Reinstatement of *Leda rhytida* Dall, 1908 and its reallocation into *Propeleda* (Bivalvia: Nuculanidae)

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ABSTRACT

In 1908, Dall described "Leda" rhytida as occurring off Acapulco, Mexico. The species was never figured, and has no subsequent published records. Despite that, it appears mentioned by several authors in check-lists. The identity of this species appears as controversial in the literature: some authors emended the type locality to either eastern South America or Chile, and the species was regarded either as a possible synonym of *Propeleda longicaudata* (Thiele, 1912), or considered as a *nomen dubium*. The aims of this study are to determine the actual provenance of the type material, to provide a proper redescription of the species, and to revise its generic placement and current status. The study of the syntypes and additional material from museum collections reveals that the species actually comes from southern Chile. Based on the elongated shell outline and distinctive hinge morphology, the species is here reallocated into *Propeleda*. Comparison of this species with P. longicaudata establishes that *P. rhytida* is a distinct and valid species.

Additional Keywords: Protobranchia, Nuculanoidea, Magellan Region, Chile, Taxonomy

INTRODUCTION

Leda (Leda) rhytida Dall, 1908 is among the numerous new bivalve species described from the collections made by the U.S. Albatross expedition along the Americas. The original description is poor and lacking in detail, and the species was never figured. According to Dall (1908) the species was collected "off Acapulco, Mexico, in 141 fathoms", at Albatross station 3422, and the type material was deposited at the United States National Museum [National Museum of Natural History, Smithsonian Institution], under number "122,918". After examining the type material, Keen (1971) detected an error in the type locality originally indicated by Dall (1908). Keen stated that the true provenance of the species was "Patagonia, eastern South America" (sic). In contrast, Bernard (1983) indicated the type locality to be

"Chile". Despite that, Zamorano and Hendrickx (2012) repeated "Acapulco" as the type locality. Apart from the original collection, no new records for the species are known. Recently, Coan and Valentich-Scott (2012) suggested that *Leda rhytida* could correspond to a synonym of *Propeleda longicaudata* (Thiele, 1912), a species described from the Gauss Expedition in eastern Antarctica, but currently regarded as widely distributed in Antarctic and sub-Antarctic waters (Dell, 1964; 1990; Villarroel and Stuardo, 1998). However, Bouchet (2014) regarded *Leda rhytida* as a *nomen dubium*. The aims of this contribution are to clarify the identity and precise provenance of *Leda rhytida*, to provide a proper redescription of the species, and revise its generic placement and its affinity with *Propeleda longicaudata*.

MATERIALS AND METHODS

We examined photographs of the type material of *Leda rhytida* and *Leda longicaudata* (the latter currently treated in the genus *Propeleda*), housed respectively at the National Museum of Natural History, Smithsonian Institution (USNM), Washington, and Zoologisches Museum Berlin (ZMB). Additional material comes from the collection of the Museo de Zoología de la Universidad de Concepción (MZUC), Chile, and material sampled by the authors at the Beagle Channel and the South Shetland (61°23′45″ S, 55°26′33″ W) and South Orkney (60°58′53.4″ S 43°26′42.6″ W) (sub-Antarctic and Antarctic waters), currently housed at the Museo de La Plata (MLP), Argentina.

Shells were measured according to the parameters and ratios indicated by Kamenev (2014), by using an ocular micrometer mounted on a stereoscopic microscope, and a caliper for larger animals. Text abbreviations are: A, length anterior to beaks; H, maximum height perpendicular to L; L, maximum shell length; W, shell width across closed specimens. Details of hinge plate and protoconch were studied with a Phillips XL-30 scanning electron microscope (SEM), at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN).

SYSTEMATICS

Genus Propeleda Iredale, 1924

Type Species: Leda ensicula Angas, 1877 (OD)

Propeleda rhytida (Dall, 1908) **new combination** (Figures 1–16)

Leda (Leda) rhytida Dall, 1908: 219 (listed only), 376 (description).

Propeleda longicaudata Thiele, 1912: Villarroel and Stuardo, 1998: 142, figs. 113, 114 (in part).

Redescription: Shell club-shaped, delicate, moderately large for genus (max. observed L = 13.2 mm), elongate $(H/L = 0.44 \pm 0.01, n = 8)$, compressed $(W/H = 0.49 \pm 0.01)$ 0.02, n = 8), slightly gapping posteriorly; equivalve; markedly inequilateral: anterior end short, widely curved; posterior end projected into a curved rostrum, three to four times longer than anterior end (Figures 1–13). Anterodorsal margin consisting of a very short, almost horizontal section near beak, followed by a longer, obliquely sloping distal section, which is widely arched to slightly straight; both parts continuous or forming a weak angulation (Figures 1–8). Anterior margin evenly curved, joining anterodorsal margin in a slight angulation and continuous to ventral margin. Ventral margin markedly convex at anterior half and nearly straight at posterior half (Figures 1–8). Posterior (rostral) margin somewhat convex, forming well-marked angles at junctions with posterior part of dorsal and ventral margins. Posterodorsal margin long, slightly to markedly concave (Figures 1–8). Umbones opisthogyrous, located on anterior third (A/L = 0.29 ± 0.02 , n = 10), only slightly raised from dorsal margin. Two strong carinae running at posterior area of shell, along rostrum: one extending from umbo to junction of ventral and posterior margins, another from umbo to junction of postero-dorsal and posterior margins (Figures 1–8). Shallow sulcus between these carinae present. Anterior and central areas of shell sculptured with regularly distributed, rounded, commarginal cords, separated by narrow interspaces. These cords extend over two posterior carinae and into sulcus. Escutcheon large, well-defined by prominent dorsal carina, sculptured with faint lines (Figure 9). Lunule not differentiated. Prodissoconch small, about 165 µm long, D-shaped, sculptured with a polygonal, net-like pattern (Figure 14). Periostracum thin, well-adhered, greenish-brown in wet specimens, straw-yellow when dry (Figures 1–8). Inner shell surface white, glossy, with a strong ridge extending along rostrum from umbo to approximately half of posterior margin, separating inhalant and exhalant siphons (Figures 10-13). Pallial sinus short, extending up to half of posterior adductor muscle (Figure 12). Anterior adductor muscle scar ovate, perpendicular to hinge; posterior adductor muscle scar narrower and smaller than anterior one, parallel to hinge plate. Hinge plate narrow, taxodont, with two series of teeth interrupted beneath beaks (Figures 12, 13). Anterior

series composed of about 15 teeth, posterior series with about 27 teeth, regarding larger specimens. Teeth variable in size and morphology within each series. Anterior series: first two teeth closest to beak, low, U-shaped; first evenly narrow, second with stronger ventral part (Figures 15, 16). One or two following teeth almost straight and lamellar. Subsequent teeth V-shaped, with ventral part gradually longer, increasing in size and height, sharply cusped. Most distal tooth greatly reduced in size. Posterior series: five to eight teeth closest to beaks lamellar, similar in solidness (Figures 15, 16). Internal ligament stout, posterior to beaks, slightly larger than resilifer, which is triangular, oblique, posteriorly directed. External ligament narrow, elongated, amphidetic, larger anteriorly and partially sunken below beaks (Figures 15, 16).

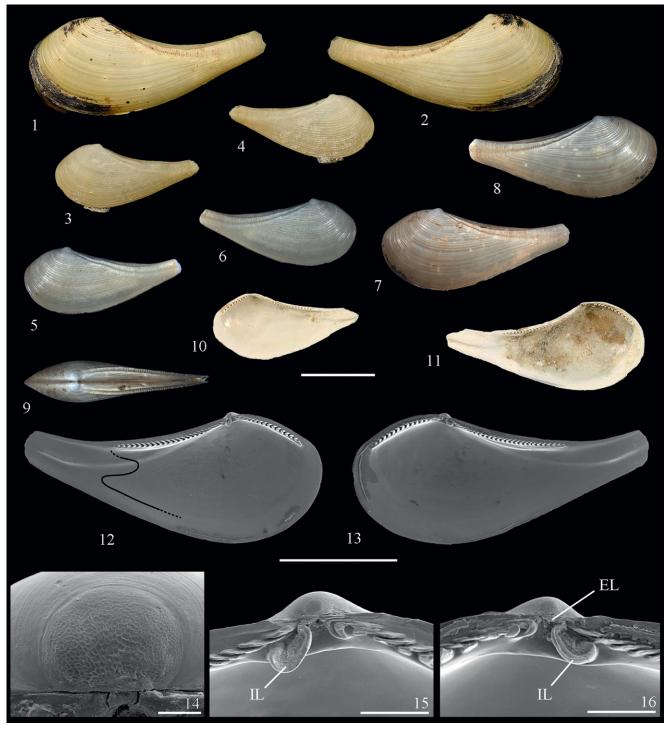
Type Locality: [Herein emended] U.S. Albatross station 2783, 51°02′30″ S, 74°08′30″ W, west coast of Patagonia, 141 fathoms [=256 m].

Type Material: 8 syntypes (USNM 96918).

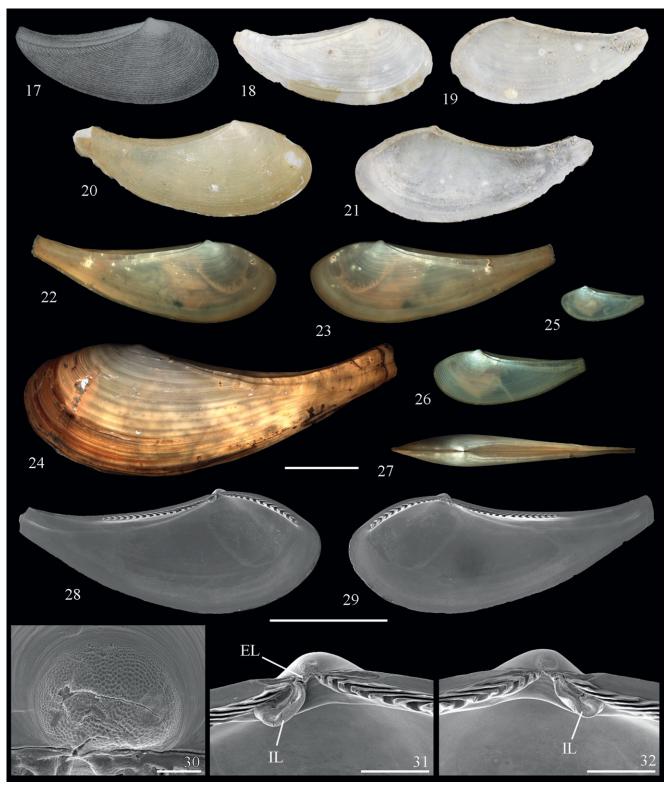
Material Examined: MZUC 10406, 1 specimen, 50°03′ S 74°41′ W, Isla Tobar, 200 m; MZUC 4642, 8 specimens, and MZUC 4610, 19 valves, 50°09′55″ S 74°43′75″ W, Confluence Canales Concepción and Trinidad, 390–460 m; MZUC 4627, 1 specimen and 4 valves, same data as previous lot, but 460 m; MZUC 4646, 4 specimens and 4 valves, 51°00′50″ S, 74°14′10″ W, Puerto Bueno, Canal Sarmiento, 215–220 m; MLP Ma14041 1 specimen, 54°52′ S, 68°28′ W, Bahía Lapataia, Beagle Channel, 120–138 m.

Distribution: Southern Chile and Beagle Channel, living at 120–460 m depth.

Remarks: Some discrepancies arise when comparing the original labels of the material currently identified as type of *Leda rhytida* (at the USNM) to information in the original description, in particular in relation to the repository number and the provenance of the types. The repository number mentioned by Dall (1908) ("USNM 122,918") actually corresponds to the holotype of Leda lobula Dall, 1908, another species described by that author in the same work. Dall indicated that this latter species also originated from ALBATROSS station 3422 (off Acapulco, Mexico). In addition, Dall did not provide a repository number for Leda lobula. The specimen in lot USNM 122918 agrees with the original description of Leda lobula, particularly differing from Leda rhytida by having an "ovate shape", with both anterior and posterior ends "rounded" (Dall, 1908: 375). In contrast, the original description of Leda rhytida refers to an "elongateovate" shell, with the anterior end rounded and the posterior one "produced" in a "strongly recurved rostrum". This set of characters is in accordance with the shell morphology of specimens in lot USNM 96918, currently labeled as syntypes of L. rhytida (Figures 1-4), whose label reads "Station 2783, west coast of Patagonia". Thus, it seems clear that there was an error in the published information of repository numbers and provenance



Figures 1–16. Propeleda rhytida. 1–4, 10, 11. Four syntypes of Leda rhytida (USNM 96918). 1–4. External views. 10, 11. Internal views. 5–9, 12–16. Specimens from $50^{\circ}09'55''$ S, $74^{\circ}43'75''$ W, southern Chile (MZUC 4642). 5–8. External views. 9. Dorsal view. 12, 13. Internal views (pallial sinus shown in black line on Figure 12). 14. Detail of prodissoconch. 15, 16. Details of hinge plate. 15. Left valve. 16. Right valve. Scale bars: 1-11=5 mm; 12, 13=5 mm; 14=50 μm; 15, 16=500 μm. Abbreviations: IL=internal ligament; EL=external ligament.



Figures 17–32. Propeleda longicaudata. 17. Original figure by Thiele (1912). 18–21. Two syntypes of Leda longicaudata (ZMB 63104). 18, 20. External views. 19, 21. Internal views. 22–32. Propeleda cf. longicaudata. 22, 23, 27. Specimens from South Orkney (MLP 7467). 24–26, 28–32. Specimens from South Shetland (MLP 7468). 22–26. External views. 27. Dorsal view. 28, 29. Internal views. 30. Detail of prodissoconch. 31, 32. Detail of hinge plate. 31. Left valve. 32. Right valve. Scale bars: 17–27 = 5 mm; 28, 29 = 5 mm; 30 = 50 μm; 31, 32 = 500 μm. Abbreviations: IL = internal ligament; EL = external ligament.

of the species. Keen (1971) already detected such error, although she mistakenly wrote "eastern South America" instead of "western South America" when emending the type locality. Bernard (1983), on the contrary, did refer to a locality on the Pacific coast, but was ambiguous in stating "Chile".

Based on the original label of the syntypes, the provenance of "Leda" rhytida is here emended to "51°02′30″ S, 74°08′30″ W, west coast of Patagonia" (which corresponds to Albatross station 2783). Study of additional (conspecific) specimens from southern Chile and the Beagle Channel allows us to confirm the occurrence of the species in that area, and the nominal species is no longer regarded as a nomen dubium (as suggested by Bouchet, 2014) but as a valid species.

Generic Allocation of the Species: The genus Leda Schumacher, 1817 in which L. rhytida was originally described is an objective junior synonym of Nuculana Link, 1807. Allen and Hannah (1986) defined this genus by the presence of robust and "moderately" posteriorly elongated shells. Allen and Sanders (1996) added as a diagnostic character the presence of a robust hinge with V-shaped teeth and a small ligament, and the absence of an internal posterior ridge running from umbo to posterior margin. The fact that all teeth are V-shaped in this genus can be confirmed from the illustrations of Nuculana pernula (Müller, 1779) in Oliver et al. (2010) (this species is currently regarded as a senior synonym of Arca rostrata Brugière, 1789, the type species of *Nuculana*). In addition, these photographs show that the internal ridge is extremely short in this species, being present only in the distal part of the rostrum.

This set of characters does not match those present in "Leda" rhytida, which has delicate, very posteriorly elongated shells, with a long internal ridge extending from the umbo to posterior margin, and bearing a large internal ligament and differentiated lamellar teeth near the beak. In contrast, the characters present in "Leda" rhytida are in agreement with those present in Leda ensicula Angas, 1877, the type species of Propeleda Iredale, 1924 (Huber, 2010; Kamenev, 2014). Consequently, "Leda" rhytida is here reallocated into Propeleda. The distinction of Propeleda from other nuculanid and siliculid genera was discussed by Huber (2010) and Kamenev (2014).

AFFINITIES BETWEEN PROPELEDA RHYTIDA AND PROPELEDA LONGICAUDATA: Coan and Valentich-Scott (2012) suggested that Propeleda rhytida (as Leda rhytida) could correspond to a synonym of Propeleda longicaudata (reported by the authors under Nuculana). The study of the syntypes of the latter species (Figures 17–21) reveals that both species show morphological resemblance. Nonetheless, P. rhytida may clearly be distinguished by having shells with shorter and more broadly rounded anterior end, more projected ventral margin and posterior rostrum, stronger and more spaced commarginal sculpture, and the two posterior carinae stronger (wider

and higher) than *P. longicaudata*. These differences lead us to consider the two taxa as distinct species.

Propeleda longicaudata is currently regarded as a widely distributed Antarctic and sub-Antarctic species, occurring in South Georgia, South Orkneys, South Shetlands, Weddell Sea, Ross Sea and East Antarctica (Dell, 1964; 1990; Hain, 1990; Aldea and Troncoso, 2010). The study of two lots of "P. longicaudata" from South Orkney and South Shetland (MLP 7467, 7468, respectively) reveals some morphological differences between these specimens and the syntypes of that species, namely the presence of a consistently less recurved and longer rostrum, which consequently generates a more elongated shell outline (Figures 22–25, 28, 29). At present, the significance of these differences could not be determined, because the syntypes are represented by only 3 valves, and no additional specimens from the type locality were available to evaluate the intraspecific variability of this taxon. Therefore, we prefer to be conservative and refer to the South Orkneys and South Shetland specimens here studied as *Propeleda* cf. *longicaudata*. The specimens here studied of *P. cf. longicaudata* (Figures 22–32) also differ from P. rhytida by having less inflated shells $(W/L = 0.16 \pm 0.01, n = 10 \text{ vs. } W/L = 0.22 \pm 0.01, n = 8)$ and a minor number of posterior teeth, even when considering specimens of similar size (23 vs. 27 in specimens about 13 mm long). Morover, in P. rhytida the lamellar teeth at the posterior series are shorter and stouter, and at the anterior series, the two teeth closest to the beaks are consistently stronger (Figs. 15, 16 vs. 31, 32), and the V-shaped teeth are taller and more delicate. Furthermore, judging from the material here available, P. cf. longicaudata reaches a larger size (23.8 mm vs. 13.2 mm long in *P. rhytida*).

Propeleda longicaudata was also previously reported as occurring in southern Chile by Villarroel and Stuardo (1998). However, the study of the specimens they mentioned (MZUC 4610, 4627, 4642, 4646) indicates that they were misidentified by those authors. The lots are here reassigned to Propeleda rhytida.

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