Polar Biology (2022) 45:777–787
https://doi.org/10.1007/s00300-022-03018-3

ORIGINAL PAPER

The smallest marine bivalves from the end of the world (Tierra del Fuego, Isla de Los Estados and Burdwood Bank)

Marina Güller[1,2] · **Diego G. Zelaya**[1,2]

Received: 22 October 2021 / Revised: 19 January 2022 / Accepted: 20 January 2022 / Published online: 20 February 2022

Abstract
Small molluscs are known to be particularly abundant towards the poles. Although recent studies on sub-Antarctic waters of the southernmost tip of South America have begun to show a highly diversified small-sized fauna, micromolluscs have not yet received sufficient attention. Recently, samplings targeting the smallest molluscan benthic fauna have been conducted in the sub-Antarctic waters of South America, providing material of three new minute species occurring in The End of the World (Tierra del Fuego, Isla de los Estados and Burdwood Bank). The present study describes *Pachykellya fuegiensis* n.sp. (Neoleptonidae), *Benthocardiella ituartei* n.sp. and *Benthocardiella finisterra* n.sp. (Condylocardiidae). These are not only the smallest bivalves currently known from the area, but are also smaller than any other species thus far known from the adjacent Antarctic waters, and are included among the smallest species of their respective genera. To confirm generic placement, the type species of *Pachykellya* (*P. edwardsi* F.B. Bernard 1897) and *Benthocardiella* (*B. pusilla* Powell 1930) are studied for the first time with scanning electron microscopy. This study allows to amend the previous descriptions of hinge teeth number, morphology and arrangement for these genera. Based on these new findings, *Pachykellya* and *Benthocardiella* are here reported for the first time in South America.

Keywords Neoleptonidae · Condylocardiidae · *Pachykellya* · *Benthocardiella* · Patagonia · Burdwood Bank/MPA Namuncurá

Introduction

Small-sized bivalve species are unusually numerous in high latitudes of the Southern Hemisphere (Nicol 1964, 1966). According to Nicol (1970), 61% of the shallow water Antarctic species are smaller than 10 mm in maximum size. These results were ratified by Rivadeneira et al. (2015), who concluded that "Antarctic bivalves are much smaller than those in any other region across global oceans". A high ratio of small-sized bivalves also appears in the neighboring areas of Antarctica. In this regard, 58% of the bivalve species in South Georgia are smaller than 10 mm (Zelaya, unp. data); and in the southernmost tip of South America (i.e., the Magellan Region), the median size among bivalves is 23 mm (Rivadeneira et al. 2015). To date the smallest Magellanic bivalves are *Malvinasia piccola* Ituarte and Zelaya (2015) (Lasaeidae: 2.2 mm maximum size) and *Cyclopecten multistriatus* Linse (2002) (Propeamussiidae: 1.8 mm maximum size) (Linse 2002; Ituarte and Zelaya 2015).

The present study represents a new contribution towards a better knowledge of small-sized sub-Antarctic bivalves, through the description of three minute new species occurring in the southern tip of South America.

Materials and methods

Most of the material reported in this contribution was personally sampled as part of a series of field trips aboard the A.R.A. *Alférez Sobral*, the B. O. *Puerto Deseado* and the GC-189 *Prefecto García*. Sea bottom samples were obtained by using a benthic dredge of 2-mm mesh size, around Tierra del Fuego,

✉ Diego G. Zelaya
dzelaya@bg.fcen.uba.ar

[1] Laboratorio de Malacología, Departamento Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Intendente Güiraldes 2160, Universidad de Buenos Aires, Ciudad Universitaria, C1428EGA Buenos Aires, Argentina

[2] Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

Isla de los Estados and Burdwood Bank/Namuncurá MPA (Fig. 1). Molluscs were sorted from the sediment under stereoscopic microscope, fixed onboard in 10% sea-water formalin, and posteriorly transferred to 80% ethanol. The number of specimens (spec), articulated valves (av) and valves (v) is informed. The studied material was deposited in the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina. Additional specimens from this area came from the collections of the Los Angeles County Museum (LACM), Los Angeles, USA. For comparative purposes, specimens of *Benthocardiella pusilla* Powell (1930a) and *B. hamatans* Powell (1930b) (housed in the collections of the Florida Museum of Natural History, Florida, USA—FlMNH), and photographs of a lot of *Pachykellya edwardsi* F.B. Bernard (1897) (housed in the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand—registration numbers prefixed 'M.') were studied.

Shells were studied and figured using a Philips XL30 TMP New Look scanning electron microscope (SEM), and measured according to the following criteria: L: maximum antero-posterior distance; H: maximum dorso-ventral distance, perpendicular to L.

Systematics

Family Condylocardiidae F.B. Bernard (1896)

Benthocardiella Powell (1930a)

Type: *Benthocardiella pusilla* Powell (1930a, b) (OD).

Remarks: Powell (1930a) introduced *Benthocardiella* to place his newly described species, *B. pusilla*. According to the author, the genus is similar to *Condylocardia* but with differences in teeth morphology. Powell (1930a) described the left valve of *Benthocardiella* as having a hooked "cardinal" tooth posterior to the resilifer, and two teeth anterior to the resilifer: an "anterior cardinal" and an "anterior lateral"; and he described the right valve as having two posterior teeth ("upper cardinal" and "lower cardinal") and a "simple" anterior tooth. However, the SEM study of a specimen of *B. pusilla* reveals that the anterior tooth of the right valve of *Benthocardiella* is not "simple" but composed of two connected elements that form a hook (Fig. 2b: "da" and "pa"); a similar condition is also present in *B. hamatans* (Fig. 2e). The above described conformation of the hinge plate is also recognizable in two Magellanic condylocardiids whose morphology, however, differs from all other species currently known in this genus. Consequently, these two Magellanic species are considered as new.

Benthocardiella ituartei Güller & Zelaya new species Fig. 3

***Benthocardiella* n. sp. 1 Zelaya 2005: 116.**

Type locality: 55° 03′ S, 66° 37′ W, Cabo San Pío, Tierra del Fuego, 30–35 m.

Type material: Holotype (MACN-In 43,855, mounted for SEM) and 19 paratypes from the type locality (MACN-In 43,856).

Zoobank registration number: 10.1007/s0030 0-020-02654 -x

Additional material examined: Beagle Channel: 55° 05.883′ S, 66° 20.233′ W, 45 m (MACN-In 43,858: 1spec, 27 av, 1 v); 55° 00.400′ S, 65° 49.683′ W, 103 m (MACN-In 43,857: 2v, 5 av). Isla de los Estados: 54° 52.450′ S, 64° 03.367′ W, 271 m (MACN-In 43,860: 3 v, 1va). Burdwood

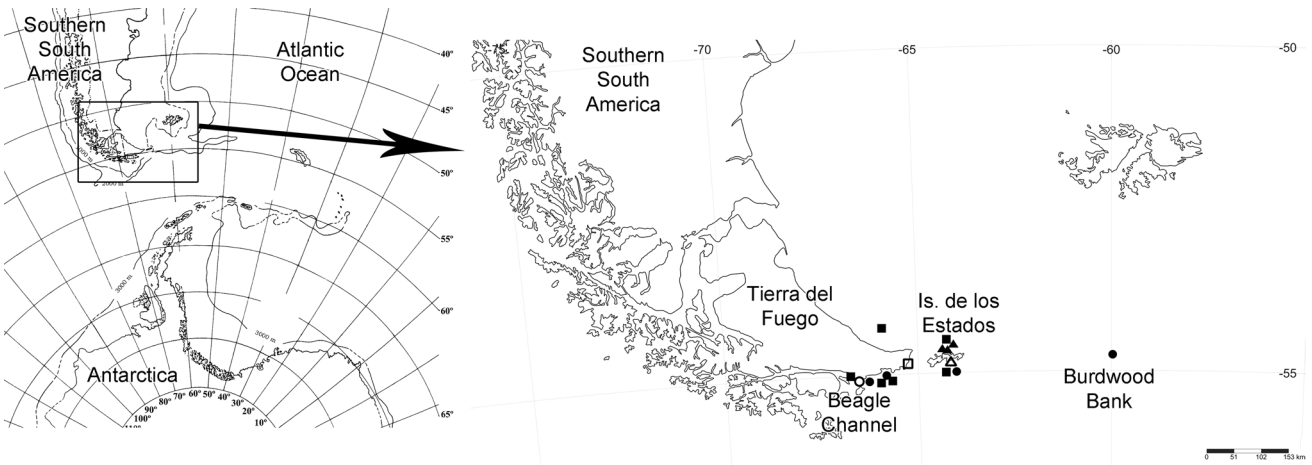

Fig. 1 Location map, showing the sites of collection of *Benthocardiella ituartei* n. sp. (circles), *B. finisterra* n. sp. (triangles) and *Pachykellya fuegiensis* n. sp. (squares). Empty shapes represent the type localities; full shapes refer to the provenance of other studied material

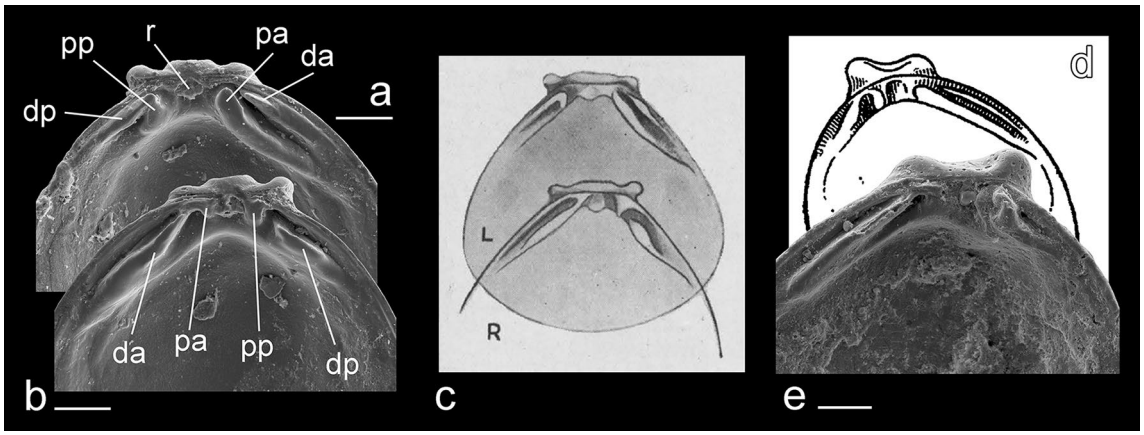

Fig. 2 *Benthocardiella pusilla* Powell (1930a) (**a**, **b**, **c**) and *Benthocardiella hamatans* Powell (1930b) (**d**, **e**). **a**, **b**. Specimen from Awanui Bay, New Zealand (FlMNH 246,240). **a** Detail of hinge plate, left valve. **b** Detail of hinge plate, right valve. **c** Original illustration (Powell 1930a: fig. 5). **d** Original illustration (Powell 1930b: fig. 7). **e**. Specimen from Doubtless Bay, New Zealand (FlMNH 246,239 in part), detail of hinge plate, right valve. Abbreviations: da = distal anterior tooth; dp = distal posterior tooth; pa = proximal anterior tooth; pp = proximal posterior tooth. Scale bars: 100 µm

Bank: 54° 34.983′ S, 59° 41.817′ W, 113 m (MACN-In 43,859: 1av).

Diagnosis: Shell ovate-trigonal, as high as long or higher than long, somewhat anteriorly projected, flat. Prodissoconch posteriorly projected. Resilifer minute. Right and left valves with two anterior and two posterior teeth. Right valve: tooth immediately behind the resilifer (proximal posterior tooth), massive. Left valve: anteriormost tooth (distal anterior tooth), narrowly elongated.

Description: Shell minute (maximum size = 0.62 mm L), ovate-trigonal, as high as long or higher than long, relatively flat, equivalve, delicate.

Anterior end somewhat projected, posterior end subtruncated. Antero-dorsal and postero-dorsal margins slightly arcuated; the anterior longer than the posterior. Ventral margin curved, insensibly connected with anterior and posterior margins.

Shell surface whitish, shiny, sculptured with prominent, regularly separated commarginal cords; interspaces narrower than or as wide as cords. Inner shell margin smooth.

Prodissoconch whitish, flat, well differentiated from dissoconch; posteriorly raised and projected. Prodissoconch I finely sculptured with commarginal elements; Prodissoconch II with thin radial sculpture. Limit between Prodissoconch I and Prodisoconch II only discernible from shell sculpture. Prodissoconch I + Prodissoconch II about 220 µm long.

Hinge plate narrow. Resilifer minute, with a small dorsal notch.

Right valve with two teeth anterior and two posterior to the resilifer. Anterior teeth comprising a U-shaped proximal element ("pa"), attached to dorsal shell margin, and a distal, sigmoid element ("da"); both teeth narrow, similar in solidness; with their bases close to each other. Posterior teeth comprising a strong, triangular, and relatively high tooth, clearly detached from the dorsal shell margin, located immediately behind the resilifer ("pp"), and a short, elongated distal element, close to the posterior margin ("dp").

Left valve with two teeth anterior and two posterior to the resilifer. Anterior teeth comprising an oblique, short and massive proximal element, completely detached from shell margins ("pa"), and an elongated, thin element, forwardly displaced, which narrows distally ("da"). Posterior teeth comprising a short, triangular knob, merged to the dorsal shell margin ("pp"), and a high and massive tooth, triangular in outline, which extends to the lower margin of the hinge plate ("dp").

Adductor muscle scars ovate, the posterior slightly higher than the anterior.

Geographical and bathymetrical distributions: Only known from Tierra del Fuego, Isla de los Estados and Burdwood Bank, from 30 to 271 m depth; living specimens only found at 30–45 m.

Etymology: The species is named after Cristián F. Ituarte, in recognition of his meticulous contributions to the knowledge of Argentine bivalves.

Remarks: In general shell outline, *Benthocardiella ituartei* new species resembles *B. pusilla*, *B. hamatans* and *B. striatula* Powell (1931), from which it differs in having a more anteriorly projected end that originates a more markedly inequilateral shell. In addition, *B. ituartei* differs from all these species in having a narrower hinge plate, and two distinctive anterior teeth in the right valve (Figs. 2 *vs.* 3f, g). *Benthocardiella ituartei* also differs from *B. pusilla* and *B. hamatans* in having less curved anterior and posterior shell margins, a flatter prodissoconch, and more pronounced commarginal sculpture on the dissoconch (Fig. 3)

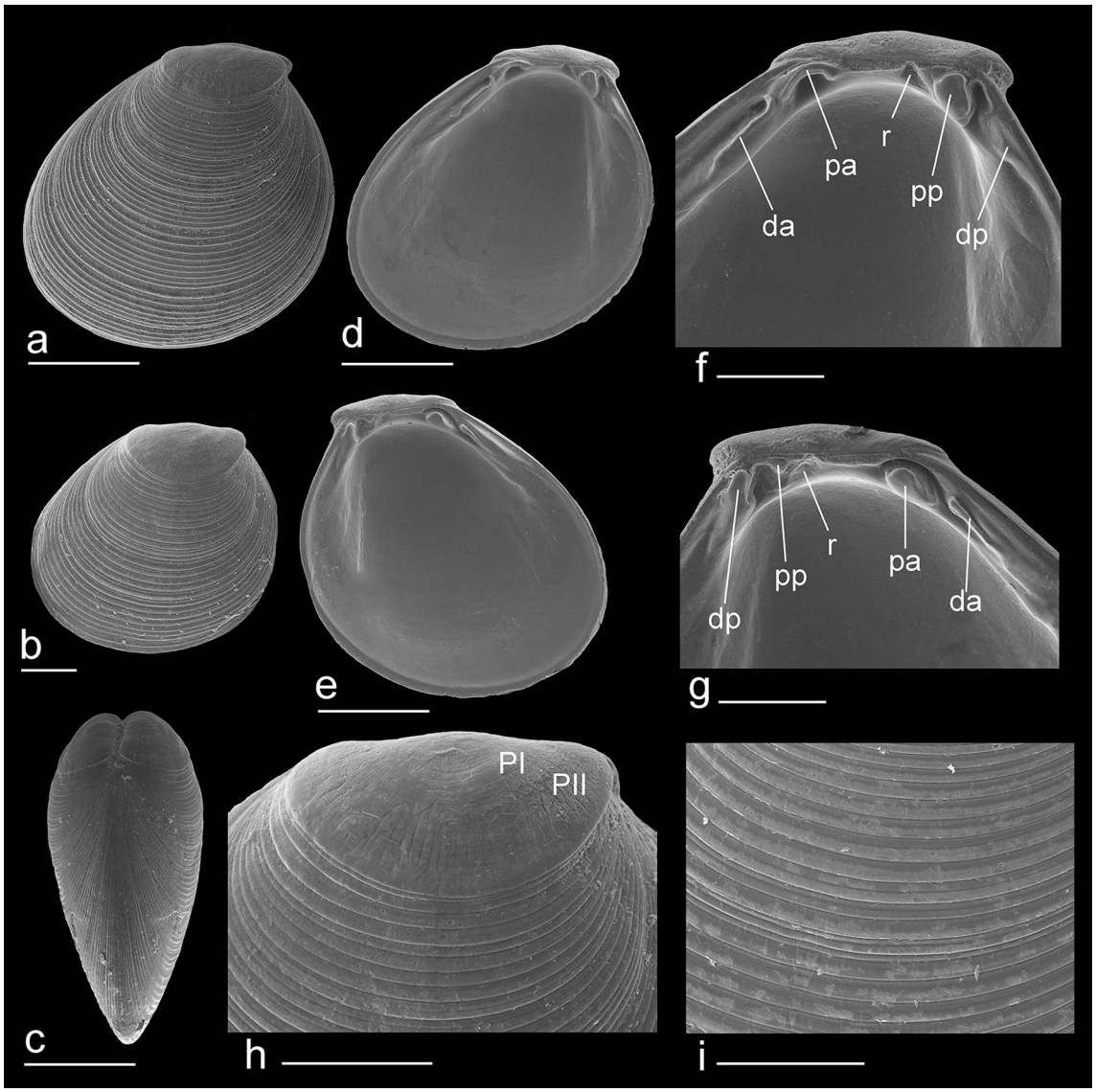

Fig. 3 *Benthocardiella ituartei* new species. **a** Holotype (MACN-In 43,855). **b–i** Paratypes (MACN-In 43,856). **a**, **b** Outer view, left valve. **c** Anterior view. **d** Inner view, right valve. **e** Inner view, left valve. **f** Detail of hinge plate, right valve. **g** Detail of hinge plate, left valve. **h** Prodissoconch. **i** Detail of dissoconch sculpture. Abbreviations: da = distal anterior tooth; dp = distal posterior tooth; pa = proximal anterior tooth; pp = proximal posterior tooth; PI = Prodissoconch I; PII = Prodissoconch II. Scale bars: **a**, **c–e** = 200 µm; **b**, **f–i** = 100 µm

Benthocardiella finisterra **Güller & Zelaya new species Fig. 4.**
Benthocardiella **n. sp. 2 Zelaya 2005: 116.**

Type locality: 54° 46.8′ S, 64° 04.0′ W, Puerto Vancouver, Isla de los Estados, 31 m.

Type material: Holotype (LACM 3785, mounted for SEM) and 14 paratypes from the type locality (LACM 3786).

Zoobank registration number: 2C25B61C-5202-4A32-B08F-1F5BD0060BD5

Additional material examined: Isla de los Estados: 54° 39.5′ S, 64° 07.1′ W, Isla Observatorio, shallow subtidal (LACM 71–310: 2 va, 1v; LACM 71–310: 2va, 2v); 54° 43.9′ S, 64° 14.1′ W, Puerto Basil Hall (LACM 71–317: 4 va, 5v); 54° 43.7′ S, 64° 14.2′ W, Cabo Colnett, 18 m (LACM 71–264: 4v).

Diagnosis: Shell markedly trigonal, longer than high, markedly anteriorly projected, somewhat inflated. Prodissoconch posteriorly raised but not projected. Resilifer large. Right valve with only one discernible tooth anterior to the resilifer and two posterior teeth; the posterior tooth closer to the resilifer (proximal posterior tooth), minute. Left valve with two anterior and two posterior teeth, the anteriormost tooth (distal anterior tooth) short and thick.

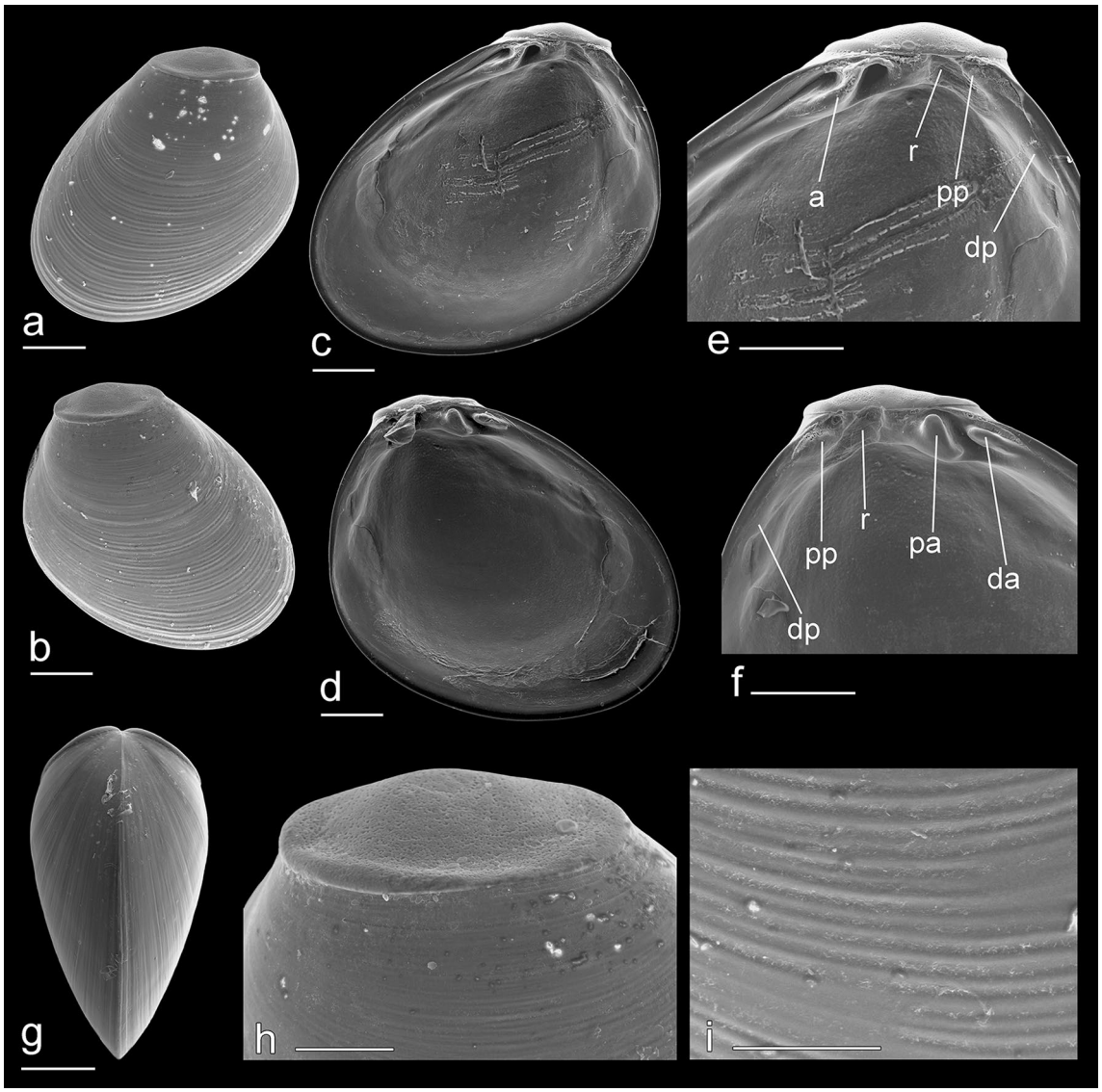

Fig. 4 *Benthocardiella finisterra* new species. **a**, **b**, **g**–**i**. Paratypes (LACM 3786). **c**–**f** Holotype (LACM 3785). **a** Outer view, left valve. **b** Outer view, right valve. **c** Inner view, right valve. **d**. Inner view, left valve. **e** Detail of hinge plate, right valve. **f**. Detail of hinge plate, left valve. **g**. Anterior view. **h**. Prodissoconch. **i**. Detail of dissoconch sculpture. Abbreviations: a = anterior tooth; da = distal anterior tooth; dp = distal posterior tooth; pa = proximal anterior tooth; pp = proximal posterior tooth. Scale bars: **a**–**g** = 200 µm; **h**, **i** = 100 µm

Description: Shell minute (maximum size = 1.2 mm L), markedly trigonal, longer than high, somewhat inflated, equivalve, solid in appearance.

Anterior end greatly projected, posterior end truncated. Anterior and posterior margins slightly arcuated, the anterior much longer than the posterior one. Ventral margin forming a wide curve, insensibly connected with anterior and posterior margins.

Shell whitish or pinkish, shiny; sculptured with densely packed, regularly separated commarginal cords; interspaces narrower than cords. Inner shell margin smooth.

Prodissoconch large (about 145 µm long), flat, delimited by a cord which is particularly evident in the posterior part, where it originates an elevation; brownish in color. Prodissoconch culpture unknown (due to the state of preservation of the studied material).

Hinge plate moderately thick. Resilifer large, with a small dorsal notch.

Right valve with only one recognizable tooth anterior and two posterior to the resilifer. Anterior tooth ("a") hooked, attached to the dorsal shell margin; its posterior branch extremely short, the anterior branch markedly projected. Posterior teeth comprising a minute tubercle, immediately behind the resilifer ("pp"), completely detached from dorsal shell margin, and an elongate, short distal element ("dp"), close to posterior margin.

Left valve with two teeth anterior and two posterior to the resilifer. The anterior teeth comprising a high element, markedly triangular in outline, short at the base, completely detached from shell margins ("pa"), and an elongated, short and thick element, parallel to anterior margin ("da"). The posterior teeth comprising a small, triangular knob, which is merged to dorsal shell margin, located just behind the resilifer ("pp"), and a prominent posterior tubercle ("dp").

Adductor muscle scars elongated, similar in size.

Geographical and bathymetrical distributions: Only known from Isla de los Estados, from the shallow subtidal to 31 m depth; living specimens only found at 31 m depth.

Etymology: From the Latin *finis terrae*, "the end of the world"; in reference to the provenance of the species.

Remarks: In general shell outline, *Benthocardiella finisterra* new species is most similar to the Australian *B. darwinensis* Middelfart (2002a), from which it differs by having a shorter and rapidly sloping posterior margin, which originates a more-markedly inequilateral shell. In addition, *B. finisterra* has a flatter prodissoconch, more conspicuous commarginal sculpture on the dissoconch and a larger resilium than *B. darwinensis*. Another difference arises in the inner shell margin, which is smooth in *B. finisterra* and crenulated in *B. darwinensis*.

Benthocardiella finisterra differs from the sympatric *B. ituartei* in having a more projected anterior end, and a longer ventral margin. In addition, the prodissoconch of *B. finisterra* is not posteriorly projected as that of *B. ituartei*. *Benthocardiella finisterra* has a wider hinge plate and a larger resilifer than *B. ituartei*. Other differences arise from the hinge teeth: in the left valve, the anteriormost tooth is short and strong in *B. finisterra* whereas in *B. ituartei* this tooth is long and narrow. In the right valve, the proximal posterior tooth is considerably smaller in *B. finisterra* than in *B. ituartei*; and there is only one discernible anterior tooth in *B. finisterra*, and two anterior teeth in *B. ituartei*.

Family Neoleptonidae Thiele (1934)
Pachykellya F.B. Bernard (1897)

Type: *Pachykellya edwardsi* F.B. Bernard (1897) (by monotypy).

Remarks: *Pachykellya* was not described separately from its type species, for which Bernard (1897) reported the presence of two anterior and two posterior elongated teeth in each valve ("A0", "AII", "P0" and "PII" in the left valve; "AI", "AIII", "PI" and "PIII" in the right valve); out of these, the most dorsal teeth ("AII", "PII", "AIII", and "PIII") were described by Bernard (1897) as hooked. The most ventral anterior tooth of the right valve ("AI") was not particularly described by the author, although the original figure also shows a hooked outline (Bernard 1897: fig. 1). Powell (1927: pl. 23, fig. 1) provided an additional figure of *P. edwardsi*, whose hinge conformation is mostly in agreement with the previous illustration by Bernard (1897), except for the fact that the right valve shows an antero-ventral tooth which is triangular in outline (instead of hooked). Powell (1927) referred to the teeth as "outers" and "inners", and for two of the new species he described (*P. bernardi* and *P. rotunda*), he considered these elements as "laterals". As part of the present study we had the opportunity to study the hinge of *P. edwardsi* with SEM for the first time (Fig. 5a–e). This study allows us to confirm that the right valve has two anterior and two posterior teeth, the most antero-ventral tooth being triangular in outline, with a wide base and proximal cusp. However, the left valve only shows one anterior and one posterior tooth, corresponding to those elements described by Bernard (1897) as "AII" and "PII", respectively. The other two elements regarded by this author as teeth ("A0" and "P0") actually correspond to the hinge plate margin. Thus, *P. edwardsi* does not fall apart from the general conformation of the hinge of the genus *Neolepton* (see for instance: Salas and Gofas 1998; Zelaya and Ituarte 2004). Consequently, and following what has been described for *Neolepton*, the anterior teeth are here considered as cardinals (CA), and the posterior teeth, as laterals (PL) (Salas and Gofas 1998; Zelaya and Ituarte 2004). The above described conformation of the hinge of *P. edwardsi* was also recognized in specimens collected in the Magellan Region, which proved to correspond to a new species, described below (Fig. 5f–l).

***Pachykellya fuegiensis* Güller & Zelaya new species-Figs.** 5f-l

Type locality: 54° 47.9′ S, 65° 14.7′ W, Bahía Buen Suceso, Tierra del Fuego, 12–18 m.

Type material: Holotype (MACN-In 43,861, mounted for SEM) and three paratypes (MACN-In 43,862).

Zoobank registration number: 3F1DE797-4896-4EDF-B58F-F4A81F9D2623

Additional material examined: Beagle Channel: 55° 01.5′ S, 66° 41.7′ W, Monte Moat, 15–20 m (MACN-In 43,863: 1 v); 55° 00.400′ S, 65° 49.683′ W, 103 m (MACN-In 43,864: 5v, 1 av); 55° 02.283′ S, 65° 46.117′ W, 118 m (MACN-In 43,866:1 spec, 10 av, 1 v). NE of Tierra del Fuego: 54° 14.617′ S, 65° 58.383′ W, 74 m (MACN-In 43,867: 1 av). Isla de los Estados: 54° 30.117′ S, 64° 08.433′ W, 99 m (MACN-In 43,868: 1 av, 2 v); 54° 52.450′ S, 64° 03.367′ W, 271 m (MACN-In 43,865: 2 v).

Diagnosis: Shell ovate, higher than long, obliquely projected anteriorly. Dissoconch sculptured with prominent commarginal cords. Umbos low, not projected. Hinge plate evenly arcuate ventrally. Resilifer wide.

Description: Shell minute (maximum size = 1025 µm H), ovate, higher than long, equivalve, solid.

Anterior end obliquely projected. Anterior and posterior margins slightly arcuated, the anterior longer than the

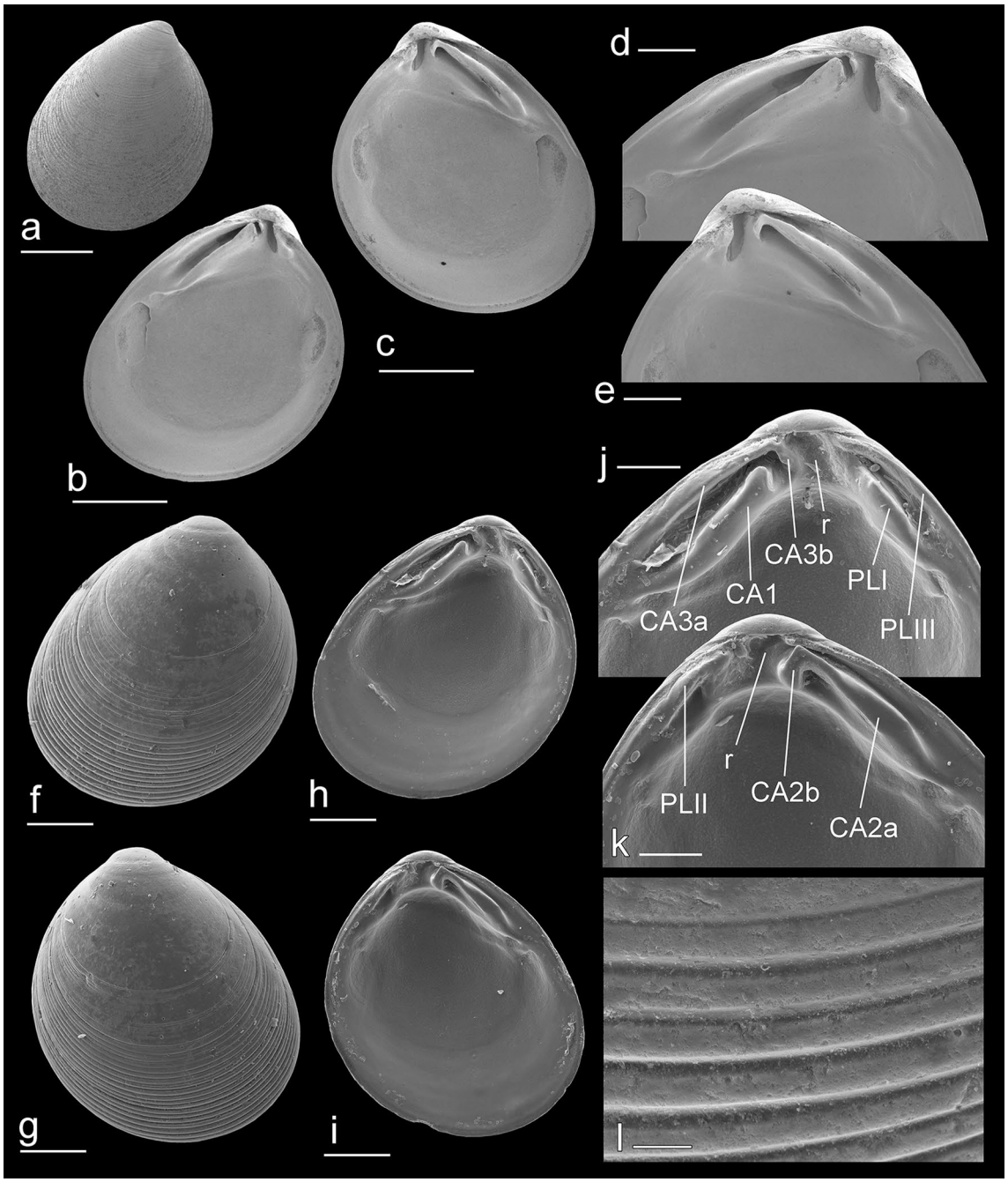

Fig. 5 *Pachykellya edwardsi* F.B. Bernard (1897) (**a**–**e**) and *Pachykellya fuegiensis* new species (**f**–**l**). **a**-**e**. Specimens from off Big South Cape Island, New Zealand (M.019059). **f**, **g** Holotype (MACN-In 43,861). **h**–**k** Paratype (MACN-In 43,862). **a**, **f**, **g** Outer views: **a**, **f** left valve, **g** right valve. **b**, **c**, **h**, **i** Inner views: **b**, **h** right valve. **c**, **i** left valve. **d**, **e**, **j**, **k**. Detail of hinge plates: **d**, **j** right valve, **e**, **k** left valve. **j**, **l** Detail of dissoconch sculpture. Abbreviations: CA = anterior cardinal teeth; PL = posterior lateral teeth; r = resilifer. Scale bars: **a**–**c** = 500 µm; **d**–**i** = 200 µm; **j**, **k** = 100 µm; **l** = 20 µm

posterior. Ventral margin markedly convex, insensibly connected with anterior and posterior margins.

Shell surface whitish, translucent; sculptured with prominent, densely packed commarginal cords; interspaces narrower than or as wide as cords. Internally, a weak fold extends obliquely, from the dorsal part of the anterior adductor muscle scar to the posterior part of the hinge plate. Inner shell margin smooth.

Prodissoconch whitish, about 185 µm long, almost circular, cap-shaped, well differentiated from dissoconch. Umbo low and rounded.

Hinge plate broad, markedly arcuated below the umbos. Resilifer obliquely elongated, wide, extending all along the height of the hinge plate; with a small dorsal notch. Ligament completely internal.

Right valve: CA1 prominent, triangular in outline, with rounded, proximal cusp and elongated base; CA3a relatively thick, close to shell margin; CA3b short and narrow, forming a right-angle with CA3a. PLI long and massive; PLIII almost indistinct from shell margin.

Left valve: CA2a long, straight, widening distally; CA2b short, forming a right angle with CA2a; both teeth well separated from shell margin. PLII elongated, strong.

Anterior and posterior adductor muscle scars ovate, subequal in size.

Geographical and bathymetrical distributions: Only known from Tierra del Fuego and Isla de los Estados, in depths from 12 to 271 m; living specimens only found at 118 m.

Etymology: The species name refers to the provenance of the studied material.

Remarks: In general shell outline, *Pachykellya fuegiensis* new species is most similar to *P. edwardsi*, from which it differs by having lower, and not projected umbos (Figs. 5f–k *vs.* 5a–e). Another difference arises from the hinge plate, which has a deeply sinuous ventral margin in *P. fuegiensis*, whereas in *P. edwardsi* the ventral margin is anterior and posteriorly straight, forming a prominent angulation below the umbo. In addition, the resilifer is shorter and wider in *P. fuegiensis* than in *P. edwardsi*. Furthermore, the right valve of *P. fuegiensis* has a shorter and higher CA1 and a more elongate PLI than *P. edwardsi*; and the left valve shows a longer PLII. *Pachykellya bernardi*, *P. concentrica*, *P. minima* and *P. rotunda* clearly differ from *P. fuegiensis* by having the anterior end more projected, and proportionally longer and lower shells.

Discussion

Despite representing the majority of molluscan diversity, micromolluscs are much more poorly know than larger species, a fact originated from the insufficient sampling and understudy of these organisms in most parts of the world (Middelfart 2002b). In this sense, the significance of the small-sized bivalves to the total species diversity of a particular area is potentially biased by the completeness of species inventories. In the Antarctic waters numerous small-sized species are known since the beginning of the twentieth century (Thiele 1912). In fact, the smallest species known to date from the area -*Thyasira debilis*- was described in 1912. The great sampling efforts made on that fauna for more than a century, indubitably contribute to the recognition of an "unusual proportion" of small-sized species in Antarctic waters (Nicol 1964, 1966, 1970; Valentine et al. 2006; Rivadeneira et al. 2015); and this fact also led to the idea that bivalve size is reduced with increasing latitudes (the so called "latitude-size rule": Moran and Woods 2012). However, the scenario in the sub-Antarctic waters around the southernmost tip of South America is very different. At this area, there have been neither researchers particularly focusing on micromolluscs nor specific samplings targeting that fauna (Zelaya 2015). Consequently, small-sized molluscs (and particularly bivalves) have been largely overlooked throughout the years. Despite that, a series of recent specific samplings and studies (e.g., Zelaya and Ituarte 2004; Ituarte and Zelaya 2015; this study) revealed that the local diversification of that fauna is considerably higher than previously thought. In particular, the present study describes the three smallest species thus far known from the Magellan Region. These species are also smaller than any other species thus far known from the adjacent Antarctic waters, and in fact, are among the smallest species of *Benthocardiella* and *Pachykellya* currently known worldwide. The minute size of these new species does not attempt against their adulthood condition. In fact, brooding shelled embryos were found in one specimen of *Benthocardiella ituartei* and in one specimen of *B. finisterra*. These new species provide new evidence arguing against the previous conception of the existence of "few" small-sized species in the neighboring areas to the Antarctica, suggesting that such conception is actually the result of a bias originated in an imperfect knowledge of that fauna. Moreover, this study provides additional evidence supporting that size-latitude trends are more spatially variable than previously thought (Roy et al. 2000; Berke et al. 2013).

Thus far involving the need of specific sampling and sorting methods, the study of such minute fauna imposes several difficulties, which had to be also addressed herein:

1) For long time, the stereoscopic microscope was the only available tool for studying small-sized bivalves, a fact that involved several limitations in the description of some characters of taxonomical value, such as for instance, the number and arrangement of hinge teeth. With the advent of the SEM, and its usage for the study of molluscs, it was possible to refine the description of minute bivalves (e.g., Salas and Gofas 1998; Zelaya and Ituarte 2004; Batistão and Passos 2020). Despite that, several elderly described species still remain only known from their original descriptions. These are the cases of the type species of *Benthocardiella* and *Pachykellya*, two taxa which were here studied for the first time with SEM. The study of these species resulted in emendations to the previous descriptions of the conformation of their hinge

teeth; a process that resulted crucial for confirming the generic placement of the new species described herein.
2) Hinge teeth identification and nomenclature: the teeth of condylocardiids are sometimes so close to the shell margin that their distinction is hard. In addition, within the family, there have been reports of teeth fusions, which obscure the recognizement of some particular teeth. Furthermore, the paucity of ontogenetic studies on condylocardiids should be considered: to date the only available information on this issue comes from the study by Bernard (1896) on *Condylocardia pauliana*, *C. crassicostata* and *C. concentrica* (the latter currently considered a member of the genus *Condylocuna* fide Middelfart (2002a). To the previous, it should be added that there is chaos surrounding the nomenclature of the teeth within the group. In this regard, and particularly focusing on *Benthocardiella*, in the left valve, the anterior "lateral" tooth of Powell (1930a) was subsequently interpreted by the same author (Powell 1930b) as a second anterior "cardinal", after considering that true laterals are absent in *Benthocardiella*. Middelfart (2002a) also interpreted this tooth as a cardinal ("CA4a"), although the author also reported the presence of an anterior lateral ("LAII"). Unfortunately such lateral was not labeled or is recognizable in the photographs Middelfart (2002a) provided. On the other hand, in the left valve, the posterior hook-like "cardinal" of Powell (1930a) was interpreted by Middelfart (2002a) as a posterior cardinal ("CP3"), which is fused to the posterior lateral ("LPII"). The interpretation of this posterior "hook" composed of two different teeth is in agreement with what was found in the two new species described herein. In addition, in the right valve, the "lower cardinal" of Powell (1930a) was not considered as a cardinal by Middelfart (2002a), but as a posterior "lateral" tooth ("LPIII"). Furthermore, Middelfart (2002a, b) regarded the anterior hook-like element of the right valve as the anterior cardinal ("CA3") merged with the anterior lateral ("LAI"), although no evidences supporting such fusion were provided by the author. In fact, in none of the species he studied, nor in *B. pusilla*, it is easy to decide what portion of this continuous tooth element should be regarded as cardinal or lateral. Nevertheless, the current finding of two teeth located anterior to the resilifer in *B. ituartei*, suggests that Middelfart's (2002a, b) interpretation of a fusion of teeth may be correct. But if such interpretation is correct, then the traditional nomenclature for referring to this tooth element does not apply. This fact, together with the discrepant nomenclatures for the other tooth elements, led us to avoid referring to the teeth as "cardinal" or "lateral" in the descriptions of *Benthocardiella* species. In the case of *Pachykellya* there was also a different use of nomenclature for referring to the teeth by Bernard (1897) and Powell (1927). However, in this case, the distinction of "cardinal" and "lateral" teeth does not seem to be a major problem, when following the criterion used in the modern literature for neoleptonids (e.g. Salas and Gofas 1998; Zelaya and Ituarte 2004).
3) The lack of phylogenetic studies. To date there is no phylogeny showing the relationships among members of *Benthocardiella* or *Pachykellya*. The great similarities in hinge teeth morphology and arrangement of *P. fuegiensis* with the type species of *Pachykellya*, do not lead to questioning the co-generic placement of these two taxa. However in the case of *B. ituartei* and *B. finisterra*, there are several similarities, but some differences with the type species of *Benthocardiella*. Middelfart (2002a) discussed that *Benthocardiella* and *Condylocardia* are the only condylocardiids with the anterior tooth of the right valve ("CA3") forming a hook, and with the left valve having an anterior tooth ("CA2") completely detached from shell margins. In addition, the author pointed out that *Benthocardiella* lacks one of the three posterior teeth in the left valve (the "CP2"), which appears in *Condylocardia*. The above set of characters led us to place the two new condylocardiid species described herein in *Benthocardiella*. However, it should be noted that these species have some differences with the type species of the genus. In the two new species described herein the posterior hook-like "tooth" of the left valve is in contact with the dorsal margin (contrary to what occurs in *B. pusilla*); and in the right valve, the tooth located immediately behind the resilifer is completely detached from shell margins (while in *B. pusilla* it is attached). Despite that, the characteristics here described for *B. ituartei* and *B. finisterra* are also present in *B. hamatans* (Fig. 2d, e) —another species described by the same author who described the type species— as well as in the two species assigned to *Benthocardiella* by Middelfart (2002a). The two new species described herein also differ from the diagnosis of *Benthocardiella* provided by Middelfart (2002a) by having a depressed prodissoconch, (i.e., lacking the "central elevation"). Whether these differences are part of the intra-specific variability or constitute evidence supporting the distinction of a different (new) genus, remains open. In the mean time, we prefer to be conservative, until a better understanding of the group is reached.
4) The affinities and family assignment of the studied taxa. Although Middelfart (2002a) "tentatively included" *Benthocardiella* in the Condylocardiidae, he pointed out the "superficial resemblance" of the hinge morphology of the two species of *Benthocardiella* that he studied to the genera *Cyamiomactra* F.B. Bernard (1897) and *Cyamium* Philippi (1845) (members of the Cyamiidae). The hinge teeth morphology and arrangement of the two species described by Middelfart (2002a) are not different from

those of the *Benthocardiella* species described herein. However, none of these hinges are actually similar to those of *Cyamiomactra* or *Cyamium*: there are differences in the number, morphology and arrangement of teeth and ligaments (for a revision of the conformation of hinge of Cyamioidea, see Zelaya et al. 2020). Alternatively, the hinge morphology of *Benthocardiella* closely resembles that of *Condylocardia* (the type genus of Condylocardiidae). The concept of this family and the genera included/excluded therein has greatly varied along the years and in fact there is at present no general consensus among authors (for a review see Passos et al. 2021). The most recent molecular studies (González and Giribet 2015; Combosch et al. 2017) provided evidence showing that some species formerly assigned to the Condylocardiidae nest within the Carditidae, thus questioning the validity of this group. However, to date, no study has considered members of the type genus of Condylocardiidae or, eventually, representatives of the morphologically similar genus *Benthocardiella*. Due to this, and until further evidences provide better definition on the relationships of the Carditoidea, we prefer to follow the traditional usage, and include the two new species described herein in Condylocardiidae.

Biogeographic implications of the present findings

The genus *Benthocardiella* is currently represented by six valid species ocurring in Neozelanic waters (*B. pusilla*, *B. striatula* Powell 1931; *B. orbicula* Powell 1931; *B. hamatans*, *B. rakiura*; Powell 1939; *B. obliquata* Powell, 1939, the latter comprising three subspecies) and two species occurring in Australian waters (*B. burtonae* Middelfart, 2002a, and *B. darwinensis* Middelfart 2002a). In addition, Middelfart (2002a) inferred that *Condylocardia io* Bartsch (1915), described from South Africa, may also possibly correspond to *Benthocardiella*. Only two of these taxa (*B. striatula* and *B. obliquata bountyensis*) have documented records in sub-Antarctic waters (Powell 1931, 1933). The two new *Benthocardiella* species described herein duplicate the number of species currently known from sub-Antarctic waters, and provide the first record of this genus in the Atlantic Ocean.

The genus *Pachykellya* comprises currently five species: *P. edwardsi*, *P. bernardi*, *P. concentrica* Powell (1927), *P. rotunda* Powell (1927), and *P. minima* Powell (1931) (WoRMS Editorial Board 2021), all of them occurring in Neozelanic waters, in a bathymetric range of 156–311 m. Only one of these species (*P. minima*) has at present published records in the sub-Antarctic waters (Bernard 1897). The present finding of a new species of this genus in the southern tip of South America accounts for a second species in sub-Antarctic waters, and provides the first record of *Pachykellya* outside New Zealand.

Acknowledgements The authors greatly acknowledge Bruce Marshall and Peter Middelfart for sharing comments on New Zealand and Australian representatives of the genera considered herein, and B. Marshall for helping us to obtain some specific literature; Gene Coan for alerting us on the presence of specimens of *Benthocardiella* in LACM; and John Slapcinsky and Gustav Paulay for the facilities provided during the visit to the FlMNH. Bruce Marshall and an anonymous reviewer provided valuable comments for improving the Ms. Photographs of *P. edwardsi* are copyrighted by the Museum of New Zealand Te Papa Tongarewa (CC BY 4.0).

Author contributions MG and DZ both designed and contributed equally to this publication, including sampling, sorting, systematic studies and manuscript writing.

Funding This study was funded by UBACYT 20020150100195BA and PICT 2016–2983. This work is contribution N° 57 MPA Namuncurá (Law 26.875). The authors are members of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

Declarations

Conflict of interest The authors declare no conflict of interests.

References

Batistão AR, Passos FD (2020) New data on *Warrana besnardi*, a tiny bivalve mollusk from the Southwestern Brazilian coast. Am Malacol Bull 38:55–59. https://doi.org/10.4003/006.038.0104

Berke SK, Jablonski D, Krug AZ, Roy K, Tomasovych A (2013) Beyond Bergmann's rule: size–latitude relationships in marine Bivalvia world-wide. Glob Ecol Biogeogr 22:173–183. https://doi.org/10.1111/j.1466-8238.2012.00775.x

Bernard FB (1896) Études comparatives sur la coquille des lamellibranches. *Condylocardia*, type nouveau de lamellibranches. J Conchyliol 44:169–207

Bernard F (1897) Sur quelques coquilles de lamellibranches de l'Île Stewart. Bull Mus Natl Hist Nat 3:309–314

Combosch DJ, Collins TM, Glover EA, Graf DL, Harper EM, Healy JM, Kawauchi GY, Lemer S (2017) Family-level tree of life for bivalves based on a Sanger-sequencing approach. Mol Phylogenet Evol 107:191–208. https://doi.org/10.1016/j.ympev.2016.11.003

González VL, Giribet G (2015) A multilocus phylogeny of archiheterodont bivalves (Mollusca, Bivalvia, Archiheterodonta). Zool Scr 44:41–58. https://doi.org/10.1111/zsc.12086

Ituarte C, Zelaya DG (2015) A redescription of *Malvinasia* Cooper & Preston, 1910 (Bivalvia: Galeommatoidea), with the description of a new species. J Molluscan Stud 81:455–465. https://doi.org/10.1093/mollus/eyv027

Linse K (2002) The shelled Magellanic Mollusca: with special reference to biogeography relations in the Southern Ocean. Theses Zool 34:1–252

Middelfart P (2002a) A revision of the Australian Condylocardiinae (Bivalvia: Carditoidea: Condylocardiidae). Molluscan Res 22:23–85. https://doi.org/10.1071/MR02001

Middelfart P (2002b) Revision of the Australian Cuninae *sensu lato* (Bivalvia: Carditoidea: Condylocardiidae). Zootaxa 112:1–121. https://doi.org/10.11646/zootaxa.112.1.1

Moran AL, Woods HA (2012) Why might they be giants? Towards an understanding of polar gigantism. J Exp Biol 215:1995–2002. https://doi.org/10.1242/jeb.067066

Nicol D (1964) An essay on size of marine pelecypods. J Paleontol 38:968–974

Nicol D (1966) Size of pelecypods in Recent marine faunas. Nautilus 79:109–113

Nicol D (1970) Antarctic pelecypod faunal peculiarities. Science 168:1248–1249

Passos FD, Batistão AR, Bieler R (2021) When size matters: the first comprehensive anatomical study of a species of "Condylocardiidae", an extremely miniaturized bivalve. Peer J 9:e12108. https://doi.org/10.7717/peerj.12108

Powell AWB (1927) Deep-water Mollusca from south-west Otago, with descriptions of 2 new genera and 22 new species. Rec Canterb Mus 3:113–124

Powell AWB (1930a) New species of New Zealand Mollusca from shallow-water dredgings. Part 1. Trans Proc N Z Inst 60:532–543

Powell AWB (1930b) New species of New Zealand Mollusca from shallow-water dredgings. Part 2. Trans Proc N Z Inst 61:536–546

Powell AWB (1931) Descriptions of some new species of recent Mollusca, mainly from the sub-Antarctic islands of New Zealand. Rec Canterb Mus 3:371–376

Powell AWB (1933) Marine Mollusca from the Bounty Islands. Rec Canterb Mus 4:29–39

Rivadeneira MM, Villafaña JA, Gordillo S, Bayer S, Nielsen SN (2015) Hobbits from the deep south: historical drivers of dwarfism in modern Antarctic bivalves. Congr Geol Chil 14:635–638

Roy K, Jablonski D, Martien KK (2000) Invariant size–frequency distributions along a latitudinal gradient in marine bivalves. Proc Natl Acad Sci USA 97:13150–13155. https://doi.org/10.1073/pnas.97.24.13150

Salas C, Gofas S (1998) Description of four new species of *Neolepton* Monterosato, 1875 (Mollusca: Bivalvia: Neoleptonidae), with comments on the genus and on its affinity with the Veneracea. Ophelia 48:35–70. https://doi.org/10.1080/00785236.1998.10428676

Thiele J (1912) Die antarktischen Schnecken und Muscheln. Deutsche Südpolar-Expedition 1901–1903. Wiss Ergeb 13 Zool 5:185–285

Valentine JW, Jablonski D, Kidwell S, Roy K (2006) Assessing the fidelity of the fossil record by using marine bivalves. Proc Natl Acad Sci USA 103:6599–6604. https://doi.org/10.1073/pnas.0601264103

WoRMS Editorial Board (2021) World register of marine species. http://www.marinespecies.org at VLIZ. Accessed Jun 19, 2021.

Zelaya DG (2005) The bivalves from the Scotia Arc Island: Species richness and faunistic affinities. Sci Mar 69:113–122. https://doi.org/10.3989/scimar.2005.69s2113

Zelaya DG (2015) Marine bivalves from the Argentine coast and continental shelf: secies diversity and assessment of the historical knowledge. Am Malacol Bull 33:245–262. https://doi.org/10.4003/006.033.0204

Zelaya DG, Ituarte C (2004) The genus *Neolepton* Monterosato, 1875 in Southern South America (Bivalvia: Neoleptonidae). J Molluscan Stud 70:123–137. https://doi.org/10.1093/mollus/70.2.123

Zelaya DG, Güller M, Ituarte C (2020) Filling a blank in bivalve taxonomy: an integrative analysis of Cyamioidea (Mollusca: Bivalvia). Zool J Linn Soc 190:558–591. https://doi.org/10.1093/zoolinnean/zlz144