenica* new species (Figs. 40–42).

*Diagnosis*. Shell small, globose. Whorls convex. Whorls with numerous spiral cords. No umbilicus present. Columella concave with weak denticle.

*Description*. The shell is relatively small and globose with convex whorls. The sculpture on the whorls and base consists of numerous subequal spiral cords. The axial sculpture is not developed, nor is an umbilicus present in adults. The oblique aperture is circular with a flattened base. A weak denticle is present at the base of the concave columella. The protoconch is unknown. Dimensions: height 6 mm (holotype).

*Etymology*. A Miocene species of this genus.

*Type material*. Holotype SGO.PI.6016 (MAT), 5 Paratypes SGO.PI.6072, 1 Paratype SMF 323626 (RQS).

*Occurrence*. MAT, RQS; Miocene, Navidad and Ranquil Formations, central to south central Chile.

*Remarks*. The Recent type species *Diloma nigerrima* is larger and has weaker spiral ornamentation. The presence of the genus in the Miocene of Chile may explain the distribution of the only extant species, which ranges from New Zealand to Chile and South Africa.

*Genus Fagnastesia new genus*

*Type species*. *Trochus veneficus* Philippi, 1887; Miocene, Chile.

*Diagnosis*. Shell low spired, whorls angulated. Spiral sculpture on upper and lower sides of whorls. Weak to strong nodes below suture. Umbilicus wide, aperture subquadrate.

*Etymology*. Free combination of the generic names *Fagnanoa, Astele*, and *Valdesia*.

*Remarks*. The two species included in *Fagnastesia* are somewhat intermediate among the genera *Fagnanoa*

Bonarelli, 1917, *Valdesia* del Río, 1985, and *Astele* Swainson, 1855. All three genera have a relatively wide umbilicus and subquadrate aperture. Species of *Fagnanoa* (del Río and Morra, 1985) have a much lower spire and more angulated whorls than those of *Fagnastesia*. Species of *Valdesia*, (del Río, 1985) in contrast, have a higher spire and more inflated whorls than those of *Fagnastesia*. *Astele*, a calliostomatine genus with a typical honeycomb pattern on the protoconch, comprises species with a much higher spire and straighter sides than those of *Fagnastesia*. However, protoconchs of species included in *Fagnanoa* and *Valdesia* and the two species described here are not known and might bear a honeycomb pattern. If so, they would represent an independent group of South American calliostomatines ranging from high-spired forms like *Astele laevis* to low-spired true *Fagnanoa* species. Until this issue is resolved, we prefer to treat the present species as a separate genus.

*Fagnastesia venefica (Philippi, 1887) new combination (Figs. 43–45).*

*Trochus veneficus* Philippi, 1887; p. 101, pl. 12, Fig. 8.

*Trochus (Gibbula) veneficus* Philippi, Tavera, 1979; p. 94–95, pl. 18, Fig. 64.

*Original diagnosis*. *Testa depresso-conica, late umbilicata, laevissima; anfractus posteriores medio angulati, ad angulum nodulosi, ultimus ambitu acute carinatus, basi infra carinam linea elevata cinctus deinde planus, ad umbilicum rotundatus*.

*Diagnosis*. Shell low-conical. Sculpture of spiral cords on upper and lower sides of whorls. Strong rounded nodes near suture. Prominent keel at periphery, second keel below first. Umbilicus wide, aperture subquadrate.

*Description*. The trochoid, low-conical shell is sculptured with spiral cords on the upper and lower sides of the whorls. Characteristic strong, rounded nodes are present below the suture. A prominent keel is present at the periphery, with a second one below it. The whorls are low and subquadrate. The umbilicus is wide, smooth, and spiraling inward. Dimensions: height 16.5 mm, diameter 30.7 mm (lectotype).

*Type material*. Lectotype SGO.PI.817 (Navidad), Paralectotypes SGO.PI.809 (three specimens, Matanzas), SGO.PI.4682 (Navidad), SGO.PI.4681 (one fragment, Navidad).

*Occurrence*. Miocene, Navidad Formation, central Chile.

*Remarks*. The only similar species from the Navidad Formation is *Fagnastesia matanzana*, which has a weak cord of nodules instead of prominent nodes below the suture. *Fagnastesia venefica* is separated from similar Argentinean species of the genus *Valdesia* by its much lower spire and angulated whorls (del Río, 1985).

*Fagnastesia matanzana new species.*

*Diagnosis*. (Figs. 46–48) Shell low-conical. Sculpture of spiral cords on upper and lower side of whorl. Weak cord of nodules below upper, prominent suture. Umbilicus wide, aperture subquadrate.

*Description*. The trochoid, low, conical shell has a sculpture of approximately 20 fine spiral cords and a weak cord of nodules below the prominent suture. The base bears approximately 22 spiral cords and becomes stronger toward the umbilicus. Whorls are very low, convex, and subquadrate. A wide, smooth, spiral umbilicus is present, characteristic of the genus. Dimensions: height 13 mm, diameter 31 mm (holotype).

*Etymology*. After the type locality near the village of Matanzas.

*Type material*. Holotype SGO.PI.6004 (MAT).

*Occurrence*. MAT; Miocene, Navidad Formation, central Chile.

*Remarks*. For a comparison with other species, see our remarks on *F. venefica*.

*Subfamily Calliostomatinae Thiele, 1924*

Genus *Calliostoma* Swainson, 1840

*Type species*. *Trochus conulus* Linnaeus, 1758; Recent, Europe.

*Calliostoma (s.l.) mapucherum new species (Figs. 49–51)*

*Diagnosis*. Shell small and straight-sided, umbilicus absent. Sculpture of three nodulous spiral cords. Six spiral lirae on base. Aperture subquadrangular.

*Description*. The small shell has steep straight sides. The protoconch is unknown. The sculpture consists of three spiral and axial cords that form prominent nodules at the intersections. The base has six spiral lirae; the outer one forms the periphery. An umbilicus is not present. The aperture is almost quadrangular. Dimensions: height 2.7 mm, diameter 2.8 mm (holotype).

*Etymology*. Of the Mapuche, the native people of south central Chile.

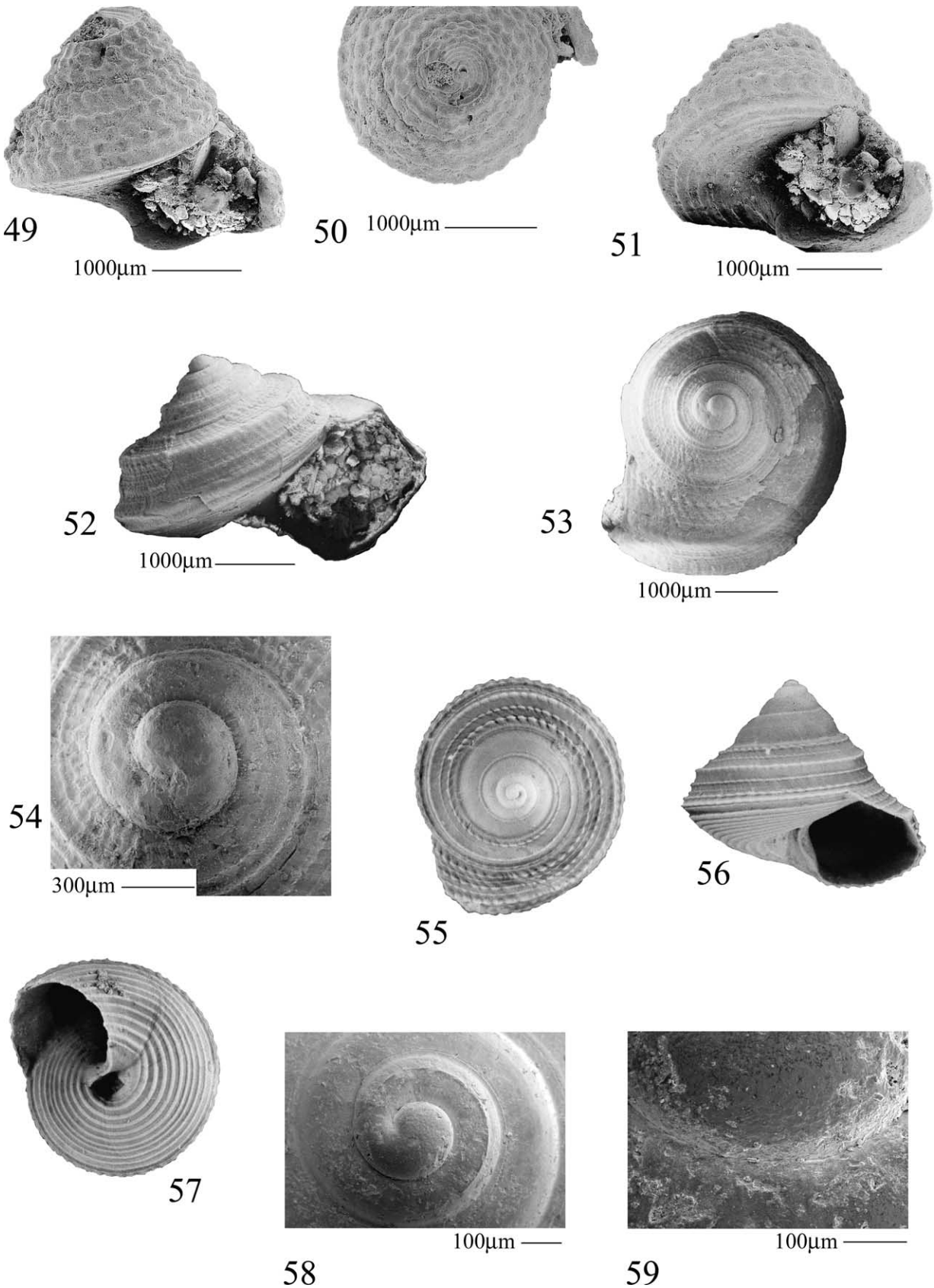
*Type material*. Holotype SGO.PI.6005 (RAP).

*Occurrence*. RAP; Miocene, Navidad Formation, central Chile.

*Remarks*. Species of *Calliostoma* can be recognized easily by their protoconch, which bears a characteristic honeycomb pattern. Although the protoconch is not preserved, the species is placed in this genus because the shell form and sculpture are typical for that group. There is no similar species known from the Miocene of Chile. *Calliostoma foncki* Philippi, 1860, which bears a similar sculpture, might be a living relative from Chile and Peru, but comparison is difficult because the holotype of *C. mapucherum* is an immature specimen.

*Calliostoma (s.l.) kleppi new species (Figs. 52–54)*

*Diagnosis*. Shell small and angulated. Sculpture of beaded spiral cords and axial threads.




Figs. 49–59. Trochidae, Calliostomatinae. 49–51. *Calliostoma mapucherum* n. sp., holotype SGO.PI.6005. 52–54. *Calliostoma kleppi* n. sp., holotype SGO.PI.6017. 55–59. *Calliostoma (Otukaia) covacevichi* n. sp., 55–57. Holotype SGO.PI.5301 (largest), 58–59. Paratype SGO.PI.5301 (middle).

*Description*. The small shell is low spired and has a stepped profile and two prominent peripheral angulations. The shell surface is sculptured with numerous beaded spiral cords and weaker axial threads. Two secondary cords appear on the subsutural ramp between the suture and the first primary cord. Below this first primary cord, a second primary cord forms the first prominent angulation, a third primary cord is on the whorl side, and a fourth primary cord forms the second prominent angulation. Between primary cords are three secondary cords between which tertiary cords are intercalated. On the base are additional spiral cords. The protoconch seems smooth (Fig. 54), and the aperture is subquadrate. Dimensions: height 3.1 mm, diameter 4.4 mm (holotype).

*Etymology*. Named after Christian Klepp (Hamburg) for his friendly support.

*Type material*. Holotype SGO.PI.6017 (MAT).

*Occurrence*. MAT; Miocene, Navidad Formation, central Chile.

*Remarks*. Although the protoconch does not show the typical calliostomatine honeycomb pattern, erosion may be the cause, as we discuss for *Calliostoma covacevichi*. The heavily angulated shell form is unique among the Chilean trochids. Angulated forms such as *C. kleppi* are atypical for calliostomatines, but *C. covacevichi* has a similar form and was probably closely related. However, *C. kleppi* can be distinguished easily from *C. covacevichi* by its different whorl shape.

*Subgenus Otukaia Ikebe, 1942*

*Type species*. *Calliostoma kiheiziebisu* Otuka, 1939; Recent, Japan.

*Calliostoma (Otukaia) covacevichi* new species (Figs. 55–59).

*Diagnosis*. A species of the subgenus *Otukaia* characterized by its smooth first three teleoconch whorls.

*Description*. The shell is small, thin, and umbilicate with convex spire whorls. The protoconch consists of three-quarters of a whorl and bears a honeycomb pattern. Teleoconch whorls are four and one-quarter. The first teleoconch whorls are smooth; later teleoconch whorls bear noded spiral cords. The subsutural cord is the least prominent and remains close to the suture. A second cord, sharply defined and strongly noded, is similar to the third cord. A fourth cord, between the second and third cord, remains weak. Three more noded cords appear below, weaker than the second and third ones. The basal keel is sharp with the suture laid directly on its lower surface. The base bears 10 cords, which become broader toward the umbilicus; the 11th (umbilical) cord is weak. The columellar wall is thick and laid on the 10th basal cord, and the outer lip is thin. Dimensions: height 6.4 mm, diameter 7 mm (holotype).

*Etymology*. After the late V. Covacevich, who contributed much to the knowledge of Chilean Tertiary mollusks.

*Type material*. Holotype SGO.PI.5301, Paratypes SGO.PI.6015, SGO.PI.6020 (all Pupuya).

*Occurrence*. Pupuya; Miocene, Navidad Formation, central Chile.

*Remarks*. Although the subgenus *Otukaia* is defined by its sculpture of three spiral cords on the early whorls, the new species is interpreted as belonging, as it develops these cords on the fourth whorl. *Calliostoma (Otukaia) covacevichi* resembles low-spired forms of the Recent Chilean *C. (O.) delli* McLean and Andrade, 1982 and the Recent New Zealand *C. (O.) alertae* Marshall, 1995, but is separated from these forms by its smooth early whorls and the presence of an umbilicus. The umbilicus might be a juvenile character, in which case the *C. (O.) covacevichi* specimens also were juveniles. *Calliostoma (O.) covacevichi* comes from a deep-water siltstone with other characteristic deep-water gastropods. This locality has quite different sedimentology and fauna than the nearby PUY.

*Genus Astele Swainson, 1855*

*Type species*. *Astele subcarinata* Swainson, 1855. Recent, Tasmania.

*Astele chilensis* (d'Orbigny, 1852) new combination (Figs. 60–69).

*Trochus laevis* Sowerby, 1846; p. 256, pl. 3, Fig. 46, 47 non Dillwyn, 1817, nec Nilsson, 1827, nec Wood, 1828.

*Trochus collaris* Sowerby, 1846; p. 256, Navidad non Sta. Cruz.

*Trochus chilensis* d'Orbigny, 1847, d'Orbigny, 1852; p. 44, new name.

*Trochus laevis* Sowerby, Philippi, 1887; p. 101, pl. 12, Fig. 5.

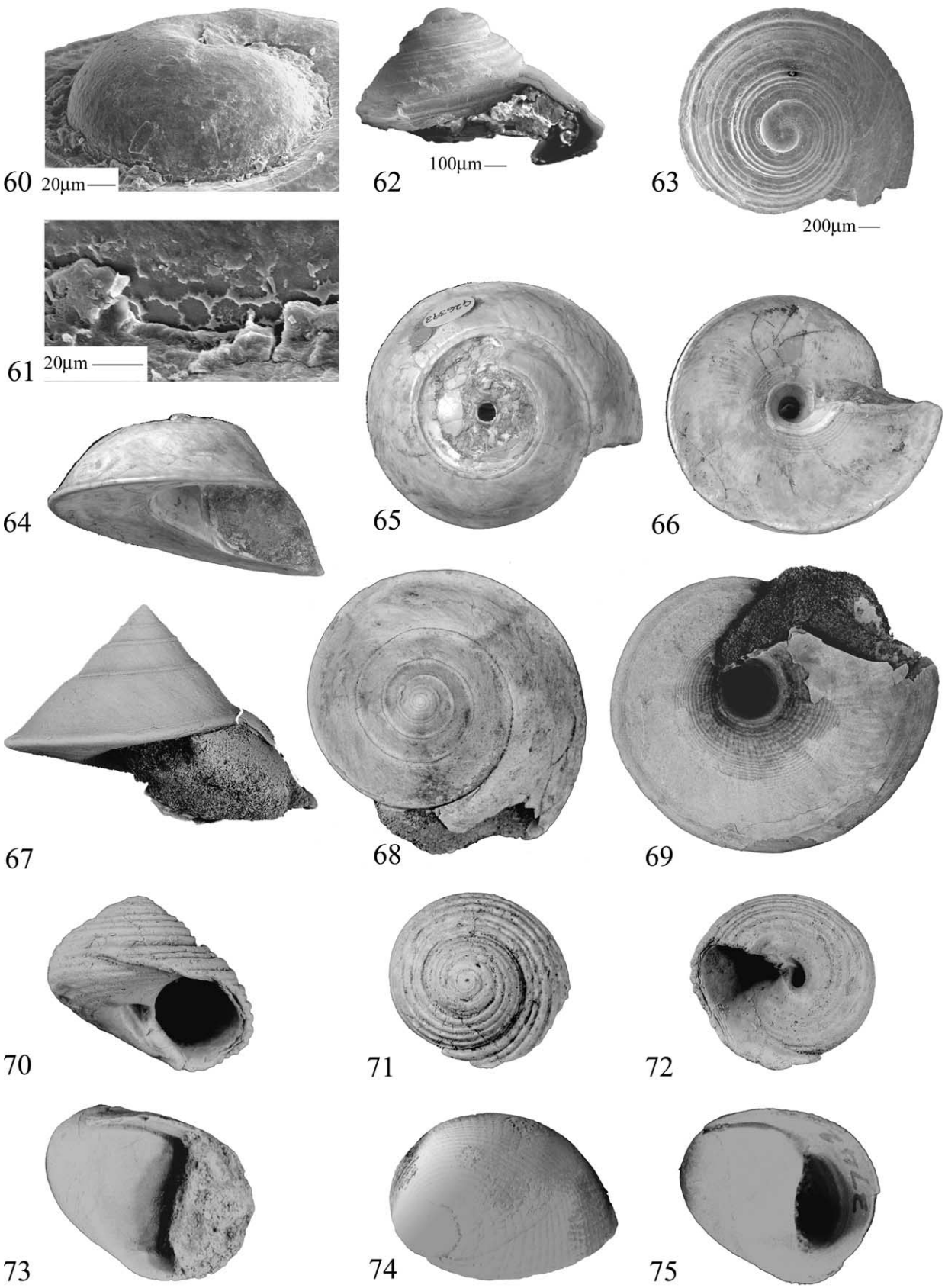
*Trochus fricki* Philippi, 1887; p. 101, pl. 12, Fig. 7.

*Trochus (Gibbula) laevis* Sowerby, Tavera, 1979; p. 94

*Original diagnosis*. *Trochus testa conica, laevi, anfractibus subaequalibus, postice turgidiusculis, antice tenuissime transversim striatis, infra subconcavis, spiraliter tenuiter striato; apertura rhomboidea, angulo externo acuto; umbilico mediocri, intus laevissimo; labio interno subincrassato*.

*Diagnosis*. Shell large, conical. Protoconch with honeycomb pattern. Early whorls with five spiral threads. Growth lines weak. Later whorls smooth. Lower side of whorls slightly convex, bearing fine spiral cords, becoming coarser near umbilicus. Umbilicus wide, smooth, with groove at the suture. Whorls straight with weak shoulder. Aperture subquadrate.

*Description*. The trochoid shell is relatively large, conical, and smooth other than its fine spirals and growth lines. On other whorls, the spiral sculpture vanishes from the center of the whorl, so the shell seems smooth. Spiral sculpture is low on the whorl side and more prominent near the umbilicus. Sides of the whorls are almost straight and have a weak shoulder. The umbilicus is wide, smooth, spirals




Figs. 60–75. Trochidae, Calliostomatinae, and Umboniinae and Neritidae. 60–69. *Astele chilensis* (d'Orbigny, 1852), 60–63. SMF 323627, 64–66. Holotype BMNH G.26393, 67–69. coll. Nielsen RAP001. 70–72. *Monilea riorapelensis* n. sp., holotype SGO.PI.6006. 73–75. *Nerita (Heminerita) chilensis* Philippi, 1887, 73–74. Holotype SGO.PI.844, 75. SGO.PI.3742.

upward and has a groove at the suture. The aperture is subquadrate. The protoconch has the typical calliostomatine honeycomb pattern (SMF 323627) and consists of approximately three-quarters of a whorl. It measures 480 μm across. Dimensions: height up to 41 mm, diameter up to 57 mm.

*Type material*. Holotype of *T. laevis* BMNH G.26393 (Navidad); Syntype of *T. fricki* SGO.PI.813 (Navidad).

*Occurrence*. RAP, PPN, RAN; Miocene, Navidad and Ranquil Formations, Chile Chico (Frassinetti and Covacevich, 1999), Isla Crosslet, central to southern Chile.

*Remarks*. The name *T. laevis* has been used several times, so *T. chilensis* has been introduced as a replacement name by d'Orbigny (1852), though this proposal has been neglected by other authors. d'Orbigny (1852) cites d'Orbigny, 1847, because he thought it would be published that year. *Trochus laevis* (i.e. *A. chilensis*) was assigned to the subgenus *Juliania* Morra and del Río, 1987 of *Valdesia* by Morra and del Río (1987). This opinion is not shared here, because *Valdesia* is regarded as more related to *Gibbula* and thus should not have a honeycomb pattern on the protoconch. However, revision of the whole species complex, including Argentinean species, is necessary. A very similar, if not conspecific, species is *Valdesia (Juliania) conica* Morra and del Río, 1987, type species of *Juliania*, from Argentina. Also very similar is *Valdesia collaris* (Sowerby, 1846) from Sta. Cruz, Argentina, which had been synonymized with *A. chilensis* by Philippi (1887), Morra and del Río (1987), and Frassinetti and Covacevich (1999) but is regarded as a distinct species by M. Griffin (pers. comm.). We share the opinion that the Chilean and Argentinean species should be considered distinct species until a more detailed comparison of the type material is carried out and well-preserved additional material from the type localities is available. The single preserved syntype of *T. fricki* is a small, worn specimen that falls into the morphological range of juvenile *A. chilensis*. Specimens of the latter show intergrades between an almost smooth shell and one that bears four well-developed spiral cords on early whorls that become obsolete on later whorls. *T. fricki* bears such spiral cords, but we are not aware of any diagnostic features separating it from *A. chilensis*.

*Subfamily Umboniinae H. and A. Adams, 1854*

Tribe Monileini Hickman and McLean, 1990.

Genus *Monilea* Swainson, 1840

*Type species*. *Trochus callifera* Lamarck, 1822; Recent, Indo-Pacific.

*Monilea riorapelensis* new species (Figs. 70–72).

*Diagnosis*. Shell globose, medium-sized, with small umbilicus; whorls convex. Sculpture of coarse spiral cords, aperture strongly inclined.

*Description*. The globose, medium-sized shell has a small umbilicus. The protoconch is unknown, and there are five convex teleoconch whorls. Whorl sculpture consists of four coarse spiral cords, and the base bears nine coarse spiral cords. Secondary cords appear on the last whorl. The aperture is strongly inclined. Dimensions: height 10.5 mm, diameter 13 mm (holotype).

*Etymology*. After the type locality north of Río Rapel.

*Type material*. Holotype SGO.PI.6006 (RAP).

*Occurrence*. RAP; Miocene, Navidad Formation, central Chile.

*Remarks*. The only similar species from the Navidad Formation is *G. poeppigii*. *Monilea riorapelensis* has a more globose shell, a rounded aperture, an open umbilicus, and 10 ribs on the upper side of whorls, whereas *G. poeppigii* has a subquadrate aperture, only about six ribs on the upper side of whorls, and an umbilicus closed by callus. *Monilea patricia* Philippi, 1851 is the only species of *Monilea* in the tropical eastern Pacific (Hickman and McLean, 1990). *Monilea riorapelensis* differs from other Recent species of *Monilea*, such as *M. callifera* (Lamarck, 1822) from the Phillipines and *M. lentiginosa* A. Adams, 1851 from New Zealand, by its coarser sculpture and less angulated whorls. *Monilea riorapelensis* seems the oldest *Monilea s.s.*; Hickman and McLean (1990, p. 127) noted that the genus 'is not recognized earlier than the Pliocene.'

*Order Neritimorpha Golikov and Starobogatov, 1975*

Superfamily Neritoidea Rafinesque, 1815

Family Neritidae Rafinesque, 1815

Genus *Nerita* Linnaeus, 1758

*Type species*. *Nerita peloronta* Linnaeus, 1758; Recent, Caribbean Sea.

Subgenus *Heminerita* Martens, 1887

*Type species*. *Nerita japonica* Dunker, 1859 ( = *N. pica* Gould, 1850); Recent, Japan.

*Nerita (Heminerita) chilensis* Philippi, 1887 (Figs. 73–75).

*Nerita chilensis* Philippi, 1887; p. 98, pl. 11, Fig. 18.

*Original diagnosis*. *Testa tenuis, obtusissima, confertim sulcata; labium (seu columella) concaviusculum, laeve, margine rectilineum, edentulum.*

*Diagnosis*. *Nerita* with visible spire. Sculpture of 38–45 flat spiral cords. Columella concave, inner lip and callus smooth, outer lip smooth.

*Description*. The spire is low but visible and, though eroded in all specimens, documents that the teleoconch has about three whorls. The sculpture consists of 38–45 flat spiral cords and weak growth lines. The inner lip, callus, and interior of the outer lip are smooth. Dimensions: width 18.3 mm, height 16 mm (holotype).

*Type material*. Holotype SGO.PI.844. Additional specimens SGO.PI.3742 (height 11.5 mm), SGO.PI.4985 (height 13.5 mm), all Matanzas.

*Occurrence*. MAP; Miocene, Navidad Formation, central Chile.

*Remarks*. Due to the smooth inner and outer lip, this species belongs in *Nerita* (*Heminerita*). It differs from other species of this subgenus, which usually appear almost

smooth but have fine spiral lirae, in that it has visible spiral ornament. *Heminerita* is a Pacific subgenus known from Japan (*Nerita pica*) and Isla de Pascua (Easter Islands) (*Nerita lirellata* Rehder, 1980 and *Nerita morio* (Sowerby, 1833)). Philippi (1887) mentioned two specimens from Matanzas, of which only one remains in his collection. One of the two specimens of Covacevich and Frassinetti's collection (SGO.PI.3742, Fig. 18) has been prepared to show the apertural features that are hidden by matrix in the holotype.

## 5. Discussion

Patelloids, which dominate the intertidal fauna of Chile, are not known from the Chilean Miocene. They seem to have appeared in Chile only in the Pliocene (Herm, 1969; personal data). It is interesting to note that among the Fissurelloidea and Trochoidea, several genera that occur in the Miocene still live at or off the Chilean coast today, whereas the composition of most other groups of gastropods (e.g. Stromboidea, Tonnoidea, Conoidea, Architectonicidae) has changed significantly since the end of the Miocene. These archaeogastropods have adapted to the various climatic changes that have occurred since the Miocene. *Nerita*, in contrast, is a tropical form and therefore not living on the Chilean coast today. However, whereas *Nerita* is strictly an inhabitant of the higher intertidal and supratidal zone, some of the trochids may have lived at greater depths with already cool temperatures during the Miocene, before water temperature generally dropped subsequently.

*Tegula* is regarded as appearing in the Miocene (Hickman and McLean, 1990). However, the high diversity shown here for the (Upper?) Miocene, with the two subgenera *Chlorostoma* and *Agathistoma*, indicates that *Tegula* may have evolved earlier, perhaps during the Late Paleogene.

In Argentina, as in Chile, the patelloids appear with *Cellana* only in the Holocene, maybe Pliocene. In the Miocene of Argentina, there are no *Diodora, Cantrainea, Bathybembix, Astele, Monilea*, or *Nerita* known, but *Tegula, Gibbula*, and *Calliostoma* are present with several species (M. Griffin, pers. comm.).

In New Zealand *Cellana* is recorded since the latest Eocene, but is absent in Chile until the Pliocene. However, even in the much larger fauna of New Zealand (c. 5000 species), *Cellana* is a rare fossil before the Pleistocene. The scarcity of 'limpets' in New Zealand before the Pleistocene is a result of the poor preservation potential of the intertidal fauna (Beu, pers. comm.). There are no species of *Diodora, Cantrainea, Tegula, Bathybembix, Gibbula*, or *Heminerita* known from the New Zealand fossil record, but *Cantrainea* is represented in the Recent fauna and likely to have lived there in the past. Calliostomatines appeared in the Late Eocene and become diverse in the Pliocene, *Astele* s.l. is present in the New Zealand Miocene with a few species, and *Monilea* s.l. is known from the Miocene (Beu and Maxwell, 1990).

In summary, the vetigastropod and neritid fauna of the Miocene of Chile shows an interesting mix of warm- and cold-water elements. Warm- and cold-water species do not occur together (except at RAP, where several fallen blocks were sampled prior to our recognition that different faunas might be present). Therefore, the interpretation that much of the sampled formations consist of sediments that were deposited in a shallow water environment and subsequently displaced into greater depths (Encinas et al., 2003; Finger et al., 2003; Nielsen et al., 2003) is strongly supported. Warm-water species are displaced from a shallow water environment, whereas the cold-water species are from the deep-water environment in which the sediments were deposited. The fauna has low affinities with the faunas of New Zealand, Argentina, and the tropical eastern Pacific and apparently none at all with the Caribbean fauna (cf. Woodring, 1957–1982).

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