



Unravelling the identity of *Pandora* species (Bivalvia: Pandoridae) from Southern South America

Marina Güller¹ and Diego G. Zelaya²

¹*División de Invertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Ángel Gallardo 470, Ciudad Autónoma de Buenos Aires, Argentina; and*

²*Departamento Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón 2, 4º Piso, Argentina*

Correspondence: M. Güller; e-mail: mguller@macn.gov.ar

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ABSTRACT

Four species of *Pandora* have been reported from southern South America: *P. cistula* Gould, 1850, *P. braziliensis* G. B. Sowerby II, 1874, *P. diffissa* Mabilie & Rochebrune, 1889 and *P. patagonica* (Dall, 1915). The group has received little taxonomic attention in this area, resulting in arbitrary and wrong usage of these names, for which several contradictory synonymies have been proposed. This study provides the first revision of *Pandora* species living in southern South America, including photographs of the type material and descriptions of shells, gross anatomy and living animals. Out of the four species previously mentioned, *P. braziliensis* is here regarded as valid, including *P. patagonica* and *P. diffissa* as synonyms. The fourth species, *P. cistula*, remains known only from its type specimen. In addition, a new species, *P. brevirostris*, is described from the shallow waters of Argentina.

INTRODUCTION

In recent years several studies have discussed the affinities of members of the Anomalodesmata (Dreyer, Steiner & Harper, 2003; Harper, Dreyer & Steiner, 2006; Morton, 2012). As a result, the traditional concept of Pandoroidea has fallen into disuse and the family Pandoridae Rafinesque, 1815 is now included within the ‘lyonsiid’ clade (Dreyer *et al.*, 2003; Harper *et al.*, 2006). These studies have revealed the poor knowledge of this group in general and the Pandoridae are no exception. Despite the numerous contributions dealing with the functional, anatomical and developmental aspects of representatives of this family (e.g. Allen, 1954a, b; Allen & Allen, 1955; Yonge & Morton, 1980; Morton, 1984; Thomas, 1994) and the catalogues provided by Carpenter (1869) and Boss (1965), there have been few systematic revisions, either at a global or local scale. Some of the main systematic contributions are those by Carpenter (1865), Dall (1915), Lamy (1934), Boss & Merrill (1965) and Valentich-Scott & Skoglund (2010). However, none of these focused on the species occurring in southern South America.

Three members of the Pandoridae have been described from southern South America: *Pandora cistula* Gould, 1850, from ‘east Patagonia’, *P. diffissa* Mabilie & Rochebrune, 1889 from Tierra del Fuego and *Kennerlyia* (sic) *patagonica* Dall, 1915 from the ‘west coast of Patagonia’. In addition, a fourth species, *P. braziliensis* G. B. Sowerby II, 1874, originally described from ‘Brazil’, has also been reported from this area. Information on these species comes mainly from their original descriptions, which usually lack details and thorough comparisons among the taxa. Given the lack of systematic study of the group, it is not surprising that species have

been frequently confused and that a number of apparently contradictory synonymies have been proposed. For example, Lamy (1934) considered *P. cistula*, *P. patagonica* and *P. braziliensis* as distinct species, with *P. diffissa* as synonym of the last. However, Osorio & Reid (2004) and Huber (2010) regarded *P. patagonica* as a synonym of *P. cistula*, although both figured material from Chile that does not agree with the specimens from the Argentine Province identified by Ageitos de Castellanos (1970) as *P. patagonica*.

This study aims to provide the first integrative revision of *Pandora* species from southern South America, with a view to clarifying their taxonomy and providing descriptions.

MATERIAL AND METHODS

The study area ranges in the southwestern Atlantic from 35°S, south to the Beagle Channel (54–55°S) and north to 42°S in the southeastern Pacific. Sediment from 28 sites along the study area was collected by means of a 2-mm mesh trawl. Living specimens were sorted from the sediment under a stereoscopic microscope and fixed in 5% seawater formalin.

The material was deposited in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires and the Museo de La Plata (MLP), La Plata. Complementary material housed at MACN; Museo Nacional de Historia Natural (MNHNM), Montevideo; Museo Nacional de Historia Natural (MNHNCL), Santiago; Museo de Zoología de la Universidad de Concepción (MZUC), Concepción, and Zoologisches Museum, Hamburg (ZMH), was examined to add distributional records.

The material examined, including number of specimens (spec.) or single valves (v.) in each studied lot, is indicated in the Supplementary Material.

For comparative purposes, the type material (or photographs of it) of all the nominal species described or reported from the area, and the syntypes of *P. bushiana*, housed at National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; Natural History Museum (NHMUK), London and Museum National d'Histoire Naturelle (MNHN), Paris, were also studied. Specimens of *P. bushiana* from off Destin, Florida, housed at the Florida Museum of Natural History (FLMNH 147894, 147896) were compared with the new species here described.

The following shell measurements were taken using a calliper: length (L) = maximum anteroposterior distance; height (H) = maximum dorsoventral distance perpendicular to L ; width (W) = maximum inflation of left valve, perpendicular to L . The ratios H/L and W/H were calculated, with their standard deviation.

SYSTEMATIC DESCRIPTIONS

PANDORIDAE Rafinesque, 1815

Pandora Bruguère, 1797

Type species: Pandora rostrata Lamarck, 1818 (subsequent designation by Children, 1823).

Pandora braziliensis G. B. Sowerby II, 1874

(Figs 1A–Q, 2A, Supplementary Material Figs S1–S3)

Pandora braziliensis G. B. Sowerby II, 1874 (ex A. A. Gould, MS): sp. 15, pl. 2, fig. 15 (Brazil; holotype NHMUK 1964464; Fig. 1A; Supplementary Material Fig. S1).

Pandora (Kennerlyia) braziliensis—Smith, 1881: 40, pl. 5, fig. 4-4c. Lamy, 1934: 110.

Pandora (Pandorella) braziliensis—Ureta, 1966: 311. Rios, 1994: 301, pl. 103, fig. 1474. Huber, 2010: 487.

Kennerleya brasiliensis [sic]—Ageitos de Castellanos, 1970: 277, pl. 26, fig. 8.

Pandora diffissa Mabille & Rochebrune in Rochebrune & Mabille, 1889: H103 (New Year Sound [southern Tierra del Fuego]; 2 syntypes MNHN; Fig. 1G, J, N; Supplementary Material Fig. S3).

Kennerlyia [sic] *patagonica* Dall, 1915: 450 (west coast of Patagonia [46°47'30"S 75°15'00"W], 61 fms; 2 syntypes USNM 96937; Fig. 1B, C, M; Supplementary Material Fig. S2). Soot-Ryen, 1959: 37. Ramorino, 1968: 223, pl. 3, figs 3, 4, pl. 10, figs 3, 4.

Pandora cistula—Osorio & Reid, 2004: 83, fig. 3C. Cárdenas, Aldea & Valdovinos, 2008: 233, fig. 7.102-103. (Both not Gould, 1850).

Pandora (Pandorella) cistula—Huber, 2010: 487 (not Gould, 1850).

? *Pandora (Pandorella) bushiana*—Huber, 2010: 487 (not Dall, 1886).

Material examined: Photographs of the holotype of *P. braziliensis*; syntypes of *P. diffissa*; photographs of syntypes of *K. patagonica*; 37 lots (see Supplementary Material).

Diagnosis: Shell subovate; anterior end short; posterior end high, produced; rostrum indistinct. Deep anterior radial sulcus in left valve, delimiting a small anterior area. Sculpture of irregular

commarginal folds and well-marked radial striae on right valve. Two massive, elongated crura in left valve; one short, massive anterior crura and one weak, elongated posterior crura in right valve.

Description: Shell (Fig. 1A–Q): L to 29.8 mm, delicate, subovate ($H/L = 0.61 \pm 0.04$ mm, $n = 24$); inequivalve: left valve inflated ($W/L = 0.19 \pm 0.02$, $n = 24$), with deep sulcus radiating from beak to anterior part of ventral margin, delimiting a small, depressed, anterior area of shell (less evident in eroded specimens) (Fig. 1A, B, D, E, G); right valve flat, with anterior area not clearly differentiated (Fig. 1C, F, I). Anterior end of shell short, posterior end produced, higher than anterior one. Anterodorsal margin sloping, straight to slightly curved, forming a weak to well-marked angle at junction with anterior margin. Ventral margin widely arcuate, anteriorly markedly sinuated by the radial sulcus in left valve, posteriorly variably expanded, evenly curved; junction of ventral and posterior margins angulated; posterior margin short, obliquely truncated. Posterodorsal margin almost straight, sometimes recurved or arcuate; twice length of anterodorsal one. Beaks low but wide, prosogyrate, raised from dorsal margin, located in anterior third of shell (Fig. 1A–E). In left valve, a well-marked radial ridge extends from beak to junction of posterior and ventral margins, delimiting a slightly depressed to flat posterior area of shell. A second, similar ridge extends along posterior area, running from beak to posterior margin (Fig. 1A, B, D, E, L). Posterior area not projecting in a distinctive rostrum. In right valve, a ridge running from beak to dorsal third of posterior margin; area dorsal to this ridge flat, bent into an almost straight angle, overlapping opposite valve (Fig. 1L). Outer shell surface chalky white in well-preserved specimens, sculptured with irregular growth folds, and well-marked radial grooves only in right valve, with additional short, medial grooves towards ventral margin (Fig. 1B–D, F). Eroded specimens with nacreous shell surface, exposing weak radial elements in left valve (Fig. 1E, H). Periostracum thick, dehiscent, orange-brown (Fig. 1E, F), extending over dorsal margin of valves, forming a periostracal ligament. Interior nacreous (Fig. 1J, K, N, O). Adductor muscle scars subcircular, subequal, deeply impressed. Pallial line interrupted, of 5 small, circular scars and a larger, irregular, elongate posterior one. Hinge plate of 2 tooth-like elements ('crura') in each valve (Fig. 1P, Q). Right valve with a massive, short, high crus below beak and a weak, elongate, low, posterior crus, approximately twice length of anterior one (Fig. 1Q). Left valve with 2 massive, elongate crura completely merged with anterior and posterior dorsal margins (Fig. 1P). Anterior crus sometimes enlarged towards beak. Ligament elongate, oblique, posteriorly directed, deeply sunken, with well-developed calcified ventral portion (i.e. the lithodesma; not shown); posteriorly limited by the posterior crura in both valves (Fig. 1P, Q).

Anatomy (Fig. 2A): Mantle with strongly developed radial musculature. Mantle margins largely fused, for about $\frac{3}{4}$ of their length, with short anterior pedal aperture, whose extent coincides with anterior area of shell. Mantle margin posteriorly hypertrophied forming inhalant and exhalant siphons, which are fused along all their length. Inhalant and exhalant apertures fringed by external ring of simple, capitate tentacles, of similar length; inhalant aperture with an additional innermost ring of alternating long and short capitate tentacles. Adductor muscles subcircular in cross section, of similar size; posterior adductor at middle of length from beak to posterior margin. Gills: both demibranchs present. Outer demibranch extremely small, reduced to descending lamella, upturned, extending between gonad and posterior adductor muscle. Inner demibranch large, heterorhabditic, of about 70 plicae (in specimens $c.$ 20 mm length); ascending lamella slightly shorter than descending one.



Figure 1. *Pandora braziliensis*. **A.** *P. braziliensis*, holotype (NHMUK 1964464). **B, C, M.** *Kennerlyia patagonica*, syntypes (USNM 96937). **D, L, P, Q.** Isla de los Estados, 86 m (MACN 22235). **E, F.** Fiordo Cahuelmo, 10–30 m (MZUC). **G, J, N.** *Pandora diffissa*, syntype (MNHN). **H.** Fiordo Cahuelmo, 70–113 m (MACN-In 40332). **I.** Golfo San Matías, 161 m (MACN-In 40326). **K, O.** Golfo San Jorge (MACN-In 40328). Scale bars: **A–O** = 1 cm; **P, Q** = 2 mm.

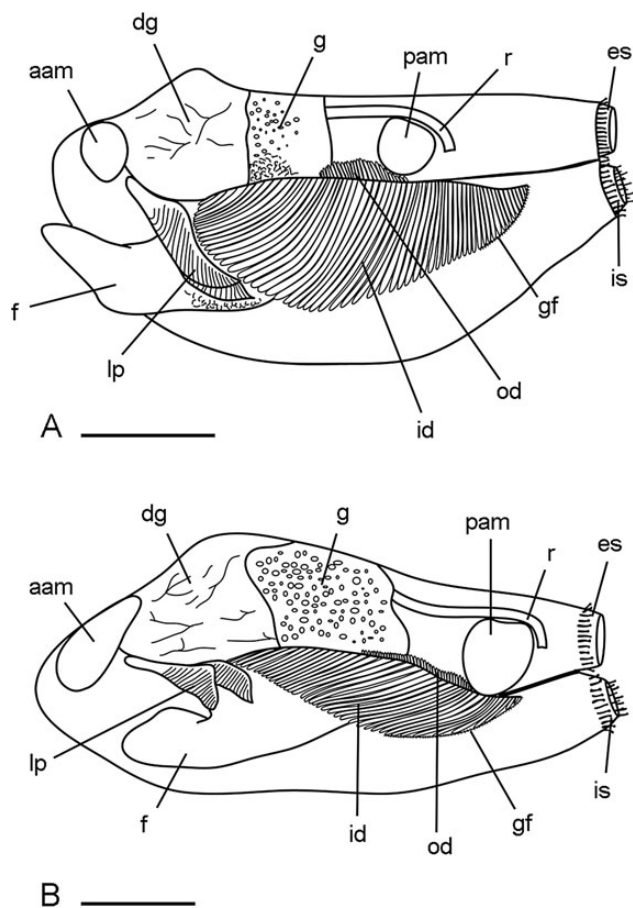


Figure 2. Anatomy. **A.** *Pandora braziliensis*. **B.** *P. brevirostris* n. sp. Abbreviations: aam, anterior adductor muscle; dg, digestive gland; es, exhalant siphon; f, foot; g, gonad; gf, gills fusion; id, inner demibranch; is, inhalant siphon; lp, labial palps; od, outer demibranch; pam, posterior adductor muscle; r, rectum. Scale bars: **A** = 5 mm; **B** = 2 mm.

Left and right outer demibranchs fused in their posterior fifth. Labial palps large, elongate, of about 25 sorting ridges in larger specimens, posterior pair slightly longer than anterior one.

Distribution: Southwestern Atlantic, from São Paulo, Brazil (Ihering, 1907; Rios, 1994) south to southern Tierra del Fuego (Rochebrune & Mabile, 1889; herein) and in southeastern Pacific north to Valparaíso (33°S) (Ramorino, 1968); 10–665 m (herein).

Remarks: Ureta (1966: 311) already noted the “great similarity” between *P. braziliensis* and *P. patagonica*, and Huber (2010), although regarding both species as distinct, included *P. diffissa* as a synonym of the former. Our study of the type material of *P. braziliensis*, *P. patagonica* and *P. diffissa*, and specimens from sites intermediate between their type localities, reveals a continuum of variation that includes specimens with curved to straight posterodorsal margin and the ventral margin smoothly curved to posteriorly expanded, consequently giving the appearance of ovate to elongate shells (resembling the outlines of the types of *P. diffissa* and *P. patagonica*, respectively). All this variability could be found among specimens from a single locality, although those from the Beagle Channel tend to be more ovate and those from the southeastern Pacific more elongate. The reasons for these morphological differences cannot be explained at present but, taking into account their continuum of variation at some

sites, we consider that they represent intraspecific variants of a single species, for which *P. braziliensis* is the oldest available name.

Pandora braziliensis is most similar to *P. wardiana* A. Adams, 1860, from the North Pacific Ocean, a species that clearly differs by having the ventral and posterior margins evenly rounded and gradually connected, which results in a much higher posterior end of the shell. Additionally, in *P. wardiana* the beaks are lower, not projecting above the dorsal shell margin, the situation of the anterior part of the ventral margin is deeper, and the anterior radial sulcus slopes from the beak straight down towards the ventral margin or posteriorly (instead of anteriorly, as in the case of *P. braziliensis*).

Pandora braziliensis is a widely distributed species, ranging from southern Brazil to Cape Horn in the southwestern Atlantic and north to central Chile in the Pacific; however, all records north of 42°S (on both Atlantic and Pacific sides of the continent) come from waters deeper than 49 m, associated with sub-Antarctic water masses. Consequently, *P. braziliensis* can be regarded as a Magellanic species.

Pandora brevirostris new species

(Figs 2B, 3A–M)

Kennerleya patagonica—Ageitos de Castellanos, 1970: 277 (not Dall, 1915).

Pandora patagonica—Scarabino, 1977: 215, pl. 10, fig. 5 (not Dall, 1915).

Type locality: 41°40′17.8″S 65°00′27.8″W, Playas Doradas, Golfo San Matías, Argentina; 16 m.

Type material: Holotype (MACN-In 40339) and 3 paratypes (MACN-In 40340: 2 spec., 1 v.) from type locality.

ZooBank registration: B90A78AC-5846-4A91-A19E-CA5D2BF94327.

Etymology: The name makes reference to the short rostrum present in this species.

Other material examined: 19 lots (see Supplementary Material).

Diagnosis: Shell elongate-cuneiform; anterior end rounded to pointed; posterior end high, with short rostrum. Shallow anterior radial sulcus in left valve delimiting large anterior area. Sculpture of irregular commarginal folds and faint radial striae on right valve. Two solid crura on each valve and an additional, weak thickening in anterior part of right valve; anterior crus of left valve small, projecting in sagittal plane.

Description: Shell (Fig. 3A–C, E–K): *L* to 17.7 mm; delicate, elongate-cuneiform ($H/L = 0.51 \pm 0.03$ mm, $n = 11$); inequivalve: left valve somewhat inflated ($W/L = 0.14 \pm 0.02$, $n = 11$), with shallow sulcus radiating nearly straight down from beak to ventral margin, delimiting a relatively large, projected anterior area of shell (Fig. 3A–C, E–G); right valve flat, with anterior area not clearly differentiated (Fig. 2I). Anterior end of shell widely rounded to pointed; posterior end produced, almost as high as anterior end, attenuate, narrowly subtruncate, with short rostrum. Anterodorsal margin short, straightly sloping to markedly concave, forming marked angulation at junction with anterior margin. Ventral margin widely arcuate, only slightly indented by radial sulcus in left valve; usually centrally straight in right valve; sometimes forming a shallow sinus at posterior part, before reaching posterior margin. Posterior margin short, straight, obliquely truncate, forming well-marked angles at junction with ventral and dorsal margins. Posterodorsal margin

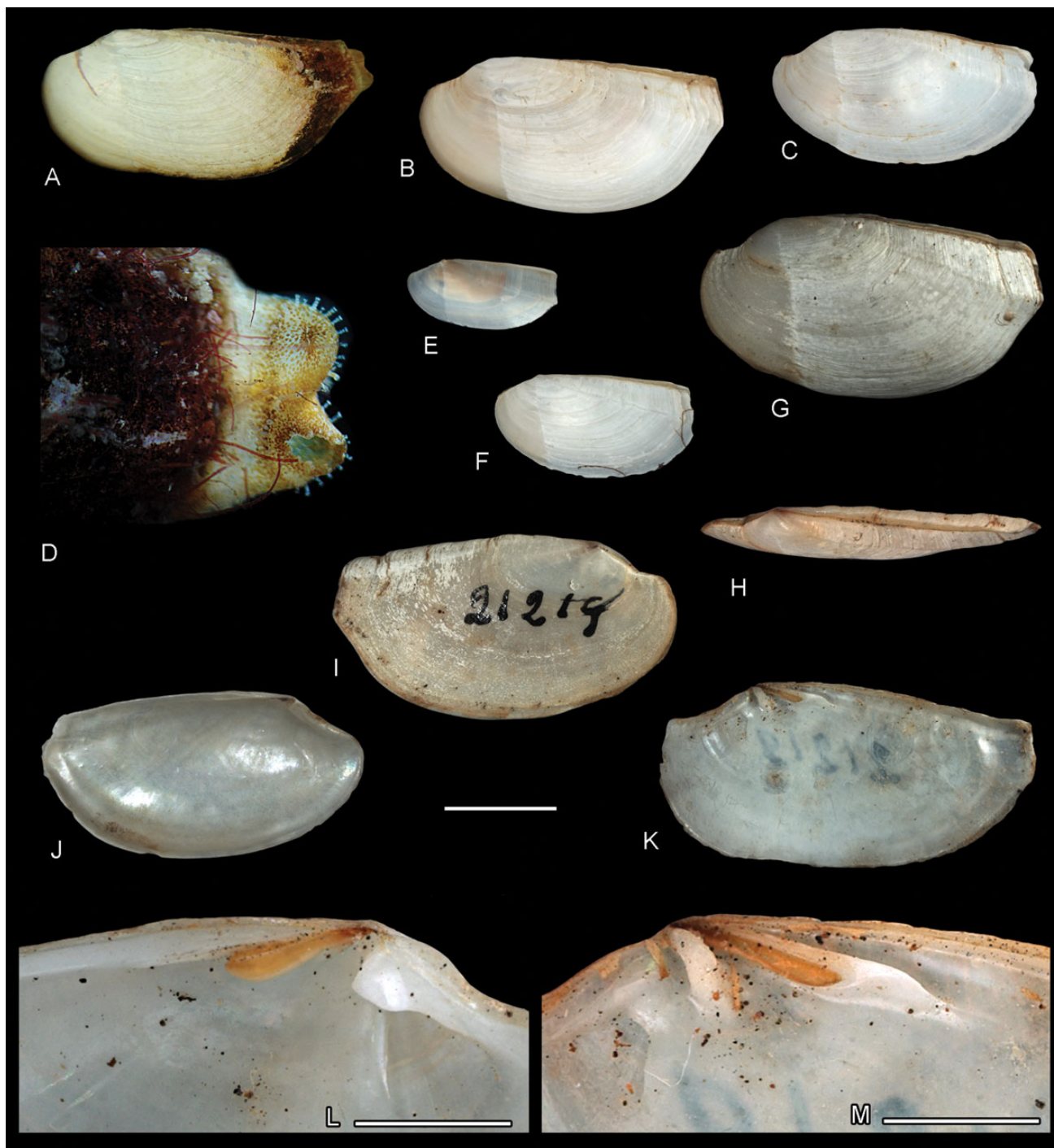


Figure 3. *Pandora brevirostris* n. sp. **A.** Holotype (MACN-In 40339). **B, C, F.** Las Grutas, 9 m (MACN-In 40348). **D.** Detail of siphons, living holotype (MACN-In 40339). **E.** Las Grutas, 9 m (MACN-In 40344). **G-I, K-M.** Golfo San Matías (MACN-In 21219). **J.** Puerto Lobos, 21 m (MACN-In 40358). Scale bars: **A-C, E-K** = 5 mm; **L, M** = 2 mm.

straightly sloping to slightly convex, 4 times length of anterodorsal one. Beaks minute, slightly prosogyrate, not projecting above dorsal margin, located in anterior fourth of shell (Fig. 3A–C, E–I). In left valve, a low but well-marked radial ridge running from beak to junction of posterior and ventral margins, delimiting a narrow, flat posterior area of shell, which extends slightly forming a short rostrum (Fig. 3A, B, E, G, I). In right valve, an obscure ridge running from beak to dorsal fourth of posterior margin; area dorsal to this ridge bent into almost straight angle,

overlapping the opposite valve (Fig. 3I, H). Outer shell surface chalky white in well-preserved specimens, sculptured with irregular growth folds, which are less marked in anterior area of shell, and faint radial grooves only in right valve. Eroded specimens with nacreous shell surface. Periostracum dehiscent, yellowish-brown, extending over dorsal margin of valves, forming a periostracal ligament. Interior nacreous (Fig. 3J, K). Adductor muscle scars slightly impressed, subequal; anterior pear-shaped, posterior ovate (Fig. 3L, M). Pallial line interrupted, of 5–7 small,

ovate scars and a larger, irregular, ovate-elongate posterior one. Hinge plate of 2 tooth-like elements ('crura') on each valve (Fig. 3L, M). Right valve with 2, straight, posteroventrally directed crura diverging from beak; the anterior one higher, 1/3 length of posterior one; posterior crus elongate, with a distally located cusp, representing posterior limit of internal ligament (Fig. 3M); in addition, a low and weak thickening, running from beak to side of anterior adductor muscle scar. Left valve with 2 crura merged to dorsal margin (Fig. 3L). Anterodorsal margin widened, with the adjacent anterior crus ranging from an elongate, indistinct element to a distinct tubercle below beak, parallel to sagittal plane. Posterior crus elongate, narrow. Ligament long, oblique, posteriorly directed, sunken (Fig. 3L, M), with well-developed ventral calcified lithodesma (not shown).

Anatomy (Fig. 2B): Mantle margins largely fused, except for anterior pedal aperture, which extends for about 1/3 of its length, coinciding with anterior area of shell. Posterior hypertrophy forming inhalant and exhalant siphons, which extend only slightly from shell in living specimens (Fig. 3D). Siphons fused along most of their length, only distally separated. Inhalant and exhalant apertures fringed by external ring of similar, simple, capitate tentacles (Figs 2B, 3D); inhalant aperture with an additional innermost ring of capitate tentacles, similar in length. Anterior adductor muscle pear-shaped in cross section, its major axis parallel to anterodorsal margin; posterior adductor muscle ovate in cross section, slightly smaller than anterior one, located slightly posterior to middle length between beak and posterior margin. Gills: both demibranchs present (Fig. 2B). Outer demibranch extremely small, elongate, reduced to descending lamella, extending between gonad and posterior adductor muscle. Inner demibranch larger, heterorhabditic, composed of about 30 plicae (in specimens *c.* 8 mm length); ascending lamella slightly shorter than descending one. Left and right outer demibranchs fused in posterior half. Labial palps triangular, composed of about 17 sorting ridges in larger specimens (Fig. 2B). Mantle pale, pigmented with orange-brown spots, which are more dense towards margin and at end of siphons (Fig. 3D).

Distribution and habitat: Currently only known from south of Buenos Aires Province to Golfo San Matías. Living animals were found in the shallow subtidal at 7–18 m depth, buried on soft bottoms of varied grain-size, ranging from thin sand or mud to coarse gravel and in layers of sand over rocky substrates.

Remarks: *Pandora brevis* is most similar *P. bushiana* Dall, 1886 (Fig. 4A–O), originally described from Tampa, Florida. However, the former clearly differs by having a shorter rostrum which, in addition, is less differentiated, due to the shallower sinus in the posterior part of the ventral margin. Another difference is found in the extension of the anterior area of the shell, which is larger in *P. brevis* than in *P. bushiana*. In addition, the anterior crus of the left valve is small and projects parallel to the sagittal plane in *P. brevis*, whereas it is large, massive and introverted towards the valve in *P. bushiana* (Fig. 3L *cf.* 4N, respectively). Furthermore, the species seem to be allopatric in distribution. Boss & Merrill (1965) reported *P. bushiana* as distributed from North Carolina to Yucatán, Mexico. Subsequently, the species was also mentioned as present in the Colombian Caribbean and Brazil (Abbott, 1974; Díaz Merlano & Puyana Hegedus, 1994; Rios, 1994; Mikkelsen & Bieler, 2008; Huber, 2010; Passos & Magalhães, 2011), although the identity of the material on which these records are based requires confirmation.

In shell outline the new species also resembles *P. granulata* Dall, 1915, from the northeastern Pacific. However, *P. brevis* is less elongate and higher posteriorly, has faint radial striae on the right valve (*cf.* the well-marked ones of *P. granulata*) and lacks the granulations on the posterior radial ribs of *P. granulata*.

In addition, *P. brevis* reaches a larger size than *P. granulata* ($L = 17.7$ vs 10 mm).

Pandora braziliensis is easily distinguished from *P. brevis* by its subovate, inflated shell, which results in the highest observed W/L and H/L proportions, and by lacking the short posterior rostrum of *P. brevis*. In addition, *P. braziliensis* has a deep anterior radial sulcus and two posterior radial ridges on the left valve, and deeply-incised radial grooves on the right valve. Although smaller specimens of both species are extremely similar, being elongate and less inflated (Figs 1H, 3C), the presence of two posterior ridges clearly allows one to recognize *P. braziliensis*. Lastly, it should be noted that *P. brevis* seems to be allopatric with *P. braziliensis*, being associated with the temperate waters of the Argentinean / Brazilian Province.

The study of the specimens from Golfo San Matías previously reported as *P. 'patagonica'* by Castellanos (1970) (MACN-In 21219, reported as 21319), revealed that these actually correspond to *P. brevis*. Judging from the figure by Scarabino (1977: pl. 10, fig. 5), his record of *P. patagonica* also applies to this species.

***Pandora cistula* Gould, 1850**

(Fig. 5A–D)

Pandora cistula was described from 'East Patagonia'. The illustration by Gould (1852: pl. 33, figs 500, 500a, 500b) matches the material currently recognized as the holotype (USNM 5887; Fig. 5A–D). This name was subsequently used several times to refer to Chilean material (e.g. Osorio & Reid, 2004; Cárdenas *et al.*, 2008); however, none of these records actually correspond to this species, and they are here reassigned to *P. braziliensis*. Thus, *P. cistula* remains at present known only from its type material, which is clearly different from the other two species described above (i.e. *P. braziliensis* and *P. brevis*) by having a high and broadly rounded anterior end, with the anterodorsal margin convex and the posterior end markedly projecting in a recurved rostrum. The shell morphology exhibited by *P. cistula* appears closely allied to the northeastern Atlantic *P. inaequalis* (Linnaeus, 1758) and *P. albida* (Röding, 1798) (these two species are regarded as synonyms by some authors, e.g. Boss & Merrill, 1965). Whether the stated type locality of *P. cistula* is incorrect, or it actually corresponds to a third (and rare) species from southern South America, never subsequently collected, remains an open question.

DISCUSSION

Only one of the four species of *Pandora* previously reported from the southern tip of South America could be validated, *P. braziliensis*, with two other species (*P. diffissa* and *P. patagonica*) here considered its synonyms. The remaining species, *P. cistula*, is only known from the type specimen and might not be from this region. Furthermore, *P. brevis* is newly described from the area.

On the (sub)generic allocation of the species

Despite the numerous generic names that have proposed to accommodate the species of this family, only six genera were regarded as valid by Valentich-Scott & Skoglund (2010): *Pandora* Bruguière, 1797 (= *Calopodium* Röding, 1798 and *Trutina* Brown, 1827); *Clidiophora* (Carpenter, 1864); *Heteroclidus* Dall, 1903; *Foveadens* Dall, 1915; *Frenamya* Iredale, 1930 (= *Coelodon* Carpenter, 1865) and *Coania* Valentich-Scott & Skoglund, 2010. *Pandorella* Conrad, 1863, previously regarded as a full genus (e.g. Bernard, Cai & Morton, 1993), has since been considered a subgenus of *Pandora* (Valentich-Scott & Skoglund, 2010), with *Kennerlia* Carpenter, 1864 (and its subsequent misspellings *Kennerlyia*, *Kennerleyia*, *Kennerleya*) as synonyms.

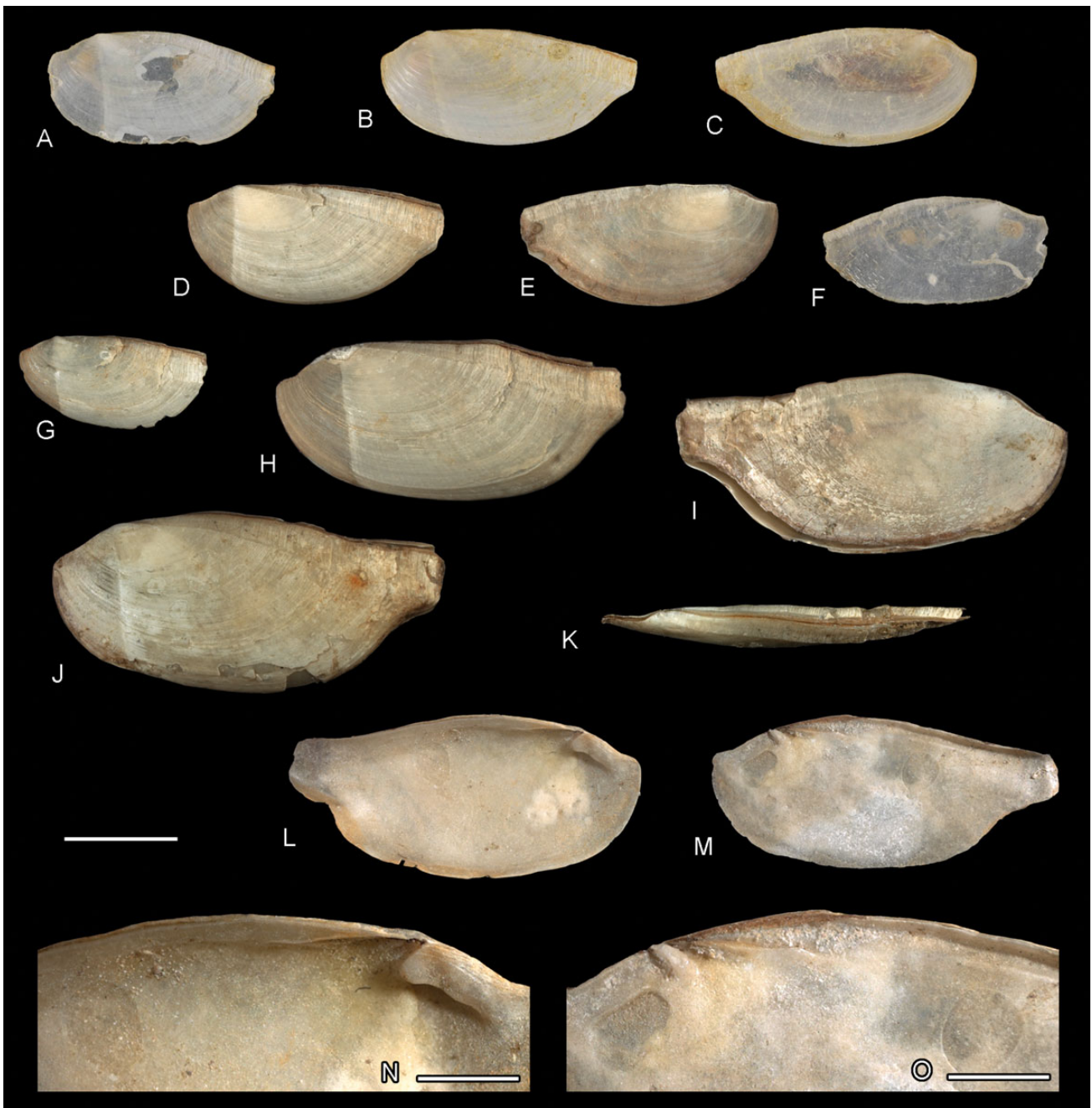


Figure 4. *Pandora bushiana*. **A–C, F.** Syntypes (USNM 61029). **D, E, G–K.** Off Destin, Florida, 36.5 m (FLMNH 147896). **L–O.** Off Destin, Florida, 32.9–36.5 m (FLMNH 147894). Scale bars: **A–M** = 5 mm; **N, O** = 2 mm.

Valentich-Scott & Skoglund (2010) confirmed that hinge morphology is the most reliable diagnostic character for the recognition of the different groups. In this regard, *P. cistula* cannot be unambiguously characterized, due to the eroded state of the material. *Pandora braziliensis* and *P. brevisrostris* fit within their concept of *Pandora* by having two solid crura in each valve, those of the left valve fused to the dorsal margin. Within this genus, *P. braziliensis* shows strong radial grooves in the right valve, a condition regarded as diagnostic of *Pandorella*; in contrast, *P. brevisrostris* has faint radial striae in the right valve, which is a diagnostic character of the nominate subgenus as defined by Valentich-Scott & Skoglund (2010). According to these authors, the lithodesma is usually present in *P. (Pandora)* and always

present in *P. (Pandorella)*. However, Huber (2010) pointed out that the type species of *Pandora* lacks a lithodesma and consequently suggested that most of the other species currently attributed to this genus could actually belong to different (new) (sub)genera. Both *P. braziliensis* and *P. brevisrostris* have a well-developed lithodesma. The gross anatomy of *P. braziliensis* and *P. brevisrostris* studied herein is in agreement with the descriptions by Boss & Merrill (1965) of '*Pandora*', as well as that of *Frenamya* by Morton (1984). The 'only' morphological differences found (mainly size or shape) in the adductor muscles, demibranchs, labial palps and extent of the mantle gaps, appear to be useful characters at species-level. Due to the uncertainties resulting from the lack of knowledge of other pandorids, and the discrepancies about the value of the lithodesma



Figure 5. A–D. *Pandora cystula*, holotype (USNM 5887). Scale bar: 1 cm.

as a diagnostic character at generic level, the species here studied are tentatively included under *Pandora* in a broad sense.

SUPPLEMENTARY MATERIAL

Supplementary Material is available at *Journal of Molluscan Studies* online.

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SUPPLEMENTARY MATERIAL

Non-type material examined:

***Pandora braziliensis* G. B. Sowerby II, 1874**

Southwestern Atlantic: 35°47'24'00''S 52°58'48''W, 199-214 m (MNHNM: 2 v.); 36°34'S 53°40'W, 182 m (MACN-In 24171: 16 spec., 15 v.); 37°31'S 56°23'W, 70 m (MACN-In 16167: 1 spec.); Golfo San Matías: 41°12'58.8''S 64°31'32.4''W, 161 m (MACN-In 40326: 1 spec., 11 v.); 41°20'50.4''S 64°55'36.6''W, 102 m (MACN-In 40327: 2 v.); 45°25'S 65°45'W (MLP-Ma 6503-1: 38 v.); [46°04'S 66°50'W], Golfo San Jorge (MACN-In 40328: 4 spec.); Isla de los Estados: [54°43'56''S 63°51'25''W], Puerto San Juan del Salvamento, 33.4 m (MACN-In 22152: 2 v.); 54°45'45''S 64°16'17''W, Puerto Basil Hall, 86 m (MACN-In 22235: 9 v.); [54°48'42''S 64°22'18''W], Puerto Parry (MACN-In 40329: 3 v.). Magellan Strait: 53°09'12''S 70°39'12''W, 127 m (ZMH 19929: 2 spec.). Beagle Channel: 54°29'26''S 69°04'38''W, 100 m (ZMH 19931: 1 spec.); 54°50'S 68°15'W, 18-21 m (MLP-Ma 14172: 1 v.); 54°54'24''S 70°12'46''W, 665 m (ZMH 19934: 3 spec.); 54°54'44.64''S 67°14'08.64''W, 38 m (MACN-In 40330: 1 spec., 4 v.). Southeastern Pacific: Fiordo Cahuelmo: 42°15'22''S 72°23'48''W, 10-30 m (MZUC: 4 spec., 2 v.); 42°15'23''S 72°24'09''W, 40-93 m (MACN-In 40331: 2 spec., 1 v.); 42°15'37''S 72°25'52''W, 70-113 m (MACN-In 40332: 5 spec., 1 v.); Golfo de Ancud: 42°20'06''S 72°55'52''W, 252 m (MZUC 32648: 1 spec.); Fiordo Comau: 42°22'S 72°24'W, 30 m (MACN-In 40333: 1 spec.), 50 m (MACN-In 40334: 6 spec., 3 v.); 42°22'47''S 72°25'07''W, 73-89 m (MACN-In 40335: 4 spec., 6 v.); 42°22'51''S 72°25'06''W, 50-97 m, (MACN-In 40336: 14 spec.); 42°22'56''S 72°25'24''W, 115-

260 m, (MACN-In 40337: 3 spec., 2 v.); 42°24'26''S 72°25'25''W, 26-144 m
(MACN-In 40338: 5 spec., 2 v.); Estero Castro: 42°30'11''S 73°45'40''W, 22 m
(MZUC 32649: 1 spec.); Boca del Guafo: 43°39'18''S 73°50'95''W, 106 m
(MNHNCL-MOL 7116: 1 spec.); Isla Toto: 44°17'43''S 73°12'46''W, 250 m
(MNHNCL-MOL 7189: 1 spec.); Estero Puyuhuapi: [44°19'S 72°30'W], 237 m
(MNHNCL-MOL 7123: 1 v.); Seno Aysén: 45°18'58''S 73°17'51''W, 330 m
(MNHNCL-MOL 7108: 14 spec.; MNHNCL-MOL 7107: 3 v.); 45°21'80''S
73°22'78''W, 200 m (MNHNCL-MOL 7155: 1 v.); 45°24'69''S 72°51'64''W, 200 m
(MNHNCL-MOL 7158: 1 spec.; MNHNCL-MOL 7160: 3 v.); 45°26'36''S
72°53'56''W, 180 m (MNHNCL-MOL 7181: 1 spec.); 45°29'56''S 73°31'03''W, 250
m (MNHNCL-MOL 7164: 46 spec.; MNHNCL-MOL 7165: 4 v.).

***Pandora brevirostris* new species**

Southwestern Atlantic: Buenos Aires: [38°51'00''S 60°05'00''W], Claromecó,
intertidal (MACN-In 40341: 1 v.); Golfo San Matías (MACN-In 21219: 4 spec.);
Golfo San Matías: Las Grutas, 16 m (MACN-In 40342: 1 spec.); Las Grutas, 18 m
(MACN-In 40343: 1 spec.); 40°49'44''S 65°05'13.5''W, 9 m (MACN-In 40344: 1
spec.); 40°50'12.8''S 65°04'42.2''W, 10 m (MACN-In 40345: 2 v.); 40°50'35.5''S
65°04'43.7''W, 12 m (MACN-In 40346: 1 v.); 40°55'17.4''S 65°08'07.6''W, 7-8 m
(MACN-In 40347: 1 spec., 2 v.); 40°56'26.6''S 65°07'59.1''W, 9 m (MACN-In
40348: 7 spec., 3 v.); 40°56'27.2''S 65°07'58.2''W, 10-11 m (MACN-In 40349: 7
spec., 4 v.); 41°37'59.2''S 65°01'23.1''W, in stomach content of *Astropecten* spec.
(MACN-In 40350: 2 spec., 1 v.); 41°38'02.6''S 65°01'13.3''W, intertidal (MACN-In
40351: 1 v.); 41°38'06.6''S 65°00'55.9''W, 7 m (MACN-In 40352: 1 v.);

41°39'03.1"S 65°00'38.3"W, 12-14 m (MACN-In 40353: 2 spec.); 41°39'41.3"S 65°00'32.9"W, 16 m (MACN-In 40354: 1 v.); 41°40'48.3"S 65°00'46.1"W, 12 m (MACN-In 40355: 1 spec.); 41°40'49.1"S 65°00'46.5"W, 12 m (MACN-In 40356: 1 v.); 41°58'22.8"S 65°03'28.6"W, 16.5 m (MACN-In 40357: 2 v.); 42°00'07"S 65°03'20.8"W, 21 m (MACN-In 40358: 2 v.).

Supplementary figures:



Figure S1. A, B. *Pandora braziliensis*, holotype (NHMUK 1964464). **A.** External view (also shown in Fig. 1A); **B.** Internal view. Scale bar = 5 mm.

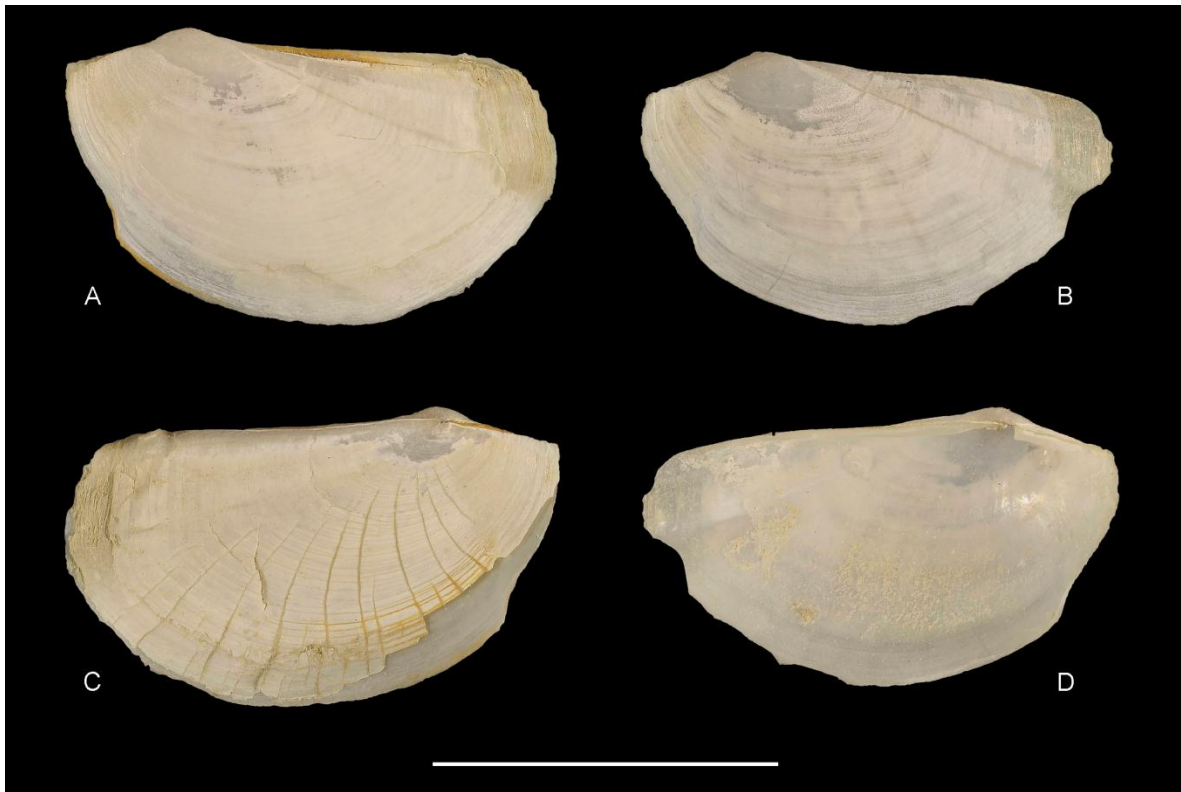


Figure S2. A–D. *Kennerlyia patagonica*, syntypes (USNM 96937). **A–C.** External views (A and C also shown in Fig. 1B, C); **D.** Internal view (also shown in Fig. 1M).

Scale bar = 1 cm.

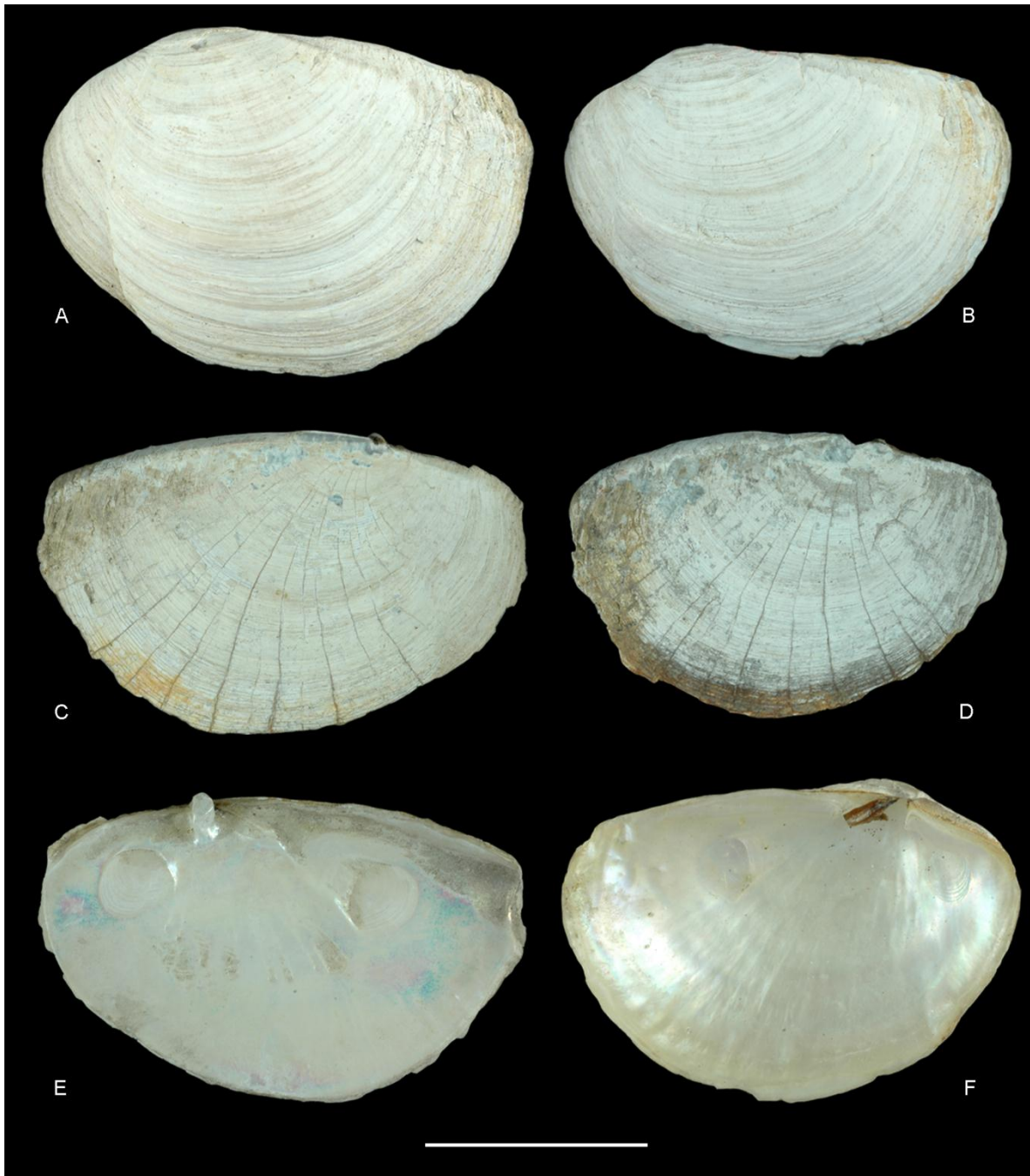


Figure S3. A–F. *Pandora diffissa*, syntypes (MNHN). A–D. External views (A also shown in Fig. 1G); E, F. Internal views (also shown in Figs. 1J, N). Scale bar = 1 cm.