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Solemyidae (Bivalvia, Protobranchia) from the lower Miocene of south-central Chile, with description of a new species

Leonardo Pérez-Barría[1,2] and Sven N. Nielsen[2]*

[1]Museo Regional de Aysén (MRA), Coyhaique, Chile <leonardo.perez@museoschile.gob.cl>;
[2]Instituto de Ciencias de la Tierra, Universidad Austral de Chile, Valdivia, Chile <sven.nielsen@uach.cl>

Abstract.—The Miocene Solemyidae of Chile are revised. The holotype of *Solemya antarctica* Philippi, 1887, originally described as *Solenomya*, is lost. Due to the lack of information on internal characters, its systematic position is considered as uncertain. A new species, *Solemya lucifuga* n. sp., is described from the lower Miocene Ranquil Formation of south-central Chile. Its dense radial external ornamentation shows that it is clearly different from *S. antarctica*. It is currently the only confirmed and described Miocene solemyid bivalve from the Southern Hemisphere.

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Introduction

Solemyidae is a family of primitive bivalves with a widespread distribution from tropical to temperate latitudes and intertidal to below 5000 m depth (Allen, 1979; Zardus, 2002; Taylor and Glover, 2010). Extant solemyids are euryhaline, some broadly tolerant to salinities >34 ppt and <20 ppt after acclimatization (Castagno and Chanley, 1973). They are well known for their ability to live under oxygen-poor conditions through symbiosis with chemoautotrophic bacteria oxidizing sulfur (e.g., Reid and Brand, 1987; Fisher, 1990; Distel, 1998; Stewart and Cavanaugh, 2006). They live infaunally in silty to sandy sediments and are able to swim briefly through expulsion of a water jet from their posterior opening (Reid, 1980).

Externally, solemyids are difficult to distinguish based only on valve morphology (Neulinger et al., 2006). They possess thin aragonitic valves with a high content of organic matrix (Taylor et al., 1969). The valves are equilateral, anteriorly elongate, subcylindrical, with dorsal and ventral margins usually parallel, and with an edentate hinge that represents an early apomorphic trait (see Bailey, 2011, and references therein). Studies using electron microscopy show a wide variety of shell microstructures, from outer layers characterized by radially elongate simple prismatic structures to reticulate structures not known in any other mollusk, and inner layers with laminar, homogeneous, and irregular complex crossed-lamellar structure (see Sato et al., 2013b). They are covered externally by a coarse and shiny periostracum that frequently extends over the shell margin. Taxonomically, there are two modern genera, *Solemya* Lamarck, 1818 and *Acharax* Dall, 1908, which are principally distinguished by the position of the ligament, internal or external, respectively (e.g., Cox et al., 1969; Coan and Valentich-Scott, 2012).

Fossil representatives of Solemyida are known since the Early Ordovician (Cox et al., 1969; Pojeta, 1988; Cope, 1996, 2000; Bailey, 2011). Recent phylogenetic analyses suggest that both *Solemya* and *Acharax* have an early Paleozoic origin (Sharma et al., 2013), and are probably among the most ancient chemosymbiotic bivalves (Taylor et al., 2008). Despite this early origin, the evolutionary history of the group is poorly documented and the fossil record shows many gaps along the Phanerozoic (Vokes, 1955; Pojeta, 1988), although the record at fossil seeps seems relatively good in comparison (e.g., Kiel, 2010; Hryniewicz et al., 2017). The solemyid fossil record from the Miocene is concentrated in the Northern Hemisphere with representatives known from Japan (Amano and Little, 2005; Amano and Ando, 2011), Russia (Ilyina, 1963), the Mediterranean (Taviani et al., 2011), Oregon (Moore, 1963), Cuba (Cooke, 1919), Panama and Costa Rica (Olsson, 1942), and Barbados and Venezuela (Gill et al., 2005). The only record from the Southern Hemisphere, apart from some undescribed species from New Zealand (Marwick, 1931; Vokes, 1955; Saether et al., 2016), seems to be *Solenomya antarctica* Philippi, 1887, coming from the early Miocene of central Chile (33°S). However, since Philippi's (1887) work (simultaneously published in German and Spanish), no other specimen has been described. The first confirmed specimen of the family in ca. 130 years comes from the Arauco Peninsula (Kiel and Nielsen, 2010, tab. dr1), at ~37°S, and is described here as a new species along with a discussion of *Solenomya antarctica* Philippi, 1887.

Geological setting

The material described here comes from the Ranquil Formation on Arauco Peninsula, south-central Chile (Fig. 1), consisting mostly of mudstones with intercalated sandstone beds. It unconformably overlies the Eocene Millongue Formation and underlies the Huenteguapi Sandstone (Le Roux et al., 2008) with an erosional discontinuity. The studied material comes from

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*Corresponding author

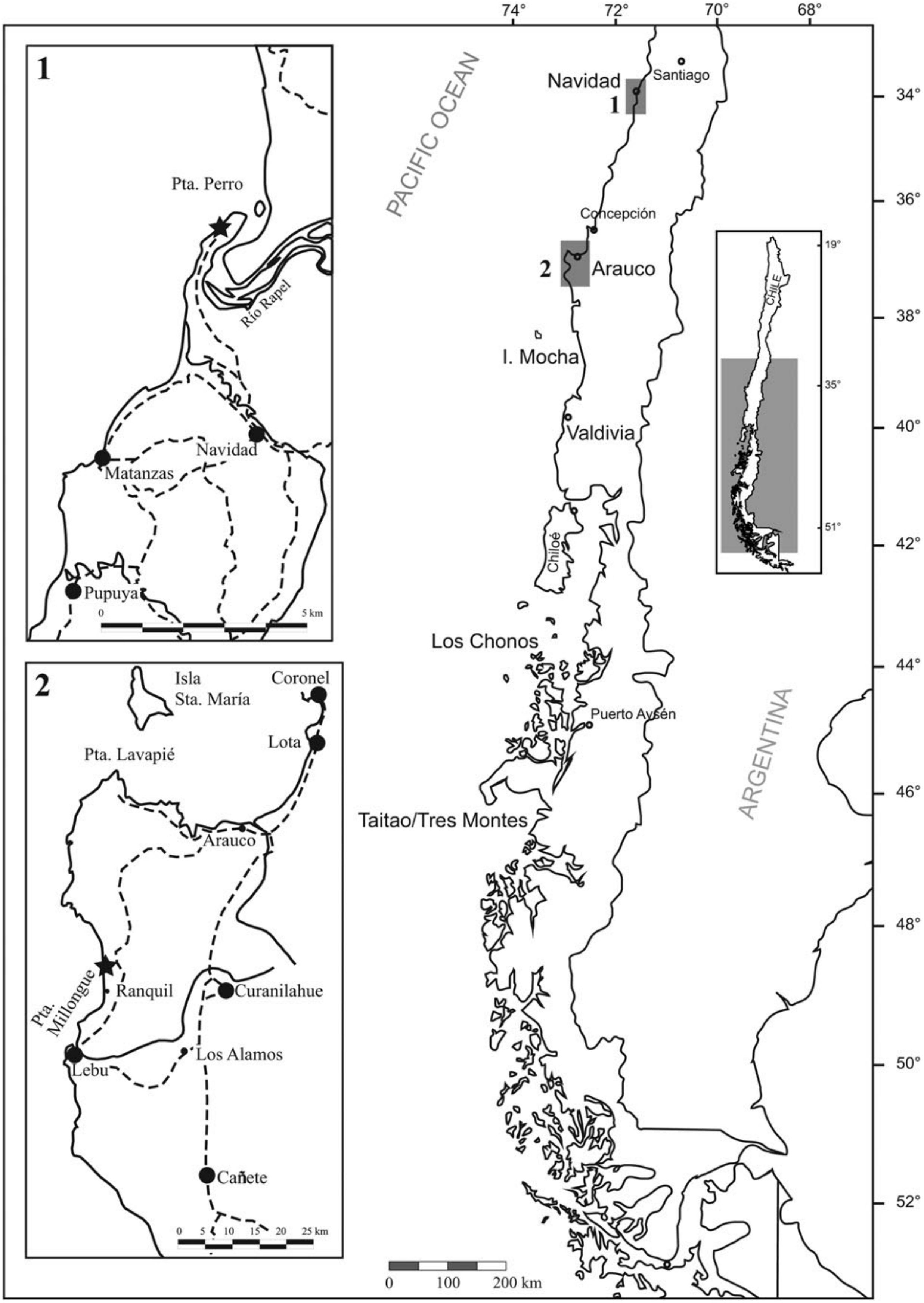

Figure 1. Type localities of early Miocene Solemyidae from Chile. (**1**) Approximate type locality of *Solemya antarctica* Philippi, 1887 from the Navidad Formation at the mouth of the river Rapel; (**2**) type locality of *Solemya lucifuga* n. sp. from the Ranquil Formation.

locality RAN (37°30’25”S, 73°35’28”W; WGS84), consisting of massive brown sandstones with intercalations of greenish glauconite-bearing sandstone beds exposed at coastal bluffs and the intertidal platform. Nielsen and Glodny (2009) gave an age of ca. 21.8–19.4 Ma using strontium isotope stratigraphy for this locality, and Finger (2013), using biostratigraphy, gave its age as 22.5–17.5 Ma based on the occurrence of the planktic foraminifera *Paragloborotalia mayeri* (Cushman and Ellisor, 1939), *Catapsydrax dissimilis* (Cushman and Bermúdez, 1937), *Globoquadrina dehiscens* (Chapman, Parr, and Collins, 1934), *Gq. praedehiscens* Blow and Banner, 1962, *Globigerina praebulloides* Blow, 1959, *G. venezuelana* Hedberg, 1937, *Globigerinoides trilobus* (Reuss, 1850), and *Globoturborotalia woodi* (Jenkins, 1960). Benthic foraminifera support a bathyal paleobathymetric interpretation for this locality based on a high number of species ranging from the upper to lower bathyal (Finger, 2013). The accompanying molluscan fauna includes, among others, *Ameranella verruculosa* (Sowerby, 1846), *Astele chilensis* (d’Orbigny, 1852), *Aturia cubaensis* (Lea, 1841), *Cancellaria medinae* Philippi, 1887, *Distorsio ringens* Philippi, 1887, *Echinophoria monilifera* (Sowerby, 1846), *Glossaulax pachystoma* (Hupé, 1854), *Lamprodomina dimidiata* (Sowerby, 1846), *Neilo volckmanni* (Philippi, 1887), *Pachycymbiola vidali* (Philippi, 1897), *Panopea* sp., *Sassia armata* (Hupé, 1854), *Scaphander remondi* (Philippi, 1887), turritellids, *Zeacuminia costellata* (Sowerby, 1846), and *Zygochlamys hupeanus* (Philippi, 1887) (Nielsen et al., 2004, 2009; Nielsen and Frassinetti, 2007a; Griffin and Nielsen, 2008; Beu, 2010), and is typical for lower Miocene units equivalent to the Navidad Formation (Kiel and Nielsen, 2010). Contrary to the microfossil record, these species represent a rather shallow-water environment (Finger et al., 2007). A detailed sedimentological description and evaluation of depositional environment and processes to clarify these ambiguous data, however, is lacking.

Materials and methods

For this work, the collections of the Museo Nacional de Historia Natural in Santiago, Chile, were revised for fossil solemyids. These include the collections of Philippi and Tavera, the latter having been transferred partially from Universidad de Chile.

Repositories and institutional abbreviations.—Museo Nacional de Historia Natural (MNHNcl), Santiago, Chile; Invertebrate Paleontology Collection (SGO.PI.) of MNHNcl; Museo de Zoología. Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción (MZUC-UCCC), Concepción, Chile.

Systematic paleontology

Class Bivalvia Linnaeus, 1758
Subclass Protobranchia Pelseneer, 1889
Incertae sedis
Solemya? *antarctica* Philippi, 1887
Figure 2

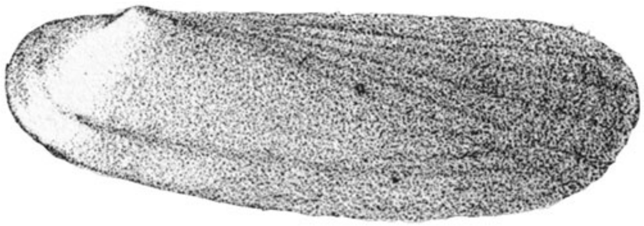

Figure 2. *Solemya antarctica* Philippi, 1887. Original drawing of holotype from Philippi (1887). Specimen length is 11 mm.

1887	*Solenomya antarctica* Philippi, p. 186, pl. 42, fig. 5.
?1942	*Solenomya antártica* [sic]; Tavera, p. 602.
?1979	*Solenomya antarctica*; Tavera, p. 139.
?1983	*Solemya* (*Petrasma*) *antarctica*; Bernard, p. 9.
1998	*Solenomya antarctica*, Villarroel and Stuardo, p. 169.

Holotype.—Philippi (1887) indicated the existence of a single specimen, which would be the holotype, that appears lost from the SGO.PI. collections. Other materials mentioned from Arauco and Navidad (Tavera, 1942, 1979), as well as a possible solemyid from Chiloé (Tavera et al., 1985), were also not found in the collections. The type locality is the mouth of the Rapel River (original designation), Navidad, Navidad Formation.

Occurrence.—Navidad Formation, lower Miocene.

Description.—From Latin, according to Philippi (1887, p. 186), “Shell elongate, rounded at both ends, anterior slightly narrower; radials not much impressed, descending from apex to posterior end; apices situated at fifth part of length. Length almost 11 mm.”

Remarks.—The generic name, *Solenomya*, used by Philippi is an unjustified emendation by Children (1823) of the valid name *Solemya* Lamarck, 1818 (Cox et al., 1969). Note that Philippi (1887) had taken the anterior (longer) for the posterior (shorter) part. He did not mention internal characters because the specimen was included in a “large rock.” The type material is not available and the limited information given by Philippi (1887, p. 186, pl. 42, fig. 5) in text and figure is insufficient to clarify the generic position of this species. The position of the ligament (internal or external) is of prime importance to differentiate between the two principal solemyid genera, *Acharax* Dall, 1908 and *Solemya* Lamarck, 1818 (see Cox et al., 1969; Taylor et al., 2008; Coan and Valentich-Scott, 2012). Nevertheless, several unique characters emphasized by Philippi deserve attention. The presence of a small and acute apex from which subtle radial grooves start that run in an oblique manner over the anterior half would not be a preservational artifact. Philippi asserted that the specimen was well preserved. Due to its small size, it is not clear if it represented a juvenile or an adult. Philippi had doubts in this respect, although he accepted the possibility of it being an adult comparing it with *Solemya velum* Say, 1822, a species of barely larger size now living in the North Atlantic. The general characters described by Philippi are consistent with a solemyid. However, similar external morphologies exist in some Siliculidae (Nuculanidae). For example, the figure given by Philippi resembles juveniles of *Silicula rouchi* Lamy, 1911, a species now living in circum-Antarctic waters (Engl, 2012). The form and position of the apex (small and acute) and the presence of subtle radial grooves in the antero-dorsal region are similar. A direct examination of several specimens present in the MZUC-UCCC collection confirm this similarity. Internally, Siliculidae are easily separable from Solemyidae by the presence of elongated teeth that run in an oblique manner along the dorsal margin (Allen and Sanders, 1973). However, internal features of Philippi's species are not known.

Despite the mentioned limitations, this species cannot be considered anything other than a protobranch, although the generic position as well as the family remain unclear. Therefore, following the opinion of Philippi (1887), the type genus of Solemyidae, *Solemya* Lamarck, 1818, is maintained with certain doubt.

Tavera (1942, p. 620) mentioned a *Solenomya antártica* [sic] from the "clays of the Navidad Beds of Isla Santa María," Gulf of Arauco, together with *Limopsis* and *Balaenoptera*? bones. He considered that this specimen was "identical to *Solenomya rossiana* Wilckens" from the Cretaceous of Seymour Island, Antarctica. However, the holotype illustrated by Wilckens (1910; see also Little et al., 2015, p. 220, fig. 5K) differs from this claim—its outline and ornamentation differing clearly through an oblique truncated anterior margin, the dorsal and ventral margins being divergent and not paralleled and its ornamentation is less dense than in *Solemya*? *antarctica* Philippi. Tavera added that his specimen was about the size of the Cretaceous species of Wilckens. The lower Miocene Ranquil Formation actually crops out on Isla Santa María (Melnick et al., 2006), but the comments of Tavera suggest the existence of a species different from *Solemya*? *antarctica*.

Later, Tavera (1979, p. 73) mentioned that he obtained his specimen in situ from the Navidad Member (Navidad Formation, sensu Encinas et al., 2006). Unfortunately, this specimen, as well as the one from Santa María Island, was neither described nor illustrated for comparison. Tavera added that *Solemya*? *antarctica* is also present in the Eocene of Arauco Peninsula (Tavera, 1979, p. 76). A sample in the Tavera collection at MNHNcl is labelled as *Solenomya* sp. (SGO.PI.19079) coming from Docas Island, situated immediately off the coast of Mocha Island (to the south of Arauco). The label says Eocene, which coincides with the local geology. The lithology also agrees with the material listed previously as *Solenomya* sp. by Tavera and Veyl (1958, p. 171), who referred to this material as part of an assemblage correlated with the Millongue Formation (Eocene of Arauco). However, examination of specimen SGO.PI.19079 revealed that there is no solemyid among the various taxa present in the rock sample. The presence of *Solenomya araucana* Philippi, 1887 in the Chilean Eocene, or any other solemyid from this age, remains doubtful until a revision of the Paleogene faunas from Arauco.

This species was also listed as extant (Bernard, 1983) with the combination *Solemya* (*Petrasma*) *antarctica* Phillippi, 1887. Unfortunately, Bernard did not give more specific data, apart from a fossil record since the Miocene, living at 50°S, in 40 m depth, and at 3–11°C temperature. He also did not indicate where the examined material was housed and the Museo Nacional de Historia Natural in Santiago is not among the institutions listed, so apparently the type material was not consulted. Furthermore, the inclusion of Philippi's species in *Petrasma* Dall, 1908 raises further doubts, since, as mentioned previously, its internal characters were never described. It is more likely, that the extant material seen by Bernard belongs to a different taxon.

According to Villarroel and Stuardo (1998), *Solenomya antarctica* Philippi, 1887 is the only fossil solemyid appropriately included in the genus *Solemya*. However, these authors did not provide any evidence to justify this claim nor did they consult the type material.

Order Solemyida Dall, 1899
Superfamily Solemyoidea Gray, 1840
Family Solemyidae Gray, 1840
Genus *Solemya* Lamarck, 1818

Type species.—*Solemya mediterranea* Lamarck, 1818 by subsequent designation of Children (1823) (=*Tellina togata* Poli, 1795). Extant, Mediterranean Sea.

Solemya (s.l.) *lucifuga* new species
Figure 3

?1942 *Solenomya antártica* [sic], Tavera, p. 620.
?1958 *Solenomya* sp., Tavera and Veyl, p. 171.
2010 *Solemya* sp., Kiel and Nielsen, tab. dr1.

Holotype.—Holotype SGO.PI.23102. A two-valved specimen in butterfly position. Right valve visible, left valve in matrix. Type locality is the intertidal platform at Ranquil (RAN), Ranquil Formation, Arauco.

Diagnosis.—*Solemya* with parallel ventral and dorsal margins. Ornamentation of >20 dense radial ribs and narrow interspaces, which cover the whole shell surface. Ribs sometimes bifurcate.

Occurrence.—Ranquil Formation (RAN), lower Miocene.

Description.—Valves small (27 mm incomplete length, 12.5 mm height), thin, equivalve, inequilateral, compressed. Outline elongate–subquadrate, anterior end elongate and well rounded. Posterior end partly unknown. Dorsal and ventral margins straight, parallel. External ornamentation weak, consisting of many narrow, poorly defined, radial ribs (~20 visible) of variable width, some bifurcating. Anteriorwards, ornamentation getting stronger. Interior unknown, except for chondrophore seen in fracture surface.

Etymology.—From the Latin *lucifugum* (n) in feminine declination, *lucifuga*. Shy of the light. Figurative in the sense of reluctant to be discovered.

Remarks.—This is the specimen listed by Kiel and Nielsen (2010, tab. dr1). The posterior end is broken and therefore prevents knowing total shell length and rib count. The section view shows a limited thickening of the shell in the form of a swelling situated behind the dorsal margin. This feature differs from *Acharax* Dall, 1908, where a similar swelling would be the place for the nymph projecting farther than the margin and

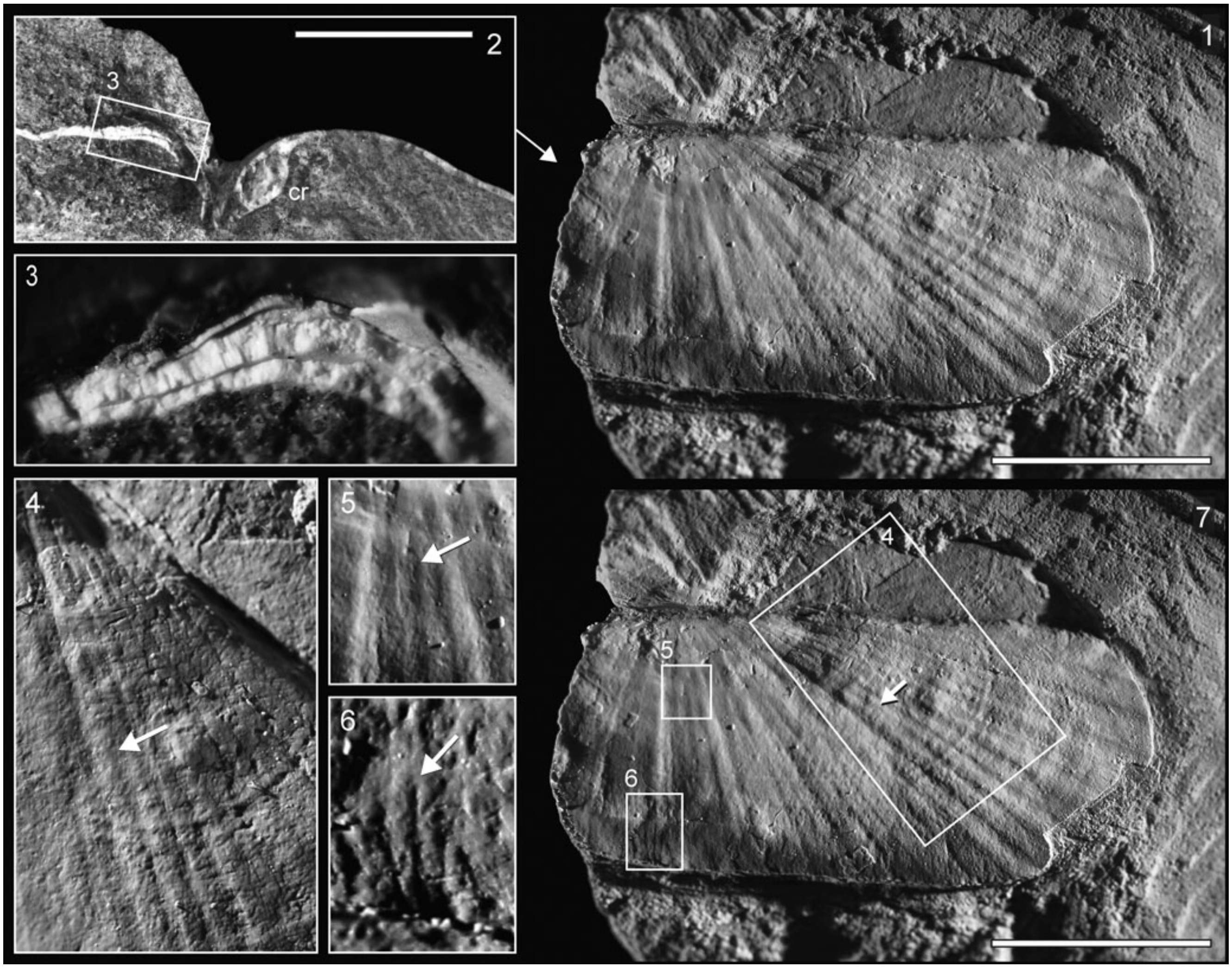

Figure 3. *Solemya lucifuga* n sp. holotype SGO.PI.23102. (**1, 7**) General view of the valves in butterfly position; (**2**) view of posterior area showing thickening of shell giving way to the chondrophore (cr) where the internal ligament is situated; white arrow indicating position of detail; (**3**) enlarged detail of the thickened shell through superposition of aragonite layers; (**4–6**) details of bifurcating ribs indicated in (**7**). Scale bars 5 mm.

where the external ligament would be attached (for reference, see Taylor et al., 2008, fig. 1; Bailey, 2011, text-fig. 2; Walton, 2015, fig. 1). The visible structure (swelling; Fig. 3.3) corresponds to development of the chondrophore (Kamenev, 2009, figs. 2–6). The ligament of the new species is internal, such as occurs in *Solemya* Lamarck, 1818 and its subgenera (*Solemya*, *Petrasma*, *Zesolemya*, *Austrosolemya*, *Solemyarina*). Absence of an internal view does not allow interpretation of other structures, therefore impeding precision of its taxonomic position. Due to this, the new species is treated as *Solemya* in a broad sense (s.l.).

Solemya lucifuga n. sp. is characterized by the high density of ribs, which are rather narrow and vary in width (~0.3–1.0 mm), thus giving the shell a slightly irregular appearance. The ribs are little divergent among each other, with generally narrow interspaces. *Solemya lucifuga* n. sp. can be differentiated from *Solemya*? *antarctica* Philippi, 1887, by its outline and the presence of ornamentation on the whole shell surface. Other solemyids, such as the extant *Acharax patagonica* (Smith, 1885), show an ornamentation that broadens notably towards the margin. Similarly, it differs from *A. yokosukensis* Kanie and Kuramochi, 1995, from the Miocene of Japan (Amano and Ando, 2011), and from the extant *A. johnsoni* (Dall, 1899), both of which show strong ribs of low density and, therefore, with wider interspaces. *Solemya lucifuga* n. sp. differs from the Oligocene *S. lomitensis* Olsson, 1931, from Lomitos in Peru, by the smooth and polished shell surface of the latter, where only about six very slight radial impressions at the anterior are visible (Olsson, 1931). It differs from *S. sulcifera* Cooke, 1919, from the Eocene of Cuba (see Kiel and Hansen, 2015, for age), whose holotype is larger but has a lower number of ribs (n = 15) while *S. pateri* Zinsmeister, 1984, from the Eocene of Seymour Island (Stilwell and Zinsmeister, 1992) has an ornamentation of wider ribs and narrower interspaces. It differs from *Solemya* sp. (Amano and Little, 2005, fig. 5G), reported from whale-fall communities in the Miocene of Hokkaido, Japan, which is higher and shorter. *Solemya lucifuga* n. sp. is similar to *Solemya puata* Walton, 2015, a living species from New Zealand, due to the subparallel dorsal and ventral margins and a rounded anterior margin, but it can be differentiated by its denser, broader, and more regular radial ornamentation.

Taylor et al. (1969) described the shell mineralogy and structure of Solemyoidea as consisting of two aragonitic layers, an outer prismatic one and an inner homogeneous one. This pattern seems consistent with that seen along almost the entire dorso-ventral section of *S. lucifuga* n. sp. although we cannot specify the structure of those layers. The knowledge about the microstructure of solemyids has been recently increased using scanning electron microscopy, showing a greater diversity of structures than previously reported (Sato et al., 2013b; Sato and Sasaki, 2015). Nonetheless, the number of layers and microstructure of thickened structures, such as the chondrophore in *Solemya* and the nymph in *Acharax*, where the ligament attached, have not been evaluated. Towards the end of the dorsal margin of *S. lucifuga* n. sp., where the chondrophore is developed, at least four layers can be seen (Fig. 3.3).

Discussion and conclusions

Since Philippi (1887) described for the first time a species from Chile assigned to the Solemyidae, no other records of this group can be confirmed due to the loss of other specimens mentioned in the literature. Loss of the type material of *Solemya*? *antarctica* Philippi, 1887 also prevents clarifying its relation to other species. The possibility that it is a morphotype with a wide chronostratigraphic range, as indicated by Bernard (1983), is at least doubtful. Although some cases exist where it has been documented that Miocene shells are indistinguishable from modern ones, such as *Architectonica karsteni* Rutsch, 1934 (Frassinetti and Covacevich, 1981; DeVries, 1985; Nielsen and Frassinetti, 2007b) and *Cyclochlamys argentina* Pastorino and Griffin, 2018, it is more likely that the modern material had been misidentified. After Bernard's work, *Petrasma atacama* Kuznetsov and Schileyko, 1984, has been described from the Peru-Chile Trench, while other solemyids are well known from the Southern Hemisphere high latitudes, including *Acharax patagonica* (=*A. macrodactila* Mabille and Rochebrune in Rochebrune and Mabille, 1889) (Smith, 1885; Osorio and Bahamonde, 1970; Osorio and Reid, 2004; Osorio et al., 2005) and *Acharax* sp. (Villarroel and Stuardo, 1998), the latter collected from Sarmiento Channel at 51°S. Modern *Petrasma* are not described from high latitudes of the Pacific coast.

The holotype of *Solemya lucifuga* n. sp. is situated in a grayish-olive, medium- to fine-grained, well-sorted sandstone. Its valves are very fragile and the internal ligament is reduced, typical of *Solemya* (s.l.). The preservation of both valves semiarticulated and in butterfly position suggests depositional conditions of very low energy. Deep-sea, soft-sediment environments provide pronounced stability and homogeneity over long periods of time (Allen, 1979). The presence of an articulated chimaeriform fish (G. Arratia, unpublished manuscript) from the same beds supports this interpretation, while benthic foraminifera indicate a bathyal depth of ~1500 m (Finger, 2013). A bathymetric separation of mostly bathyal *Acharax* (>400 m) and more shallow water *Solemya* (<600 m) has been noted by Neulinger et al. (2006) and Huber (2010), but deep-dwelling *Solemya* certainly do occur (Kamenev, 2009; Sato et al., 2013a). With regard to the bathyal depth indicated by benthic foraminifera for this locality (Finger, 2013), this could indicate that the new species is a bathymetric exception, or that the sediment package containing it derived from more shallow water and was displaced into greater depth, as indicated by the additional mollusk fauna (Finger et al., 2007). The rather fragile shell and butterfly position makes a more exceptional deeper water presence of *S. lucifuga* n. sp. more likely, but detailed sedimentological studies are needed to clarify the situation.

More than a century since Philippi's (1887) description of *Solemya*? *antarctica*, the name-bearing specimen of *Solemya lucifuga* n. sp. is the only confirmed solemyid from the Miocene of Chile and the only known species of *Solemya* (s.l.) from the Neogene of the Southern Hemisphere.

Acknowledgments

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