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A NEW GENERIC PLACEMENT FOR "*CALLIOSTOMA*" *BLAKEI* CLENCH & AGUAYO, 1938 (GASTROPODA: TROCHOIDEA)

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ABSTRACT

"Calliostoma" blakei Clench & Aguayo, 1938, described from Río Negro Province, Argentina, appears in the literature either under the genera *Calliostoma*, *Photinula* (Calliostomatidae) or as a member of the Umboniinae (Trochidae). The study of live-collected specimens allows to revise its generic placement.The species is characterized by a bipectinate ctenidium with short afferent membrane, isolated appendices in the left side of the neck, and the rachidian and the first lateral teeth reduced to their base. This set of characters, not present in any other trochoid, leads us to propose the new genus *Carolesia* for this species.

Key words: Gastropoda, Trochoidea, *Carolesia*, southwestern Atlantic.

INTRODUCTION

The Trochoidea is one of the most diversified gastropod superfamilies, with a large number of genera and species (Hickman & McLean, 1990). Traditional classification within the group has been based upon shell characters alone (e.g., Carcelles, 1945; Clench & Turner, 1960; McLean, 1964, 1970; Quinn, 1992a, b; Nascimento de Barros, 2010). Hickman & McLean (1990) recognized the plasticity and convergent nature of the shell morphology in the group, suggesting the combination of this information with anatomical characters from such structures as the ctenidium, radula, epipodial elements, snout and foot. On the basis of this information, they recognized two formal families (Turbinidae and Trochidae), and a third "provisional" and paraphyletic (Skeneidae) group. However, a number of subsequent molecular studies showed some inconsistencies between morphological / anatomical and molecular characters, mainly arising in the fact that both Trochidae and Turbinidae [in Hickman & McLean's (1990) sense], appear as polyphyletic (Geiger & Thacker, 2005; Williams & Ozawa, 2006; Kano, 2008; Williams et al., 2008, 2010). This resulted in the splitting of these taxa into up to eight families (Williams, 2012). Despite the numerous contributions and new findings that have been published in the recent years on the global Trochoidea, the diversity and taxonomy of the species of this group occurring in Argentinean waters remain obscure. The only exceptions are the genera *Calliostoma* Swainson, 1840, and *Margarella* Thiele, 1893, revised by Clench & Turner (1960) and Castellanos & Fernández (1976), and Zelaya (2004), respectively.

Clench & Aguayo (1938) described "*Calliostoma*" *blakei* from off Cape Bermeja, Río Negro Province, Argentina. Clench & Turner (1960), although with doubts, placed it in *Photinula* Adams & Adams, 1854, also a member of the the Calliostomatidae. This generic placement was followed in the subsequent literature (Figueiras & Sicardi, 1970, 1980; Scarabino, 1977; Castellanos, 1982; Ageitos de Castellanos & Landoni, 1989; Rios, 1994; Rosenberg, 2013). However, the radula of "*Photinula*" *blakei* (figured by Calvo, 1987: fig. 30) clearly differs from that of *Photinula caerulescens* (King, 1832), the type species of the genus (figured by McLean, 2012: fig. 7). Quinn (1992a) stated that the correct placement of "*Photinula*" *blakei* is among the Lirulariinae (= Umboniinae, Trochidae; Williams et al., 2010), and Aguirre & Farinati (2000) tentatively listed the species under *Tegula* (*Agathistoma*), but without any argument for this proposed placement.

The objective of this contribution is to provide a new generic placement for "*Calliostoma" blakei*, and to discuss the familial affinities of this species.

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MATERIALS AND METHODS

This study is based on living specimens collected in the Golfo San Matías, Río Negro Province, Argentina. Samples were hand-collected from the intertidal zone during the lowest low tides, by diving in the shallow subtidal, and with a 2 mm mesh-size net at greater depths. Information of living animals was obtained and documented from specimens maintained in aquaria. Specimens for anatomy were relaxed in magnesium chloride and fixed in 10% sea-water formalin. The gross anatomy and radulae were studied with ten specimens from different sites and depths. Radulae were removed by dissection, cleaned by rinsing in a sodium hypochlorite solution and mounted for scanning electron microscopy (SEM); soft parts were hexamethyldisilazane prepared for SEM. Voucher specimens were deposited in the collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires. This collection was also studied in search for additional information on the distribution of the species. The number of specimens (spec.) and shells (s.) for each lot is indicated in the material examined section. The terminology used throughout the text follows Hickman & McLean (1990). The ratio height/width is refered to as H/W. For comparative purposes live-collected specimens of *Tegula patagonica* d'Orbigny, 1835, were also studied. *Tegula* Lesson, 1832, is here used in a broad sense, including some species formerly assigned by different authors to the (sub)genera *Chlorostoma* Swainson, 1840, and *Agathistoma* Olsson & Harbison, 1953. This is due to the uncertainties concerning the distinctive characters for these (sub)genera, the consequently differing opinions on the usage of these names, and the lack of a recent world-wide revision on the (sub)generic placement of most species of this / these group(s).

SYSTEMATICS

Carolesia, new genus

Type species: Calliostoma (*Calliostoma*) *blakei* Clench & Aguayo, 1938.

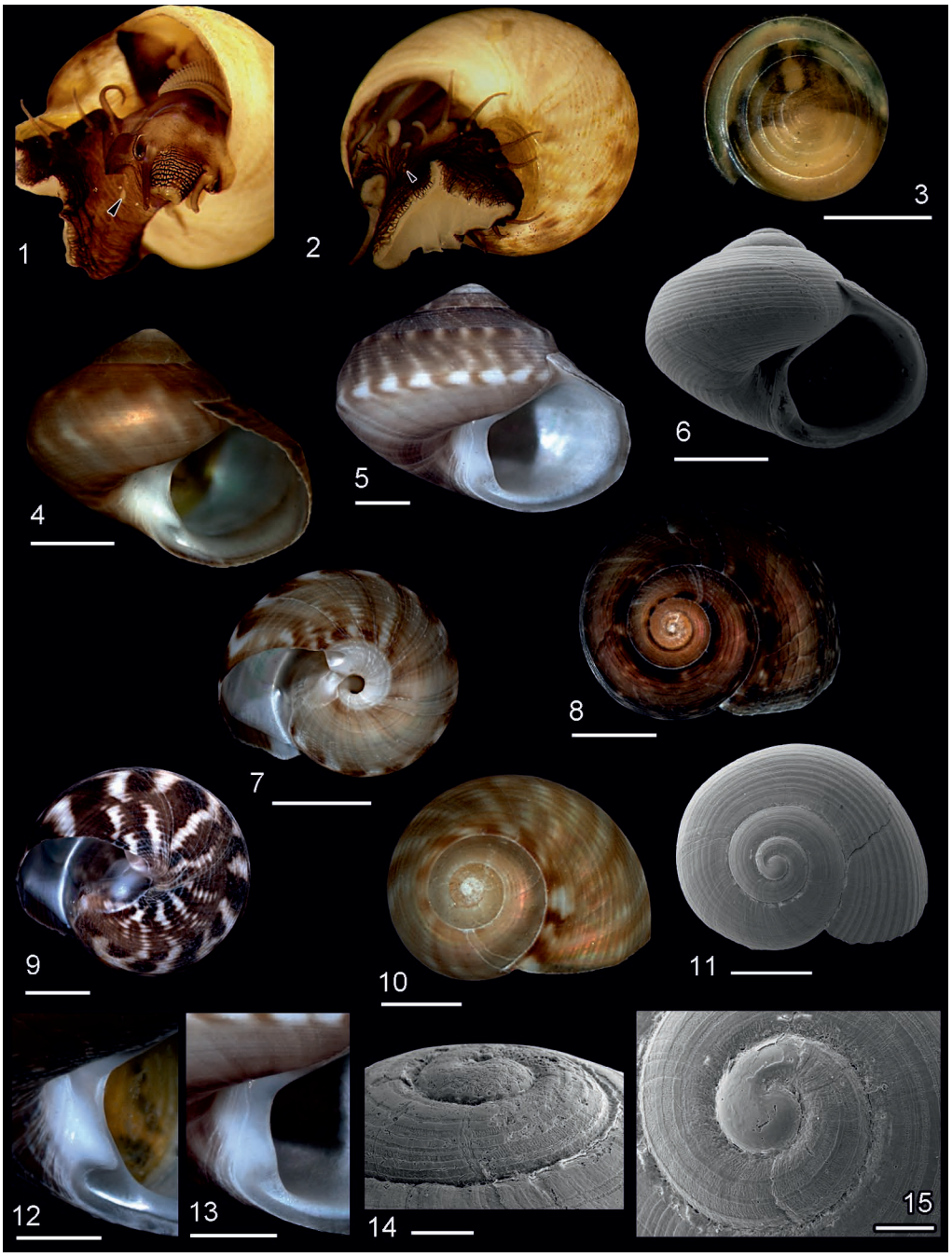
Distinctive Characters: Shell solid, with low spiral sculpture. Columella with moderately to well-developed basal denticle and a depression beneath it. Left side of the neck with a triangular, flattened projection at the anteriormost part, and two or three smooth, tentaculiform processes posteriorly. Ctenidium bipectinate, with short afferent membrane. Radula with rachidian and first lateral teeth reduced to rectangular, wider than high, basal plates; remaining laterals narrower, with well-developed shaft and cusp. First marginal with well developed shaft and cusp, and inner projection at the base.

Ethymology: The new genus is named after Carole S. Hickman, in recognition for her contributions to the understanding of Trochoidea.

Comparisons: The shell of *Carolesia* closely resembles that of *Tegula mariana* Dall, 1919 (figured by Hickman & McLean, 1990: fig. 35E). *Tegula* (as defined by Hickman & McLean, 1990) and *Carolesia* share the presence of a bipectinate ctenidium, with a short afferent membrane and four pairs of epipodial tentacles. However, *Tegula* strikingly differs from *Carolesia* in having: (1) a smooth or digitated longitudinal and continuous fringe, extending all along the left side of the neck (i.e., from the posterior part of the left eye stalk to the base of the first epipodial tentacle) (Hickman & McLean, 1990; Collado, 2008), while in *Carolesia* the left side of the neck shows discontinuos elements: a short, triangular, flat, anterior projecton, followed by two or three smooth tentaculiform processes; (2) all five lateral teeth narrow, similar, and with well-developed cusps, while in *Carolesia*, the first laterals differ from the other laterals in being widened and in lacking of distinct cusp.

Carolesia blakei
(Clench & Aguayo, 1938)
new combination
Figs. 1–23

Calliostoma (*Calliostoma*) *blakei* Clench & Aguayo, 1938: 376, pl. 28, fig. 6.
Photinula blakei: Figueiras & Sicardi, 1970: 31, pl. 8, fig. 115; Scarabino, 1977: 181, pl. 2, fig. 15; Figueiras & Sicardi, 1980: 184 [listed only]; Calvo, 1987: 65, fig. 30; Ageitos de Castellanos & Landoni, 1989: 23, pl. 4, fig. 2; Rios, 1994: 35, pl. 10, fig. 103.
Photinula blackei [sic]: Castellanos, 1982: 42 [listed only].
Tegula (*Agathistoma*)? *blakei*: Aguirre & Farinati, 2000: 256, pl. 2, figs. 16, 17.



FIGS. 1–15. *Carolesia blakei*. FIGS. 1, 2: Living specimens (arrowhead showing the lateral papillae); FIG. 3: Operculum; FIGS. 4–15: Shell. FIGS. 4–6: Apertural view; FIGS. 7, 9: Umbilical view; FIGS. 8, 10, 11: Apical view; FIGS. 12, 13: Detail of columella; FIGS. 14, 15: Protoconch. FIG. 14: Lateral view; FIG. 15: Apical view. Figs. 1, 2: Specimen from El Buque, MACN-In 3946; Figs. 3–15: Specimens from Las Grutas. Figs. 3, 5, 8, 10, 12, 13: MACN-In 39455; Fig. 4: MACN-In 39459; Figs. 6, 14: MACN-In 39464; Fig. 7: MACN-In 39458; Fig. 9: MACN-In 39462; Figs. 11, 15: MACN-In 39463. Scale bars: Figs. 3–5, 10, 12, 13 = 1 mm; Figs. 6, 11 = 500 µm; Figs. 7–9 = 2 mm; Figs. 14, 15 = 100 µm.

Type Material: Holotype and 50 paratypes at Museum of Comparative Zoology, Harvard; [n?] Paratypes at Museum Poey, Havana (*fide* Clench & Aguayo, 1938).

Type locality: off Cape Bermeja, Argentina (41°17'S), 17 fathoms [31 m].

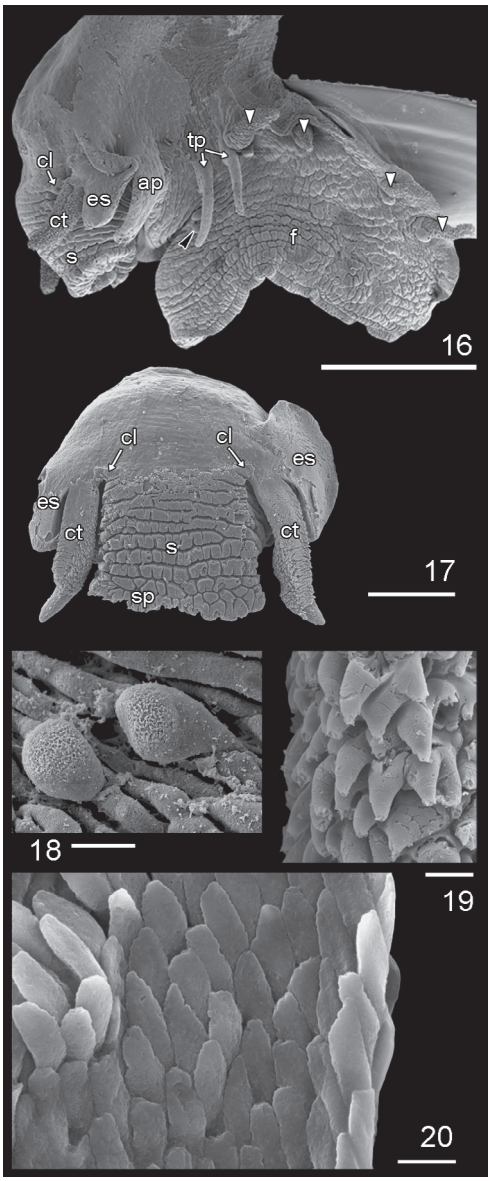
Material Examined: Uruguay: 34°40'00"S, 53°59'30"W, Rocha, 30 m (MACN-In 15359: 47 s.); [34°40'S, 54°10'W], Cabo Santa María (MACN-In 15289: 3 s.). Argentina: [38°22'S, 57°30'W], Mar del Plata, Buenos Aires (MACN-In 8731: 1 s.); [38°22'S, 57°30'W], Mar del Plata, Buenos Aires (MACN-In 8587-2: 1 s.); [38°22'S, 57°30'W], Mar del Plata, Buenos Aires, 33–37 m (MACN-In 8727: 1 s.); [38°22'S, 57°30'W], Mar del Plata, Buenos Aires (MACN-In 8729: 3 s.); [38°22'S, 57°30'W], Mar del Plata, Buenos Aires (MACN-In 14344: 7 s.); [38°22'S, 57°30'W], Mar del Plata, Buenos Aires (MACN-In 16539: 7 s.); [38°17'S, 57°29'W], Mar del Plata, Buenos Aires (MACN-In 8728: 6 s.); [38°22'S, 57°30'W], Mar del Plata, Buenos Aires (MACN-In 8655: 156 spec., 2 s.); [38°22'S, 57°30'W], Mar del Plata, Buenos Aires (MACN-In 8730: 3 s.); [38°22'S, 57°30'W], Mar del Plata, Buenos Aires (MACN-In 8726: 8 s.); [38°22'S, 57°30'W], Mar del Plata, Buenos Aires (MACN-In 29452: 3 s.); [38°35'S, 58°41'W], Puerto Quequén, Buenos Aires, 18 m (MACN-In 19545: 1 s.); [38°37'S, 57°32'W], Punta Mogotes, Buenos Aires, 39 m (MACN-In 8629: 15 s.); [38°37'S, 57°32'W], Punta Mogotes, Buenos Aires (MACN-In 8653-2: 5 s.); 38°40'S, 56°00'W, Buenos Aires, 93 m (MACN-In 8725-1: 2 spec.); Golfo San Matías, Río Negro (MACN-In 21299: 8 s.); [40°51'S, 65°3'W], San Antonio Oeste, Río Negro (MACN-In 23695: 2 s.); 40°25'47.4"S, 65°25'14.1"W, Las Grutas, 8 m (MACN-In 39455: 16 spec., 3 s.); 40°25'47.4"S, 65°30'01.2"W, Las Grutas, 8 m (MACN-In 39456: 2 spec.); 40°29'35.2"S, 65°31'44.7"W, Las Grutas, 6 m (MACN-In 39457: 8 spec., 62 s.); 40°29'46.2"S, 65°28'20.1"W, Las Grutas, 10–11 m (MACN-In 39458: 11 spec., 1 s.); 40°30'16.2"S, 65°27'29.6"W, Las Grutas, 10 m (MACN-In 39459: 8 spec., 1s.); 40°32'00.6"S, 65°47'29.5"W, El Buque, intertidal (MACN-In 39460: 14 spec., 18 s.; MACN-In 39461: 24 spec., 10 s.); 40°49'56.6"S, 65°05'16.2"W, Las Grutas, 7 m (MACN-In 39462: 28 spec., 27 s.); 40°50'12.8"S, 65°04'42.2"W, Las Grutas, 10 m (MACN-In 39463: 37 spec., 48 s.); 40°50'35.5"S, 65°04'43.7"W, Las Grutas, 12 m (MACN-In 39464: 2 spec., 5 s.); 41°58'22.8"S, 65°03'28.6"W, Puerto Lobos, 16.5 m (MACN-In 39465: 6 s.); 41°58'31.7"S, 65°03'38.6"W, Puerto Lobos, 13 m (MACN-In 39466: 1 s.); 42°15'25"S, 62°54'53"W–42°14'15"S, 62°59'42"W, 60 m (MACN-In 39467: 1 spec., 5 s.).

Known Distribution: Rio Grande do Sul, Brazil (Rios, 1994) to Golfo San Matías, Argentina. Living specimens: lower intertidal to 93 m.

Description

Shell: small (up to 9.7 mm wide), trochoid, of up to 5 whorls, solid. Spire moderately elevated (H / W = 0.84 ± 0.05, n= 22) (Figs. 4–6). Protoconch of one whorl, about 200 µm wide, with one or two spiral threads at peripheral margin; raised from teleoconch (Figs. 14, 15). Spire whorls obliquely straight, slightly angulated or evenly convex; separated by well-marked suture (Figs. 4–6, 10, 11, 14). Last whorl usually biangulated in larger specimens, sometimes evenly rounded (Figs. 4–6). In the first case, adapical area straight or concave. Base convex. Umbilicus open, deep in small specimens; partially to fully closed by columellar callus in larger specimens; umbilical area sunken (Figs. 7, 9). Shell surface sculptured with low spiral cords and microscopic granules between cords (Fig. 15). First ¾ teleoconch whorl with 3–4 spiral cords, narrower than interspaces; intercalated thread-like cords appear, gradually increasing their width on subsequent whorls. Last whorl (in larger specimens) with 17–29 cords between suture and lower angulation; base with 17–25 low cords as wide as or wider than interspaces (Figs. 4–11). Growth disruptions frequent along the shell (Fig. 11). Outer shell surface shiny in living specimens. Color highly variable, even among specimens from the same site (Figs. 4, 5, 7–10): brown, reddish-brown, tan, greenish-brown to whitish; uniform, variegated or spirally banded; in last case, frequently alternating dark and light stains. These bands usually wider near suture, at periphery of last whorl, and sometimes in umbilical area (Figs. 5, 7, 9). Sometimes this pattern also present in intermediate areas, resulting in irregular axial bands along spire and radial bands on base (Figs. 5, 9).

Aperture: large, obliquely ovate; aperture lip finely crenulated by external sculpture; peristome interrupted (Figs. 4–6). Collumella solid, arched, widening towards base, with moderately to well-developed denticle, and depression beneath (Figs. 12, 13). Inner shell surface nacreous.



FIGS. 16–20. *Carolesia blakei*, anatomy. FIG. 16: Left side view of an HMDS specimen (black arrowhead showing lateral papillae, see Fig. 18); FIG. 17: Detail of head; FIG. 18: Detail of lateral papillae; FIG. 19: Detail of cephalic tentacle's micropapillae; FIG. 20: Detail of jaw. Figs. 16, 18: Specimens from Las Grutas, MACN-In 39455; Figs. 17, 19, 20: Specimens from El Buque, MACN-In 39461. Scale bars: Fig. 16 = 1 mm; Fig. 17 = 500 µm; Fig. 18 = 50 µm; Fig. 19 = 20 µm; Fig. 20 = 5 µm. Abbreviations: ap = anterior projection; cl = cephalic lappet; ct = cephalic tentacle; es = eye stalk; f = foot; s = snout; sp = snout papillae; tp = tentaculiform processes; white arrowhead = epipodial tentacle (see epipodial sense organ below).

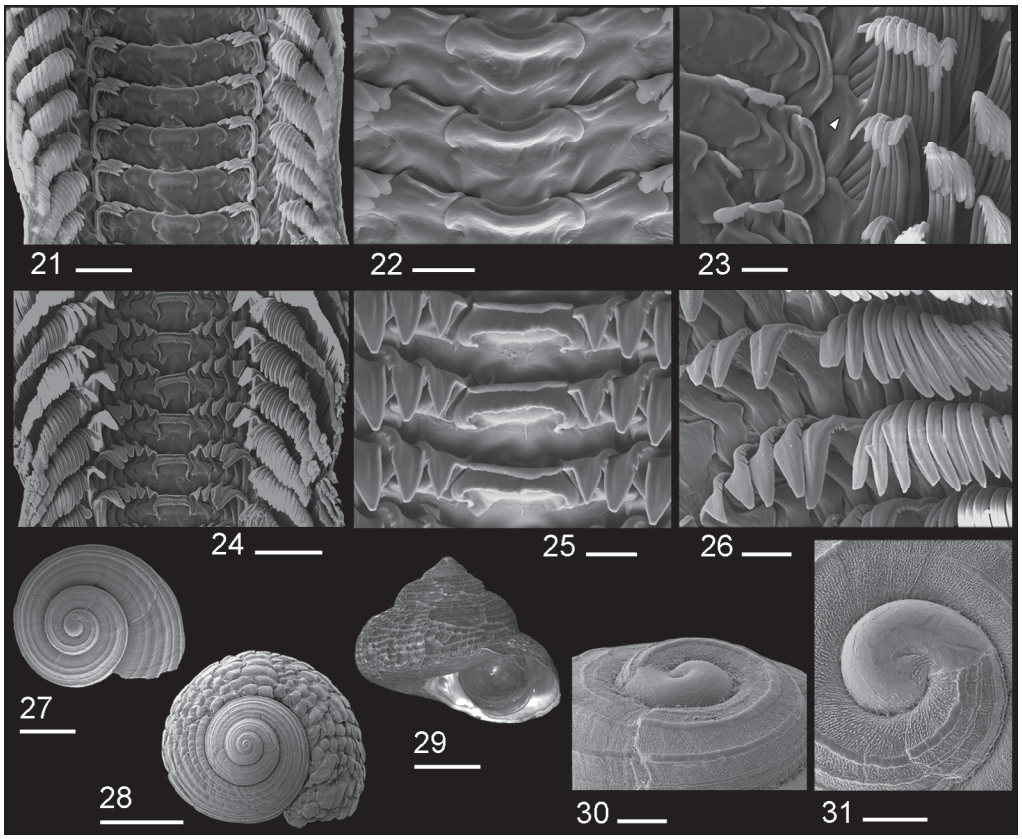
Operculum: corneous, circular, multispiral, with slightly expanded growing edge (Fig. 3); deeply retractable into shell.

Radula (Figs. 21–23): rhipidoglossate, bilaterally symmetrical, regularly arched. Rachidian tooth reduced to ovate, wider than high basal plate, without cutting edge; with deep depression at anterior front (Fig. 22); anterior margin thickened; secondary attachment membrane absent. Five unequal lateral teeth. First (innermost) laterals wider than high, resembling rachidian tooth in outline, also lacking distinct cutting edge (Figs. 21–22). Remaining four laterals on each side gradually narrowing their overlapping bases, increasing size and serrations of cutting edges outwards (Fig. 21). First marginal with well developed shaft and cusp, and inner projection at the base; cusp similar to other inner marginals (Fig. 23). Remaining marginal teeth (up to 49 according to this study; 60 *fide* Calvo, 1987) long, narrow; cusps elongate, strongly serrated on both sides; well-developed compressional ridge in midregion (Fig. 23). Marginal teeth gradually decreasing in size and robustness outwards. Jaws well developed, with elongate, juxtaposed, rod-like scales in anterior area (Fig. 20).

Anatomy: Snout short, broad, somewhat tapering, with short papillae and slit ventral lip (Figs. 1, 16, 17). Cephalic lappets extremely small, wide, lobed (Figs. 1, 2, 16, 17). Cephalic tentacles elongate, cylindrical, micropapillate (Figs. 17, 19). Eye stalks short, right one stout, left one widely expanded forming posterior flap (Fig. 17). Right neck lobe formed by wide, simple fringe, extending from eye stalk to first epipodial tentacle; left side of the neck with a short, triangular, flat projection immediately behind the eye stalk, separated from two (sometimes three) smooth, posterior tentaculiform processes (Figs. 2, 16). Posterior process sometimes bifurcated. Below neck, two or three conspicuous papillae on each side (Figs. 1, 2, 16, 18). Four pairs of narrow, micropapillate epipodial tentacles, with conspicuous epipodial sense organs at their bases (Figs. 1, 2, 16); sometimes one additional epipodial tentacle on left side. Foot anteriorly rounded. Animal dark brown to black; snout sometimes with fine, irregular, transverse lines (Figs. 1, 2). Ctenidium bipectinate, with short afferent membrane and long free tip.

Remarks: The shells of *Carolesia blakei* resemble small specimens of *Tegula patagonica* (Fig. 27), and the two are found living together.

The latter may be differentiated by having a higher spire with more evenly convex whorls; the protoconch sunken, partially covered by the first teleoconch whorl (Figs. 30, 31); stronger spiral cords; and uniform dark-color. The larger specimens of *T. patagonica* are consistently stouter, show irregular granules or scales, have the last whorl evenly curved (not angulated), and reach a greater size (~ 21 mm wide) (Figs. 28, 29). Additionally, in *T. patagonica* the columellar denticle(s) project(s) towards the umbilicus (which may be open, partially or entirely covered), and the outer lip may be smooth or conspicuously denticulated. Anatomically, the main difference between these species is found on the left side of the neck, which in *T. patagonica* shows a longitudinal fringe, either evenly smooth or with one or two digitations at the posterior part (Collado, 2008: fig. 2E; pers. obs.), while in *C. blakei* there is a short, triangular flat projection at the anterior part separated from two or three smooth tentaculiform projections. The radula of *T. patagonica* (Figs. 24–26), like other species of *Tegula* (*s.l.*), shows an additional difference with that of *C. blakei* (see below).



FIGS. 21–31. *Carolesia blakei* and *Tegula patagonica.* FIGS. 21–23: *Carolesia blakei*, radula; FIG. 21: Full radula width; FIG. 22: Detail of central field (rachidian and innermost lateral) tilt, showing the depression at anterior front of rachidian; FIG. 23: Detail of outer laterals and inner marginal teeth (arrowhead showing first marginal tooth). FIGS. 24–31: *Tegula patagonica*; FIGS. 24–26: Radula; FIG. 24: Full radular width; FIG. 25: Detail of central field, tilt radula; FIG. 26: Detail of lateral and marginal teeth; FIGS. 27–31: Shell; FIGS. 27, 28: Apical view; FIG. 29: Apertural view; FIG. 30: Protoconch, lateral view; FIG. 31: Protoconch, apical view. Figs. 21, 22, 24–26, 28, 30, 31: Specimens from Las Grutas; Figs. 27, 29: Specimens from Puerto Lobos; Figs. 21, 22: MACN-In 39455; Fig. 23: MACN-In 39467; Figs. 24–26: MACN-In 39471 (intertidal); Figs. 27, 29: MACN-In 39469 (21 m); Fig. 28: MACN-In 39470 (9 m); Figs. 30, 31: MACN-In 39468 (6 m). Scale bars: Figs. 21, 25, 26 = 50 µm; Figs. 22, 23 = 20 µm; Fig. 24 = 200 µm; Fig. 27 = 500 µm; Fig. 28 = 2 mm; Fig. 29 = 5 mm; Figs. 30, 31 = 100 µm.

In the original description of *Carolesia blakei*, Clench & Aguayo (1938) compared this species with *Calliostoma coppingeri* (Smith, 1880), pointing out as main differences in the latter the presence of beaded cords, a closed umbilicus, and the lack of a columellar denticle. The radula of *Calliostoma coppingeri* (figured by Clench & Turner, 1960: pl. 4, fig. 4) confirms the correct generic placement of that species under *Calliostoma*, and the distinction with that of *Carolesia*.

DISCUSSION

Carolesia blakei had been previously assigned to the calliostomatid genera *Calliostoma* and *Photinula*. However, both the ctenidium and radula morphology precludes the inclusion of this species under these genera: calliostomatids (as currently defined) have extremely narrow, flexible rachidian and lateral teeth, all with elongate, finely serrated tapering cusps; and the ctenidium with a long afferent membrane. In addition members of *Calliostoma* and *Photinula* possess a pseudoproboscis, which is absent in *Carolesia*. Furthermore, *Calliostoma* shows a characteristic protoconch with reticulate ("honey-comb" or "hexagonal spaces") pattern (Hickman & McLean, 1990; Marshall, 1995), clearly distinct from the condition present in *Carolesia blakei*.

Quinn (1992a) stated that according to "characters of the animal and radula … [*Carolesia blakei*] should be assigned to the Lirulariinae Hickman & McLean, 1990 (Quinn, in preparation)", although the manuscript he mentioned was never subsequently published. On the basis of molecular evidence, Lirulariinae is currently regarded as a synonym of Umboniinae (Williams et al., 2010). Members of this subfamily show the rachidian and lateral teeth reduced to basal plates, with shafts and cusps extremely reduced or, more often, absent; and with bases either completely separated or only slightly overlapping (Hickman & McLean, 1990; Herbert, 1992). On the contrary, in *Carolesia blakei* the reduction of the central field involves only the rachidian and innermost lateral teeth, while the remaining laterals have well-developed shafts and cusps, and the laterals show interlocking bases. Other characters reported for Umboniinae are the presence of a monopectinate or bipectinate ctenidium with long afferent membrane, the foot with a bifid propodium, and the snout with long papillae ("processes") (Hickman & McLean, 1990; Herbert, 1992). None of these characters are present in *Carolesia blakei*.

Carolesia blakei shows a number of similarities with the Tegulidae [as defined by Williams, 2012; corresponding to Hickman & McLean's (1990) Tegulinae]. Among such similarities are the presence of a ctenidium with short afferent membrane, the snout with a shallowly-slit ventral lip, the anterior end of the foot broadly rounded, and the radula with the base of laterals complexly interlocking and the marginals with compressional ridges. *Carolesia blakei* also shows an operculum with slightly expanded growing edge, which is a typical tegulid character (McLean, pers. com.). Another shared character is the presence of a denticle at the base of columella, although this character was reported by Hickman & McLean (1990) as present in other trochoideans. As mentioned above, the shell of *Carolesia blakei* closely resembles that of *Tegula mariana* (from northwest America), although several studies proved that shells in Trochoidea appear as plastic characters, frequently showing convergence among distantly related groups (Hickman & McLean, 1990). Aguirre & Farinati (2000), in fact, tentatively referred this species under *Tegula*. Despite the overall similarities above mentioned, *Carolesia blakei* differs from the current concept of Tegulidae by lacking the "rolled" anterior margin of the rachidian tooth, by having very distinctive (wide) innermost laterals, without shaft and cusp, and by the laterals that gradually become narrower outwards. In addition, the left neck lobe of tegulids is a wide longitudinal fringe, either smooth or with digitiform projections (Hickman & McLean, 1990; Collado, 2008; Collado et al., 2012), whereas the left side of the neck in *Carolesia blakei* shows isolated projections: a flat anterior projection and two tentaculiform posterior processes.

The unique combination of shell, anatomical and radular characters present in *Carolesia blakei* leads us to propose a new genus to include this species. The distinctive characters used here to define *Carolesia* were not previously reported for any other species thus far anatomically investigated. This study highlights once again the importance of considering anatomical characters in addition to shell morphology, for a proper classification of trochoids. *Carolesia* is here tentatively located under Tegulidae, although the above-mentioned differences with other members of this family should not be diminished. These differences suggests that *Carolesia* may even

belong to a new (sub)family, but we prefer to avoid introducing a new family-group name considering the high instability of trochoidean classification at this time.

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