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Trophonella (Gastropoda: Muricidae), a New Genus from Antarctic Waters, with the Description of a New Species

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Abstract. The new genus *Trophonella* is described from the outer shelf and upper continental slope of Antarctica and islands within the Antarctic Convergence. Four previously known species that had been attributed to the genus *Trophon* (*Trophon scotianus* Powell, 1951; *T. echinolamellatus* Powell, 1951; *T. enderbyensis* Powell, 1958; and *T. eversoni* Houart, 1997) are included in *Trophonella*, as is one new species (*Trophonella rugosolamellata*) described herein. *Trophonella* resembles *Trophon* in gross shell morphology: the members of both genera have large, globose shells, paucispiral protoconchs, prominent axial lamellae, and short siphonal canals. *Trophonella* differs from *Trophon* in having shells with evenly rounded whorls that lack a well-defined shoulder; rachidian teeth with distinctive, broadly triangular central cusps, but that lack the marginal cusps of *Trophon*; characteristic spherical accessory salivary glands; and a circumpapillar fold on the penis that is absent in *Trophon*. Relationships of the genera *Trophon* and *Trophonella*, as well as of the subfamily Trophoninae are reexamined by supplementing the data matrix of Kool (1993b, Table 3) with data for additional taxa. Results support the segregation of *Trophonella* from *Trophon* at the generic level. Based on the relationships of the type species of their respective nominotypical genera, Trophoninae is either the sister taxon of a narrowly circumscribed Ocenebrinae, or both are part of a larger clade. A better resolved phylogeny containing a much broader sampling of the more than 50 genus-level taxa that have been attributed to these two subfamilies will be required in order to delineate more precisely the membership of the clade and to identify its diagnostic synapomorphies.

INTRODUCTION

Although the family Muricidae is best known for its temperate and tropical shallow-water representatives, it also includes a group of taxa inhabiting polar seas and intervening deeper waters that have generally been grouped in the subfamily Trophoninae. Cossmann (1903) proposed the subfamily Trophoninae to contain the genera *Trophon* Montfort, 1810, and *Aspella* Mörch, 1877. The genus *Trophon* was subdivided into the subgenera *Trophon* and *Trophonopsis* Bucquoy and Dautzenberg, 1882. Under *Trophon sensu stricto*, he included the sections *Trophon*, *Xanthochorus* Fischer, 1884, and *Forreria* Jouseaume, 1880. *Trophonopsis* was further subdivided into *Trophonopsis* and *Boreotrophon* Fischer, 1884. The genus *Aspella* was not subdivided.

Over the past several decades, there has been general agreement among researchers that Trophoninae is not a monophyletic group. As was noted by Radwin and D'Attilio (1976, p. 175), Trophoninae "has been the site of assignment of many dissimilar forms that seem, on the basis of the shell and radular morphology of the type species of *Trophon* (*T. geversianus*), unlikely to belong there." The genus *Aspella* is presently assigned to the subfamily Muricinae on the basis of radular morphology (Radwin & D'Attilio, 1976, p. 21). These authors went on to exclude from the subfamily Trophoninae a number of genera (e.g., *Austrotrophon* Dall, 1902; *Forreria*; *Zacatrophon* Hertlein & Strong, 1951) because they "... had radulae characteristic of the family Thaididae." In a phylogenetic study, Kool (1993a, fig. 65) showed that, based on the morphology of its type species, the genus *Trophon* was closely related to the genera *Nucella* and *Ocenebra*, and he suggested that future studies would reveal Trophoninae to be polyphyletic.

Our continuing studies on the Muricidae represented in the collections of the United States Antarctic Program (USAP) have revealed that four species previously described in the genus *Trophon* (i.e.,

Trophon scotianus Powell, 1951; *T. echinolamellatus* Powell, 1951; *T. enderbyensis* Powell, 1958; and *T. eversoni* Houart, 1997) appear to be closely related to each other, but they differ substantially from the type species of the genus *Trophon*. In this paper, we propose the new genus *Trophonella* to include these species, and we describe an additional new species that we attribute to this genus. A review of each of the species included in this new genus is provided, based on more recently collected specimens.

We also examine the relationships of the genus *Trophon* and the subfamily Trophoninae by reanalyzing Kool's (1993b, table 3) data matrix of primarily ocenebrine and rapanine taxa supplemented by the addition of data for (1) *Trophon geversianus* (Pallas, 1769), the type species of the type genus of Trophoninae; (2) *Ocenebra erinaceus* (Linnaeus, 1758), the type species of the type genus of Ocenebrinae; (3) *Trophonella scotiana* (Powell, 1951), the type species of the new genus *Trophonella*; (4) *Boreotrophon aculeatus* Watson, 1882; and (5) *Paziella pazi* (Crosse, 1869), the type species of the genus *Paziella*.

MATERIALS AND METHODS

This study is based primarily on specimens collected for the United States Antarctic Program (USAP) aboard the vessels R/V Hero, R/V Eltanin and R/V Professor Sedlacki and housed in the collections of the National Museum of Natural History, Smithsonian Institution (USNM). Additional specimens from several Antarctic expeditions of the Argentine Republic deposited in the Museo Argentino de Ciencias Naturales (MACN) were examined, as were specimens at the Zoological Institute and Museum, Hamburg (ZMH), and the Senckenberg Museum, Frankfurt (SMF), collected by the vessels R/V Walther Herwig and R/V Polarstern. The notation "w/n" following an institutional acronym indicates that no catalog number was associated with the specimen at the time it was examined. All specimens were compared with the holotypes of their respective species, which are housed in The Natural History Museum, London (NHM), the South Australian Museum (SAM), and at USNM.

Alcohol-preserved animals of most species of *Trophonella* were dissected, and the gross anatomy of the anterior part of the alimentary system and pallial gonoducts were compared. Radulae were prepared according to the method described by Solem (1972) and examined using a Scanning Electron Microscope (SEM). Terminology for rachidian-tooth morphology follows Kool (1987, fig. 1). Shell ultrastructure data was obtained from fracture surfaces of shell fragments removed from the central portion of the lip along the last shell whorl.

In order to determine the generic and subfamilial relationships of this distinctive group of Antarctic muricids, we reanalyzed the data matrix in Kool (1993b, table 3), to which we added data for *Trophon geversianus*, *Ocenebra erinaceus*, *Trophonella scotiana*, *Boreotrophon aculeatus*, and *Paziella pazi*. Harasewych (1984) was the source of data for *T. geversianus*, *B. aculeatus*, and *P. pazi*. Data for *T. geversianus* and *O. erinaceus* were obtained from Kool (1993a). Data on shell ultrastructure of *Boreotrophon aculeatus* and *Paziella pazi* were newly obtained from the voucher material from Harasewych's (1984) study. Each of the newly added taxa were scored for the 18 characters and their character states, as defined in Kool (1993b). The data were analyzed using maximum parsimony (MP) and neighbor-joining algorithms of PAUP* 4.0 Macintosh Beta Version 10 (Swofford, 2002).

SYSTEMATICS

Class GASTROPODA Cuvier, 1797

Order NEOGASTROPODA Wenz, 1938

Family MURICIDAE Rafinesque, 1815

Trophonella new genus

Type species: *Trophon scotianus* Powell, 1951.

Diagnosis: Shell large, fusiform, inflated. Protoconch paucispiral (1.5–2 whorls). Teleoconch (6–7 whorls) globose, without distinct shoulder, with tall, conical spire. Sculpture of low, rounded, spiral cords and axial lamellae that may be broadly flaring to short and rugose. Aperture broadly rounded, with flaring outer lip and thin inner lip. Siphonal canal short. Operculum large, oval, with subterminal nucleus. Rachidian teeth with rectangular basal plate; three major cusps, central cusp exceptionally broad, triangular, with small denticle on each side; marginal cusps absent. Accessory salivary glands small, spherical. Esophageal gland reduced. Penis with conical papilla surrounded by collar.

Description: Shell large (to 76 mm), fusiform, often broadly ovate, with strongly convex, evenly rounded whorls that do not form a distinct shoulder. Protoconch paucispiral, occasionally with weak, irregular, spiral cords. Teleoconch sculpture of low, rounded, spiral cords with or without scales, and axial lamellae that range from broadly flaring to short and rugose. Aperture large, suboval, with thick outer lip, and thin inner lip. Siphonal canal short, scabrous. Shell ultrastructure of three layers, the inner two of orthogonally oriented crossed-lamellar aragonite, the outermost layer of calcite. Operculum large, filling aperture, corneous, oval, with subterminal nucleus, thick rim, and large attachment area.

Animal large, unpigmented. Cephalic tentacles wide, blunt. Mantle edge smooth, siphon short. Pleuroem-

bolic proboscis short, broad. Radular ribbon small, thin, extending beyond rear of buccal mass. Rachidian teeth with subrectangular, weakly recurved basal plate and smooth, broad, marginal surfaces that lack marginal cusps. Central cusp long, exceptionally broad, triangular; flanked by a single, small to nearly obsolete lateral denticle on each side; lateral cusps short, robust, smooth. Lateral teeth of moderate size, basal plate shorter and narrower than in rachidian teeth, with single scythelike cusp along outer edge that is slightly longer than the basal plate. Esophagus short. Salivary glands very large, ascinous, enveloping esophagus. Accessory salivary glands small, spherical, and completely embedded in corresponding salivary gland. Gland of Leiblein compact, with terminal ampula. Penis large, wide, with conical papilla rising from a concavity at its distal end.

Etymology: *Trophon* (Gr., that which feeds) + *ella* (L., suffix added to form the diminutive).

Included species: *Trophonella scotiana* (Powell, 1951), new combination [Type species]; *T. echinolamellata* (Powell, 1951), new combination; *T. eversoni* (Houart, 1997), new combination; *T. enderbyensis* (Powell, 1958), new combination; *T. rugosolamellata*, new species.

Remarks: *Trophonella* is similar to *Trophon* in gross shell morphology, as both have globose shells of comparable size with paucispiral protoconchs, prominent axial lamellae, and short siphonal canals. Species of *Trophonella* can be distinguished most readily by their evenly rounded whorls that lack a well-defined shoulder. The main differences appear to be anatomical. *Trophonella* has a circumpapillar fold on the penis that is absent in *Trophon*. The accessory salivary glands of *Trohonella* are globular, while those of *Trophon* are elongate.

The rachidian teeth of *Trophonella* have distinctively broadly triangular central cusps and lack the marginal cusps of *Trophon*.

Trophonella is restricted in geographic distribution to Antarctica and islands within the Antarctic Convergence. Records range in depth from 18 m to 474 m (both for *T. scotiana*), with the majority of specimens sampled at outer-shelf and upper continental-slope depths (Figures 20–21). In terms of size and biomass, species of *Trophonella* are the largest muricids occurring within the Antarctic Convergence.

Trophonella scotiana (Powell, 1951), new combination

(Figures 1–13, 20)

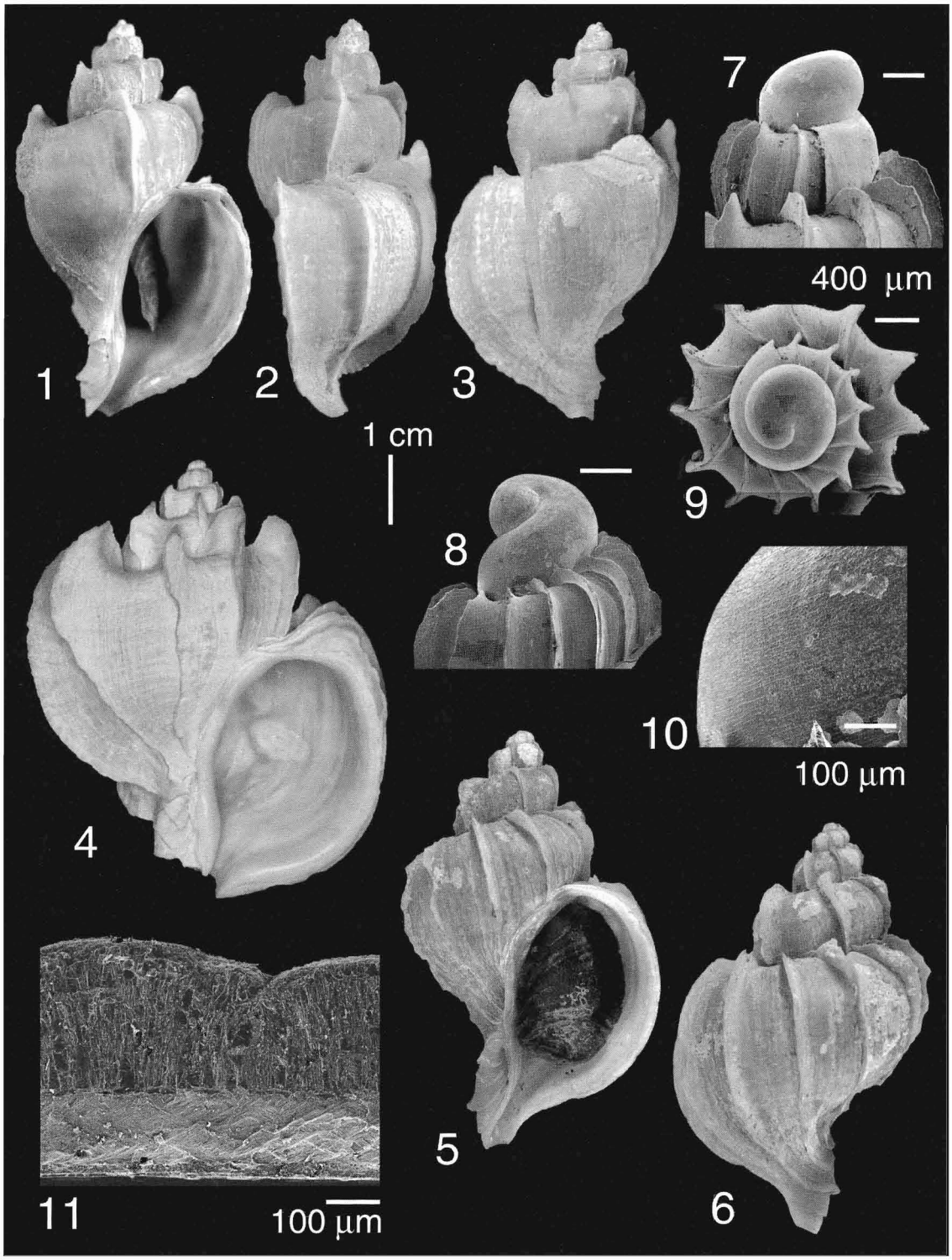
Synonymy: *Trophon scotianus* Powell, 1951, p. 153, pl. 9, figs. 48–49, M88; Carcelles, 1953, p. 189, pl. 2, fig. 51; Powell, 1960, p. 154; Okutani, 1986, p. 279, pl. 1, figs. 3–6; Dell, 1990, p. 207, figs. 346–347; Castellanos & Landoni, 1993, p. 13, fig. 36; Numanami, 1996, p. 138, figs. 91 a–c.

Trophon sp. 1 Hain, 1990, p. 63, pl. 6, fig. 9 a,b; pl. 25, fig. 2.

Description: Shell (Figures 1–6) large (to 70 mm), fusiform, thin shelled, chalky. Protoconch (Figures 7–10) tall, increasing in diameter from 450 μm to 1.2 mm in 1½ to 1¾ evenly rounded whorls, surface with very fine, irregular and discontinuous spiral threads. Transition to teleoconch marked by broadly flaring lip. Teleoconch of up to 6 slightly globose whorls; spire tall, conical, less than 50% of shell length. Suture impressed to abutting. Spire angle 62°–84°. Aperture subpolygonal to evenly rounded, deflected from the coiling axis by 20°–25°; interior glossy. Siphonal canal moderately short, narrow, slightly deflected dorsally. Siphonal fasciole scabrous; pseudoumbilical chink nearly closed or reduced to a very narrow slit. Outer lip rounded with reflected edges. Columellar lip narrow, adpressed. Axial sculpture of regular, thin, strongly developed lamellae (4–11 on last whorl) that span whorl surface from suture to siphon, expanded in shoulder region. Fine, closely spaced growth lines cover whorls and lamellae. Spiral sculpture, of low, rounded, spiral cords, broader than interspaces (18–32 on body whorl, 2–6 on siphonal canal) becoming reduced to obsolete on larger specimens. Shell color white to pale orange-tan. When color present, lighter bands may be evident, one below suture, the other above the juncture to the siphonal canal.

Shell composed of three layers (Figure 11). Innermost layer, of crossed lamellar aragonite with crystal planes oriented perpendicular to the growing edge, comprises roughly 2% of shell thickness. Middle layer, also aragonitic, arranged with crystal planes parallel to growing edge, comprises roughly 36% of shell thickness. Outermost layer is calcitic, comprising the major part (62%) of the shell's thickness. Operculum (Figure 43) oval, with terminal nucleus, outer surface with regular growth lines, inner surface with broad, thickly glazed rim along posterior edge, and large, round/oval attachment area, often with 2–3 horseshoe-shaped scars.

Animal large, compact. Foot short, broad, with accessory boring organ situated along ventral midline, opening via ventral pedal gland in females. Tentacles large, broad, closely situated, with large black eyes. Mantle edge smooth, osphradium (Figure 48, os) small, slightly asymmetrical, with 45–55 leaflets per side, less than 50% the length of the ctenidium (Figure 48, ct). Proboscis large, muscular, cylindrical, pleurombolic. Radula (Figures 12–13) short (radular



Figures 1–11. *Trophonella scotiana* (Powell, 1951). 1. Apertural, 2. lateral, and 3. dorsal views of a medium-sized specimen with few axial lamellae, USNM 897411, off South Georgia Island, 54°53′S, 35°49′W, in 127–140 m. 4. Apertural view of large specimen with well-developed lamellae, USNM 901644, Off Borchgrevink Coast, Victoria Land, Antarctica, 74°01′S, 178°53′E, in 256–258 m. 5. Apertural and 6. dorsal views of average specimen, USNM 897560, off South Georgia Island, 54°39′S, 37°22′W, in 140–150 m. 7–8. Lateral, and 9. apical views of the protoconch. 10. Detail of protoconch sculpture. USNM 901645, W of Graham Land,

length roughly 30% of aperture length), narrow (roughly 550 μm wide), extending beyond rear of retracted proboscis. Rachidian tooth subrectangular, basal plate moderately concave anteriorly, with short, smooth marginal area. Central cusp large, broad, lateral cusps shorter, narrower, with single denticle between central and lateral cusps (Figure 13, d) often almost obsolete, but present, even in juvenile specimens. Lateral teeth L-shaped, with single cusp along outer edge roughly equal in length to width of basal plate. Juvenile specimens have proportionally larger denticles, and thinner cusps on rachidian and lateral teeth. Esophagus very thin. Valve of Leiblein (Figure 49, vL) ovate. Salivary glands (Figure 49, sg) very large, envelop the valve of Leiblein and the small, nearly spherical accessory salivary glands, joining esophagus via two thick ducts anterior to the valve of Leiblein. Mid-esophagus very thin, lacks conspicuous esophageal gland, passes under gland of Leiblein. Gland of Leiblein large, compact, with blind duct terminating posteriorly in large ampulla. Stomach (Figures 50, 51, sto) large, lining the anterior and dorsal surface of the digestive gland, into which it opens via ducts (Figure 51, dd). Intestine (Figures 50, 51, i) broad. Penis (Figures 45–47, p) large (> 4 × tentacle length), broad, dorsoventrally flattened, elongate, with laterally situated sperm duct, dorsal blood sinus, and conical papilla (Figures 46, 47, 52, pp) surrounded by a collar. Pallial oviduct broad. Albumin gland thin, capsule gland (Figure 53, cg) short, globose. Bursa copulatrix (Figure 53, bc) onion-shaped, with distal female opening (Figure 53, fo). Rectum (Figure 53, r) overlays pallial oviduct; rectal gland (Figure 53, rg) lines anterior dorsal surface of rectum; anus (Figure 53, a) adjacent to female opening. Egg capsules of *T. scotiana* lenticular, subcircular in outline, attached to substrate (Hain, 1990, pl. 6, fig. 9b, *Trophon* sp. 1). Each capsule is about 19 mm in diameter, contains 140 eggs that hatch as crawling juveniles in 24–25 months (Hain & Arnaud, 1992, p. 307, table 3).

Type locality: Off South Georgia Island, 53°55′S, 38°01′W, in 107 m (Figure 20, ❍).

Type material: Holotype, NHM 1961542.

Material examined: D indicates empty shells, L indicates live-collected specimens.

NHM 1961542, Holotype; USNM 887834, 1 L, off South Georgia Island, 53°50′36″S, 36°18′36″W, 185–205 m, R/V Islas Orcadas, cr. 575, stn. 30, 19 May 1975; USNM 887835, 1 L, off South Georgia Island, 54°01′18″S, 36°50′42″W, 108–119 m, R/V Islas Orcadas, cr. 575, stn. 24, 17 May 1975; USNM 896099, 4 D, off South Georgia Island, 53°51′S, 37°38′W, in 97–101 m, R/V Eltanin cr. 22, stn. 1535, 7 Feb 1966; USNM 896982, 1 L, off South Georgia Island, 53°57′S, 36°06′W, 151–158 m, R/V Professor Siedlecki, cr. 601, stn. 97, 13 Dec 1986; USNM 897411, 2 L, off South Georgia Island, 54°53′S, 35°49′W, in 127–140 m, R/V Professor Siedlecki, cr. 601, stn. 71, 9 Dec 1986; USNM 897416, 1 L, off South Georgia Island, 55°24′S, 35°22′W, 207–218 m, R/V Professor Siedlecki, cr. 601, stn. 60, 8 Dec 1986; USNM 897422, 1 L, off South Georgia Island, 55°08′S, 35°06′W, 145–153 m, R/V Professor Siedlecki, cr. 601, stn. 66, 9 Dec 1986; USNM 897427, 2 L, off South Georgia Island, 55°01′S, 35°27′W, 117–122 m, R/V Professor Siedlecki, cr. 601, stn. 67, 9 Dec 1986; USNM 897433, 2 L, off South Georgia Island, 55°05′S, 35°23′W, 116–121 m, R/V Professor Siedlecki, cr. 601, stn. 68, 9 Dec 1986; USNM 897434, 5 L, off South Georgia Island, 54°31′S, 38°11′W, 180–190 m, R/V Professor Siedlecki, cr. 601, stn. 36, 4 Dec 1986; USNM 897444, 1 L, off South Georgia Island, 53°55′S, 37°08′W, 104–122 m, R/V Professor Siedlecki, cr. 601, stn. 109, 14 Dec 1986; USNM 897459, 1 L, off South Georgia Island, 53°52′S, 37°33′W, 104–112 m, R/V Professor Siedlecki, cr. 601, stn. 111, 15 Dec 1986; USNM 897475, 3 L, off South Georgia Island, 53°52′S, 38°20′W, 113–120 m, R/V Professor Siedlecki, cr. 601, stn. 120, 16 Dec 1986; USNM 897490, 1 L, off South Georgia Island, 54°11′S, 37°53′W, 113–118 m, R/V Professor Siedlecki, cr. 601, stn. 40, 5 Dec 1986; USNM 897521, 2 L, off South Georgia Island, 54°05′S, 38°25′W, 197–207 m, R/V Professor Siedlecki, cr. 601, stn. 24, 3 Dec 1986; USNM 897560, 1 L, off South Georgia Island, 54°39′S, 37°22′W, 140–150 m, R/V Professor Siedlecki, cr. 601, stn. 46, 6 Dec 1986; USNM 897564, 5 L, off South Georgia Island, 54°51′S, 35°38′W, in 84–103 m, R/V Professor Siedlecki, cr. 601, stn. 72, 9 Dec 1986; USNM 901642, 1 D, Ross Sea, Moubray Pennell Bank, Victoria Land, Antarctica, 73°22′S, 177°37′E, in 465–474 m, R/V Eltanin, cr. 27, stn. 1933, 30 Jan 1967; USNM 901644, 1 L, Ross Sea, Moubray Pennell Bank, Victoria Land, Antarctica, 74°01′S, 178°53′E, in 256–258 m, R/V Eltanin, cr. 32, stn. 2018, 14 Jan 1968; USNM 901645, 1 L, W of Graham Land, Palmer Peninsula, Antarctica, 66°21.7′S, 66°47′W, in 70–106 m, R/V Hero, cr. 731, stn. 1861, 1 Mar 1973; MACN-In 18991, 1 D, Schlieper Bay, South Georgia Island, in 18 m; MACN-In 18990, 1 L, Cumberland

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Palmer Peninsula, Antarctica, 66°21.7′S, 66°47′W, in 70–106 m. Scale bars = 400 μm. 11. Shell ultrastructure. Fracture surface parallel to growing edge. USNM 887835, off South Georgia Island, 54°01′18″S, 36°50′42″W, 108–119 m.

Figures 12–19. Radulae of species of *Trophonella*. 12. Dorsal and 13. right lateral views of the radular ribbon of *T. scotiana*, specimen in Figure 4. 14. Dorsal and 15. right lateral views of the radular ribbon of *T. echinolamellata*, USNM 896041, 2L, NW of Brabant Island, Palmer Archipelago, Antarctic Peninsula, 63°51′S, 62°38′W, in 128–165 m. 16. Dorsal and 17. right lateral views of the radula of *T. enderbyensis*, specimen in Figures 38–40. 18. Dorsal and 19. right lateral views of the radula of the holotype of *T. rugosolamellata* n. sp. ZMH 2777.

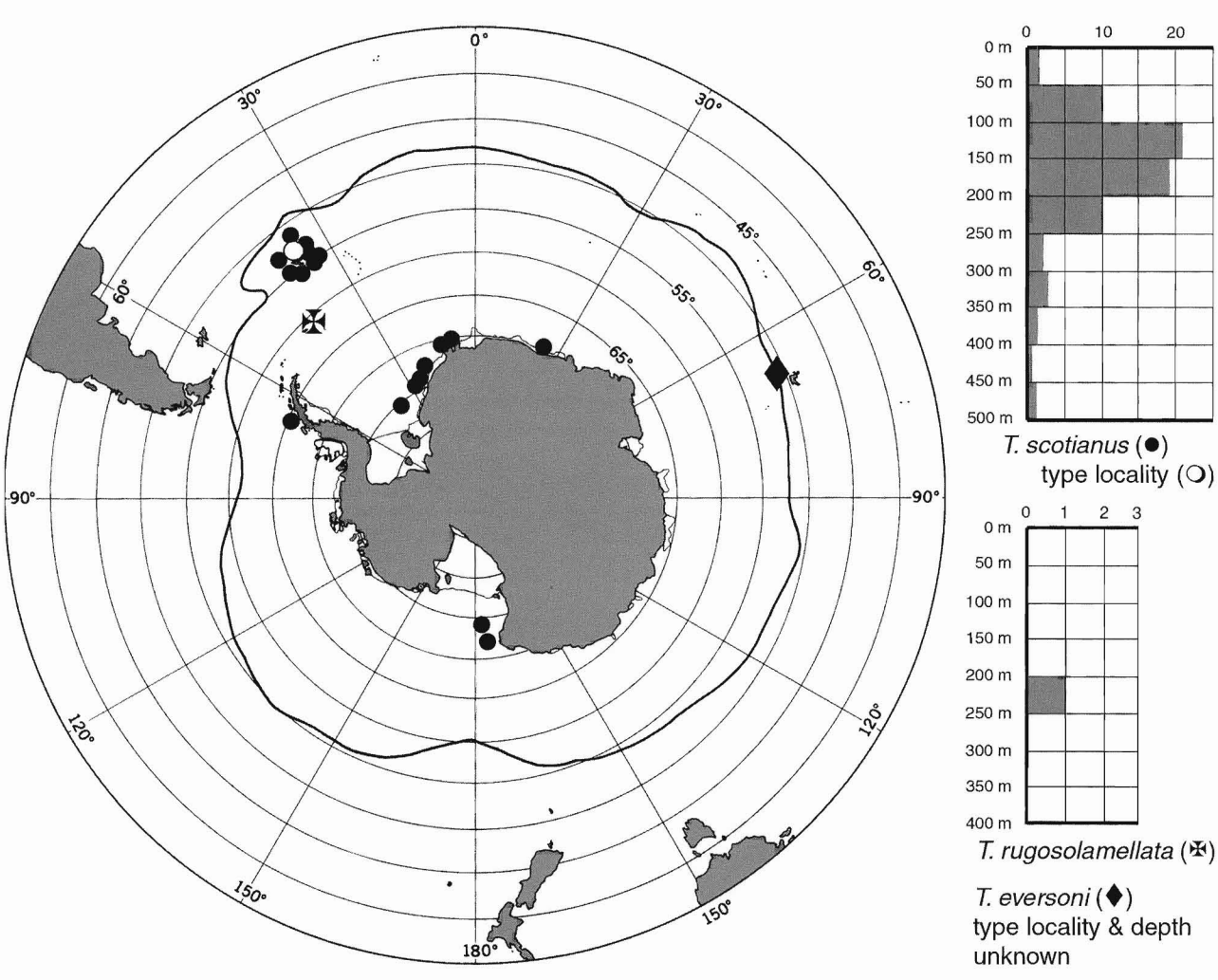


Figure 20. Geographic and bathymetric distributions of *Trophonella scotiana*, *T. rugosolamellata* n. sp., and the only locality reported for *T. eversoni*.

Bay, South Georgia Island, in 36 m; ZMH w/n, 1 D, off South Georgia Island, 54°13.2′S, 37°49.6′W, in 122 m, R/V Walther Herwig, cr. 68, stn. 15; ZMH w/n, 1 L, off South Georgia Island, 53°55.9′S, 38°29.6′W, in 145 m, R/V Walther Herwig, cr. 68, stn. 19; ZMH w/n, 3 L, 1 D, off South Georgia Island, 53°39.5′S, 37°8.9′W, in 155 m, R/V Walther Herwig, cr. 68, stn. 30; ZMH w/n, 1 D, off South Georgia Island, 53°47.3′S, 37°12.2′W, in 141 m, R/V Walther Herwig, cr. 68, stn. 31; ZMH w/n, 3 L, off South Georgia Island, 53°59.8′S, 36°56.2′W, in 150 m, R/V Walther Herwig, cr. 68, stn. 35; ZMH w/n, 1 L, off South Georgia Island, 53°43.3′S, 36°26′W, in 230 m, R/V Walther Herwig, cr. 68, stn. 40; ZMH w/n, 1 L, off South Georgia Island, 53°59.1′S, 36°20.6′W, in 198 m, R/V Walther Herwig, cr. 68, stn. 44; ZMH w/n, 1 L, off South Georgia Island, 53°52.9′S, 36°4.2′W, in 235 m, R/V Walther Herwig, cr. 68, stn. 55; ZMH w/n, 4 L, off South Georgia Island, 54°32.6′S, 35°58.1′W, in 155 m, R/V Walther Herwig, cr. 68, stn. 64; ZMH w/n, 1 L, off South Georgia Island, 54°48′S, 35°23.6′W, in 215 m, R/V Walther Herwig, cr. 68, stn. 70; ZMH w/n, 4 L, off South Georgia Island, 55°15.2′S, 34°46.8′W, in 240 m, R/V Walther Herwig, cr. 68, stn. 78; ZMH w/n, 2 L, off South Georgia Island, 55°0.37′S, 35°03.8′W, in 124 m, R/V Walther Herwig, cr. 68, stn. 79; SMF w/n, 1 D, off the Princess Martha Coast, Queen Maud Land, Antarctica, 70°29′S, 8°07′W, in 270–303 m.

Literature records: PS ANT V/3 St. 593, 73°55′S, 23°38′W, in 330 m (Hain 1990); JARE-25, St. A, 70°14′S, 24°23.9′E, Breid Bay, in 310 m (Okutani 1986; Numanami 1996).

Distribution: Off South Georgia Island, the Antarctic Peninsula, and the Ross Sea, the Weddell Sea, and Breid Bay, Antarctica, at depths of 18–474 m. See Figure 20.

Remarks: This distinctive taxon, the largest species of *Trophonella* in terms of biomass, had, until recently, been known from less than a dozen specimens (Dell, 1990:208; Numanami, 1996:138). A survey of the collections of Antarctic mollusks at USNM, SMF and ZMH, as well as a search of the literature, has uncovered more than 60 specimens and/or records, most from the vicinity of South Georgia Island and the Weddell Sea. Dell (1990:208) and Numanami (1996:140) both noted variation in shell morphology of this species, with the degree of whorl inflation and the number of axial lamellae per whorl both increased in large specimens.

Trophonella echinolamellata (Powell, 1951) new combination

(Figures 14, 15, and 21–28)

Synonyms: *Trophon echinolamellatus* Powell, 1951:152, pl. 9, figs. 44, 45. *Trophon equinolamellatus* [*sic*] Pastorino, 2002:fig. 22.

Description: Shell (Figures 22–24) large (to 69.8 mm), fusiform, inflated, thin shelled, with scabrous surface. Protoconch (Figures 25–27) tall, increasing in diameter from 300 to 920 μm in 1¾ to 2 evenly rounded whorls, surface smooth, frequently pitted. Transition to teleoconch distinguished by weak flare in lip. Teleoconch of up to 7 evenly rounded whorls; spire tall, conical, slightly less than half the shell length. Suture distinctly impressed. Spire angle 66–72°. Aperture broadly ovate, deflected from the coiling axis by about 25°, interior with glazed, lustrous white layer that does not extend to the end of the flared, rounded, outer lip, nor to the edge of thick, adpressed, columellar lip. Demarcation between apertural glaze and apertural lip very pronounced, especially in pigmented shells. Siphonal canal short, narrow, slightly deflected dorsally. Siphonal fasciole scabrous; pseudoumbilical chink pronounced, constricted to varying degrees by thick columellar lip. Outer lip rounded, weakly reflected. Columellar lip thick, overlaying sculpture of previous whorl. Axial sculpture of numerous (14–16 on first teleoconch whorl, 42–50 on last whorl), extremely short lamellae that intersect with closely spaced spiral cords that are as broad as interspaces (16–20 on body whorl, 2–4 on siphonal canal) to produce a scaly surface. On the final whorl of very large specimens, several lamellae may be close together and thickened, giving the appearance of varices that may be spaced ¼ to ½ whorl apart. Shell white, or, more commonly pale orange-cinnamon. When color is present, lighter bands may be evident, one below the suture, the other above the juncture to the siphonal canal.

The shell is composed of three layers (Figure 28). Innermost layer very thin (approximately 2% of shell thickness), consisting of crossed lamellar aragonite with crystal planes oriented perpendicular to growing edge of the shell. Middle layer of crossed lamellar aragonite, with crystal planes colabrally oriented, accounts for approximately 30% of shell thickness. Outermost layer thickest (~ 68% of shell thickness), calcitic. Operculum (Figure 42) D-shaped, with straight adaxial margin, terminal nucleus, fine growth lines along external surface, and broad, glazed rim along inner surface. Attachment area without scars.

The animal is similar to that of *T. scotiana* in most respects. The radula (Figures 14, 15) is slightly longer (radular length ~ 0.45 aperture length) and has proportionally broader rachidian teeth with more pronounced denticles.

Type locality: Off Cape Bowles, Clarence Island, Antarctica, 61°25′S, 53°46′W, in 342 m. (Figure 21, ▽).

Type material: Holotype and one paratype, NHM 1961541.

Material examined: D indicates empty shells, L indicates live collected specimens.

NHM 1961541, Holotype and one paratype; USNM 638874, 1 L, off Victor Hugo Island, west coast of Palmer Peninsula, Antarctica, 65°08′S, 66°04′W, in 135 m, stn. ED28, 22 Mar 1959; USNM 678397, 3 L, off Palmer Peninsula, Antarctica, 60°48′S, 44°13.5W, in 188 m, R/V Eastwind, stn. EW66-028, 11 Feb 1966; USNM 846180, 1 D, east of Victor Hugo Island, west coast of Palmer Peninsula, Antarctica, 65°04′S, 65°53′W, in 150 m, R/V Polar Duke, 8 Sept 1985; USNM 870316, 1 L, NW of Brabant Island, Palmer Archipelago, Antarctic Peninsula, 63°51′S, 62°38′W, 128–165 m, R/V Eltanin, cr. 6, stn. 439, 9 Jan 1963; USNM 870593, 2 L, NE of Joinville Island, Antarctic Peninsula, 62°41′S, 54°43′W, 210–220 m, R/V Eltanin, cr. 12, stn. 1003, 15 Mar 1964; USNM 881728, 1 L, off Visokoi Island, South Sandwich Islands, 56°42′18″S, 27°00′24″W, 93–121 m, R/V Islas Orcadas, cr. 575, stn. 61, 30 May 1975; USNM 881906, 1 L, D'Urville Island, Bransfield Strait, Antarctic Peninsula, 62°39′S, 56°10′W, 426–311 m, R/V Eltanin, cr. 6, stn. 418, 2 Jan 1963; USNM 881907, 1 L, D'Urville Island, Bransfield Strait, Antarctic Peninsula, 62°39′S, 56°10′W, 426–311 m, R/V Eltanin, cr. 6, stn. 418, 2 Jan 1963; USNM881939, 1 L 2 D, off South Georgia Island, 54°41′S, 38°38′W, 220–320 m, R/V Eltanin, cr. 9, stn. 671, 23 Aug 1963; USNM 896041, 2 L, NW of Brabant Island, Palmer Archipelago, Antarctic Peninsula, 63°51′S, 62°38′W, in 128–165 m, R/V Eltanin, cr. 6, stn. 439, 9 Jan 1963; USNM 896056, 2 L, E of South Orkney Islands, 60°51′S, 42°57′W, in 155 m, R/V Eltanin, cr. 12, stn. 1083, 14 Apr 1964; USNM 901636, 2 D, off Zavodovski Island, South Sandwich Islands, 56°28.8′S, 27°24.6′W, in 161–210 m, R/V Islas Orca-

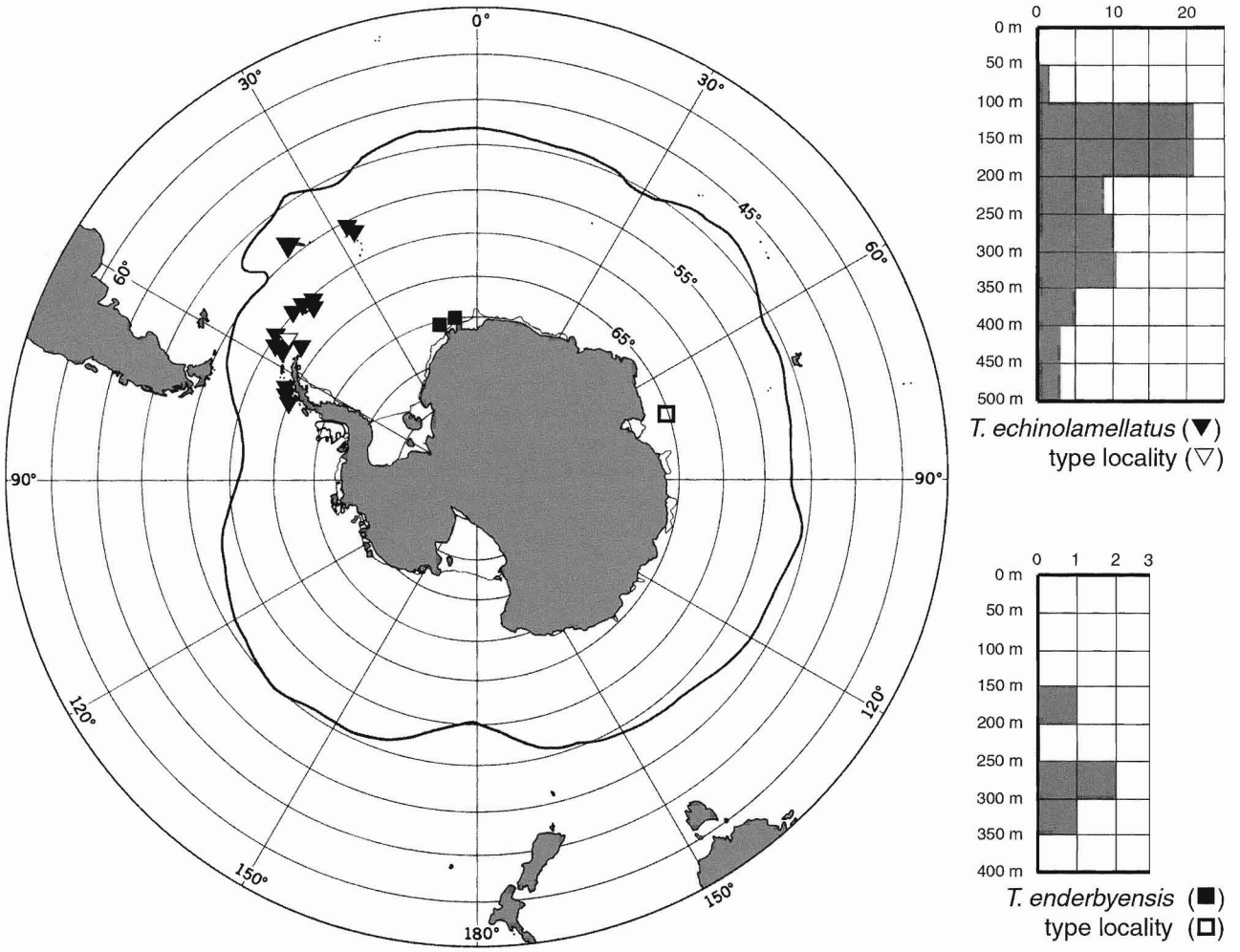
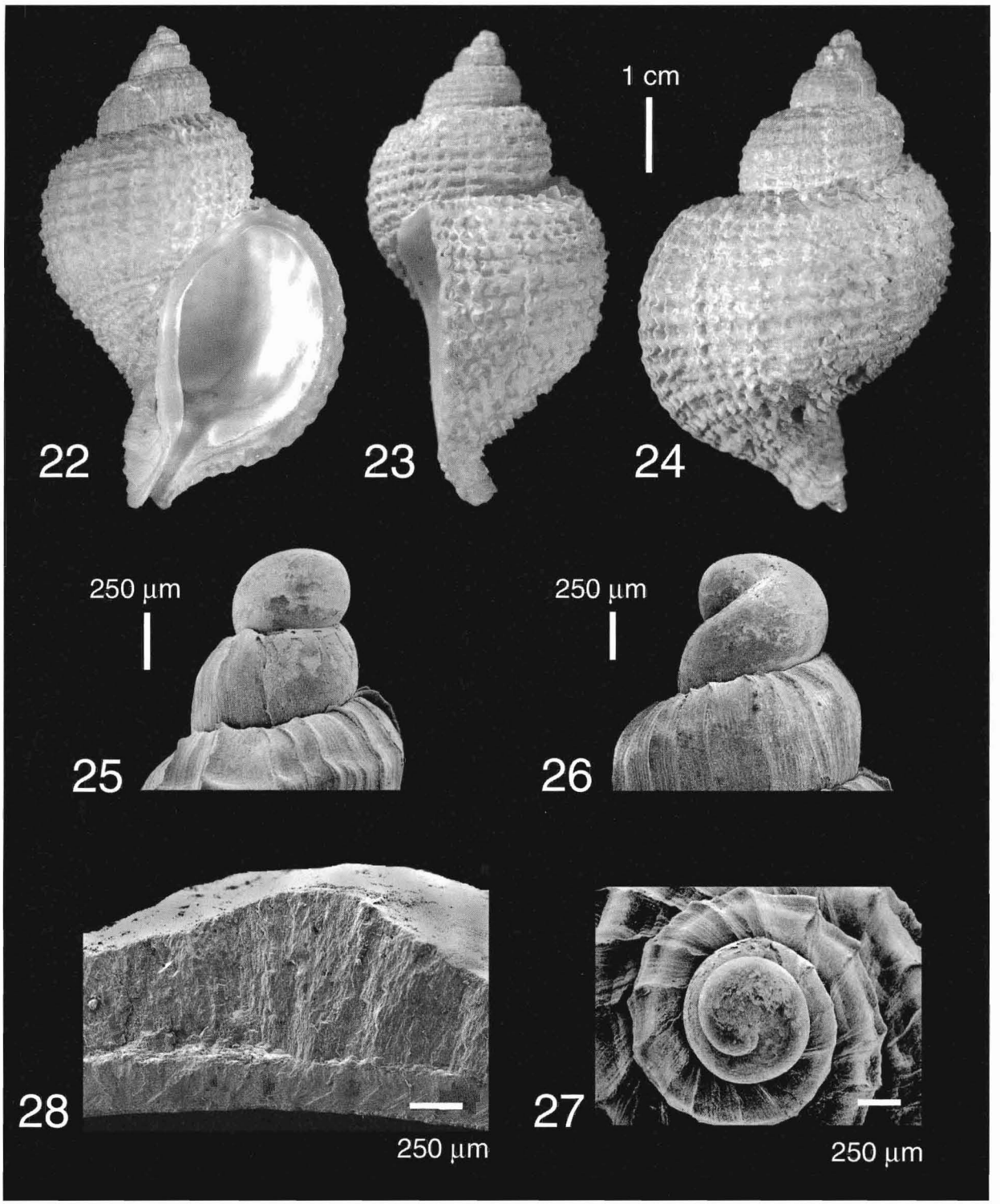


Figure 21. Geographic and bathymetric distributions of *Trophonella echinolamellatus* and *T. enderbyensis*.

das, cr. 575, stn. 70, 2 Jun 1975; USNM 901638, 1 L, Gibbs Island, Bransfield Strait, South Shetland Islands, Antarctica, 61°25′S, 56°30′W, in 300 m, R/V Eltanin, cr. 12, stn. 998, 14 Mar 1964; USNM 901639, 1 L, Low Island, South Shetland Islands, Antarctica, 63°26′S, 62°15′W, in 119–124 m, R/V Hero, cr. 691, stn. 26, 10 Feb 1969; USNM 901640, 1 L, Aspland Island, South Shetland Islands, Antarctica, 61°17′S, 56°26′W, in 421–462 m, R/V Polarstern, cr. 2, stn. 22, 21 Nov 1996; USNM 901641, 4 L, Elephant Island, South Shetland Islands, Antarctica, 60°53′S, 55°32′W, in 178–120 m, R/V Polarstern, cr. 2, stn. 79, 9 Dec 1996; col. P. Arnaud, 200–220 m, South Shetland Islands, Antarctica; ZMH w/n, 1 L, NW of Elephant Island, South Shetland Islands, Antarctica, 60°56′S, 55°32.9′W 81 m, R/V Walther Herwig, cr. 68, stn. 68; ZMH w/n, 2 L, E of Laurie Island, South Orkney Islands, Antarctica, 60°48.9′S, 43°34′W 257 m, R/V Walther Herwig, cr. 68, stn. 87; ZMH w/n, 2 L 2 D, E of Laurie Island, South Orkney Islands, Antarctica, 60°41.6′S, 43°57.1′W 290 m, R/V Walther Herwig, cr. 68, stn. 88; ZMH w/n, 1 D, NNE of Laurie Island, South Orkney Islands, Antarctica, 60°34.9′S, 44°17.3′W 240 m, R/V Walther Herwig, cr. 68, stn. 89; ZMH w/n, 4 L, 2 D, SE of Laurie Island, South Orkney Islands, Antarctica, 60°51.3′S, 44°12′W 178 m, R/V Walther Herwig, cr. 68, stn. 90; ZMH w/n, 3 L, 1 D, WNW of Coronation Island, South Orkney Islands, Antarctica, 60°25′S, 46°25.7′W 150 m, R/V Walther Herwig, cr. 68, stn. 118; ZMH w/n, 1L, NW of Aspland Island, South Shetland Islands, Antarctica, 61°21.8′S, 56°0.6′W 368 m, R/V Walther Herwig, cr. 68, stn. 138; ZMH w/n, 1 L, 3 D, NW of Aspland Island, South Shetland Islands, Antarctica, 61°19.8′S, 56°9.9′W 328 m, R/V Walther Herwig, cr. 68, stn. 139; ZMH w/n, 1 L, 1 D, NW of Aspland Island, South Shetland Islands, Antarctica, 61°12.5′S, 56°23.4′W 460 m, R/V Walther Herwig, cr. 68, stn. 141; ZMH



Figures 22–28. *Trophonella echinolamellata* (Powell, 1951). 22. Apertural, 23. lateral, and 24. dorsal views of a large specimen, USNM 901636, Off Zavodovski Island, South Sandwich Islands, 56°28.8′S, 27°24.6′W; 161–210 m. 25. Lateral, 26. abapertural, and 27. apical views of the protoconch, USNM 870593, NE of Joinville Island, Antarctic Peninsula, 62°41′S, 54°43′W, 210–220 m. 28. Shell ultrastructure. Fracture surface parallel to growing edge. USNM 901638, off Gibbs Island, Bransfield Strait, South Shetland Islands, Antarctica, 61°25′S, 56°30′W, in 300 m.

w/n, 2L, W of Elephant Island, South Shetland Islands, Antarctica, 61°12.7′S, 55°56.4′W 134 m, R/V Walther Herwig, cr. 68, stn. 148; ZMH w/n, 2 L, W of Elephant Island, South Shetland Islands, Antarctica, 61°8′S, 55°56.2′W 125 m, R/V Walther Herwig, cr. 68, stn. 150; ZMH w/n, 1 L 1 D, NW of Elephant Island, South Shetland Islands, Antarctica, 60°53.9′S, 55°30.4′W 135 m, R/V Walther Herwig, cr. 68, stn. 159.

Literature records: Only the type locality has been reported in the literature previously.

Distribution: Known from Antarctic Peninsula, South Shetland Islands, South Georgia Island, South Sandwich Islands and South Orkneys Islands, at depths ranging from 93 m to 460 m (Figure 21).

Remarks: The characteristic sculpture of the shell, consisting of sharply raised spiral cords overlain by closely spaced lamellae to produce a scabrous surface, distinguishes *T. echinolamellata* from all other known species of *Trophonella*. *Trophonella echinolamellata* and *T. scotiana* have similar bathymetric ranges, and they overlap in portions of their geographical ranges. However, *T. echinolamellata* appears to be restricted to the Scotia tectonic plate, based on the material thus far available.

Trophonella enderbyensis (Powell, 1958), new combination

(Figures 21, 29–31)

Synonymy: *Trophon enderbyensis* Powell, 1958:197, pl. 3, fig. 1.

Description: Shell (Figures 29–31) large (to 70 mm), fusiform, moderately thin-shelled, with regular spiral sculpture and widely spaced lamellose varices. Protoconch and transition to teleoconch unknown. Teleoconch with 7 or more evenly convex whorls; sutural shelf obsolete; spire tall, narrow, conical, approximately 50% of shell length; suture abutting; spire angle about 55°. Aperture broadly ovate, deflected from the coiling axis by 25°, interior glossy white. Siphonal canal short; siphonal fasciole conspicuous, with recurved, scabrous processes; pseudoumbilical chink reduced to a narrow slit. Outer lip rounded, reflected; columellar lip thin. Axial sculpture of low, generally distantly spaced thin lamellae covering entire whorl, obsolete on early whorls, approximately 3 per whorl except for the final whorl, where 3 lamellae are closely adjacent in the holotype. Spiral sculpture of low, rounded cords (3 or 4 on early whorls, 20 on last whorl), about as wide as interspaces, which may have 1–4 fine spiral threads between adjacent cords. Shell whitish. Shell composed of three layers, as in *T. scotiana*. Operculum (Figure 44) oval, with terminal nucleus; outer surface with regular growth lines, inner surface with broad, thickly glazed rim along posterior edge.

A single, male animal was examined and found to be anatomically similar to *T. scotiana*. The radula (Figures 16–17) is similar to that of *T. scotiana* but has more prominent denticles between the central and lateral cusps of the rachidian.

Type locality: (Figure 21:□), off Enderby Land, Antarctica, 65°48′S, 71°24′E in 193 m. [British, Australian, and New Zealand Antarctic Research Expedition, St. 41, January 24/25 1930].

Type material: Holotype, SAM D15497.

Material examined: Holotype; SMF w/n, 1 D, Off the Princess Martha Coast, Queen Maud Land, Antarctica, 70°30′S, 8°4′W, 261–263 m; SMF w/n, 1 L, off the Princess Martha Coast, Queen Maud Land, Antarctica,71°23′S, 13°58′W, 293–357 m.

Literature records: None, apart from the original description.

Distribution: Presently known from three specimens, one from type locality (off Enderby Land) and two from off Queen Maud Land, Antarctica.

Remarks: In his description of *Trophon enderbyensis*, Powell (1958:198) noted that this species resembled *T. scotianus*, which, at the time, was known only from South Georgia Island. The specimens presently available indicate that the geographic and bathymetric ranges of these two species overlap. Both Dell (1990:208) and Numanami (1996:140) commented that larger specimens of *T. scotiana* tend to have an increased number of axial lamellae and a more inflated final whorl of the shell. The adult holotype of *Trophonella enderbyensis* is comparable in size to the largest specimens of *T. scotiana*, yet it has far fewer, shorter, axial lamellae and a narrower, more fusiform shell. The intermediate denticle on the rachidian teeth of *T. endebryensis* is pronounced, but it is reduced or absent in *T. scotiana*. As more material becomes available, especially from off Enderby Land and Wilkes Land, the status of *T. enderbyensis* may require reevaluation.

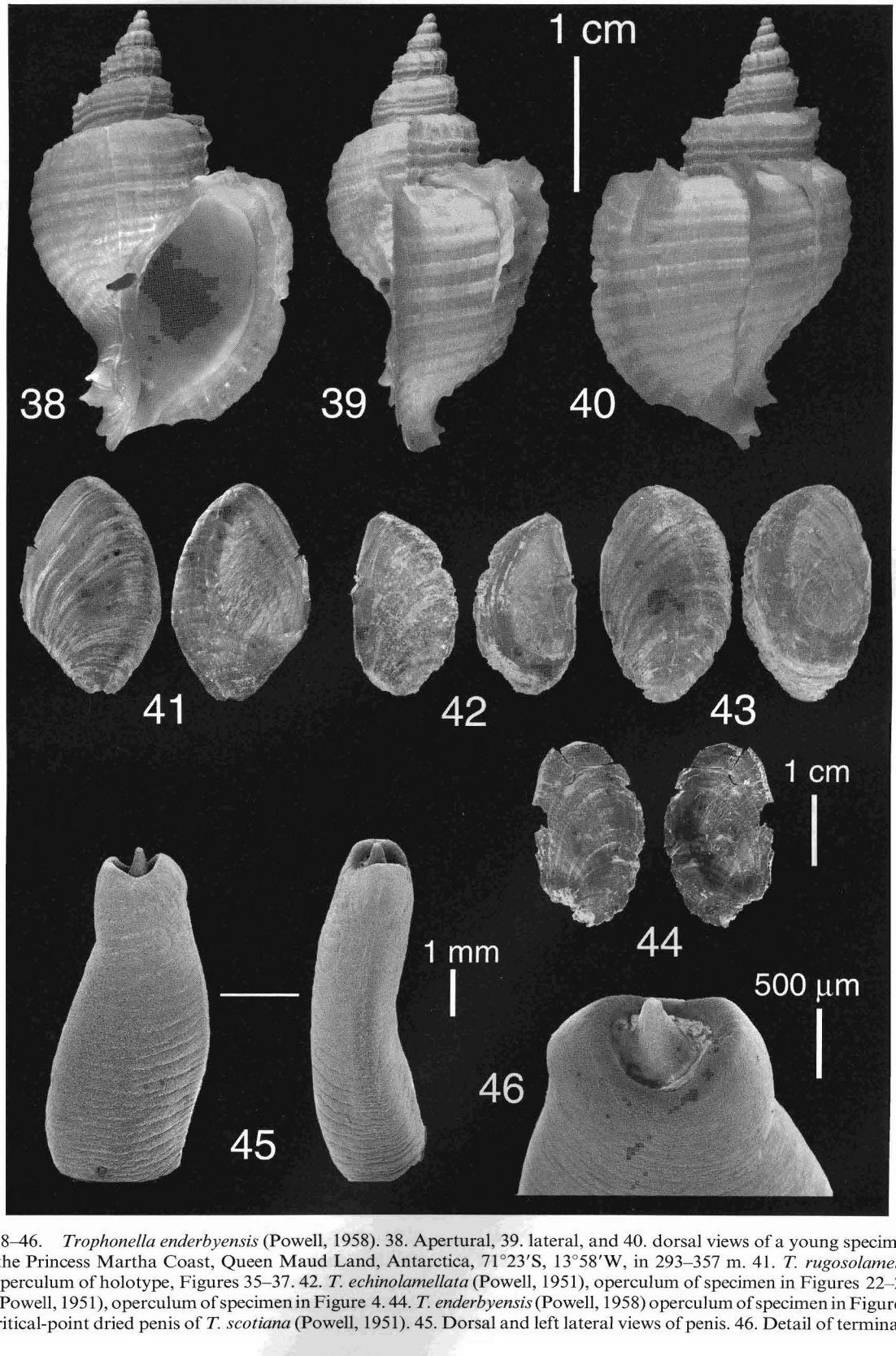
Trophonella eversoni (Houart, 1997) new combination

(Figures 32–34)

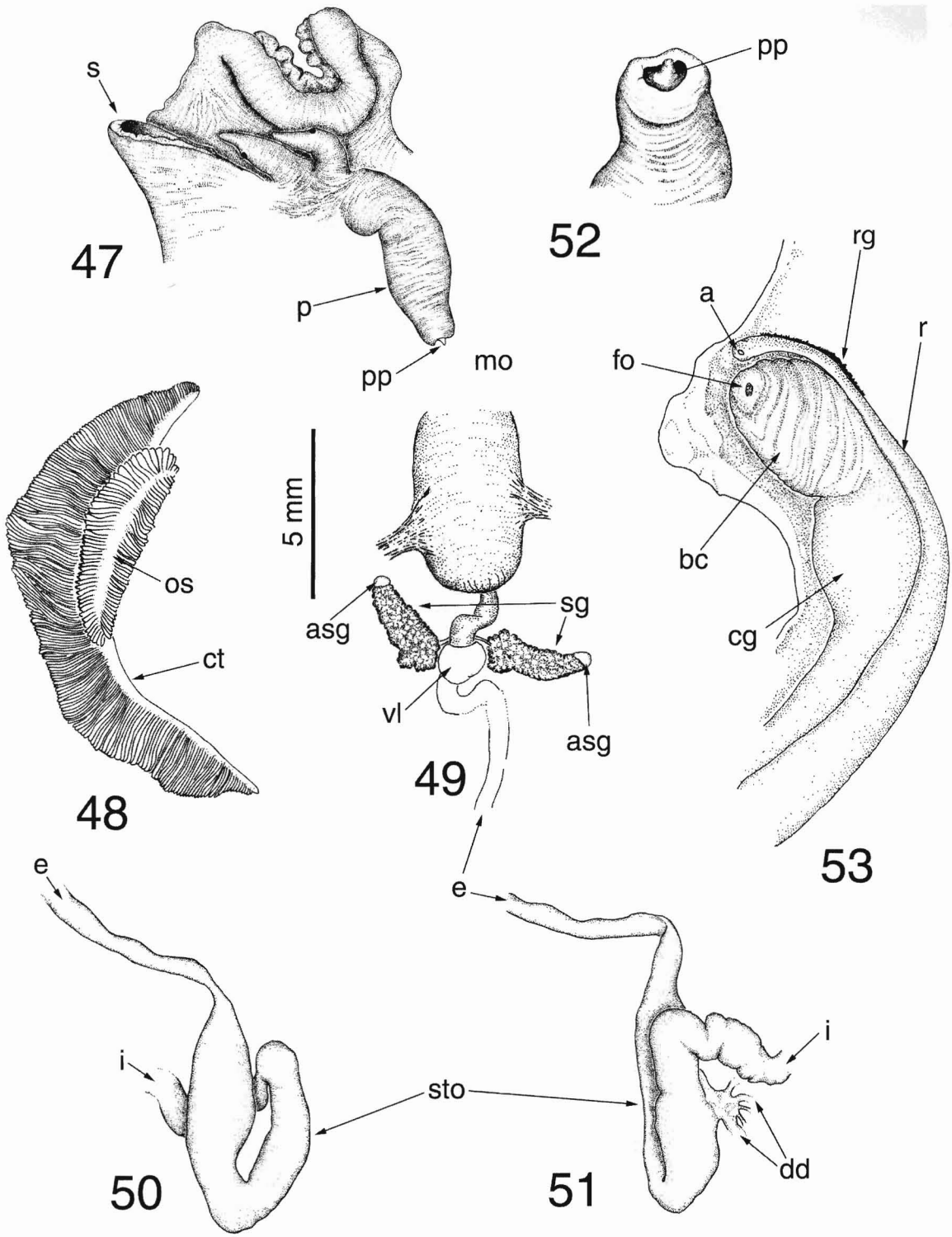
Synonymy: *Trophon eversoni* Houart, 1997:9, figs. 1–2, 4, 6.

Description: Shell (Figures 32–34) large (to 75.8 mm), fusiform, of medium thickness, strongly sculptured with spiral cords and axial lamellae. Protoconch and transition to teleoconch unknown. Teleoconch with 6

Figures 29–37. *Trophonella enderbyensis* (Powell, 1958). 29. Apertural, 30. lateral, and 31. dorsal views of the holotype, SAM D15497, off Enderby Land, Antarctica, 65°48′S, 71°24′E in 193 m. 32–34. *Trophonella eversoni* (Houart, 1997). 32. Apertural, 33. lateral, and 34. dorsal views of the holotype USNM 880177, South Atlantic Ocean, ? Antarctica, ? Kerguelen Is. 35–37. *Trophonella rugosolamellata* new species. 35. Apertural, 36. lateral, and 37. dorsal views of the holotype, ZMH 2777, off South Orkney Islands, 60°52.2′S, 44°28.4′W, in 205 m.



Figures 38–46. *Trophonella enderbyensis* (Powell, 1958). 38. Apertural, 39. lateral, and 40. dorsal views of a young specimen, SMF w/n, off the Princess Martha Coast, Queen Maud Land, Antarctica, 71°23′S, 13°58′W, in 293–357 m. 41. *T. rugosolamellata* new species, operculum of holotype, Figures 35–37. 42. *T. echinolamellata* (Powell, 1951), operculum of specimen in Figures 22–24. 43. *T. scotiana* (Powell, 1951), operculum of specimen in Figure 4. 44. *T. enderbyensis* (Powell, 1958) operculum of specimen in Figures 38–40. 45–46. Critical-point dried penis of *T. scotiana* (Powell, 1951). 45. Dorsal and left lateral views of penis. 46. Detail of terminal papilla.



Figures 47–53. *Trophonella scotiana* (Powell, 1951). 47. Anterior portion of male specimen, mantle reflected. 48. Ctenidium and osphradium. 49. Anterior alimentary system. 50. Dorsal and 51. right lateral views of stomach. 52. Distal tip of penis. 53. Pallial oviduct. Abbreviations for these figures: a, anus; asg, accessory salivary gland; bc, bursa copulatrix; cg, capsule gland; ct, ctenidium; dd, ducts to digestive diverticula; e, esophagus; fo, female opening; i, intestine; mo, mouth; os, osphradium; p, penis; pp, penial papilla; r, rectum; rg, rectal gland; s, siphon; sg, salivary gland; sto, stomach; vl = valve of Leiblein.

or more globose whorls. Sutural shelf present in last whorls. Spire conical, about 33% of total shell length. Suture abutting. Spire angle about 56°–59°. Aperture large, suboval, deflected from the coiling axis by 27°; interior glossy white; siphonal canal moderately short, slightly inclined; siphonal fasciole scaly. Outer lip rounded with reflected edges; columellar lip thin, tightly adpressed, pseudoumbilical chink absent. Axial sculpture of pronounced, regularly spaced, thin lamellae, 12–14 on last whorl, running along whorl surface from adapical suture to the siphonal fasciole. Spiral sculpture of low, rounded, spiral cords: 3, 8, and 24 on the first, second, and last whorls, respectively. Cords most pronounced along shell periphery, reduced near suture and siphonal canal. Cords cover the lamellae but became obsolete along their edges. Shell opaque white. Regular growth lines covering whorls and lamellae. Operculum, radula, and anatomy unknown.

Type locality: (Figure 20:♦), Antarctica, 185 m.

Material examined: Holotype, USNM 880177.

Literature records: Kerguelen Islands (Paratype 2); submarine bank "South" off the Kerguelen Islands, in "approximately" 250 m (Houart, 1997).

Distribution: This species is based on a holotype collected by a Russian trawler "in the Antarctic," from a depth of 185 m. Paratype 2 is reported, with some certainty, to have been taken off the Kerguelen Islands. Houart (1997:9) mentions two additional specimens from a submarine bank south of the Kerguelen Islands, at depths of 250 m.

Remarks: *Trophonella eversoni* is known from five specimens, four of which are in private collections. The geographic and bathymetric distributions of this species are apocryphal, and they have yet to be confirmed by subsequent collections. Powell (1957:113) reported the occurrence of five species of *Trophon* in the Kerguelen Islands, although all but two of the stations sampled by the British, Australian, and New Zealand Antarctic Research Expedition were from substantially shallower depths. Houart (1997:11) noted that *T. albolabratus* Smith, 1875, one of the Kerguelen Island species, differs from *T. eversoni* in having "low, thin, and more numerous axial lamellae, stronger spiral cords, and a shorter siphonal canal. He distinguished *T. eversoni* from *T. scotiana* on the basis of the former having more numerous spiral cords, more numerous and abapertu-rally sloping axial lamellae that are not as strongly produced adapically. As with *T. enderbyensis*, additional collections from off Enderby Land, Wilkes Land, and the islands off their coasts will be required to assess more accurately the distribution and relationships of *T. eversoni*.

Trophonella rugosolamellata new species

(Figures 20, 35–37)

Description: Shell (Figures 35–37) large (to 76 mm), fusiform, solid, chalky, with strong spiral cords and thick axial lamellae that are furrowed and reflected at the shoulder. Protoconch unknown. Teleoconch of at least six narrowly convex whorls; spire 33% of total shell length. Suture abutting. Spire angle about 59°. Aperture large, oval, deflected from the coiling axis by about 22°, interior glossy white. Siphonal canal moderately long and narrow, slightly inclined, siphonal fasciole strongly scabrous, pseudoumbilical chink closed. Outer lip rounded with reflected edge. Columellar lip broad, with thick, expanded callus. Axial lamellae thick, more or less evenly spaced (11 on last whorl, 8 on the penultimate whorl), running along whorl surface from suture to the siphonal fasciole, narrowest at midwhorl, most pronounced near and on the siphon and especially at a position corresponding to the shoulder, where they are enlarged, furrowed and strongly reflected. Regular growth lines evident on the whorls and lamellae. Spiral sculpture of rounded, closely spaced cords (3 or 4 on early whorls, 20 on last whorl) that extend onto the outer surfaces of the lamellae. Cords most pronounced from siphonal canal to region corresponding to the shoulder. Shell color whitish. Shell composed of three layers, as in *T. scotiana*. Operculum (Figure 41) subpolygonal, thick, brownish, with terminal nucleus. Growth lines on external surface; broad, glazed rim covering nucleus; attachment area smaller.

Animal large. Foot short, broadly rectangular. Tentacles very wide, blunt, with small black eyes; mantle edge smooth, siphon very short. Osphradium small, asymmetrical, about 50% ctenidium length. Pleurembolic proboscis short and broad. Radular ribbon (Figures 18, 19) short (radular length ~ 0.44 aperture length), thin, extending beyond rear of buccal mass. Rachidian tooth subrectangular, and basal plate weakly concave anteriorly. Central cusp broadly triangular, flanked by short stout denticles. Outer cusps shorter and narrower, slightly outwardly directed. Marginal cusps absent, marginal area smooth. Lateral teeth L-shaped, narrower than rachidian teeth. Esophagus short. Salivary glands large, ascinous, whitish, with ducts entering esophagus just anterior to the wide valve of Leiblein. Accessory salivary glands small, spherical, located in the anterior part of the buccal mass, totally embedded in salivary glands. Gland of Leiblein compact, without lobules, brownish in color, overlaying esophagus. Penis similar to that of *T. scotiana*; large, wide, flat, > 4 times tentacle length; with terminal, conical papilla surrounded by narrow collar.

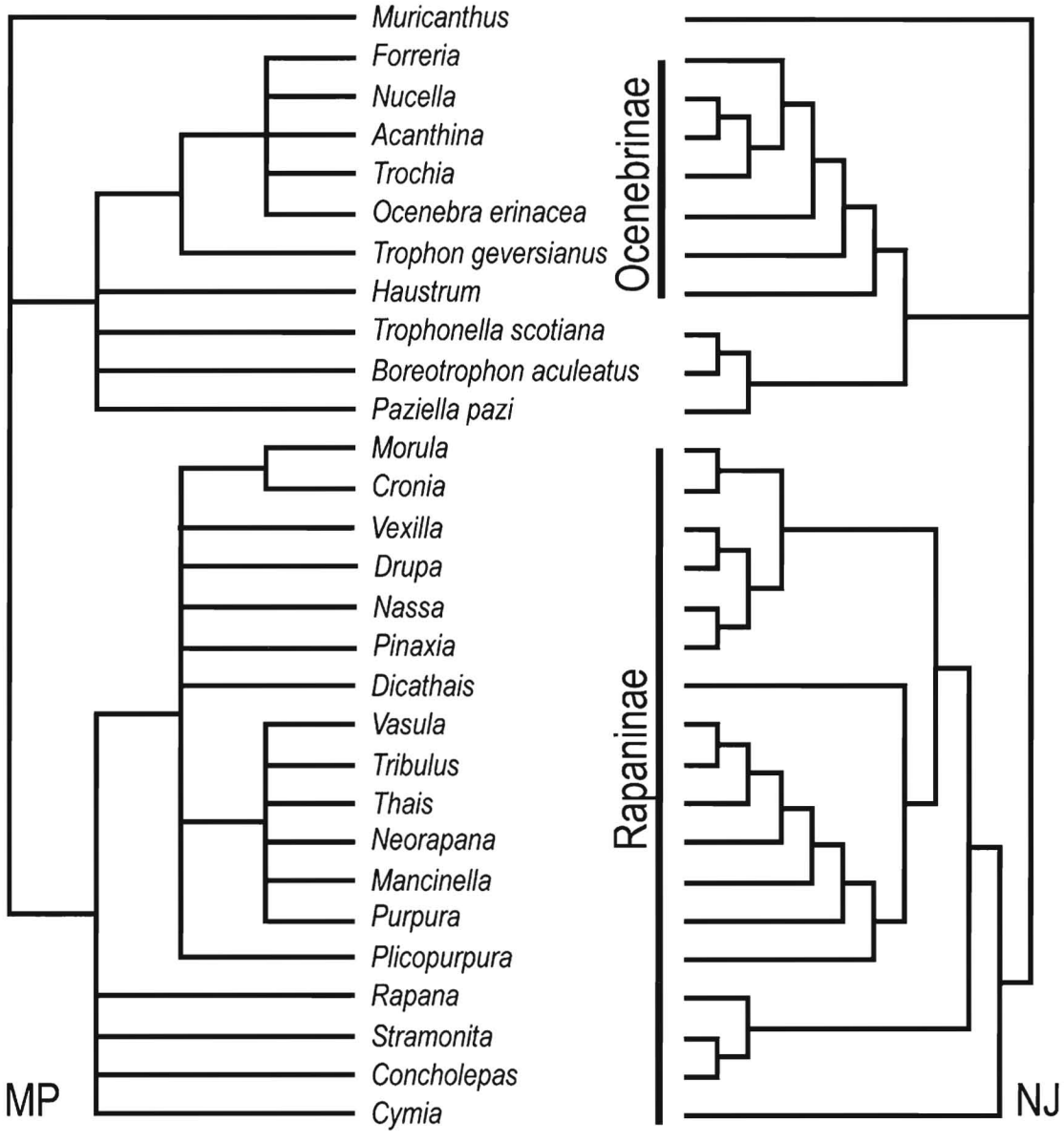


Figure 54. Strict consensus maximum parsimony [MP] and neighbor-joining [NJ] trees depicting the relationships of genera based on data derived from their type species. Data from Kool (1993b:Table 3) have been supplemented by data for *Ocenebra erinaceus*, *Trophon geversianus*, *Trophonella scotiana*, *Boreotrophon aculeatus*, and *Paziella pazi*.

Type locality: S of Laurie Island, South Orkney Islands, 60°52.2′S, 44°28.4′W, in 205 m.

Type material: Holotype, ZMH 2777.

Material examined: This species is presently known only from the holotype.

Distribution: Known only from the type locality, collected by the R/V Walther Herwig cr. 68, stn. 91 (Figure 20).

Etymology: *rugosolamellata* from Latin *rugosus* and Latin *lamellata* (with lamellae, or thin plates) referes to the extension of the spiral cords onto the axial lamellae.

Remarks: *Trophonella rugosolamellata* most closely resembles *T. eversoni*, but it can be distinguished by its thicker shell, with slightly fewer lamellae and fewer, coarser spiral cords. The axial lamellae of *T. rugosolamellata* are distinctive in that they are reflected along the outer edges, especially at a position corresponding to the shoulder, where they are enlarged, furrowed, and

Table 1

Taxa, characters, and character states used in an analysis of the relationships of Trophoninae. The data matrix is that of Kool (1993b:table 3), to which have been added the taxa *Trophon geversianus*, *Ocenebra erinaceus*, *Trophonella scotiana*, *Boreotrophon aculeatus*, and *Paziella pazi*. See Kool (1993b) for detailed descriptions of characters and character states.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Taxa from Kool (1993b):																		
Muricanthus	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Forreria	b	b	b	a	b	a	b	a	a	a	b	a	a	a	b	?	b	c
Nucella	b	b	b	a	b	a	b	a	a	a	b	b	c	a	b	b	b	c
Haustrum	b	?	c	a	b	a	a	a	a	a	b	b	b	a	e	b	a	b
Morula	a	a	a	a	c	b	a	b	b	b	c	c	d	b	c	a	a	e
Cronia	c	a	a	a	c	b	a	b	b	b	d	c	d	b	b	a	a	f
Rapana	a	a	c	a	d	a	a	a	b	c	d	e	d	b	b	a	a	f
Cymia	?	?	c	a	e	a	b	a	b	a	?	d	d	b	b	a	a	d
Stramonita	a	a	b	a	e	a	a	a	b	c	d	e	d	b	b	a	a	g
Concholepas	a	a	b	a	e	a	a	a	b	c	d	e	d	b	b	a	a	g
Dicathais	c	a	b	a	e	a	a	b	b	c	?	e	d	b	c	a	a	g
Vasula	?	?	?	b	e	a	a	b	b	c	d	e	d	b	c	?	a	j
Vexilla	d	a	a	a	f	a	c	b	b	c	d	f	d	b	d	a	a	?
Nassa	a	a	a	a	e	a	a	b	b	c	d	f	d	b	c	a	a	?
Pinaxia	a	a	a	a	e	a	a	b	b	c	d	f	d	b	c	a	a	h
Drupa	?	?	?	a	e	a	a	b	b	c	d	e	d	b	d	a	a	h
Plicopurpura	a	a	?	a	e	a	a	b	b	c	d	e	d	b	c	a	a	?
Thais	?	a	c	b	e	a	a	b	b	c	d	e	d	b	c	a	a	j
Purpura	?	a	c	b	e	a	a	b	b	c	d	e	d	b	c	a	a	h
Mancinella	?	?	c	b	e	a	a	b	b	c	?	e	d	b	c	a	a	i
Neorapana	?	a	c	b	e	a	a	b	b	c	d	e	d	b	c	a	a	j
Tribulus	?	a	c	b	e	?	a	b	?	?	?	e	d	?	?	?	a	j
Acanthina	b	b	?	a	b	?	b	?	a	?	?	b	?	?	?	?	?	?
Trochia	b	b	b	a	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Newly added taxa:																		
Ocenebra erinaceus	b	b	b	a	a	?	b	a	a	a	b	b	d	a	b	b	b	c
Trophon geversianus	b	a	b	a	a	?	a	a	a	a	b	b	c	a	c	b	b	c
Trophonella scotiana	d	a	b	a	a	?	a	a	a	a	b	b	a	a	c	b	a	a
Boreotrophon aculeatus	d	a	c	a	a	?	a	a	a	a	b	b	a	a	c	b	a	a
Paziella pazi	b	a	c	a	a	?	a	a	a	a	a	b	a	a	c	b	a	a

strongly reflected to produce a tapering structure similar to the open shoulder "spine" of *Pterochelus* Jousseaume, 1880. The spiral cords of *T. eversoni* are more numerous and thinner, and they are not as pronounced along the siphonal canal or on the axial lamellae as in *T. rugosolamellata*. *Trophonella enderbyensis* has a higher spire, fewer, smaller, and more widely spaced lamellae, and fainter spiral cords than *T. rugosolamellata*.

PHYLOGENETIC RELATIONSHIPS

A maximum parsimony analysis of the data matrix shown in Table 1 [PAUP* 4.0 beta version 10 Heuristic search, Accelerated transformation, TBR Swapping algorithm] produced 475,972 equally parsimonious trees (length = 60; consistency index = 0.783; retention index = 0.903]. A strict consensus of these trees is shown in Figure 54 (MP). Figure 54 (NJ) shows the neighbor joining tree based on the same data.

Ocenebra erinaceus, the type species of the type genus of Ocenebrinae, emerges in an unresolved pentatomy with the genera *Nucella*, *Trochia*, *Forreria*, and *Acanthina* in the strict-consensus tree and as sister taxon to these genera in the neighbor-joining tree. *Trophon geversianus*, the type species of the type genus Trophoninae, emerges as the sister group to this clade in both the MP analysis and the NJ analysis. While the NJ tree shows *Haustrum* to be the sister taxon to this clade, which, in turn, was joined by the clade [(*Trophonella* + *Boreotrophon*) *Paziella*], the MP analysis groups the genera *Haustrum*, *Trophonella*, *Boreotrophon*, and *Paziella* into an unresolved polytomy that is sister to *Trophon* and the polytomy containing *Ocenebra*.

These results indicate that the type species of

Trophonella is more closely related to *Boreotrophon* than to the type species of *Trophon* and thus support the segregation of *Trophonella* from *Trophon* at the generic level. They also confirm the contentions by various authors that Trophoninae, as defined by Cossmann (1903:9), is not monophyletic. Based on the relationships of the type species of their respective type genera, either Trophoninae is the sister taxon of Ocenebrinae or both are part of a larger clade.

In his phylogenetic study, Kool (1993b:fig. 30) considered Ocenebrinae to include *Haustrum*. Tan (2003) subsequently erected the subfamily Haustrinae (with *Haustrum* as the type genus) to encompass a clade of nonrapanine muricids endemic to Australia and New Zealand. However, the relationship of this clade to Ocenebrinae and Rapaninae varied significantly, depending on the choice of outgroup. Beu (2004:216) concluded that it seemed preferable to retain the taxa included by Tan in Haustrinae within the subfamily Ocenebrinae. This broader delineation of Ocenebrinae includes the type species of Trophoninae in both MP and NJ trees. The genera *Trophonella* and *Boreotrophon* emerged as part of an unresolved polytomy with *Haustrum* in the strict-consensus MP tree, but were depicted as being more distantly related in the NJ tree.

Both Ocenebrinae and Trophoninae were proposed in the same publication (Cossmann, 1903:10), so neither has priority. Although it is likely that these two subfamilies will be synonymized, based on the close relationship between the type species of their type genera, a better resolved phylogeny, including a more comprehensive sampling of the more than 20 genus-level taxa attributed to each of these two subfamilies, will be required to delineate more precisely the membership of the clade and to identify its diagnostic synapomorphies.

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