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Undercover speciation of wentletraps (Caenogastropoda: Epitoniidae) in the Southwestern Atlantic

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Abstract

Despite being one of the most speciose families, Epitoniidae still remains at present as one of the least understood gastropod families worldwide. This is a consequence of most of the species being only known from shell morphology, added to the wide intraspecific variability of this character and the fact that shell morphology has proven to have frequent examples of parallelisms and convergences among different (unrelated) species. Knowledge of other morphological and anatomical characters in this group is still in its first steps, and such information is currently available for a limited number of species, thus being difficult (when not impossible) to evaluate its taxonomic value. The aim of this study is to re-evaluate the diversity of Epitoniidae occurring in the Atlantic coast of Patagonia. As part of this study, the validity of only four of the six species described / reported from this area could be confirmed: *Epitonium georgettinum*, *E. striatellum*, *E. fabrizioi* and *"Cirsotrema" magellanicum.* In addition, three new species were recognized and are described herein: *Epitonium evanidstriatum, "Cirsotrema" ctenodentatum* and *"Cirsotrema" strebeli*. Information on the shell (including the protoconch), operculum, radula and jaw for these species is here provided, in most cases for the first time. A neotype for *Scalaria magellanica* is here designated. Furthermore, *"Cirsotrema" georgeanum* is here proposed as a replacement name for *Scalaria fenestrata* Strebel, 1908 (not Meneghini in de Stefani, 1875, nor *Scalaria fenestrata* Wöhrmann, 1889); and that taxon is regarded as a full species, instead of as a synonym of *"Cirsotrema" magellanicum*, as suggested in some previous publications. This study reveals that the usage of isolated (either morphological or anatomical) characters is usually insufficient for identifying some of the species from Patagonia; however, if these characters are combined, all species may be clearly recognized.

Key words: Mollusca, Gastropoda, Patagonia, Pampa Azul

Introduction

The Epitoniidae is a widely distributed family of hypsogastropods, occurring from the tropics to the poles, and from the intertidal to abyssal waters (Weil *et al.* 1999). According to Brown & Neville (2015), the family comprises a total of 704 "potentially valid" species, although most of them still remain known only known from their shells. In the last years, several contributions combining shell morphology with anatomical, molecular or ecological data (e.g., Gittenberger & Gittenberger 2005; Gittenberger *et al.* 2006; Kokshoorn *et al.* 2007), revealed that the complexity of this family is greater than previously thought; and confirmed that shell morphology alone is usually insufficient for properly recognizing the species and, more so, for defining most (sub)genera.

The current knowledge on the epitoniids occurring in the Atlantic coast of Patagonia is still in its first steps. According to the literature, six nominal epitoniid species are currently known from this area. The first species was described by Philippi (1845) under the name *Scalaria magellanica*. Strebel (1905) recognized a "variety" (= subspecies) of this species, which he named *Scalaria magellanica latecostata*. This taxon was subsequently retained by some authors as a subspecies (e.g., Powell 1951, 1960; Castellanos 1970), but others (e.g., Cárdenas *et al.* 2008; Brown & Neville 2015) regarded it as a synonym or possible synonym of Philippi's species. Later, and nearly simultaneously, Kiener (1938) and d'Orbigny (1839) described *Scalaria georgettina* and *Scalaria elegans*,

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respectively. The latter was subsequently renamed *Scalaria orbignyi* by Nyst (1871), due to its homonymy with *Scalaria elegans* Risso, 1826, and *Scalaria elegans* Lea, 1841. This taxon was regarded as a valid species by Mörch (1876) and Carcelles & Parodiz (1938), although Clench & Turner (1951) included it in the synonymy of *Epitonium georgettinum*. Another species described by d'Orbigny (1839) from northern Patagonia is *Scalaria tenuistriata*, a name subsequently used in the local bibliography by several authors (e.g., Clench & Turner 1952; Castellanos 1970; Scarabino 1977; Rios 1994). More recently, Pastorino & Penchaszadeh (1998) described, also from northern Patagonia, *Epitonium fabrizioi*. All of the above-mentioned species are currently known based on a small number of documented records, a fact that does not contribute to understanding their intraspecific variability. In addition, with the exception of *Epitonium fabrizioi* and *E. georgettinum*, the other species remain known from shell morphology only. Another Patagonian species formerly placed in *Scalaria* is *S. brevis* d'Orbigny, 1840, described from the Malvinas / Falkland islands, although Zelaya *et al.* (2006) suggested that this species seems to belong in the genus *Benthobrookula* Clarke, 1961, consequently not being an Epitoniidae.

The aim of this contribution is to provide a revision of the living species of Epitoniidae occurring in the Atlantic coast of Patagonia, considering the intra- and interspecific variability of the morphological characters previously described for these taxa, and by describing other characters not studied before.

Material and methods

The main source of information for this study comes from the material collected during numerous sampling trips to Patagonia (south of 40°S), comprising 139 sampling stations in total. Samples from the intertidal zone were hand-collected; those from the shallow subtidal (up to 30 m depths) were obtained by diving, by using a 2 mm mesh-size hand-net; and specimens from deeper waters were collected with a 45 x 50 cm net (also of 2 mm mesh-size) operated from a motorboat. In the field, epitoniids were sorted from the sediments under a stereoscopic microscope, and fixed in a 5% formalin solution. Additional information comes from the study of the material (including types) housed at the following museums:

MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires
MLP	Museo de La Plata, La Plata
MMUM	The Manchester Museum, Manchester
MNHN-Cl	Museo Nacional de Historia Natural, Santiago de Chile
MZUC	Museo de Zoología de la Universidad de Concepción, Concepción
NHMG	Museum de Genève, Geneva
NHMUK	Natural History Museum, London
SMNH	Swedish Museum of Natural History, Stockholm
USNM	United States National Museum, Smithsonian Institution, Washington
ZMB	Museum für Naturkunde, Berlin
ZMH	Zoologisches Museum, Hamburg

The number of specimens (spm.) and empty shells (sh.) in each of the studied lots is indicated. Photographs of the studied type material are here provided. The syntypes of *S. candeana* (NHMUK 1854.10.4.206), consisting of one shell and four fragments, are currently badly affected by Byne's disease and remain at present completely unrecognizable. Therefore, this material is not figured herein.

Jaws and radulae were dissected under stereoscopic microscope, cleaned in a 5% sodium hypochlorite solution, and mounted for scanning electron microscopy (SEM). The constancy of the teeth morphology described herein was corroborated by examining radulae from at least three specimens of each species, except in the case of *Epitonium evanidstriatum* **n. sp.** (for which only one live-collected specimen was available) and *E. fabrizioi* (of which six radulae were examined). Descriptions of the jaw surface refer to the inner side.

Details of the outer surface of the operculum, protoconch, and teleoconch sculptures were also studied and figured with SEM. Measurements provided in the text refer to: shell / protoconch length (L): the maximum linear distance, parallel to the columellar axis; width (W): the maximum diameter of the shell / protoconch, perpendicular to L.

Results

Epitoniid species occurring in the Atlantic coast of Patagonia

Genus *Epitonium* Röding, 1798

Type species: *Turbo scalaris* Linnaeus, 1758, subsequent designation by Suter (1913)

Epitonium georgettinum (Kiener, 1838)

(Figures 1, 2)

Scalaria georgettina Kiener, 1838: 14, pl. 5, fig. 15
Scalaria elegans d'Orbigny, 1839: 389–390, pl. 54, figs. 1–3
Scalaria orbignyi Nyst, 1871: 124–125 (*nomen novum* for *Scalaria elegans* d'Orbigny *non* Risso, 1826); Mörch, 1876: 197–198; Boury, 1911: 36–37
Scala aff. orbignyi: Carcelles, 1944: 248, pl. 2, fig. 29 (in part)
Epitonium (Epitonium) georgettina: Clench & Turner, 1951: 265–266, pl. 116, figs. 1, 2; pl. 117, fig. 1; Castellanos, 1970: 62–63, pl. 4, fig. 5; Rios, 1994: 97, pl. 32, fig. 386

Type localities. "Océan Atlantique" (*Scalaria georgettina*); "baie de San Blas", "baie Blanche" and "embouchure du Rio Negro" [Buenos Aires Province, Argentina] (*Scalaria elegans*).

Type material. 8 syntypes of *Scalaria georgettina* (NHMG Inve 75290); 15 syntypes of *Scalaria elegans*, only one of them examined herein (NHMUK 1854.12.4.358).

Additional material examined. Uruguay: Rocha: [33º54'00''S 53º31'00''W], La Coronilla (MACN-In 19215: 16 sh.); [34º39'00''S 54º10'00''W], La Paloma (MACN-In 28773: 7 sh.; MACN-In 17547: 11 sh.); 34º40'00''S 53º59'30''W, off La Paloma, 27 m (MACN-In 15352: 2 sh.). Maldonado: [34º58'00''S 54º57'00''W], Punta del Este (MACN-In 15204: 2 sh.; USNM 180870: 4 sh.). Argentina: Buenos Aires Province: [36º17'23''S 56º46'53''W], Punta Rasa, Bahía San Borombón (MACN-In 28770: +50 sh.); [36º17'35''S 56º46'37''W], Cabo San Antonio (MACN-In 1248**:** 25 sh.; MACN-In 16304: 14 sh.); 36º53'S; 53º54'W, 61.9 m (MACN-In 23443: 1 spm.); [37º09'00''S 56º52'49''W], Ostende (MACN-In 20101: 4 sh.); 37º35'03''S 54º55'03''W, 175.5 m (MACN-In 25169-1: 1 sh.); 37º59'49.96''S 57º34'35.69''W, Mar del Plata (MACN-In 25362: 12 sh.); [38º00'S 57º33'W], Mar del Plata, 42 m (MACN-In 8890: 1 sh.); [38º00'S 57º33'W], off Mar del Plata (MACN-In 14331: 4 sh.); [38°16′13″S, 57°50′W], Miramar (MLP-Ma 1449: 1 sh.; MLP-Ma 1472-1: 1 sh.; MLP-Ma 3245: 1 sh.); 38º25'18.50''S 56º30'37.07''W, off Mar del Plata (MACN-In 10245, 2 sh.; MACN-In 10741: 4 sh.; MACN-In 10322: 1 sh.; MACN-In 10296: 1 sh.; MACN-In 12211: 1 spm.); 38º34'28.7''S 58º42'42.1''W, Puerto Quequén (MACN-In 18676: 4 sh.; MLP-Ma 2403-1: 1 sh.); 38º59'05.25''S 61º17'58.68''W, Monte Hermoso (MACN-In 9209-24: 8 sh.; MACN-In 6619-44: 1 sh.; MACN-In 11214: 1 sh.; MLP-Ma 1407-1: 2 sh.; MLP-Ma 2024 in part: 3 sh.; MLP-Ma 3213: 12 sh.; MLP-Ma 3214: 4 sh.); [39º35'18.6''S 62º06'10.2''W], Bahía Brigman (MACN-In 16138: 4 sh.); [38º52'00''S 62º04'00''W], Arroyo Pareja, Bahía Blanca (MACN-In 11213: 5 sh.); [38º53'13''S 62º05'52''W], Base Naval Puerto Belgrano, Punta Alta (MACN-In 11212: 1 sh.); [39º08'34''S 61º58'08''W], Isla Trinidad, Bahía Blanca (MACN-In 19668: 2 sh.); [39°42'S 62°07'W], mouth of Río Colorado (MLP-Ma 1369: 10 sh.; MLP-Ma 1372: 16 sh.; MLP-Ma 1377: 8 sh.); 40º18'29.79''S 62º14'15.66''W, Bahía San Blas (MACN-In 20265: 3 spm., +100 sh.; MACN-In 20267-1: 1 sh.); [40°47'S 62°58'W], Carmen de Patagones (MLP-Ma 2608: 1 sh.); off Buenos Aires (MACN-In 10421: 1 sh.; MACN-In 11724: 2 sh.). Río Negro Province: Golfo San Matías (MACN-In 30809: 1 sh.); [41º00'S 64º07'W], Aguada de los Loros, San Antonio Este (MACN-In 13339: +300 sh.); [40º49'S 64º54'W], Punta Villarino, San Antonio Este (MACN-In 9379-44: 1 sh.; MACN-In 13150: 2 sh.; MACN-In 13364: 9 sh.); [40º44'00''S 64º57'00''W], Puerto San Antonio Oeste (MACN-In 9379-43: 2 sh.); 41º02'S; 62º24'W, 20 m (MACN-In 20667: 1 sh.); 40º25'47.4''S 65º25'14.1''W, 8 m (MACN-In 40359: 1 sh.); 40º45'18.7''S 64º56'31.8''W, La Mar Grande, intertidal (MACN-In 40360: 18 sh.); 40º54'08.3''S 65º06'28.0''W, 9 m (MACN-In 40361: 1 sh.); 40º55'17.4''S 65º08'07.6''W, 7-8 m (MACN-In 40362: 1 sh.); 40º56'27.2''S 65º07'58.2''W, 10-11 m (MACN-In 40363: 1 sh.); 41º16'S 65º12'W, 45.7 m (MACN-In 23742: 1 sh.); 41º38'06.6''S 65º00'55.9''W, Playas Doradas, 7 m (MACN-In 40364: 3 sh.); 41º38'49''S 65º01'25.9''W, Playas Doradas, intertidal (MACN-In 40365: 1 spm.); 42º15'24.6''S 62º54'52.8''W, 60 m (MACN-In 40366: 2 sh.).

Chubut Province: [42º25'49''S 64º08'26''W], Puerto San José (MACN-In 11479: 3 sh.); [42º34'S 64º17'W], Puerto Pirámides, Chubut (MLP-Ma 5404: 2 spm.); 42º45'26.91''S 65º02'33.13''W, Puerto Madryn (MACN-In 22478: 4 sh.).

Known distribution. Santa Catarina (27º16'S), Brazil (Rios 1994) to Puerto Madryn (42º45'S), Chubut Province, Argentina. Living specimens: intertidal to 61.9 m; dead shells up to 175.5 m.

Cárdenas *et al.* (2008) identified as *Epitonium georgettinum* specimens from the Chilean Fjords Region, in the Southeastern Pacific Ocean. The study of these specimens (housed at the MZUC and MNHN-Cl) reveals that they do not actually correspond to this species. The identity of this material will be discussed elsewhere.

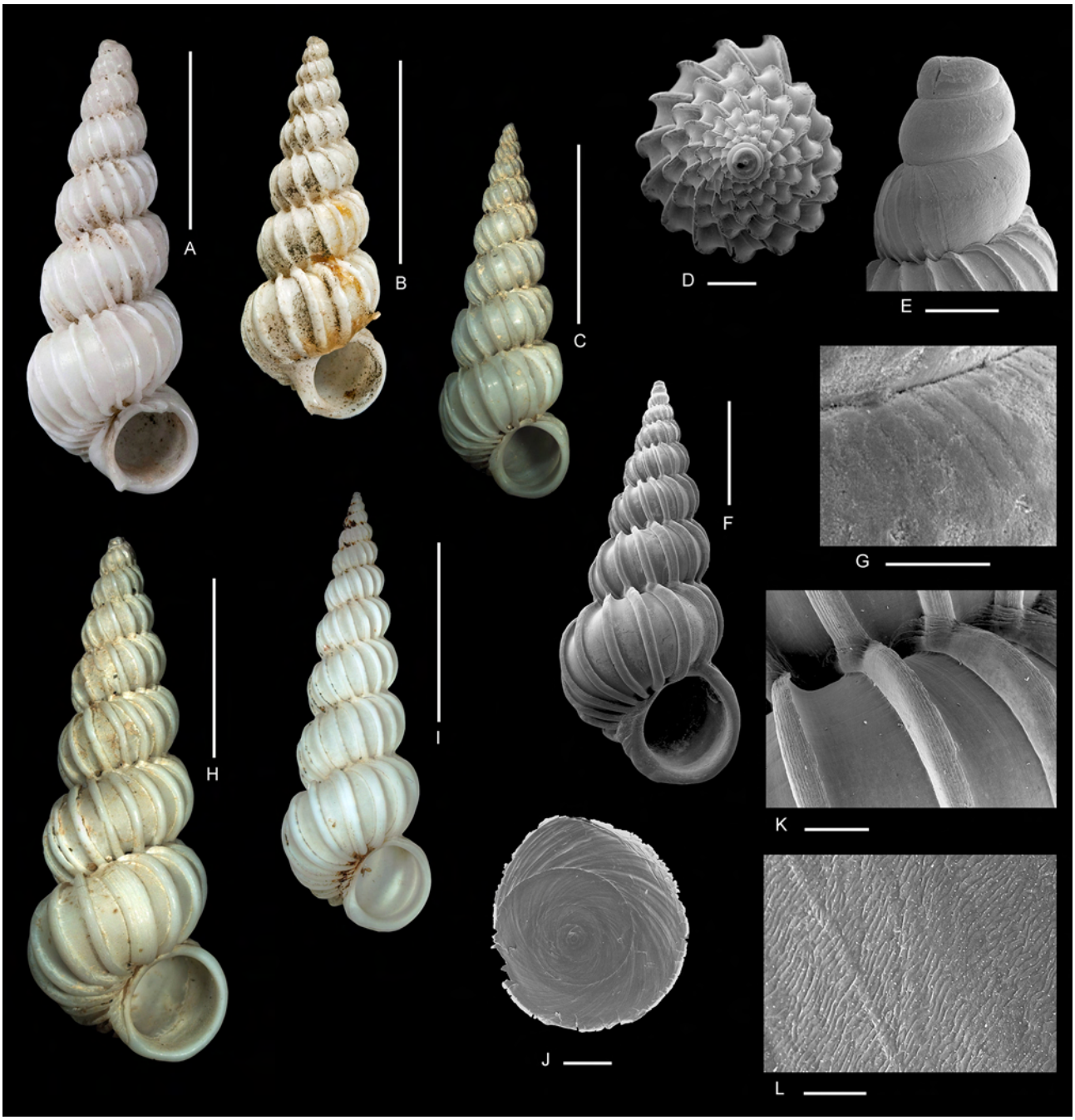

FIGURE 1. *Epitonium georgettinum* (Kiener, 1838), shell and operculum. A. Syntype of *Scalaria georgettina* (NHMG Inve 75290). B. Syntype of *Scalaria elegans* (NHMUK 1854.12.4.358). C, H. Specimens from La Mar Grande (MACN-In 40360). D–E. Specimens from Bahía San Blas (MACN-In 20265). F, G, K. Specimen from Puerto Quequén (MACN-In 18676). G. Detail of protoconch sculpture, K. Detail of teleoconch sculpture at last whorl. I, J, L. Specimen from Playas Doradas (MACN-In 40365). L. Detail of operculum sculpture. Scale bars: A–C, H, I = 10 mm; D, K = 500 µm; E = 200 µm; F = 2 mm; G = 50 µm; J = 1 mm; L = 20 µm.

Description. Shell large (maximum L observed = 37.3 mm, protoconch missing), narrowly elongated, moderately solid, white, porcelainous (Fig. 1A–C, F, H, I). Protoconch elongated, about 500 µm long and 350 µm in maximum diameter; composed of 2½, evenly-rounded whorls (Fig. 1E); usually lost in larger specimens; sculptured with faint axial threads (Fig. 1G). Transition between protoconch and teleoconch well-defined. Teleoconch with up to 10½ whorls, markedly convex in outline; suture deep, fenestrate (Fig. 1K). Last whorl evenly curved at the base. Aperture subovate, slightly expanded at its base. Outer margin thick; inner margin completely attached to last whorl (Fig. 1A–C, F, H, I). Umbilicus usually absent, narrow when present. Fasciole small to large.

Teleoconch only sculptured with slightly prosocline, widely-separated axial ribs, formed by fusion of several layers (Fig. 1K). Number of ribs constant throughout the whorls: usually 12 to 15, but as few as 10 (Fig. 1D). Ribs on the first whorl are low and rounded, increasing in height in subsequent whorls, where they may remain either as narrow, erected elements or, more frequently, as strongly recurved elements that give the appearance of rounded cords (Fig. 1A–D, F, H, I). In the first case, a flattened, sloping part of the ribs is evident near the suture (Fig. 1A, C, I); in the second case, the flattening is less noticeable (Fig. 1F, H). Ribs of adjoining whorls obliquely aligned and in contact at their bases (Fig. 1K). Axial ribs extending to the umbilical area (Fig. 1A–C, F, H, I). Interspaces between ribs smooth.

Operculum: Moderately solid, subcircular, multispiral, with subcentrally-located nucleus (Fig. 1J); whorls without raised edges. Outside surface sculptured with 35–43 fine threads per 0.1 mm, obliquely oriented with respect to growth lines (Fig. 1L). Colour: light-brown, translucent.

Jaw (Fig. 2E, F)*:* Anterior margin with a row of flat, ovate, distally-blunt denticles, pitted along their entire surface; followed by two to four rows of polygonal, densely-pitted plates; remaining surface granulate to smooth in appearance.

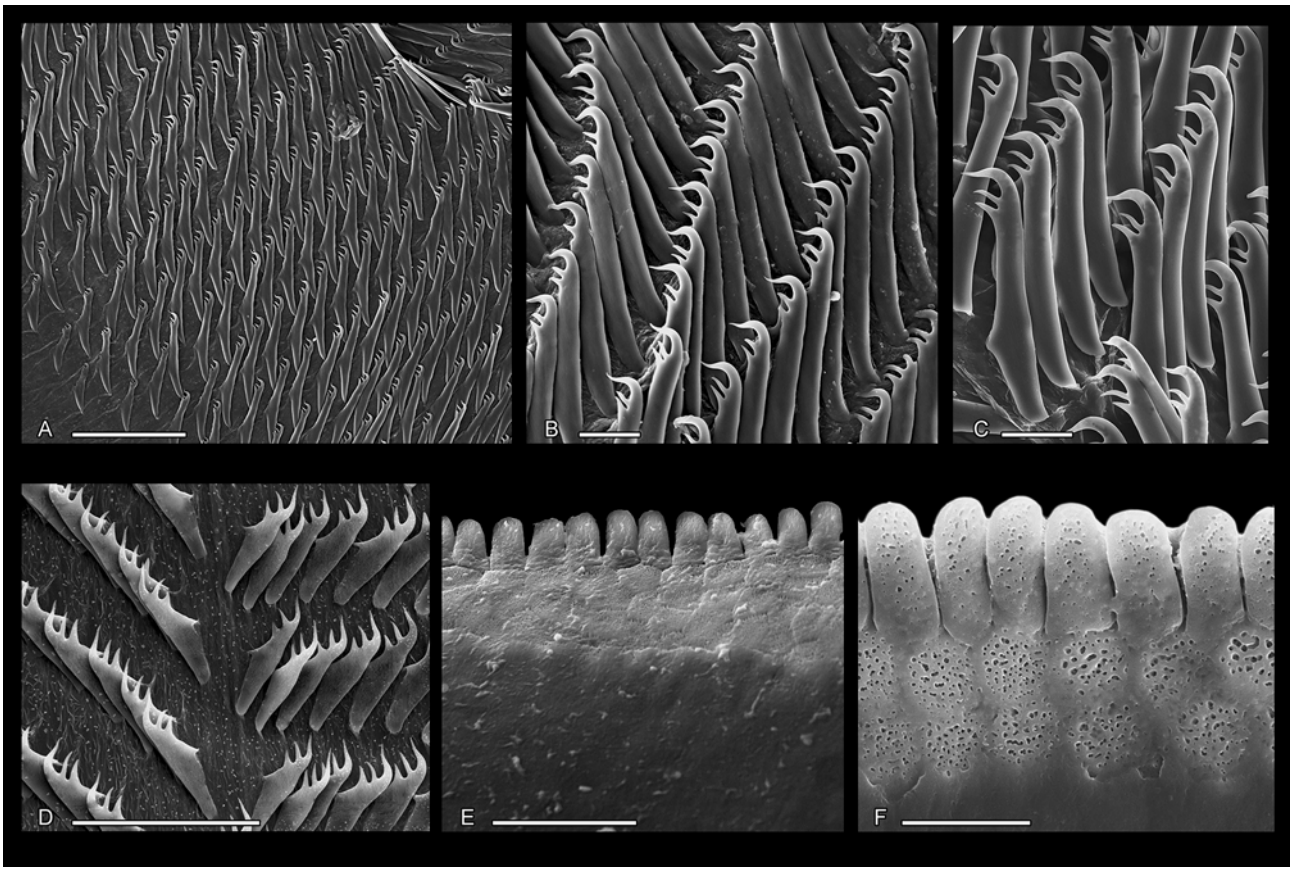

FIGURE 2. *Epitonium georgettinum*, radula and jaw. A, B, E. Specimen from off Mar del Plata, with "blade-like" ribs (MACN-In 12211). C, D, F. Specimen from Playas Doradas with "cord-like" ribs (same specimen as Fig. 1I: MACN-In 40365). A–D. Radula. A. Half radular field. B, C. Intermediate teeth. D. Detail of teeth of central field. E, F. Jaw. E. Anterior margin. F. Detail of marginal denticles. Scale bars: A = 100 µm; B, C, E = 20 µm; D = 50 µm; F = 10 µm.

Radula: With numerous teeth per row, each with a well-developed basal denticle (Fig. 2A). Teeth of the central field with short and stout blades (Fig. 2D); subsequent teeth with elongate, strong blades, reducing in size near the outer margin (Fig. 2A–C). Cusps similar along all radular field, comprising an acute apical denticle and two somewhat shorter secondary denticles (Fig. 2C).

Remarks. The sculpture of this species was usually previously described as wide, rounded axial ribs (e.g., Clench & Turner 1951; Castellanos 1970). In fact, d'Orbigny (1839) when describing *Scalaria elegans* (here regarded as a synonym of *E. georgettinum*) pointed out that this species differs from *Epitonium albidum* by lacking the lamellate ribs that are present in the latter. However, Weil *et al.* (1999) described for the species the presence of "narrow" ribs. This apparent contradiction disappears when considering that both alternatives are present in specimens with the same radular, jaw and opercular morphologies. These observations indicate that erect and markedly recurved axial ribs are part of the intraspecific variability of this species. Clench & Turner (1951) described the protoconch of *E. georgettinum* as being smooth. However, a relatively well-preserved specimen allows us to confirm (herein) that it actually shows faint axial threads when examined under high magnification. Concerning discrepancies with the previous description of the radula of this species, see remarks under *Epitonium fabrizioi*.

D'Orbigny (1839) reported "baie de San Blas", "baie Blanche" and "embouchure du Rio Negro" as the provenance of *Scalaria elegans*. Clench & Turner (1951) limited the type locality of this species to the first locality alone; but taking into account that there has been no formal designation of a lectotype for the species, all the material reported by d'Orbigny (1839) should be regarded as syntypes, and consequently the type localities of the species correspond to all the sites mentioned by the author (ICZN arts. 73.2.3 and 76.1). The syntypes of *Scalaria georgettina*, currently labelled as NHMG Inve 75290, have been previously divided into "probable syntypes" (previously numbered as 989.11.1 to 989.11.3) and "possible syntypes" (previously numbered as 989.11.4 to 989.11.8). In this case, there has not been a formal designation of a lectotype either.

Epitonium fabrizioi Pastorino & Penchaszadeh, 1998

(Figures 3, 4)

Scala aff. orbignyi: Carcelles, 1944: 248 (in part)
Epitonium albidum: Clench & Turner, 1951, pl. 114, fig. 3 (only) (*non* d'Orbigny, 1842)
Epitonium georgettina: Scarabino, 1977: 183, pl. 2, fig. 8 (*non* Kiener, 1839)
Epitonium georgettinae: Pastorino, 1995: 8, pl. 2, fig. 10 (*non* Kiener, 1839)
Epitonium fabrizioi Pastorino & Penchaszadeh, 1998: 63–68

Type locality. 42°34'S 64°17'W, Puerto Pirámides, Chubut Province, Argentina.

Type material. Holotype (MLP-Ma 5402), 10 paratypes from the type locality (USNM 880252).

Additional material examined. Buenos Aires Province: [36°21'S 56°43'W], San Clemente del Tuyú (MLP-Ma 3951: 1 sh.); [38º33'20''S 58º42'58''W], Puerto Quequén (MACN-In 25697: 7 sh.); 38º34'28.7''S 58º42'42.1''W, Puerto Quequén (MACN-In 18676-2: 1 sh.); off Buenos Aires (MACN-In 30331: 2 sh.). Río Negro Province: [40º49'00''S 64º45'00''W], Baliza Plata, Puerto San Antonio Este (MACN-In 14828: 1 sh.); 40º52'30''S 65º07'31''W, intertidal (MACN-In 40367: 1 spm.); 40º54'00.0''S 65º06'43.1''W, 6 m (MACN-In 40368: 1 sh.); 40º54'08.3''S 65º06'28.0''W, 9 m (MACN-In 40369: 7 sh.); 40º55'17.4''S 65º08'07.6''W, 7-8 m (MACN-In 40370: 1 sh.); 41º38'02.6''S 65º01'13.3''W, Playas Doradas, intertidal (MACN-In 40371: 1 spm.); 41º38'06.6''S 65º00'55.9''W, Playas Doradas, 7 m (MACN-In 40372: 3 sh.); [42º00'00''S 65º04'19''W], Puerto Lobos (MACN-In 40373: 2 sh.; MACN-In 40374: 1 sh.). Chubut Province: [42°34'S 64°17'W], Puerto Pirámides (MLP-Ma 5171: 1 sh.); [42º46'S 65º03'W], Puerto Madryn (MACN-In 10954: 3 sh.; MACN-In 37236: 1 sh.; MACN-In 9171-22: 27 spm.; MACN-In 9673: 13 spm., +50 sh.; MLP-Ma 12197: 4 spm.); [42º46'50''S 64º59'58''W], Punta Cuevas, Puerto Madryn, intertidal (MACN-In 40375: 10 spm.; MLP-Ma 6739: 3 sh.); [42º49'00''S 64º53'00''W], Punta Loma, Puerto Madryn (MACN-In 37516: 3 sh.); [42°37'S 64°16'W], Punta Pardelas (MLP-Ma: 1 sh.).

Known distribution. San Clemente del Tuyú (36º21'S), Buenos Aires Province to Puerto Madryn (42º49'S), Chubut Province, Argentina; living specimens only found in the intertidal zone.

Description. Shell medium sized (maximum L observed = 15 mm, protoconch broken), broadly conical, solid, white, dull (Fig. 3A–C, E, F, I). Protoconch of 4¼ convex whorls, of 485 µm in length and 390 µm in maximum

diameter (Pastorino & Penchaszadeh 1998); usually partially or completely lost in larger specimens; smooth (?). Teleoconch with up to 8 inflated whorls (Fig. 3A–C, E, F, I); suture deep, fenestrated by axial sculpture (Fig. 3J). Last whorl evenly curved at the base. Aperture subovate; peristome somewhat expanded at the base; outer margin thick. Umbilicus indistinct. Fasciole moderate to wide (Fig. 3A–C, F, I).

Teleoconch sculptured with markedly-prosocline axial ribs, formed by fusion of several layers; ribs constant in number along the shell, usually 13 to 15 per whorl, but up to 18, separated by wide interspaces (Fig. 3A–F, H–J). Ribs on the first whorl are low, slightly increasing in height on subsequent whorls, where they remain either erect or somewhat recurved (Fig. 3D, H). Ribs of adjoining whorls obliquely aligned and greatly overlapping ("connected") (Fig. 3J). Ribs on the last whorl regularly arched at base, extending to umbilical area (Fig. 3A–C, F, I). Interspaces between ribs smooth.

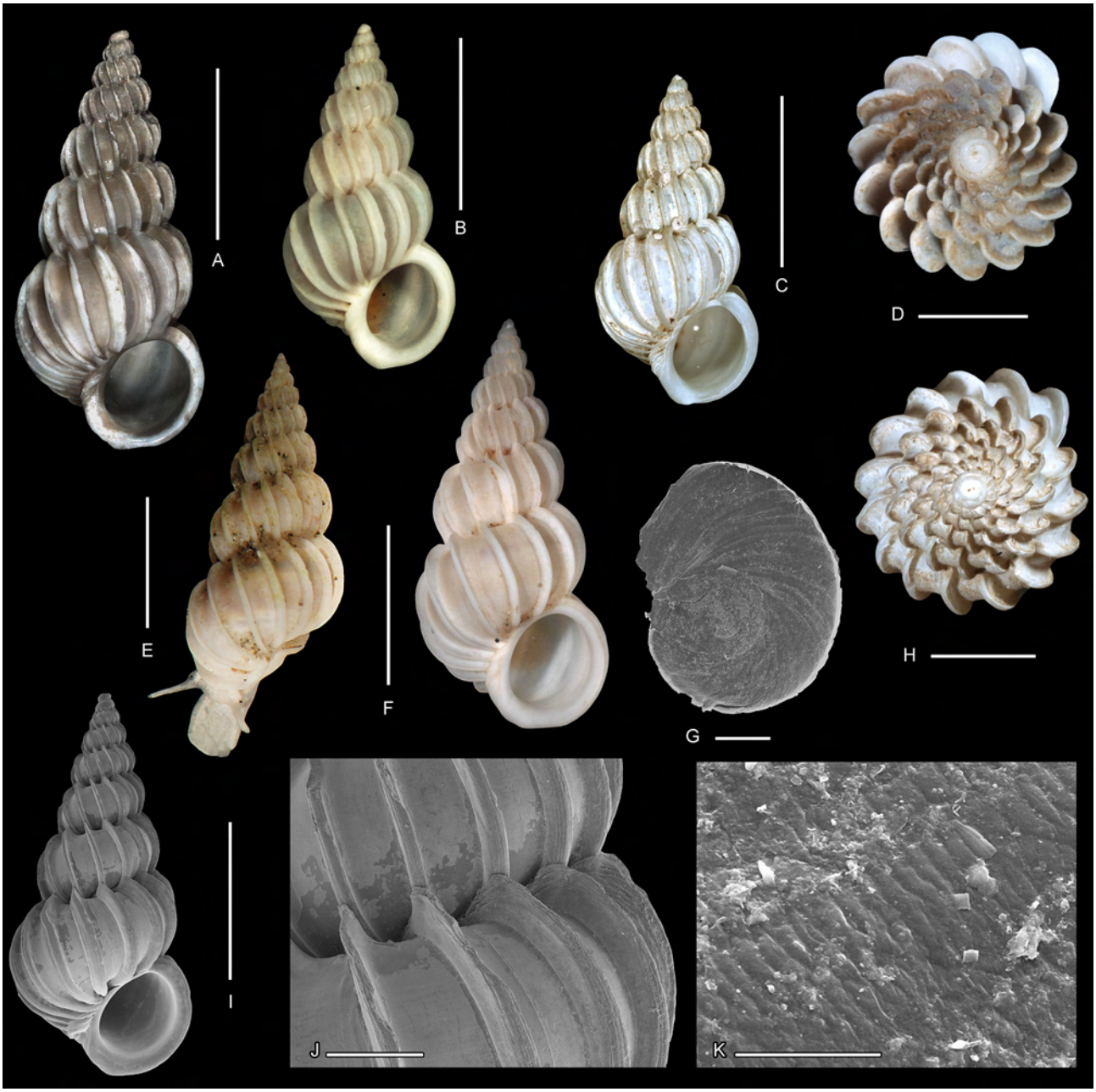

FIGURE 3. *Epitonium fabrizioi* Pastorino & Penchaszadeh, 1998, shell and operculum. A. Holotype (MLP-Ma 5402). B. Specimen from Puerto Madryn (MACN-In 9171-22). C, D, G, H, K. Specimens from Punta Cuevas (MACN-In 40375). K. Detail of operculum sculpture. E, F. Specimen from Las Grutas (MACN-In 40367). I, J. Specimen from Puerto Lobos (MACN-In 40374). J. Detail of teleoconch sculpture at last whorl. Scale bars: A–C, E, F, I = 5 mm; D, H = 2 mm; G, J = 500 µm; K = 20 µm.

Operculum: Thin, oval; paucispiral, with eccentric, slightly-sunken nucleus (Fig. 3G). Outside surface sculptured with about 40 wide bars per 0.1 mm (Fig. 3K). Colour: yellowish-brown; translucent.

Jaw (Fig. 4D, E): Anterior margin with a row of blunt, "mushroom-like" denticles. Each denticle composed of an elongate, densely-pitted, solid base ("buttress") that distally expands forming a disc, with a marginal reinforcement ("inner plate"). Adjacent surface irregular, pitted.

Radula: With numerous teeth per row, all of them with a minute basal denticle and slender blades (Fig. 4A). Teeth of the central field small, widely separated (Fig. 4A); subsequent teeth larger, with longer blades, closely set (Fig. 4A, B). Cusps composed of an acute, narrow apical denticle, followed by a large, wide, secondary denticle, which is rounded at the tip, directed towards the apical denticle (Fig. 4C). An additional, secondary denticle present, varying from a small, conical structure in the central field, to a knob in the outer teeth.

Remarks. *Epitonium fabrizioi* is most similar to *E. georgettinum*, particularly those specimens having erect axial sculpture. However, in contrast to these specimens, in *E. fabrizioi* ribs are evenly arcuate throughout the whorls (*i.e.*, lacking the straight slope near apical suture that appears in *E. georgettinum*), and the ribs of adjoining whorls are more widely overlapping. Furthermore, *E. fabrizioi* has a higher incremental rate of whorls, which results in a broad shell profile. Other differences arise from the number of protoconch whorls (4¼ in *E. fabrizioi vs*. 2½ in *E. georgettinum*), the morphology of the operculum (multispiral in *E. georgettinum vs*. paucispiral in *E. fabrizioi*), the jaw (with the denticles of the anterior margin "mushroom-like" in *E. fabrizioi vs*. flat, ovate, distally blunt in *E. georgettinum*), and radula (see discussion below). Pastorino & Penchaszadeh (1998) also mentioned that *E. fabrizioi* has smaller egg capsules, each one containing a lower number of eggs. *Epitonium fabrizioi* was previously confused with *E. albidum*. A comparison with the syntypes of that species shows that *E. fabrizioi* has a higher incremental rate of whorls and the ribs of adjoining whorls more widely overlapping, thus making the separation of the whorls less evident and its outline less convex. Furthermore, *E. fabrizioi* has a dull shell surface, while in *E. albidum* it is shiny.

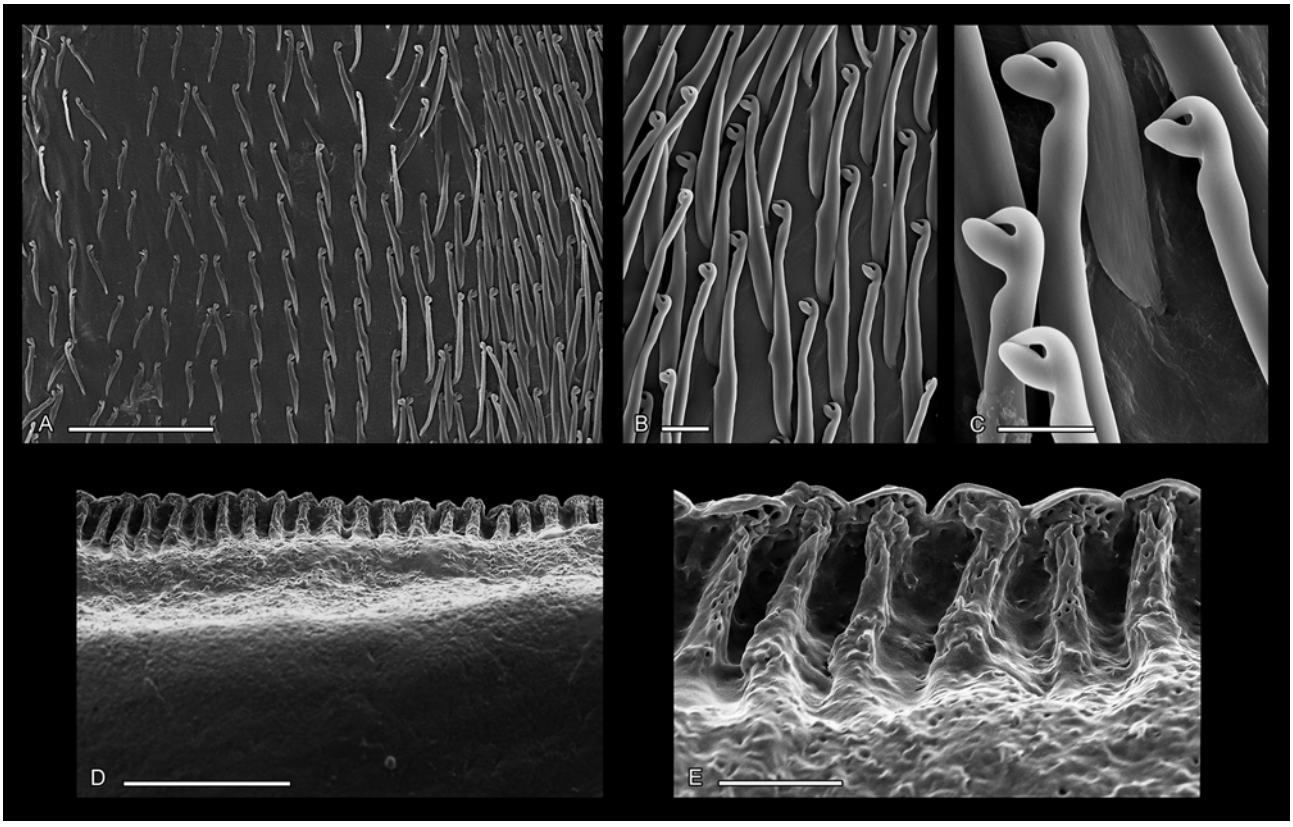

FIGURE 4. *Epitonium fabrizioi*, radula and jaw. A, D, E. Specimens from Punta Cuevas (A same specimen as Fig. 3C) (MACN-In 40375). B, C. Specimen from Las Grutas (same specimen as Fig. 3E, F: MACN-In 40367). A–C. Radula. A. Detail of half field of radula. B. Intermediate teeth. C. Detail of cusps. D, E. Jaw. D. Anterior margin. E. Detail of marginal denticles. Scale bars: A = 100 µm; B = 20 µm; C, D = 10 µm; E = 2 µm.

The shell and opercular characters here recognized as diagnostic for *E. fabrizioi* are consistent with those previously described by Pastorino & Penchaszadeh (1998); however, the morphology of the radula does not agree with their observations. According to the authors, *E. fabrizioi* shows "… tricuspid marginal teeth, identical in shape. Outermost cusps large and hook-like, central and inner cusps similar in size and shorter". In the same paper, the authors included information on the radula of a specimen of *Epitonium georgettinum* that they described as having "… one sharp terminal cusp… and two blunt cusps, one almost obsolete". Our study of the radulae of these two species consistently reveal for *E. fabrizioi* the morphology showed in figures 15 and 16 of Pastorino & Penchaszadeh's (1998) paper (*i.e.*, the morphology they attributed to *E. georgettinum*), and for *E. georgettinum* a morphology which corresponds to their description and figures for *E. fabrizioi*. These results suggest that at the time that *E. fabrizioi* was described, the two species' radulae were confused.

Among the specimens reported by Carcelles (1944) as "*Scala aff. orbignyi*" from Quequén, Buenos Aires Province, one specimen of *E. fabrizioi* (currently MACN-In 18676-2) was found mixed in.

Epitonium striatellum **(Nyst, 1871)**

(Figure 5)

Scalaria tenuistriata d'Orbigny, 1839: 390, pl. 54, figs. 4–6
Scala striatella Nyst, 1871: 134–135 (*nomen novum* pro *Scalaria tenuistriata* d'Orbigny, 1839 *non* Bronn, 1831)
Epitonium (Asperiscala) tenuistriatum: Clench & Turner, 1952: 299–300, pl. 138; Rios, 1994: 98, pl. 32, fig. 397
Epitonium tenuistriatum: Castellanos, 1970: 63, pl. 4, fig. 8; Scarabino, 1977: 183, pl. 2, fig. 9

Type locality. Bahía Blanca [38º42'S 62º10'W, Buenos Aires Province, Argentina].

Type material. Lectotype (NHMUK 1854.12.4.359/1) and one paralectotype (NHMUK 1854.12.4.359/2) [not examined].

Material examined. Uruguay: Rocha: [33º54'00''S 53º31'00''W], La Coronilla (MACN-In 19214: 2 sh.); [34°23'S 53°47'W], Cabo Polonio (USNM 359204: 1 sh); [34º39'0''S 54º10'0''W], La Paloma (MACN-In 29687: 13 sh.; MACN-In 28767: 3 sh.); [34º39'36''S 54º09'21''W], Cabo Santa María, Rocha (MACN-In 15305: 1 sh.). Argentina: Buenos Aires Province: 38º25'18.50''S 56º30'37.07''W, off Mar del Plata (MACN-In 10740: 1 sh.; MACN-In 11995: 1 sh.); [38º53'13''S 62º05'52''W], Base Naval Puerto Belgrano, Punta Alta (MACN-In 6620-23: 1 sh.; MACN-In 11211: 2 sh.); [39°42'S 62°07'W], mouth of Río Colorado (MLP-Ma 1375: 9 sh.); 40º18'29.79''S 62º14'15.66''W, Bahía San Blas (MACN-In 20266: 2 sh.). Río Negro Province: [41º00'S 64º07'W], Aguada de los Loros, San Antonio Este (MACN-In 13339-1: 3 sh.; MACN-In 13340: + 100 sh.); [40º49'S 64º54'W], Punta Villarino, San Antonio Este (MACN-In 13365: 3 sh.); 40º29'35.2''S 65º31'44.7''W, Las Grutas, 6 m (MACN-In 40376: 1 sh.); 40º45'18.7''S 64º56'31.8''W, La Mar Grande, intertidal (MACN-In 40377: 8 sh.); 40º54'00.0''S 65º06'43.1''W, 6 m (MACN-In 40378: 1 sh.); 40º54'08.3''S 65º06'28.0''W, 9 m (MACN-In 40379: 1 sh.).

Known distribution. Rio de Janeiro (22º54'S), Brazil (Rios 1994) to Golfo San Matías (40º54'S), Río Negro Province, Argentina. Bathymetric range of living specimens unknown; shells found from the intertidal to 9 m.

Description. Shell large (maximum L observed = 23.9 mm, apex missing; to 28.5 mm according to Clench & Turner (1952)), elongate, thin, white, translucent (Fig. 5A–C, E, F). Protoconch and first whorls of teleoconch very eroded in all available specimens (Fig. 5D). Teleoconch with up to 8 whorls, slightly convex in outline; suture deep, partially covered by axial sculpture (Fig. 5A–C, E, F, H); last whorl evenly curved at the base. Aperture ovate; peristome with a small basal expansion. Outer margin slightly thickened. Fasciole small. Umbilicus absent (Fig. 5A–C, E, F).

Teleoconch densely sculptured with axial and spiral elements, which form a cancellate pattern (Fig. 5A–C, E, F, H, I). Axial ribs prosocline, extremely low, recurved, giving the appearance of thin, rounded cords, formed by fusion of several layers, obliquely aligned between adjoining whorls (Fig. 5G–I). Number of ribs increasing in successive whorls: from 36–40 in the first whorl to 52–58 in the last whorl of larger studied specimens. Ribs evenly curved along the whorl, well-entering into the suture, fused at their bases with the ribs of adjacent whorl (Fig. 5H); ribs on the last whorl extending to the umbilical area. Interspaces between ribs with numerous, thick spiral threads, as wide as axial elements in the first whorl, slightly narrower than axial sculpture in subsequent whorls (Fig. 5H, I). Among spiral elements it is possible to recognize primary and secondary threads, which produce rectangular interspaces in their intersection with axial sculpture (Fig. 5H, I). Spiral sculpture not crossing over axial sculpture.

Operculum, jaw and radula: Unknown.

Remarks. Although Nyst (1871) noted the homonymy of *Scalaria tenuistriata* d'Orbigny, 1839 and *Scalaria tenuistriata* Bronn, 1831, and proposed *Epitonium striatellum* (formerly under *Scala*) as a replacement name for the first, subsequent literature (e.g., Clench & Turner 1952; Castellanos 1970; Scarabino 1977; Rios 1994) retained the usage of d'Orbigny's name.

Lima *et al.* (2012) provided a list of the *Epitonium* species present in the Atlantic coast of South America. In their list, the authors omitted both *E. tenuistriatum* and *E. striatellum*, but listed *Epitonium striatissimum* (Monterosato, 1878) as being present in Argentine waters. That species is distributed in the Mediterranean, Madeira, and SE United States, from North Carolina to Florida (Bouchet & Warén 1986), with no documented records in Patagonia thus far known.

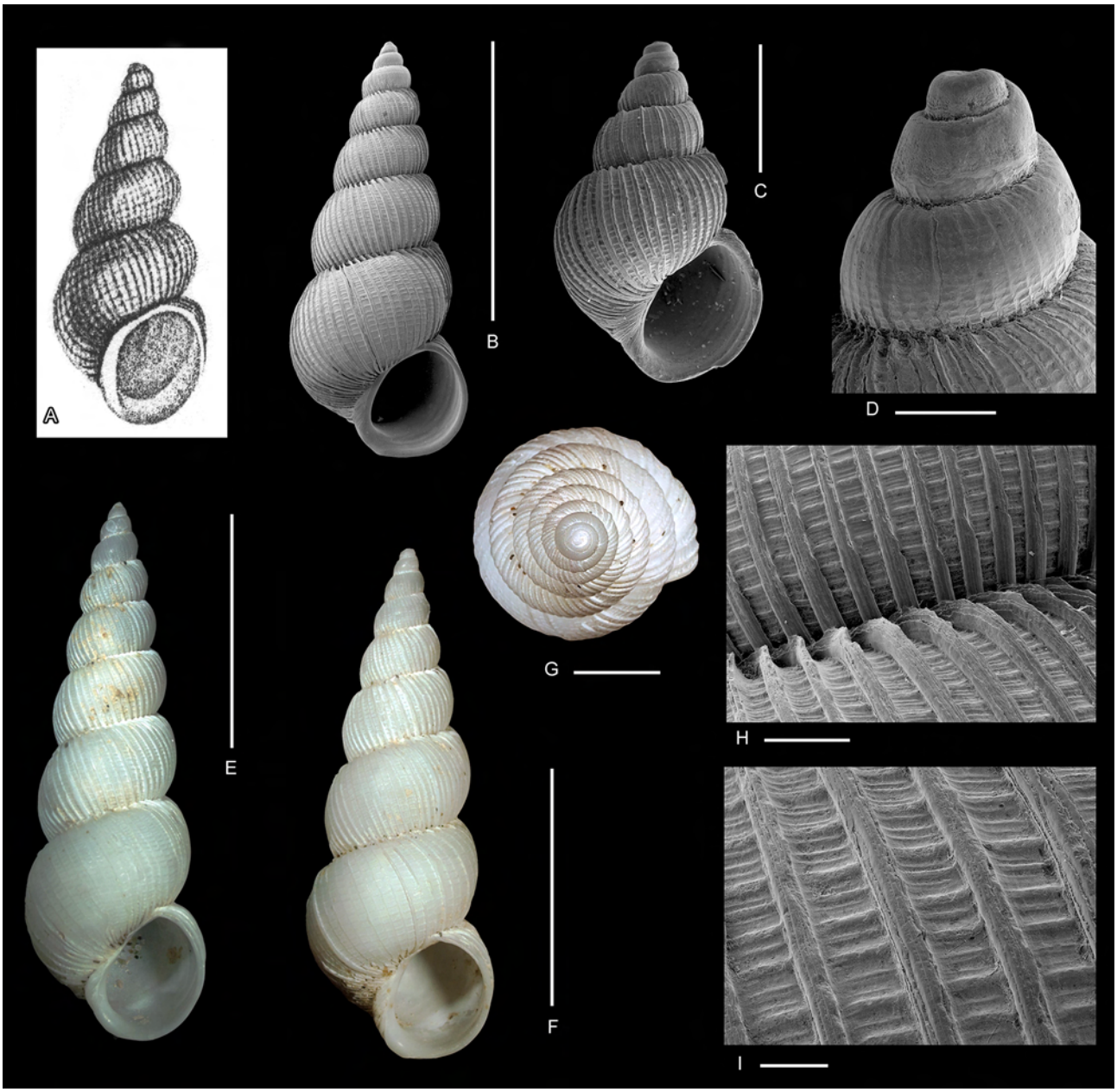

FIGURE 5. *Epitonium striatellum* (Nyst, 1871), shell. A. Original illustration of *Scalaria tenuistriata* (d'Orbigny, 1842: pl. 54, fig. 6). B, D–I. Specimens from La Mar Grande (MACN-In 40377). C. Specimen from 40º54'00.0"S 65º06'43.1"W (MACN-In 40378). H. Detail of fourth and fifth whorls. I. Detail of teleoconch sculpture at last whorl. Scale bars: B, E, F = 10 mm; C = 1 mm; D = 500 μm; E = 2 mm; G = 5 mm; H = 500 μm; I = 200 μm.

***Epitonium evanidstriatum* new species**
(Figures 6A–L, 7)

Type locality. 40º55'17.4''S 65º08'07.6''W, Golfo San Matías, Río Negro Province, Argentina, 7–8 m.

Type material. Holotype (MACN-In 40380) and 3 paratypes (MACN-In 40381) from the type locality; 2 paratypes from 40º55'29.5''S 65º08'32.7''W, 3–4 m (MACN-In 40382).

Additional material examined. Argentina: Río Negro Province: 40º48'46.80''S 65º05'45.18''W, Las Grutas (MACN-In 40383: 1 sh.); 40º50'12.8''S 65º04'42.2''W, 10 m (MACN-In 40384: 2 sh.); 40º54'08.3''S 65º06'28.0''W, 9 m (MACN-In 40385: 6 sh.); 40º54'21.7''S 65º06'39.8''W, 6 m (MACN-In 40386: 1 sh.); 40º56'27.2'S 65º07'58.2''W, 10–11 m (MACN-In 40387: 11 sh.); 41º38'06.6''S 65º00'55.9''W, Playas Doradas, 7 m (MACN-In 40388: 22 sh.); 41º39'03.1''S 65º00'38.3''W, 12–14 m (MACN-In 40389: 2 sh.); 41º39'41.3''S 65º00'32.9''W, 16 m (MACN-In 40390: 2 sh.); 41º40'17.8''S 65º00'27.8''W, 16 m (MACN-In 40391: 2 sh.); 42º00'54.2''S 65º03'40.9''W, Puerto Lobos, 10–12 m (MACN-In 40392: 1 sh.).

Known distribution. Only known from Golfo San Matías (40º48'S to 42º00'S), Río Negro Province, Argentina.

Ethymology. *evanid* - Latin for disappearing + *striatum* for striae; in reference to the spiral threads that fade in the last whorls of larger specimens.

Diagnosis. Shell broadly conical to narrowly elongate. Protoconch conical, of 3 to 3¼ whorls. Teleoconch with convex whorls, sculptured with lamellate or recurved axial ribs, which decrease in number with growth, and spiral threads, clearly visible in the first whorls but fading in the last whorls of larger specimens. Jaw with a row of flat, distally-blunt denticles at the anterior margin. Teeth with two secondary denticles in the central field, reduced to knobs or completely absent in the outermost teeth.

Description. Shell medium sized (maximum L observed = 11.5 mm), broadly conical to narrowly elongate, thin, white, shiny (Fig. 6A, C, E, F). Protoconch conical, of about 300 µm in length and 310 µm in maximum diameter, composed of 3 to 3¼ whorls; whorls slightly convex in outline; usually lost in larger specimens; surface glossy, sculptured with faint axial threads (Fig. 6D, G, I). Limit between protoconch and teleoconch clearly defined by a change in sculpture. Teleoconch with up to 7½ whorls, the first ones slightly convex, then gradually increasing in convexity (Fig. 6A, C, E, F); suture moderately deep (Fig. 6J, K). Last whorl slightly flattened at base. Aperture subovate, expanded at the base. Outer margin thick. Umbilicus absent. Fasciole narrow (Fig. 6A, C, E, F).

Teleoconch sculptured with prosocline axial ribs and delicate spiral threads (Fig. 6A, C, E, F, J). Axial ribs evenly convex along the whorl, sometimes forming a weak shoulder adapically, but without angulation at the base of last whorl; formed by fusion of several layers. Ribs on adjoining whorls discontinuous, extending well into the suture (Fig. 6J, K). Number of ribs consistently decreasing with shell growth: from 18–27 on the first whorls to 13–19 from the fifth whorl onwards (Fig. 6B); ribs in the first whorl are relatively low, but gradually increasing in height in subsequent whorls, where they are either erect (lamellar) or slightly to moderately recurved (Fig. 6B, J, K); in the last whorl, ribs extending to the umbilical area (Fig. 6A, C, E, F). Interspaces between ribs with widely-separated spiral threads, regularly spaced along the whorl, although somewhat weaker near the suture; in number of 8–9 in the first teleoconch whorl, increasing up to 15–19, but fading from the fourth to sixth whorl onwards (Fig. 6J, K). Spiral sculpture not crossing over axial sculpture.

Operculum: Thin, subovate, paucispiral, with eccentric nucleus (Fig. 6H). Adjacent whorls without raised edges. Outside surface sculptured with 34 to 36 irregular threads per 0.1 mm, obliquely oriented with respect to growth lines (Fig. 6L). Colour: light brown, translucent.

Jaw (Fig. 7D, E): Anterior margin with a row of flat, distally-blunt denticles, followed by a series of irregular, pitted plates.

Radula: With numerous teeth per row, all of them showing an obscure basal denticle. Teeth of the central field short and stout, with an acute apical denticle and one or two, variably-developed secondary denticles (Fig. 7A). Subsequent teeth with a markedly-elongate, narrow blade, and an upturned, acute apical denticle (Fig. 7B, C). A minute, knob-like secondary denticle sometimes present. Outermost teeth slightly smaller (Fig. 7B).

Remarks. The variability in shell outline described above for *E. evanidstriatum* **n. sp.** is size-related: smaller specimens are broadly conical, and gradually become narrowly elongate with growth. This variation is associated with the change in the incremental rate of whorls, which in the first teleoconch whorl is high (with an increase in width of 50–70% from the last protoconch whorl to the first teleoconch whorl), but in subsequent whorls gradually

decreases (to about 20% from the sixth to seventh whorls), showing a particularly marked decrease from the first to the second teleoconch whorl. This change in the incremental rate of whorls gives origin to a narrowly elongated aspect of the shell outline of larger specimens.

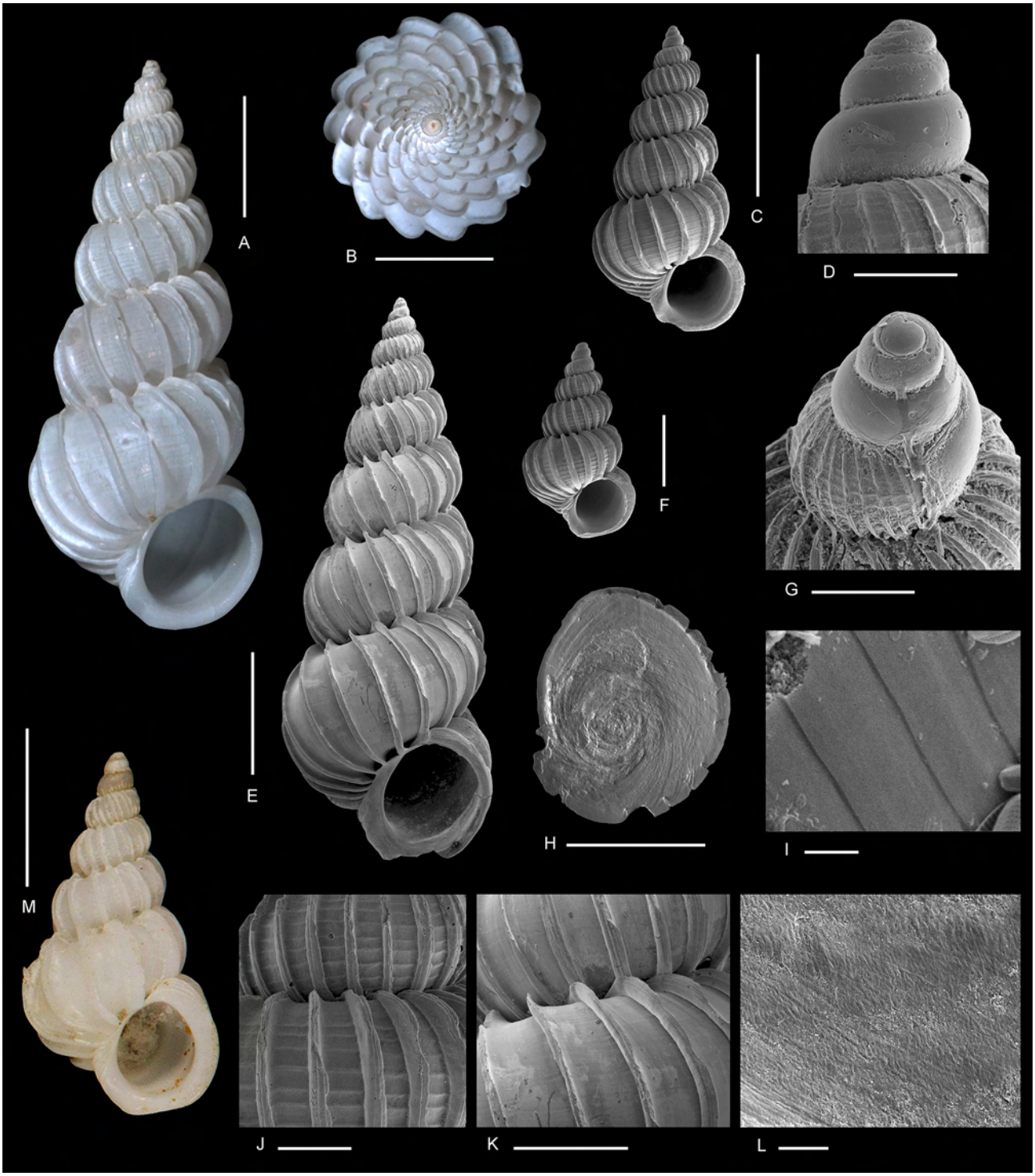

FIGURE 6. A–L. *Epitonium evanidstriatum* new species, shell and operculum. A, B. Holotype (MACN-In 40380). C, D, F, G, J. Specimens from 40º56'27.2'S 65º07'58.2"W (MACN-In 40387). E, K. Paratype (MACN-In 40381). H, I, L. Paratype (MACN-In 40382). I. Detail of protoconch sculpture. J, K. Detail of teleoconch sculpture between second and third whorls (J) and last two whorls (K); L. Detail of operculum sculpture. M. Lectotype of *Scala apiculata* (USNM 94890). Scale bars: A–C, E, M = 2 mm; D, G, J = 200 µm; F, H, K = 1 mm; I = 5 µm; L = 20 µm.

In shell outline, *Epitonium evanidstriatum* **n. sp.** closely resembles that referred to as *Epitonium candeanum* (d'Orbigny, 1842) by different authors (e.g., Clench & Turner 1951; Rios 1994; Redfern 2000). Although the

concept of *E. candeanum* is variable among different authors (e.g., d'Orbigny 1842; Clench & Turner 1951; Diaz Merlano & Puyana Hegedus 1994; Redfern 2000), there is a general agreement on the presence of fine, secondary axial sculpture running across the spiral threads, between the strong, primary axial ribs. This condition clearly differs from that present in *E. evanidstriatum* **n. sp.**, where this secondary sculpture is completely absent. Furthermore, *E. evanidstriatum* **n. sp.** is narrower and with less inflated whorls than *E. candeanum*.

In *E. evanidstriatum* **n. sp.** the spiral sculpture fades towards the last teleoconch whorls. The vanishing condition of spirals has been previously described for a few species: *Surrepifungium costulatum* (Kiener, 1838), *S. oliverioi* (Bonfitto & Sabelli, 2000), *S. patamakanthini* Gittenberger & Gittenberger, 2005, all from the Indo-West Pacific, and *Epitonium apiculatum* (Dall, 1889), described from the East coast of the United States (Fig. 6M). However, in these species the spiral sculpture disappears completely at some point, whereas in *E. evanidstriatum* **n. sp.** the spirals fade in the last whorls of larger specimens but are still visible under high magnification (SEM). In addition, *Epitonium evanidstriatum* **n. sp.** reaches larger sizes than *E. apiculatum*, but smaller than *Surrepifungium costulatum, S. oliverioi* and *S. patamakanthini* (11.5 mm *vs*. 4.5 mm *vs*. 44.0 mm, 20.0 mm and 22.8 mm, respectively); but even when comparing similarly-sized specimens, *E. evanidstriatum* **n. sp.** shows a consistently more narrowly-elongated outline than the other four species, which are widely conical all along their ontogeny. In addition, *Epitonium apiculatum* differs from *E. evanidstriatum* **n. sp.** by having a greater number of whorls at the same size (9 *fide* Clench & Turner 1952 in 4.5 mm long specimens *vs.* 7 whorls in *E. evanidstriatum*); fewer axial ribs on the fourth and fifth teleoconch whorl (10–11 *vs.* 14–20 in *E. evanidstriatum*) and the whorls only attached by axial ribs (Clench & Turner 1952). Additional characters for distinguishing *Epitonium evanidstriatum* **n. sp.** from *Surrepifungium costulatum, S. oliverioi* and *S. patamakanthini* come from the radula and jaw: the latter three species have all radular teeth with a single denticle at the cusp (the apical denticle), and the anterior margin of the jaw with several rows of acute, slender denticles. In fact, these two characters were used by Gittenberger & Gittenberger (2005) to reunite these species under the genus *Surrepifungium*. On the contrary, *E. evanidstriatum* **n. sp.** has the anterior margin of the jaw with a single row of blunt denticles, and the teeth of the central field of the radula with three denticles. The radula and jaw of *Epitonium apiculatum* remain unknown.

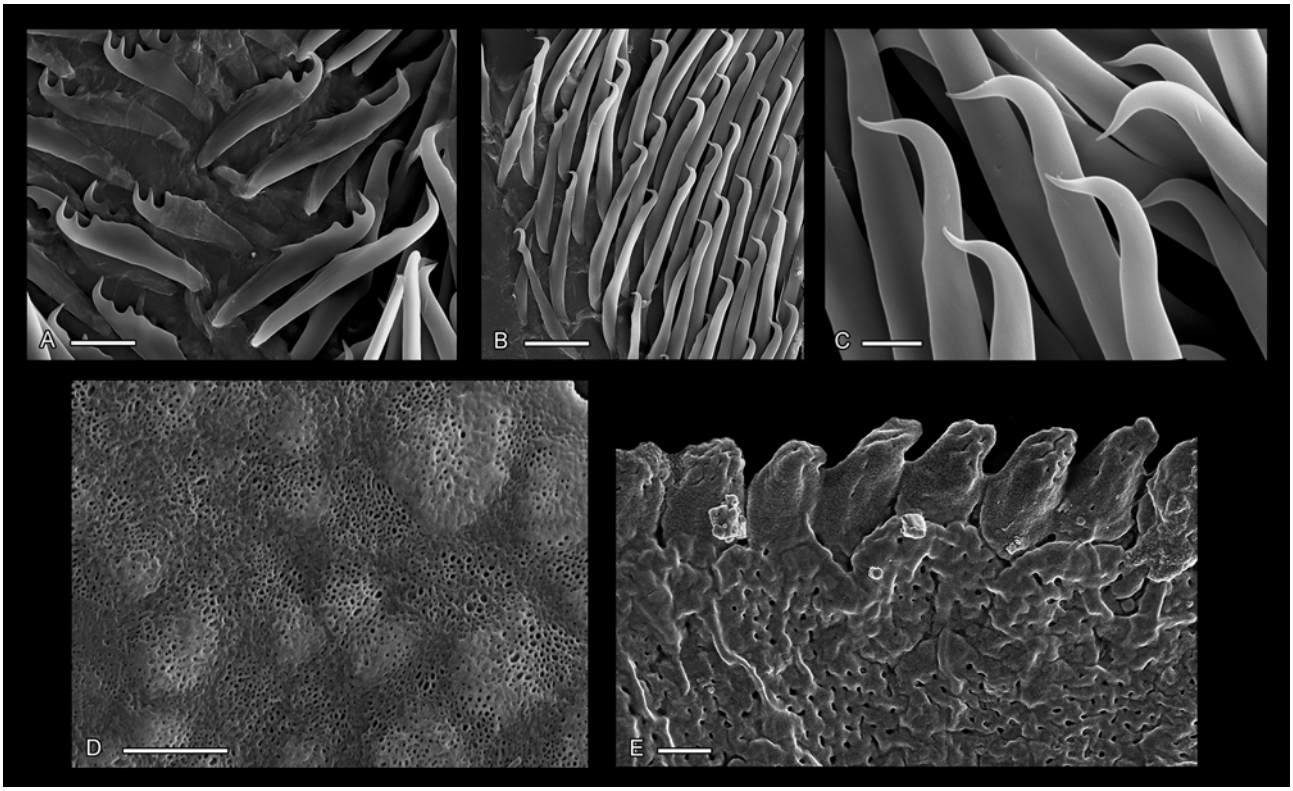

FIGURE 7. *Epitonium evanidstriatum*, radula and jaw. Paratype (same specimen as Fig. 6H, I, L: MACN-In 40382). A–C. Radula: A. Central field. B. Outer teeth. C. Detail of cusps of intermediate teeth. D, E. Jaw. D. Anterior inner surface; E. Detail of marginal denticles. Scale bars: A = 10 μm; B = 20 μm; C, D = 5 μm; E = 1 μm.

Specimens of *Epitonium evanidstriatum* **n. sp.** could be confused with the sympatric *E. georgettinum*, particularly if seen under low magnification. However, the former clearly differs by having spiral sculpture, and the adjacent whorls in tight contact instead appearing as "detached". In addition, the protoconch of *Epitonium evanidstriatum* **n. sp.** is smaller than that of *E. georgettinum* (300 *vs*. 500 µm long), even when having a greater number of whorls (3–3¼ *vs*. 2½); the number of axial ribs in the teleoconch of *E. evanidstriatum* **n. sp.** decreases with growth, instead of being constant, as it is the case of *E. georgettinum*; and the first teleoconch whorl shows almost twice the number of ribs than those present in *E. georgettinum* (18–27 *vs*. 12–15). Another difference arises in the morphology of the operculum, which is paucispiral in *Epitonium evanidstriatum* **n. sp.** and multispiral in *E. georgettinum*. Concerning the radula, *Epitonium evanidstriatum* **n. sp.** shows the outermost teeth with minute or absent secondary denticles, whereas in *E. georgettinum* the outer teeth have two well-developed secondary denticles.

The only other species sympatric with *E. evanidstriatum* **n. sp.** having both axial and spiral sculpture is *E. striatellum*. *Epitonium evanidstriatum* **n. sp.** differs from this species by having a deeper suture, and the axial sculpture comprises fewer, more widely separated, higher and stronger ribs. *Epitonium evanidstriatum* **n. sp.** also has weaker and fewer spiral threads, which fade in the last whorls, whereas in *E. striatellum* the spiral sculpture is regularly present along all the shell whorls. The aperture in *E. striatellum* is larger and more markedly ovate, and this species reaches larger sizes than *E. evanidstriatum* **n. sp.** (28.5 *vs.* 11.5 mm long, respectively).

Genus: *Cirsotrema* Mörch, 1852

Type species: *Scalaria varicosa* Lamarck, 1822, by monotypy

The following species are tentatively placed in *Cirsotrema*, due to the similarity in jaw morphology. However, they differ strikingly in shell sculpture (see further information in the Discussion section).

"Cirsotrema" magellanicum (Philippi, 1845)
(Figures 8, 9)

Scalaria magellanica Philippi, 1845: 65
Scalaria magellanica var. latecostata Strebel, 1905: 658, pl. 23, fig. 43a–d
Scala aff. orbignyi: Carcelles, 1944: 248 (in part)
Epitonium (Boreoscala) magellanicum: Clench & Turner, 1952: 324–325, pl. 156; Rios, 1994: 98, pl. 32, fig. 398
Epitonium magellanicum: Castellanos, 1970: 63–64 (in part), pl. 4, fig. 15; Cárdenas *et al*., 2008: 213–214, fig. 3.34
Epitonium magellanicum latecostatum: Castellanos, 1970: 64–65 (in part)
Boreoscala magellanica: Weil *et al.*, 1999: 12, fig. 9

Type localities. Fretum Magellanicum [= Magellan Strait] (*Scalaria magellanica*). Magalhen-Str. [= Magellan Strait]; Lennox Island [Beagle Channel] (*Scalaria magellanica var. latecostata*).

Type material. Two syntypes of *Scalaria magellanica var. latecostata* (one of them ZMB 2574, here designated as neotype of *Scalaria magellanica magellanica*; the other SMNH Type-6045).

Additional material examined. Uruguay: 35º37'10''S 54º55'03''W, 210.3 m (MACN-In 25696: 5 spm., 2 sh.); 35º42'S 52º52' W, 184 m (MACN-In 24186: 1 sh.); 36º30'S 54º44'W, 26.5 m (MACN-In 23693-1: 1 sh.); 36º42'S 53º50' W, 382 m (MACN-In 15648-10: 41 sh.). Argentina: Buenos Aires Province: 38º31'S 55º42'W, 109 m (MACN-In 23356: 1 sh.); [38º34'S 58º42'W], Quequén, 18 m (MACN-In 18676-1: 1 spm.); 38º40'S 56º00'W, 90 m (MACN-In: 8635-7: 1 sh.); 39º28'S 57º02'W, 90.5 m (MACN-In 25130: 2 sh.). Río Negro Province: 41º51'25.2''S 58º09'12''W, 106 m (MACN-In 40399: 1 spm., 1 sh.); 42º30'S 59º15'W, 96 m (MACN-In 37901: 1 spm., 18 sh.). Chubut Province: 42º31'24.6''S 59º20'37.8''W, 91 m (MACN-In 40398: 1 spm.); 44º30' to 44º00'S 59º30' to 60º30'W (MACN-In 40397: 1 spm.). Santa Cruz Province: 46º32.13'S 64º41.74'W, 107 m (MACN-In 40400: 3 spm., 1 sh.); [47°45'S 65°54'W], Puerto Deseado (MLP-Ma 13531: 6 sh.). Tierra del Fuego Province: 54º26'30''S 64º53' W, 111.6 m (MACN-In 25028: 4 sh.); 55º06'S 66º29' W, Cabo San Pío, 65-80 m (MLP-Ma 14175: 1 sh.). Burdwood Bank: 54°53'13.08''S 59°48'54''W, 785 m (MACN-In 40781: 1 sh). Chile: 41°50'56.4''S

73º23’52.8’’W, Golfo de Ancud, 214 m (MZUC 32579: 1 spm., 1 sh.); 42º43’40.8’’S 73º23’31.2’’W, Golfo Corcovado, 169 m (MNHN-Cl 7250: 1 spm.).

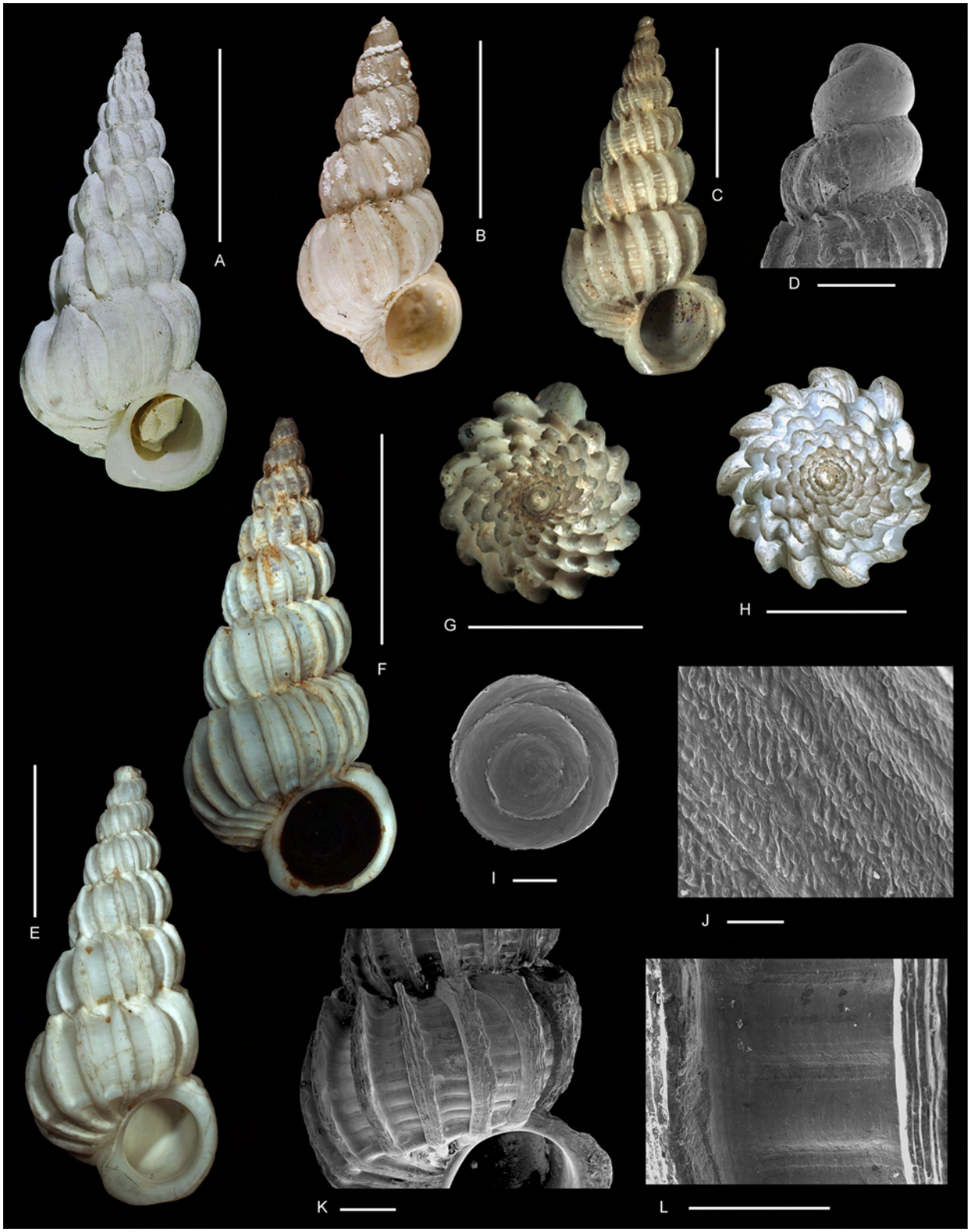

FIGURE 8. *“Cirsotrema” magellanicum* (Philippi, 1845), shell and operculum. A. Syntype of *Scalaria magellanica var. latecostata* (SMNH Type-6045). B. Lectotype of *Scalaria magellanica magellanica*, herein designated (ZMB 2574). C, D, G, K, L. Specimen from off Tierra del Fuego (MACN-In 25028). E. Specimen from Cabo San Pío (MLP-Ma 14175). F, I, J. Specimens from off Santa Cruz Province (MACN-In 40400). H. Specimen from off Río de la Plata (MACN-In 25676). J. Detail of operculum sculpture. K, L. Details of teleoconch sculpture at last whorl. Scale bars: A, B, F = 10 mm; C, E, G, H = 5 mm; D, L = 500 µm; I, K = 1 mm; J = 20 µm.

Known distribution. Rio Grande do Sul (30ºS), Brazil (Rios 1994), south to Tierra del Fuego Province (55º41'S), and in the Pacific Ocean north to Golfo de Ancud (41º50'S), Chile. Living specimens: 18 to 214 m; shells up to 785 m.

Weil *et al.* (1999) also mentioned Antarctica in the distribution of "*Cirsotrema*" *magellanicum* (under *Epitonium*), although the source of this record is unknown and no other finding from this area is currently available to confirm its presence therein.

Description. Shell large (maximum L observed = 28.2 mm, apex missing; to 30 mm *fide* Clench & Turner (1952)), narrowly conical, thick, white, chalky (Fig. 8A–C, E, F). Protoconch glossy, elongate, of about 1,000 µm in length and 500 µm in maximum diameter; composed of 2 bulbous whorls (Fig. 8D); usually lost in larger specimens. Protoconch sculpture unknown (eroded in the available material). Limit between protoconch and teleoconch clearly evidenced by a change in sculpture. Teleoconch with up to 8 whorls, markedly convex in outline, attached (Fig. 8A–C, E, F); suture crossed by axial sculpture (Fig. 8K). Last whorl markedly flattened at the base. Aperture subcircular; outer margin thick, auriculate at base; inner margin either completely attached to last whorl or partially or completely detached; in the last two cases, originating a narrow and small to wide and large umbilicus. Fasciole small or absent (Fig. 8A–C, E, F).

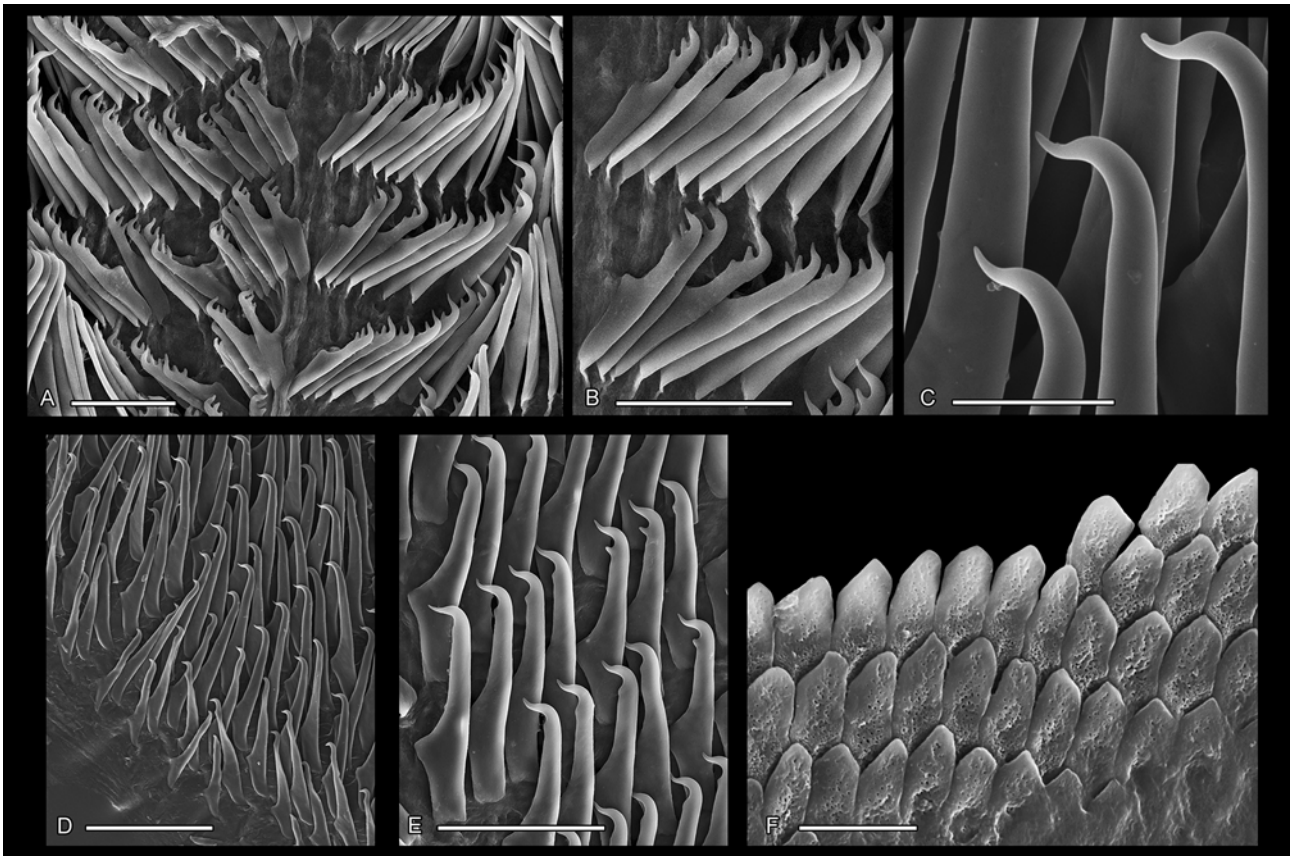

FIGURE 9. *"Cirsotrema" magellanicum*, radula and jaw. Specimens from off Santa Cruz (A, B, E same specimen as in Fig. 8F; C, D, F same specimen as in Fig. 8I, K) (MACN-In 40400). A–E. Radula. A. Central field. B. Inner teeth. C. Cusps of intermediate teeth. D. Outer teeth. E. Intermediate teeth. F. Jaw margin. Scale bars: A, B = 50 µm; C, E = 20 µm; D = 100 µm, F = 10 µm.

Teleoconch sculptured with slightly prosocline, widely-separated axial ribs and spiral elements. Ribs constant in number throughout the whorls: usually 13 to 15, but exceptionally as few as 10 and up to 18 (Fig. 8G, H). Ribs on the first whorl are low and rounded, gradually increasing in height in subsequent whorls, where they may either remain erect (Fig. 8C, F, G) or slightly to markedly recurved (Fig. 8A, B, E, H); this variation is present even among ribs of a single specimen (Fig. 8B). Ribs formed by fusion of several layers (Fig. 8K, L); evenly arcuate along the first two whorls, but showing a flattened, sloping part near the apical suture in subsequent whorls (Fig. 8C, F). Minute coronations sometimes present on the top, although generally lost by erosion. Ribs of adjoining

whorls obliquely aligned and usually fused at their bases. In the last whorl, axial ribs extending to umbilical area, with an abrupt change in curvature at the periphery of base, which is delimited by a strong spiral cord that emerges from the insertion of the outer lip of aperture (Fig. 8A–C, E, F, K). Interspaces of the axial sculpture showing 5–8 low but wide spiral cords, separated by extremely narrow interspaces, where secondary spiral cords and small, spirally aligned punctae are present (Fig. 8K, L). Secondary sculpture clearly visible in all whorls, but missing at the base. Spiral sculpture not crossing over axial sculpture.

Operculum: Thick, circular, multispiral, with edge of adjacent coils with raised edges, and subcentrally-located nucleus (Fig. 8I); outside surface sculptured with 20 to 28 massive, irregular bars per 0.1 mm, obliquely oriented with respect to growth lines (Fig. 8J). Colour: dark brown.

Jaw (Fig. 9F): Anterior part uniformly paved with several rows of polygonal, bluntly-pointed, pitted plates that continue to the margin.

Radula: With numerous teeth per row, all of them with a well-developed basal denticle (Fig. 9B, E). Teeth of the central field short and solid, with an acute apical denticle and two shorter but well-developed, bluntly-pointed secondary denticles (Fig. 9A). Subsequent teeth gradually increasing the length of the blade, and reducing the number of secondary denticles (Fig. 9B, E); the outer teeth only having the upturned, acute apical denticle (Fig. 9C, D). Outermost teeth reduced in size.

Remarks. The original description of *"Cirsotrema" magellanicum* is rather poor and the species was not figured by Philippi. Despite that, two characters clearly stand out from Philippi's description: 1) the species reaches a large size "Alt. 9½"', diam. 4½"' [= 24. 3 mm L, 11.4 mm W]; and 2) the shell is sculptured by "circa 15 oblique" axial cords, with spiral threads in the interspaces. No specimen matching exactly that description was found at the MNHN-Cl, ZMB or NHMUK, where other Chilean species studied by Philippi are housed. However, the ZMB houses a topotypic specimen, with an original handwritten label by Philippi, using this name (Fig. 8B). This is a 20.2 mm L specimen, with 10 axial ribs in the last whorl. Taking into account that this specimen comes from the type locality and was identified by Philippi himself as *Scalaria magellanica*, and considering the historical confusion surrounding the identity of *"Cirsotrema" magellanicum* (see below), the above-mentioned specimen (ZMB 2574), is here designated as neotype, with the express purpose of clarifying the taxonomic status of this species (ICZN, art. 75).

Strebel (1905) expanded the diagnostic characters of *"Cirsotrema" magellanicum*, particularly focusing on the axial sculpture, which he described as high, recurved ribs that abruptly slope from the suture. Based solely on the number of axial ribs in the last whorl, Strebel (1905) distinguished two varieties: one of them with 14–20 ribs (referred by him as *Scalaria magellanica s.s.*), and the other, represented by two specimens, one with 10 ribs per whorl, and the other with 12–13 ribs, which he named *Scalaria magellanica latecostata*. The "subtle" difference in the number of ribs could, at first, suggest that all these specimens correspond to variants of a single entity; however, the excellent figures provided by Strebel (1905: figs. 43a *vs*. 44a) reveal that he had actually two different taxa in hand. Unfortunately, Strebel (1905) failed to see that these taxa were not particularly different by the number of ribs; the "novelty" actually lay in the lots he referred to as *Scalaria magellanica s.s.*, and not in the lots he assigned his new subspecies. One of these specimens had been originally identified by Philippi as *Scalaria magellanica*, had come from the type locality and agreed with the original description, except for the lower number of ribs. Under this scenario, *Scalaria magellanica* Philippi (not Strebel) and *Scalaria magellanica latecostata* are here regarded as synonyms. However, the specimens misidentified by Strebel (1905) as *Scalaria magellanica s.s.*, correspond to one, or perhaps two new species, described below.

Castellanos (1970) identified specimens housed at the MACN as both *Epitonium magellanicum* and *Epitonium magellanicum latecostatum*. The study of this material reveals that some of the lots mentioned by the author (*i.e.*, MACN-In 25130, MACN-In 24186 and MACN-In 25018 in part) actually correspond to *"Cirsotrema" magellanicum*; the identity of the other lots is discussed below. Another specimen of *"Cirsotrema" magellanicum* (currently MACN-In 18676-1) was found among the specimens of "*Scala aff. orbignyi*" reported by Carcelles (1944) from Quequén, Buenos Aires Province, Argentina.

In shell morphology and sculpture *"Cirsotrema" magellanicum* resembles *"Cirsotrema" georgeanum nomen novum*, *"Cirsotrema" ctenodentatum* **n. sp.** and *"Cirsotrema" strebeli* **n. sp.** (see distinguishing characters under these species).

Cirsotrema douvillei Fenaux, 1937, described on the basis of a single, broken, large fossil specimen (95 mm L, according to the original reconstruction) from "rivière Santa Cruz", Santa Cruz Province, Argentina, was regarded

as a synonym, and as a possible synonym of *"Cirsotrema" magellanicum*, by Clench & Turner (1952) and by Brown & Neville (2015), respectively. However, the large size reached by *C. douvillei*, the age of its record, and the fact that in this species the spiral sculpture crosses the axial ribs —a condition absent in *"Cirsotrema" magellanicum*— preclude us from accepting this synonymy.

"Cirsotrema" georgeanum nomen novum
(Figure 10)

Scalaria fenestrata Strebel, 1908: 63–64, pl. 4, fig. 61a–d (*non* Meneghini in de Stefani, 1875 nor Wöhrmann, 1889)
Cirsotrema fenestrata: Powell, 1951: 114; Zelaya, 2005: 121

Type locality. 54°11' S 36°18'W, Cumberland Bay, South Georgia 252–310 m.

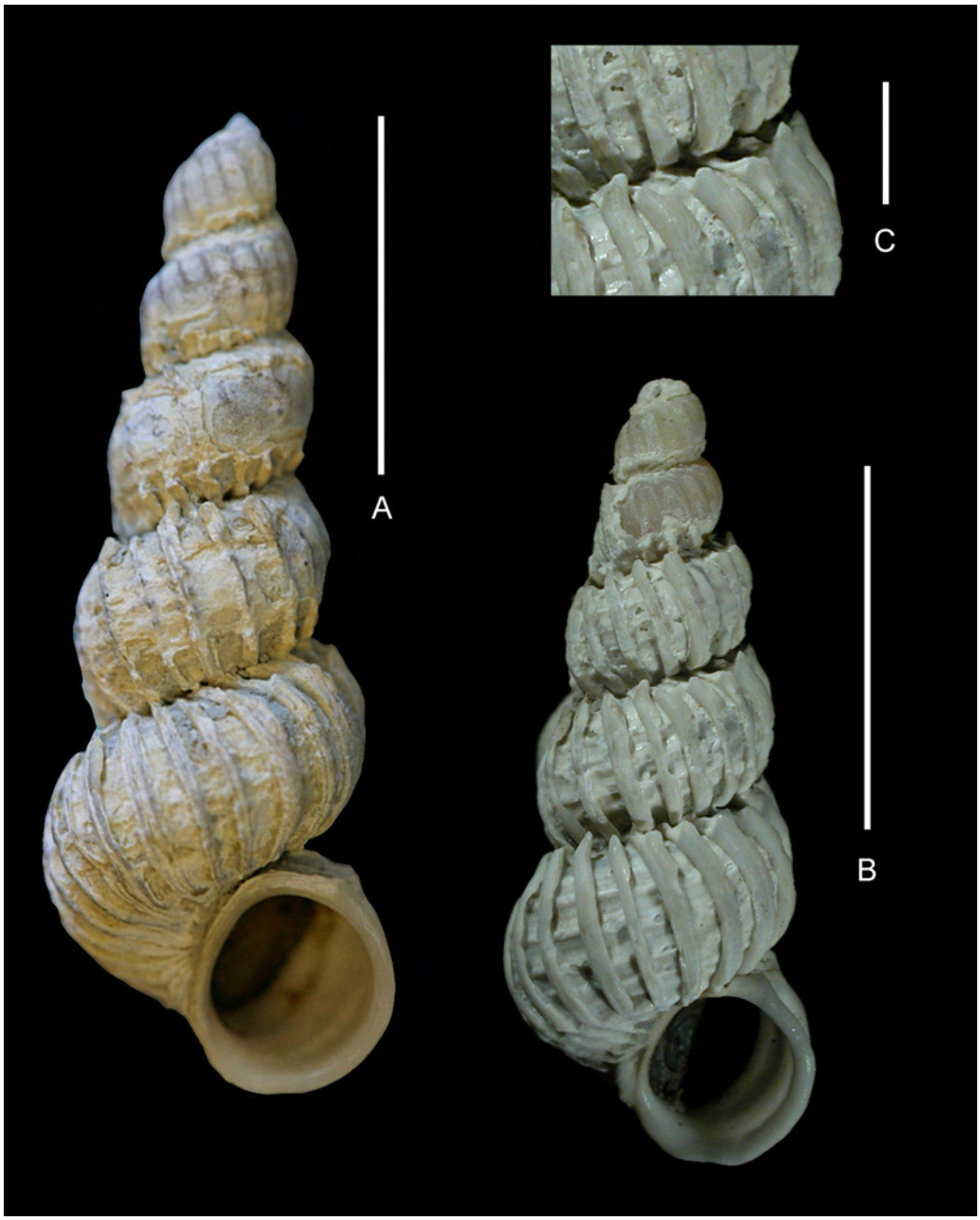

FIGURE 10. *"Cirsotrema" georgeanum* new name, shell. A. Syntype of *Epitonium fenestratum* (SMNH type-918). B, C. Syntype of *Epitonium fenestratum* (ZMH 3139). C. Detail of teleoconch sculpture at the suture. Scale bars: A, B = 10 mm; C = 2 mm.

Type material. Two syntypes (one syntype at SMNH type-918: Fig. 10A; the other syntype at ZMH 3139: Fig. 10B, C).

Known distribution. Only known from South Georgia.

Etymology. The name of the species refers to its provenance.

Remarks. *Scalaria fenestrata* Strebel, 1908 appears at present as a junior (primary) homonym of *Scalaria fenestrata* Meneghini in de Stefani, 1875 and *Scalaria fenestrata* Wöhrmann, 1889. Due to the above, *"Cirsotrema" georgeanum* is here proposed as a replacement name for Strebel's species.

In shell morphology, *"Cirsotrema" georgeanum* resembles *"Cirsotrema" magellanicum*; both species reach large sizes, and are sculptured with widely separated, lamellate axial ribs, with low but strong spiral elements in the interspaces of axial sculpture, and with a prominent spiral cord at the base. In fact, Brown & Neville (2015) suggested that both are probably synonyms. However, *"Cirsotrema" georgeanum* differs from *"Cirsotrema" magellanicum* by being slender, with whorls separated by a deeper suture, axial ribs with prominent coronations, and by lacking the auriculate peristome that is present in *"Cirsotrema" magellanicum*. Given these differences, both taxa are here regarded as distinct.

"Cirsotrema" ctenodentatum new species

(Figures 11, 12)

Epitonium magellanicum latecostatum: Castellanos, 1970: 64–65 (in part), pl. 4, fig. 13 (*non* Strebel, 1908)

Type locality. 54°47'54''S 65°14'42''W, Bahía Buen Suceso, Tierra del Fuego Province, Argentina, 18 m.

Type material. Holotype (MACN-In 40401) and one paratype (MACN-In 40402) from the type locality.

Additional material examined. Argentina: Malvinas / Falkland Islands: Lively Island (MACN-In 10138: 1 sh.; MM EE 7942.2: 11 sh.). Tierra del Fuego Province: 52°55'S 75°00'W, 92-101 m (USNM 870443: 1 sh.); 54°50'S 64°01'W, south of Isla de los Estados, 153.6 m (MACN-In 22733: 1 spm.); 54°41'35''S 64°01'37''W, 50.2 m (MACN-In 22614: 1 sh.); 55°41'S 66°34'W, 25 m (MACN-In 24975: 6 sh.); off Tierra del Fuego (MACN-In 40403: 3 spm.). Burdwood Bank: 54°30'23.4''S 59°48'39.24''W, 105 m (MACN-In 40782: 1 spm.).

Known distribution. Tierra del Fuego Province, Argentina; living specimens: 18 to 153.6 m.

Etymology. The name of the species refers to the comb-like morphology of the radular teeth, whose cusps are composed of several denticles.

Diagnosis. Shell elongated to broadly conical; protoconch of 2 rounded whorls; teleoconch sculptured with numerous, reflexed ribs, forming shoulders; interspaces between ribs with spiral cords; a stronger spiral cord delimiting the base. Operculum ovate, paucispiral. Jaw with several rows of polygonal plates at the anterior part. All radular teeth with three or four denticles at the cusp.

Description. Shell large (maximum L observed = 25.0 mm, apex missing), narrowly elongated to broadly conical, with gradated whorls; thick, white, chalky (Fig. 11A, B, E, F, H). Protoconch of about 1,000 µm in length and 700 µm in maximum diameter, composed of 2 evenly-rounded whorls (Fig. 11D), usually lost in larger specimens. Protoconch sculpture unknown, eroded in the available specimens. Limit between protoconch and teleoconch readily discernible, marked by a simple growth scar. Teleoconch with up to 7 whorls; whorls convex in outline (Fig. 11A, B, E, F, H); adjacent whorls attached; suture deep, crossed by axial sculpture. Last whorl flattened at the base. Aperture ovate; peristome continuous, thick, slightly auriculate at the base (Fig. 11A, B, E, F, H). Inner margin of aperture either completely attached to last whorl or partially detached, in the last case originating a narrow umbilicus. Fasciole usually well-developed.

Teleoconch sculptured with numerous, slightly- to markedly-prosocline axial ribs and spiral elements (Fig. 11A, B, E, F–H). Axial ribs usually 16 to 19 per whorl, but up to 25; either constant in number throughout whorls or with a greater number of ribs in the second and third teleoconch whorls. Ribs on the first whorl are low, narrow and evenly arcuate; in subsequent whorls, ribs become stronger, gradually increasing in height and slightly reflexed, formed by fusion of several layers (Fig. 11A–C, E–H). Apically, ribs projecting perpendicular to columellar axis, forming a straight shoulder that gradates the whorls (Fig. 11B, E, H), becoming convex anteriorly. Ribs of adjoining whorls obliquely aligned and fused, extending to umbilical area in last whorl, markedly changing their curvature at periphery of base (Fig. 11A, B, E, F, H). Interspaces of the axial sculpture showing 6–8 lower but

wide spiral cords, separated by extremely narrow interspaces, where secondary spiral cords and small, spirally aligned punctae are present. Spiral sculpture clearly visible in all whorls, but missing at the base. A strong basal spiral cord emerging from the insertion of the outer lip of aperture, delimits the base (Fig. 11G). Spiral sculpture not crossing over axial sculpture.

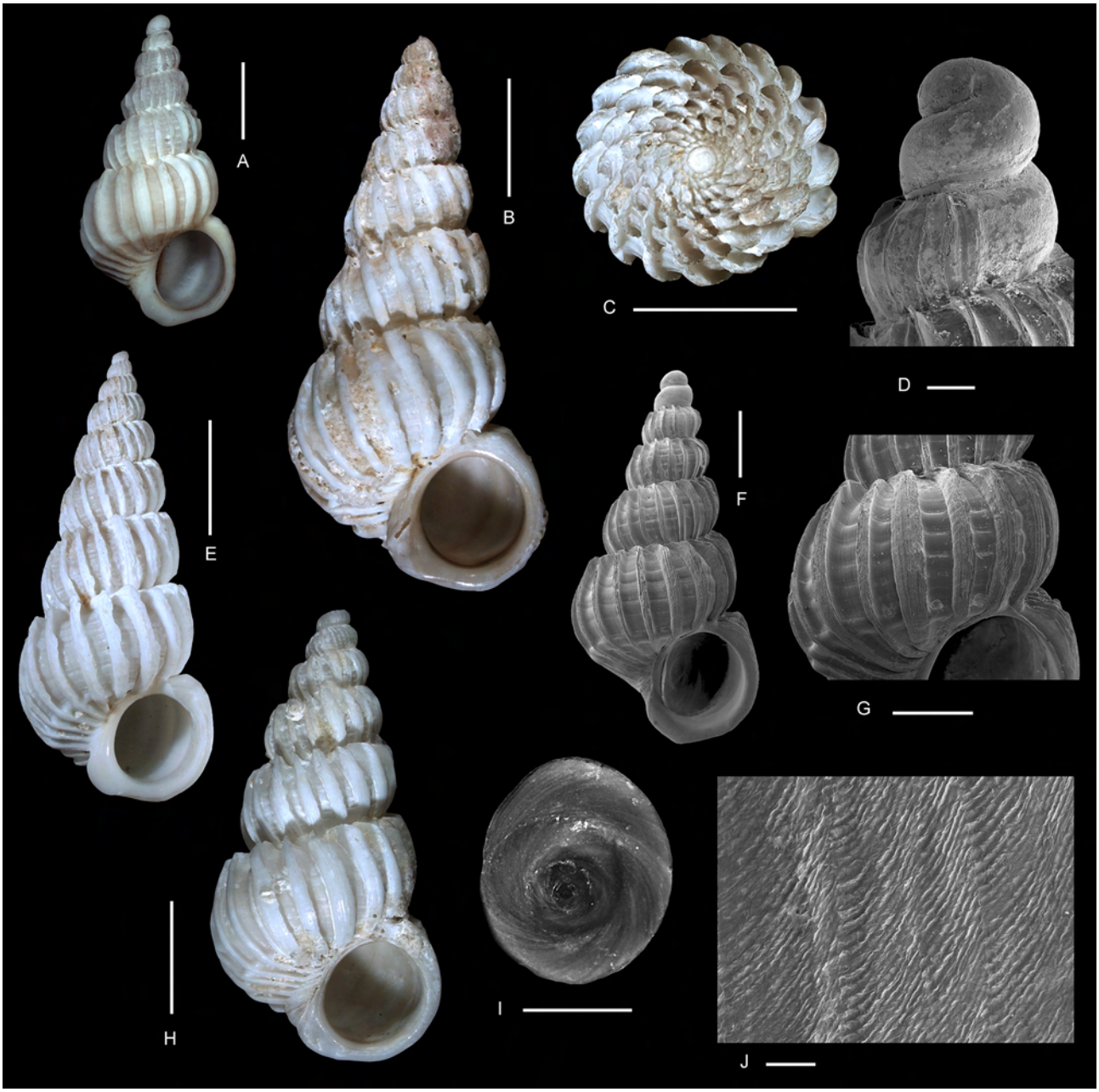

FIGURE 11. *"Cirsotrema" ctenodentatum* new species, shell and operculum. A, G, I. Holotype (MACN-In 40401). G. Detail of teleoconch sculpture at last whorl. B, H. Specimens from off Tierra del Fuego (MACN-In 24975). C, E. Specimen from off Tierra del Fuego (MACN-In 22614). D, F. Paratype (MACN-In 40402). J. Detail of operculum sculpture, specimen from off Tierra del Fuego (MACN-In 40403). Scale bars: A = 2 mm; B, C, E, H = 5 mm; D = 200 µm; F, G, I = 1 mm; J = 50 µm.

Operculum: Thin, ovate, with eccentric nucleus; paucispiral, with edge of adjacent coils with raised edges (Fig. 11I). Outside surface sculptured with about 23 regular bars per 0.1 mm, obliquely oriented with respect to growth lines (Fig. 11J). Colour: light brown.

Jaw (Fig. 12D, E): Anterior part uniformly paved with several rows of superimposed polygonal, bluntly-pointed, pitted plates that continue to the margin.

Radula: With numerous teeth per row, each with a well-developed basal denticle (Fig. 12A). Teeth of the central field with stout blades; subsequent teeth with elongate, strong blades, reducing in size near the outer margin

(Fig. 12A, B). Cusps similar along all radular field, comprising a short, acute apical denticle and usually two longer, blunt secondary denticles (Fig. 12C). An additional, smaller proximal denticle, sometimes present, varying from a knob to a well-developed structure, always smaller than the other denticles (Fig. 12C).

Remarks. In shell morphology, *"Cirsotrema" ctenodentatum* **n. sp.** closely resembles *"Cirsotrema" magellanicum*, from which it differs by having consistently more, lower and more markedly recurved axial ribs, which result in narrower interspaces. Another difference between these species arises in the straight shoulder of the axial ribs of *"Cirsotrema" ctenodentatum* **n. sp.**, which results in a markedly-gradated outline of the whorls. In *"Cirsotrema" magellanicum*, instead, the axial ribs slope apically. The distinction between *"Cirsotrema" ctenodentatum* **n. sp.** and *"Cirsotrema" magellanicum* becomes even more evident when comparing the operculum and radula: *"Cirsotrema" ctenodentatum* has a thin, ovate, paucispiral operculum, whereas that of *"Cirsotrema" magellanicum* is thick, subcircular and multispiral. With regard to the radula, *"Cirsotrema" ctenodentatum* **n. sp.** has three / four denticles in the cusp of outer teeth, while in *"Cirsotrema" magellanicum* these teeth invariably show a single denticle (the apical denticle). Another similar species to *"Cirsotrema" ctenodentatum* **n. sp.** is *"Cirsotrema" strebeli* **n. sp.** A comparison between these taxa is provided in the Remarks section of the following species.

Castellanos (1970) included under the name *Epitonium magellanicum latecostatum*, one lot belonging to this species (MACN-In 22733).

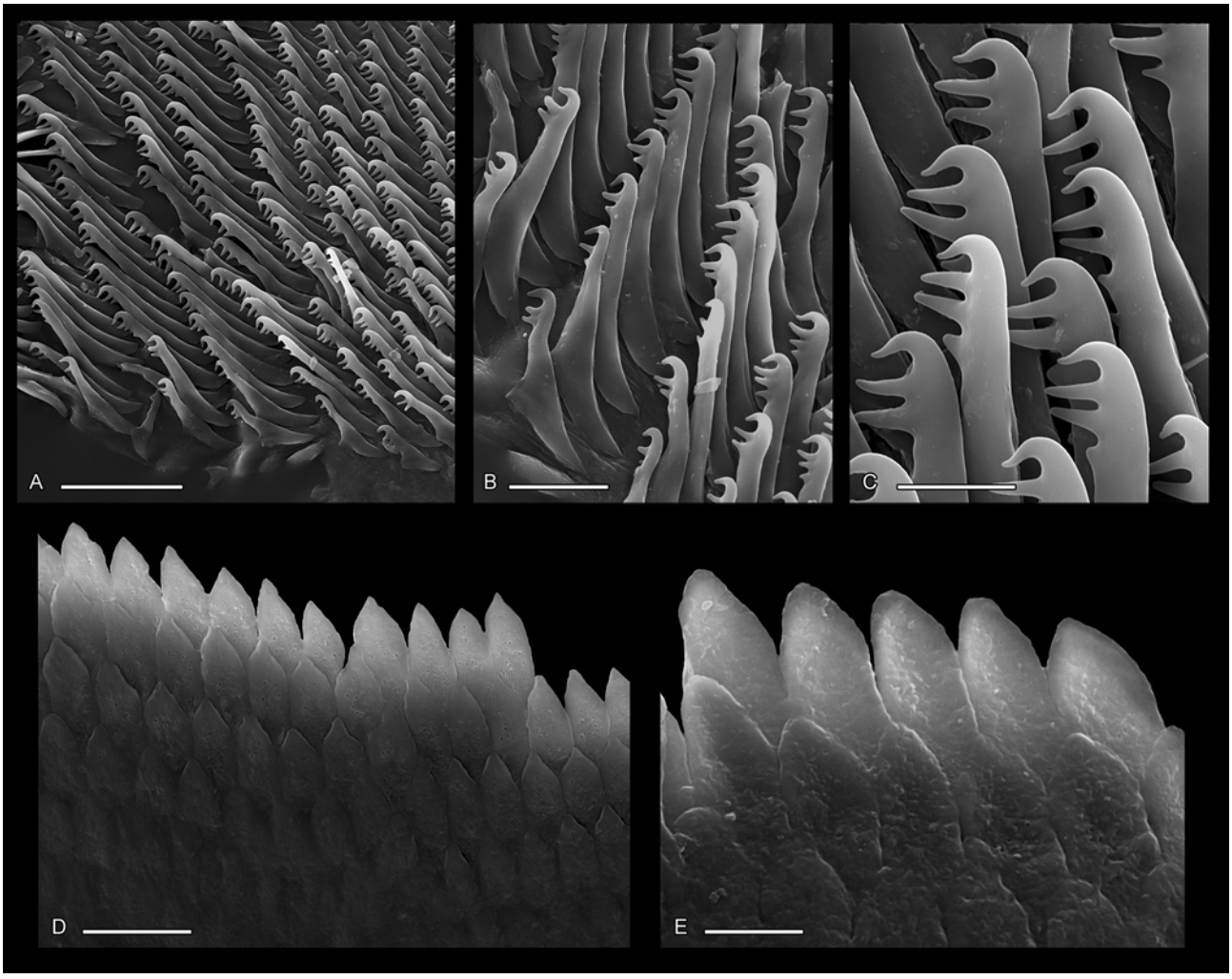

FIGURE 12. *"Cirsotrema" ctenodentatum*, radula and jaw. A–D. Holotype (same specimen as in Fig. 10A: MACN-In 40401). E. Specimen from off Tierra del Fuego (MACN-In 40403). A–C. Radula. A. Half radular field. B. Outer teeth. C. Cusps of intermediate teeth. D, E. Jaw. D. Anterior inner surface. E. Detail of plates. Scale bars: A = 50 µm; B = 20 µm; C, D = 10 µm; E = 5 µm.

***"Cirsotrema" strebeli* new species**
(Figures 13, 14)

Scalaria magellanica Strebel, 1905: 656–658 (in part), pl. 23, fig. 44a–e (not fig. 44f) (*non* Philippi, 1845)
Epitonium magellanicum: Castellanos, 1970: 63–64 (in part)

Type locality. 54°08'45.6''S 64° 57'36''W, off Tierra del Fuego Province, Argentina, 110 m.

Type material. Holotype (MACN-In 40393) and 10 paratypes (MACN-In 40394), all of them from the type locality.

Additional material examined. Argentina: Santa Cruz Province: [49°14'57''S 67°36'50''W], Punta Desengaño, San Julián (MACN-In 36924: 4 sh.). Tierra del Fuego Province: 54º26'30''S 64º53' W, 111.6 m (MACN-In 25028-1: 1 sh.); 54º45'40.6''S 63º49'06.8''W, Isla de los Estados (MACN-In 21969: 1 sh.); 54º47'S 63º35'W, 133.7 m (MACN-In 22296: 1 sh.); off Tierra del Fuego (MACN-In 40396: 3 spm.); 53º38'S 72º22'W, Canal David, 40 m (MACN-In 40395: 4 sh.); 55º01'S 66º42'W, Punta Moat, 15-20 m (MLP-Ma 14173: 1 spm., 1 sh.); 55º03'S 66º37'W, Cabo San Pío, 30-35 m (MLP-Ma 14174: 1 spm., 1 sh.). Burdwood Bank: 54°30'23.4''S 59°48'39.24''W, 105 m (MACN-In 40783: 4 sh.); 54°31'40.78''S 61°27'58.74''W, 137 m (MACN-In 40784: 1 spm.).

Known distribution. Santa Cruz (49º14'S) to Tierra del Fuego (55º03'S) Provinces, Argentina. Living specimens: 15 to 137 m.

Etymology. The species is dedicated to Hermann Strebel, in recognition for his contributions to the knowledge of the Magellanic molluscs.

Diagnosis. Shell narrowly elongate. Protoconch angulated. Teleoconch sculptured with numerous markedly-recurved axial ribs, not forming shoulder or coronations; a strong spiral cord at periphery of base; and weak spiral cords between axial ribs. Operculum ovate, paucispiral. Jaw margin with sharply-pointed denticles, followed by hexagonal to lanceolate plates. Most of the teeth with three denticles at the cusp; the outermost ones, with two denticles.

Description. Shell medium sized (maximum L observed = 13.2 mm), slender, moderately solid, white, dull (Fig. 13A, B, G, H). Protoconch glossy, of about 630 µm in length and 730 µm in maximum diameter; composed of 1¼ to 1½ whorls (Fig. 13D); apical ¼ whorl smooth; subsequent whorl(s) with a strong spiral keel at the middle of whorl or slightly apically displaced, producing an angulated protoconch outline (Fig. 13D). Spiral keel gradually increasing in strength, although not reaching protoconch margin. Above and below spiral keel, one or two irregular spiral cords, with bifurcations that form a branched sculpture pattern (Fig. 13D). Limit between protoconch and teleoconch delimited by a low cord. Teleoconch with up to 6¾ whorls, markedly convex in outline (Fig. 13A, B, G, H). Last whorl flattened at the base. Aperture subovate; peristome continuous, thick, projected at the base. Inner margin of aperture completely attached to last whorl (Fig. 13A, B, G, H). Umbilicus absent.

Teleoconch sculptured with prosocline, closely-arranged axial ribs and spiral elements (Fig. 13A, B, F–H). Axial ribs usually number 16 to 18 on the first whorls, and 18 to 22 in the last whorl of larger specimens. Ribs on the first whorl are low and narrow; on subsequent whorls, ribs gradually increase in height and become markedly recurved, thus giving the appearance of low but solid elements formed by fusion of several layers (Fig. 13C). Ribs evenly curved along the whorls, not forming shoulders, angulations or coronations, except at periphery of base, where they show an abrupt change and extend almost straight, reaching the umbilical area. Ribs of adjoining whorls obliquely aligned, fused. Interspaces of the axial sculpture showing 5 or 6 lower but wide spiral cords, separated by extremely narrow interspaces, where secondary spiral cords and small, spirally aligned punctae are present. Spiral sculpture clearly visible in all whorls, but missing at the base. A strong spiral cord that emerges from the insertion of the outer lip of aperture surrounds the base (Fig. 13F). Spiral sculpture not crossing over axial sculpture.

Operculum: Thin, ovate, with eccentric nucleus; first whorls slightly sunken; penultimate whorl with edge slightly upraised from last whorl, forming indentations (Fig. 13E). Outside surface with 19 to 22 wide, irregular bars per 0.1 mm, obliquely oriented with respect to growth lines (Fig. 13I). Colour: light brown.

Jaw (Fig. 14D, E): Anterior margin with a row of strong, sharp, triangular denticles; followed by numerous rows of densely-pitted, hexagonal plates, which gradually become lanceolate.

Radula: With numerous teeth per row, each having a well-developed basal denticle (Fig. 14A); innermost teeth and outermost tooth shorter than the others. Teeth of the central field usually with three (an apical and two

secondary) denticles, similar in length and solidness (Fig. 14B); an additional smaller, knob-like, proximal secondary denticle, sometimes present. Secondary denticles usually reducing in size and number (up to one) in outer teeth (Fig. 14C).

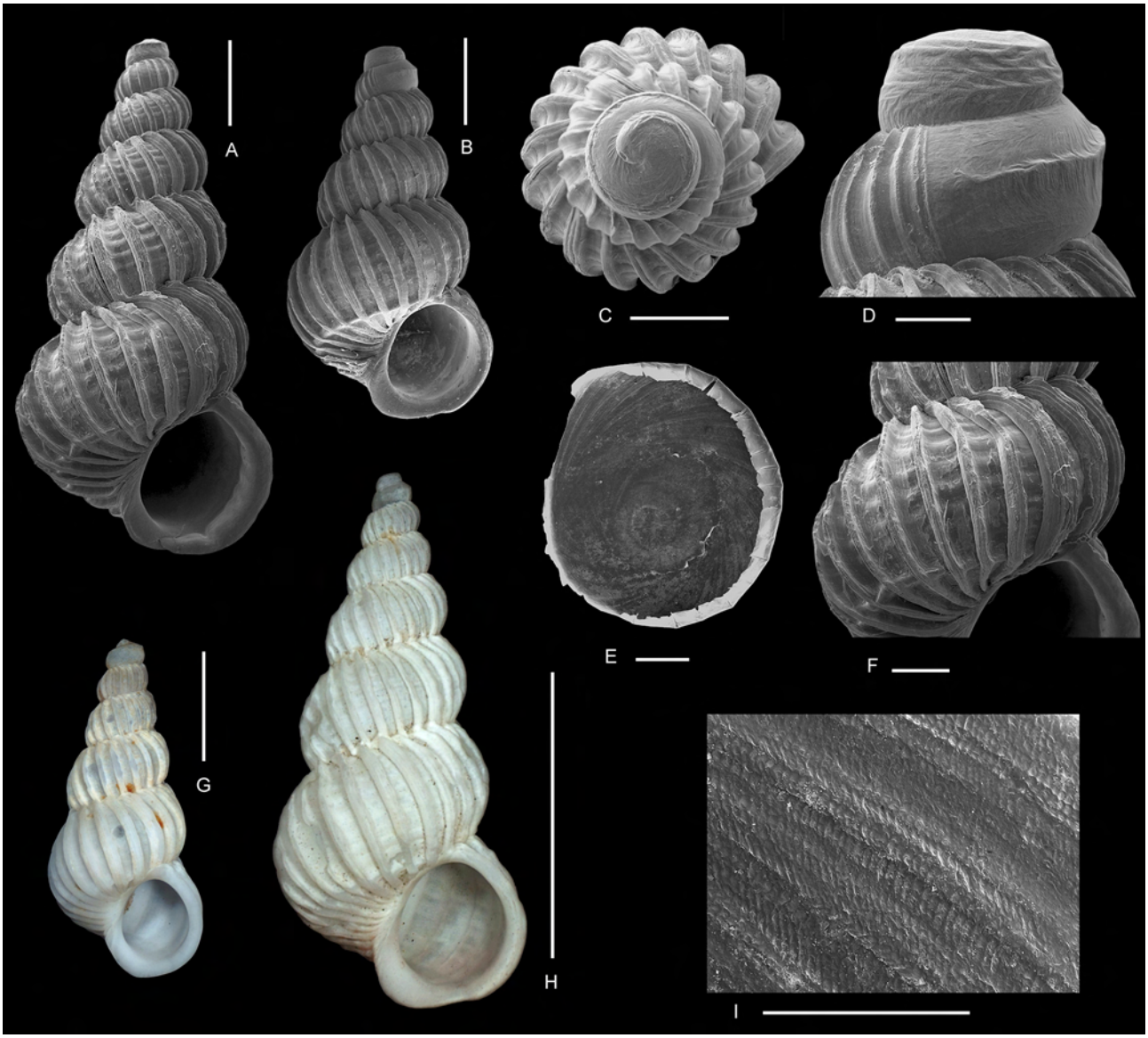

FIGURE 13. *"Cirsotrema" strebeli* new species, shell and operculum. A, F. Holotype (MACN-In 40393). F. Detail of teleoconch sculpture at last whorl. B–E, H, I. Specimens from off Tierra del Fuego (MACN-In 40396). I. Detail of operculum sculpture. G. Specimen from Cabo San Pío (MLP-Ma 14174). Scale bars: A, B = 1 mm; C, F = 500 µm; D, E = 200 µm; G = 2 mm; H = 5 mm; I = 20 µm.

Remarks. *"Cirsotrema" strebeli* **n. sp.** resembles *"Cirsotrema" magellanicum* and *"Cirsotrema" ctenodentatum* **n. sp.** by having a solid shell, sculptured with prominent axial ribs, low but solid spiral elements in the interspaces, and a strong spiral cord surrounding the base. Despite these overall similarities, *"Cirsotrema" strebeli* **n. sp.** consistently has more markedly recurved axial ribs, which consequently give the appearance of lower and wider elements. In addition, the ribs in *"Cirsotrema" strebeli* **n. sp.** are uniformly curved below the suture, lacking either the flat slope or the straight shoulder, as in the cases of *"Cirsotrema"magellanicum* and *"Cirsotrema"ctenodentatum* **n. sp.**, respectively. Another very distinctive character is the protoconch, which is angulated in *"Cirsotrema" strebeli* **n. sp.**, and evenly conic in *"Cirsotrema" magellanicum* and *"Cirsotrema" ctenodentatum* **n. sp.** Both *"Cirsotrema" magellanicum* and *"Cirsotrema" ctenodentatum* **n. sp.** reach larger sizes than *"Cirsotrema" strebeli* **n. sp.** The anterior part of the jaw in *"Cirsotrema" strebeli* **n. sp.** also differs from that of *"Cirsotrema" magellanicum* and *"Cirsotrema" ctenodentatum* **n. sp.**; in the former, there is a clear difference

between the marginal (denticles) and the subsequent (plates) elements, whereas in the latter two species, the margin and the subsequent rows are composed of similar polygonal plates. The operculum of *"Cirsotrema" strebeli* **n. sp.**, like that of *"Cirsotrema" ctenodentatum* **n. sp.** is ovate and paucispiral, while *"Cirsotrema" magellanicum* has a circular and multispiral operculum. Also similar to *"Cirsotrema" ctenodentatum* **n. sp.** is the morphology of the radula, with most of the teeth having three denticles at the cusp, although in the case of *"Cirsotrema" strebeli* **n. sp.**, the outermost teeth show two denticles. On the contrary, in *"Cirsotrema" magellanicum* the number of denticles is reduced outwards, showing only one in the outermost teeth (the apical denticle).

Judging from the excellent figures provided by Strebel (1905: fig. 44a–d) there is no doubt that the author had *"Cirsotrema" strebeli* **n. sp.** in hand, although he misidentified it as the nominotypical *Scalaria magellanica*. Strebel (1905) figured specimens of *"Cirsotrema" strebeli* **n. sp.** from Punta Arenas [53°10'S 70°56'W], Puerto Harris [53°50'S 70°27'W] and Strait le Maire [54°50'S 64°55'W], although none of these lots is currently preserved (B. Hausdorf, pers. com. 9/2014; A. Warén, pers. com. 7/2014). All of these figured specimens are small (less than 12.3 mm L) and show numerous and low axial ribs, which project roundly below the suture. Curiously, Strebel (1905) also included under the studied material of *Scalaria magellanica* two larger specimens (22.2 mm L) from Lively Island, Malvinas / Falkland, for which he did not mention illustrations but also provided a detail of axial ribs (Strebel 1905: fig. 44e), which was not referred to when mentioning the previous lots. This detail of the ribs, strikingly differs from the ribs of *"Cirsotrema" strebeli* n. sp., in being considerably wider. Unfortunately, the above-mentioned material from Lively Island could not be traced at the Manchester Museum to confirm its identity (H. McGhie, pers. com. 8/2014). If the details of these ribs actually correspond to the specimens from Lively Island, then this lot could correspond to *"Cirsotrema" ctenodentatum* **n. sp.** The large size of these specimens, and the finding herein of additional material of this species at the same place, could support this hypothesis.

One specimen of *"Cirsotrema" strebeli* **n. sp.** (currently MACN-In 25028-1) was found in a mixed lot, among specimens previously identified by Castellanos (1970) as *Epitonium magellanicum* (MACN-In 25028).

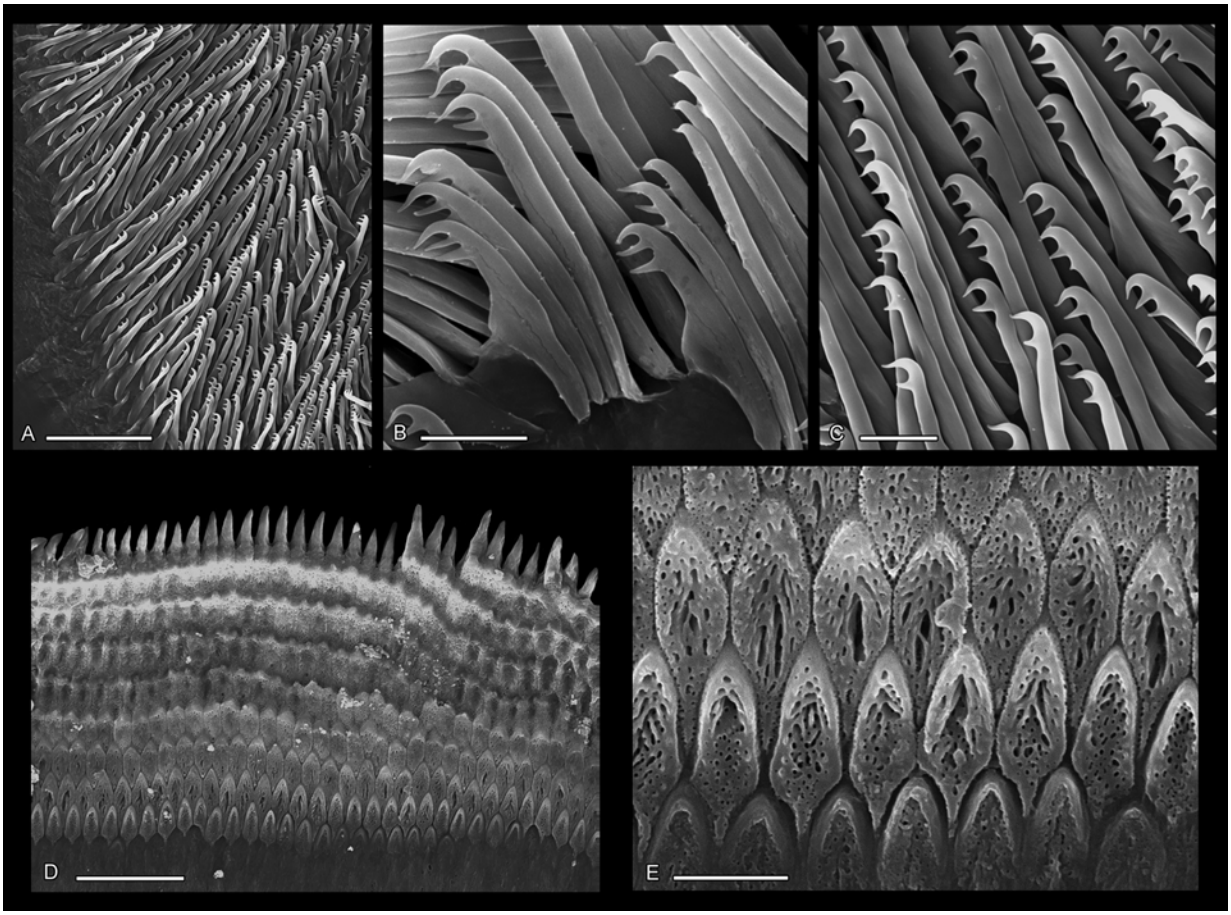

FIGURE 14. *"Cirsotrema" strebeli*, radula and jaw. Specimen from off Tierra del Fuego (same specimen as in Fig. 12E, I: MACN-In 40396). A–C. Radula. A. Half radular field. B. Inner teeth. C. Cusps of intermediate teeth. D, E. Jaw. D. Anterior inner surface. E. Detail of plates. Scale bars: A = 50 µm, B, C = 10 µm, D = 20 µm, E = 5 µm.

Discussion

This study provides the first comprehensive revision on the diversity of living species of Epitoniidae occurring in the Atlantic coast of Patagonia. From this area, a total of six nominal species had been mentioned in the literature, although until now, knowledge on most of these taxa appeared limited. With the only exception of *Epitonium fabrizioi*, the original descriptions of all other species have been based on shell morphology, with sculpture as the preponderant diagnostic character. Under this scenario, it is not surprising that species have been frequently confused, and that wrong names have been applied. Such is the case of "*Epitonium magellanicum*", a name previously used to refer to three different species.

An overview of morphological characters. When considering the information coming from teleoconch morphology, two main groups can be recognized among the species studied herein: one of them, represented by *Epitonium georgettinum*, *E. fabrizioi*, *E. evanidstriatum* and *E. striatellum*, in which the last whorl is uniformly convex at the base, thus making the axial sculpture appear evenly arched throughout the whorl; and a second group having a clearly differentiated, flat basal disc, surrounded by a prominent spiral cord, where the axial sculpture is remarkably angulated. The latter condition is present in *"Cirsotrema" magellanicum*, *"Cirsotrema" georgeanum*, *"Cirsotrema" ctenodentatum* and *"Cirsotrema" strebeli*. This second group in addition has few, low but wide spiral cords in all the whorls, contrary to the members of the first group, where the spiral sculpture is either completely absent (*Epitonium georgettinum* and *E. fabrizioi*), evident in the first whorls only (in *E. evanidstriatum*) or, if present in all the whorls (in *E. striatellum*), represented by numerous thin spiral elements.

The number of whorls, the size, the sculpture and / or the shape of the protoconch appear as useful characters for recognizing some of the species with similar teleoconch morphologies. For instance, *"Cirsotrema" strebeli* has a small (about 630 µm long), angulated and strongly sculptured protoconch, composed of 1¼ to 1½ whorls, whereas *"Cirsotrema" magellanicum* and *"Cirsotrema" ctenodentatum* have larger (about 1,000 µm long), evenly rounded and smooth protoconchs, of 2 to 2½ whorls. The protoconch morphology also allows to differentiate *Epitonium georgettinum*, *E. fabrizioi*, *E. striatellum* and *E. evanidstriatum*; although it fails to distinguish *"Cirsotrema" magellanicum* and *"Cirsotrema" ctenodentatum*.

The presence or absence of an umbilicus and the development of the fasciole are morphological characters with great intraspecific variability. In the case of *"Cirsotrema" magellanicum*, the presence or absence and, eventually, the width of the umbilicus, are related to the degree of attachment or detachment of the aperture to the last whorl. In the case of *Epitonium georgettinum*, *E. fabrizioi* and *"Cirsotrema" magellanicum* the fascioles range from scarcely- to well-developed, even among specimens of a single locality.

Exploring other characters. The operculum. The microsculpture of the opercula of the species from the Atlantic coast of Patagonia is relatively regular: all of them show threads, obliquely oriented with respect to growth lines. However, the density of such threads appears also as a difference between the two morphological groups recognized before: the opercula of *"Cirsotrema" magellanicum, "Cirsotrema" ctenodentatum* and *"Cirsotrema" strebeli* have a lower density than those of *Epitonium georgettinum*, *E. fabrizioi* and *E. evanidstriatum* (19 to 28 threads per 0.1 mm *vs*. 35 to 43 threads per 0.1 mm).

Furthermore, the outline, solidness, and number of whorls of the operculum proved to be a useful character for distinguishing some morphologically similar species, such as *Epitonium georgettinum* from *E. fabrizioi*, and *"Cirsotrema" magellanicum* from *"Cirsotrema" ctenodentatum* and *"Cirsotrema" strebeli*; although the last two species cannot be separated based on this character.

Radula and jaw. The radulae of all epitoniids occurring in the Atlantic coast of Patagonia are composed of numerous teeth per row, with the innermost and outermost teeth smaller than the intermediate ones, and each tooth having a basal denticle (although reduced in size in *Epitonium fabrizioi* and *E. evanidstriatum*) and an apical denticle. In addition, all species show secondary denticles in at least some of the teeth.

The radula appears as a useful character for distinguishing most of the morphologically similar species considered in this study. This is particularly noticeable in the case of *Epitonium georgettinum* and *Epitonium fabrizioi*, which differ in the number, morphology and orientation of the secondary denticles, as well as in the separation of the teeth in the central field. Differences in radular morphology are less evident in other cases, but still useful for species distinction. For instance, the morphology of the outermost teeth allows the distinction of *"Cirsotrema" magellanicum* with respect to *"Cirsotrema" ctenodentatum* and *"Cirsotrema" strebeli*, while the constancy / variation in the number of secondary denticles enables the distinction between the last two species.

However, great similarities were found between the radulae of *Epitonium georgettinum* and *"Cirsotrema" ctenodentatum*, and between those of *E. evanidstriatum* and *"Cirsotrema" magellanicum*, species that clearly differ in their shell morphology. The presence of different radular morphologies in closely-related species, and similar radular morphologies in unrelated ones, induced Gittenberger & Gittenberger (2005) to suggest that radulae cannot be used to define most epitoniid genera. Alternatively, Gittenberger & Gittenberger (2005) concluded that jaw morphology "seems to be useful to identify the genera".

Concerning the jaw, two main groups are distinguished among the species considered herein: one of them showing only one discernible row of denticles at the anterior edge, and a second group of species in which the anterior part of the jaw is paved with multiple rows of plates. The first condition appears in *Epitonium georgettinum*, *E. fabrizioi* and *E. evanidstriatum*, while the second in *"Cirsotrema" magellanicum*, *"Cirsotrema" ctenodentatum* and *"Cirsotrema" strebeli*. Once again, it should be noted that some species with similar shell morphologies, such as *Epitonium georgettinum* and *E. fabrizioi*, can be separated regarding jaw morphology. The same is valid when comparing *"Cirsotrema" strebeli vs*. *"Cirsotrema" magellanicum* and *"Cirsotrema" ctenodentatum*; although this character does not allow the distinction between the last two species. On the other hand, it should be noted that two species having quite distinct shell morphologies, such as *E. georgettinum* and *E. evanidstriatum* show indistinguishable jaw morphologies.

On the (sub)generic placement of the species. Different (sub)generic combinations have been used in the past to refer to the species considered in this study. In this regard, *"Cirsotrema" magellanicum* was previously listed under the (sub)genera *Epitonium* Röding, 1798 (Castellanos 1970; Cárdenas *et al*. 2008); *Scalaria* Lamarck, 1801 (Philippi 1945; Strebel 1905); *Scala* Mörch, 1852 (Melvill & Standen 1912); *Opalia* H. and A. Adams, 1853 (Ihering 1907; Carcelles 1950); *Coroniscala* Boury, 1910 (Boury 1911; Powell 1960); *Nitidiscala* Boury, 1909 (Nielsen & Valdovinos 2007) and *Boreoscala* Kobelt, 1902 (Clench & Turner 1952; Weil *et al.* 1999); the latter sometimes regarded either as a subgenus of *Gyroscala* Boury, 1887 (e.g., Kilburn 1985) or *Cirsotrema* Mörch, 1852 (Nakayama 2003). On the other hand, *Epitonium georgettinum* was attributed to *Nitidiscala* (Weil *et al.* 1999; Bonfitto & Sabelli 2001) and *Clathrus* Agassiz, 1837 (Carcelles 1950; Carcelles & Williamson 1951), while *Epitonium striatellum* was placed in *Asperiscala* Boury, 1909 (Clench & Turner 1952) and *Sodaliscala* Boury, 1909 (Weil *et al.* 1999). None of the above-mentioned (sub)generic allocations was properly discussed or justified. Pastorino & Penchaszadeh (1998) commented that *Epitonium fabrizioi* could be allocated in *Hirtoscala* Monterosato, 1890, although the authors pointed out some differences between this species and other species of that subgenus.

Regarding shell morphology*, Epitonium georgettinum*, *E. fabrizioi*, *E. evanidstriatum*, and *E. striatellum* agree well with the traditional concept of *Epitonium*, for which *Scala, Nitidiscala, Asperiscala, Sodaliscala* and *Hirtoscala* (among many others names) are currently regarded as subjective synonyms; *Scalaria* as an objective junior synonym; and *Clathrus* Agassiz, 1837 (not *Clathrus* Oken, 1815, a name rejected by the ICZN; nor *Clathrus* Gray, 1842 = *Opalia* H. & A. Adams, 1853), a genus restricted to fossils (Brown & Neville 2015). The jaw morphologies of *Epitonium georgettinum*, *E. fabrizioi* and *E. evanidstriatum* are also in agreement with that shown by Gittenberger & Gittenberger (2005: figs. 219–225) for other *Epitonium* species. On the other hand, the presence of a prominent basal cord in *"Cirsotrema" magellanicum, "Cirsotrema" strebeli, "Cirsotrema" ctenodentatum* and *"Cirsotrema" georgeanum* exclude these species from the traditional concept of *Epitonium*, and moreover distinguish these species from *Scalaria greenlandica* Perry, 1811, the type species of *Boreoscala*. The significance of this character was previously questioned by some authors. In fact, Kilburn (1985: 241) recognized that "the presence or absence of a basal cord… appears to have been independently derived in several lineages, and within a group may be present or absent in apparently related species". However, Gittenberger & Gittenberger (2005: 201) concluded that "presence of a basal cord is a more informative character state than most other teleoconch characters". This condition led the authors to consider *Gyroscala* more closely related to *Cirsotrema* than to *Epitonium*, as had been previously suggested by other authors (e.g., Abbott 1974).

The distinction of *Cirsotrema* and *Gyroscala* from *Epitonium* is also supported by molecular data (Gittenberger & Gittenberger 2005; Gittenberger *et al*. 2006). Furthermore, Gittenberger & Gittenberger (2005) found that the jaws of *Cirsotrema* and *Gyroscala* "differ distinctly" from those of *Epitonium* by having multiple rows of plates at the anterior edge of jaw. The latter condition was also found in this study in *"Cirsotrema" magellanicum, "Cirsotrema" ctenodentatum* and *"Cirsotrema" strebeli*. Due to this, the above-mentioned species are tentatively assigned to *Cirsotrema*. Nevertheless, it should be noted that none of these species has the "minutely

beaded" opercula reported by Bouchet & Warén (1986) for several species of *Cirsotrema*, or such elaborate sculpture as present in *Scalaria varicosa* Lamarck, 1822, the type species of *Cirsotrema*. In the latter the axial lamellae are completely recurved and undulating at their crests which, when contacting each other, produce a typically "multiperforate" shell surface (Kokshoorn *et al*. 2007). Alternatively, *"Cirsotrema" magellanicum, "Cirsotrema" ctenodentatum* and *"Cirsotrema" strebeli* appear more similar in shell sculpture to "*Cirsotrema*" *zelebori* Dunker, 1866 (shown by Beu (2011): fig. 5) and *Scalaria coronalis* Deshayes, 1861, the latter an Eocene species of the Paris Basin, designated as the type of *Coroniscala*. However, in the first case the spiral sculpture crosses over the axial sculpture, consequently originating ridges and nodules over the axial ribs. This condition is not present in the species from the Atlantic coast of Patagonia. Furthermore, the jaws of *S. zelebori* and *S. coronalis* are unknown, making it impossible to discount that these similarities could be originated solely through morphological convergence. In fact, shell characters have proven to be subject of convergent or parallel evolution among unrelated epitoniid groups (Kilburn 1985; Gittenberger & Gittenberger 2005; Gittenberger *et al.* 2006); and it should also be taken into account that some epitoniid (sub)genera have no consistently distinct shell characters to define them (Gittenberger & Gittenberger 2005).

Conclusion

The generic placement of the species considered in this study is tentative, due to the chaotic state of worldwide epitoniid taxonomy and the numerous limitations that exist at present for properly recognizing most of the (sub)genera of this family. Despite that, and based on the information coming from shell morphology, jaw characters and opercula microsculpture, two main groups of species are recognized among the living epitoniid species occurring in the Atlantic coast of Patagonia: one group, represented by *Epitonium georgettinum*, *E. fabrizioi*, *E. evanidstriatum*, and *E. striatellum*, agrees with the current concept of *Epitonium* (although the monophyly of this genus was recently questioned by some authors; e.g.: Gittenberger *et al.* 2006). A second group, represented by *"Cirsotrema" magellanicum, "Cirsotrema" strebeli, "Cirsotrema" ctenodentatum* and *"Cirsotrema" georgeanum*, closely resembles *Cirsotrema* and *Gyroscala* in jaw morphology (namely, by the presence of multiple rows of plates in the anterior edge of the jaw), but greatly differs in shell sculpture. These discrepancies suggest that a new genus for allocating the Patagonian species could be needed; but due to the numerous (sub)generic names of Epitoniidae currently available, and the unclear diagnostic characters for most of these taxa, we prefer to postpone the introduction of new names until more information is available for these taxa, and the degree of variation for these characters is well understood in the group. If in fact, if the shape of the jaw plates proved to be a diagnostic character at genus level, then *"Cirsotrema" strebeli* would require a different generic allocation from that of "*Cirsotrema" magellanicum* and *"Cirsotrema" ctenodentatum* (despite their overall teleoconch similarities). The distinction of these species could be also supported by the different protoconch morphologies present in these taxa. Finally, this study reveals that the usage of isolated (either morphological or anatomical) characters is usually insufficient for identifying some of the species considered herein; however, if these characters are combined, all species may be clearly recognized.

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