

THE MOLLUSCAN GENERA *MACTRELLA* AND *MACTRINULA*:
TAXONOMIC REVISION AND REDESCRIPTION OF TYPE SPECIES

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ABSTRACT

The genera *Mactrella* and *Macrinula*, both described by Gray in 1853, have generally been considered synonyms. Additionally, five species had been included in *Mactrella* were later placed in the genus *Mactrellona* Marks, 1951. The diagnosis of type species of these genera, as well as the study of their type material, have clarified the taxonomic status of the three related genera. The genus *Micromactra* Dall, 1894, is added to the synonymy of *Mactrella*. The complete shell morphology of type species *Mactrella striatula* and *Macrinula plicataria*, both introduced by Linnaeus, 1767, is described. An updated synonymy list of each species is provided. In addition, an expanded geographical distribution of the genus *Mactrella* is given. Illustrations of *Mactrellona alata* (Spengler, 1802), *Mactrellona exoleta* (Gray, 1837), *Mactrellona clisia* (Dall, 1915), *Mactrella californica* (Conrad, 1837), *Harvella elegans* (G. B. Sowerby I, 1825), and *Mactrella janeiroensis* (E. A. Smith, 1915) are included.

Key words: Bivalves, Macrtrinae, taxonomy, Gray, Linnaeus, *Mactra striatula*, *Mactra plicataria*.

INTRODUCTION

The family Macrtridae first appeared in the Lower Cretaceous (Saul, 1973; Skelton & Benton, 1993) of North America. One key morphological character that defines macrtrids is an inverted V-shaped tooth in the left valve formed by the fusion of two cardinal teeth (Keen, 1969). The anterior and posterior lateral teeth have, in general, only one cusp. Several authors have studied such anatomical characters as ctenidial morphology, labial palp fusion, siphons, stomach, and shell ultrastructure, to better understand the morphology and its variation within the group (Atkins, 1937; Yonge, 1948; Purchon, 1960; Stasek, 1963; Taylor, 1973). The Macrtridae includes about 90 generic-level entities, several of which are taxonomically unresolved.

During the first half of the nineteenth century, Gray (1837) split the genus *Mactra* into five sections. Two of them were "*Mactra* B," in which he placed *Mactra striatula* Linnaeus, 1767, and "*Mactra* C," which included *Mactra plicataria* Linnaeus, 1767. All sections mentioned by Gray in 1837 were formalized in 1853 when he introduced the genera *Mactrella* and *Macrinula* for the *Mactra* B and C

groups, respectively. The original composition included only the two Linnean species mentioned above. Throughout the twentieth century, *Mactrella* and *Macrinula* have been generally considered synonyms (e.g., Marks, 1951; Keen, 1969). Dall (1915) included five species in the genus *Mactrella*, two from the Atlantic and three from the Pacific Ocean. Marks (1951) later said that these should be assigned to his new genus *Mactrellona*, with type species *Mactra alata* Spengler, 1802. He based the description of this new genus on the diagnosis of *Mactrella* given by Gray, which actually fits with the morphology *M. alata* better than it does that of *M. striatula*. However, the type species designated by an author must be accepted assuming the correct identification of the species proposed (ICZN, 1945, Opinion 168). For this reason, Marks (1951) introduced a new genus to group the species *M. alata* and its congeners.

During an ongoing revision of western Atlantic Macrtridae (i.e., Signorelli & Scarabino, 2010; Signorelli & Pastorino, 2011, 2012a, b), it became necessary to undertake a taxonomic revision and redescription of the type species of genera *Mactrella* and *Macrinula*, the object of the present work.

MATERIALS AND METHODS

Examined type material and additional specimens illustrated in this paper are deposited in the following institutions: American Museum of Natural History (AMNH), New York; Linnean Society of London (LSL), London; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-In), Buenos Aires; The Natural History Museum (NHMUK), London; Natural History Museum (NHMW), Vienna. Digital pictures were made with a Nikon D5000 equipped with a 60-mm Nikkor micro lens. The hinge was described with the method developed by Bernard and Munier Chalmas (according to Cox, 1969), in which Arabic numbers were used to designate the cardinal teeth and Roman numbers for the lateral teeth. Additionally, all teeth in a right valve were assigned odd numbers, and all teeth in a left valve were assigned even numbers.

SYSTEMATIC RESULTS

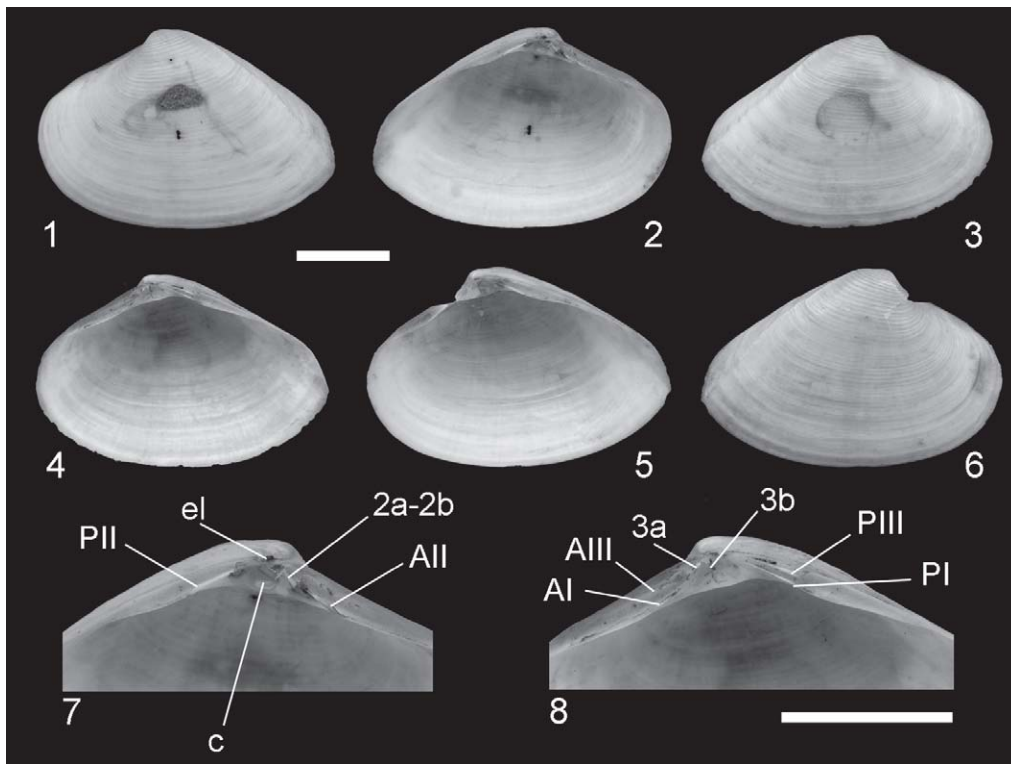
Order Cardiida Férussac, 1822
Superfamily Mactroidea Lamarck, 1809
Family Mactridae Lamarck, 1809

Genus *Mactrella* Gray, 1853.
[*Micromactra* Dall, 1894: 40; type species:
Mactra californica Conrad, 1837: 240;
monotypy]

Type species: Mactra striatula Linnaeus, 1767:
1125; monotypy.

Diagnosis: Shell trigonal to oval, beaks and umbones with concentric ribs; moderately fragile, pallial sinus deep, broad.

Distribution: West North America, East Central and South America, Europe.



FIGS. 1–8. Shells of *Mactrella striatula* (Linnaeus, 1767), syntypes LSL 78. FIGS. 1–6: General aspect; FIGS. 7, 8: Detail of hinge plate, el: external ligament, c: chondrophore. Scale bars = 1 cm.

Mactrella striatula (Linnaeus, 1767)
(Figs. 1–8)

Mactra striatula Linnaeus, 1767: 1125; Gmelin, 1791: 3257; Spengler, 1802: 99; Hanley, 1855: 55, pl. 2, fig. 3; Mörch, 1870: 122.

Mactrella striatula Linnaeus. Gray, 1853: 41.

Mactrinula striatula Linnaeus. H. Adams & A. Adams, 1856: 377; Conrad, 1868: 35.

Mactra (Mactrinula) striatula Linnaeus. Lamy, 1917: 270.

Diagnosis: Shell trigonal, with low commarginal ribs in the umbonal area; posterior end with a well-defined carina; umbos moderately inflated; pallial sinus deep, rounded.

Description: Shell trigonal, elongate, inflated, inequilateral, fragile; umbones moderately inflated, with commarginal striae, especially laterally, becoming smoother toward the ventral shell margin; anterior dorsal margin straight, longer than posterior margin; anterior end rounded; ventral margin curved; posterior carina defined by a line from the umbo to the posterior end, well marked, forming a striated, depressed area; posterior end low. Internally white, pellucid in juveniles; hinge plate with one anterior and one posterior (AI & PII) lateral teeth in the left valve, the anterior longer, inverted V-shaped cardinal tooth fragile formed by two single teeth, the posterior longer; right valve with two anterior (AI & AIII) and two posterior (PI & PIII) lateral teeth, anterior cardinal tooth (3a) oriented in the same axis as anterior ventral lateral (AI); posterior cardinal vertically oriented; internal ligament placed in a well-developed chondrophore, but not enlarged beyond the hinge plate; pallial sinus rounded, wide, deep, about half of shell length.

Type Material: LSL 78.

Type Locality: "in Mare Mediterraneo?"

Distribution: Europe, Mediterranean Sea.

Remarks: The nominal species *Mactra laevis* Chemnitz, 1782 (a rejected work; ICZN, 1944, Opinion 184); *Mactra subplicata* Lamarck, 1818 (*non M. subplicata* Lamarck of W. Wood, 1828: pl. 1, *Mactra* fig. 6) and *Mactra spengleri* Linnaeus of Born, 1780 (*non* Linnaeus, 1767) have been regarded as synonyms of *Mactrella striatula* Linnaeus (e.g.,

Gmelin, 1791, Reeve, 1854; Lamy, 1917). However, after analysis of all type material, as well as the Born collection, three distinguishable species can be recognized.

The original illustration of Chemnitz of *Mactra laevis* (1782: 214, pl. 21, figs. 205, 206) coincides with the type material of *Mactra subplicata* Lamarck (Figs. 9, 10; Figs. 11–17), but clearly differs from the types of *Mactra striatula* Linnaeus deposited at LSL. Finally, the studied material from the Born collection (Figs. 18–21) clearly matches the types of *Mactrellona alata* (Spengler, 1802) (Figs. 34–36). The type locality given by Linnaeus was the Mediterranean Sea, whereas the type localities mentioned by Chemnitz and Lamarck were "Indian Ocean." *Mactra dolabrata* Reeve, 1854, ex Deshayes ms, considered a synonym of *M. striatula sensu* Huber (2010), is, in fact, *Mactra subplicata* Lamarck. The morphology of the type material described by Reeve (NHMUK 1996.444) coincides with the characters observed in the Lamarck species.

Genus *Mactrinula* Gray, 1853

[= *Papyrina* Mörch, 1853: 4, *Mactra plicataria* Linnaeus, 1767, subsequent designation by Keen, 1969: N598]

Type species: *Mactra plicataria* Linnaeus, 1767: 1125, monotypy.

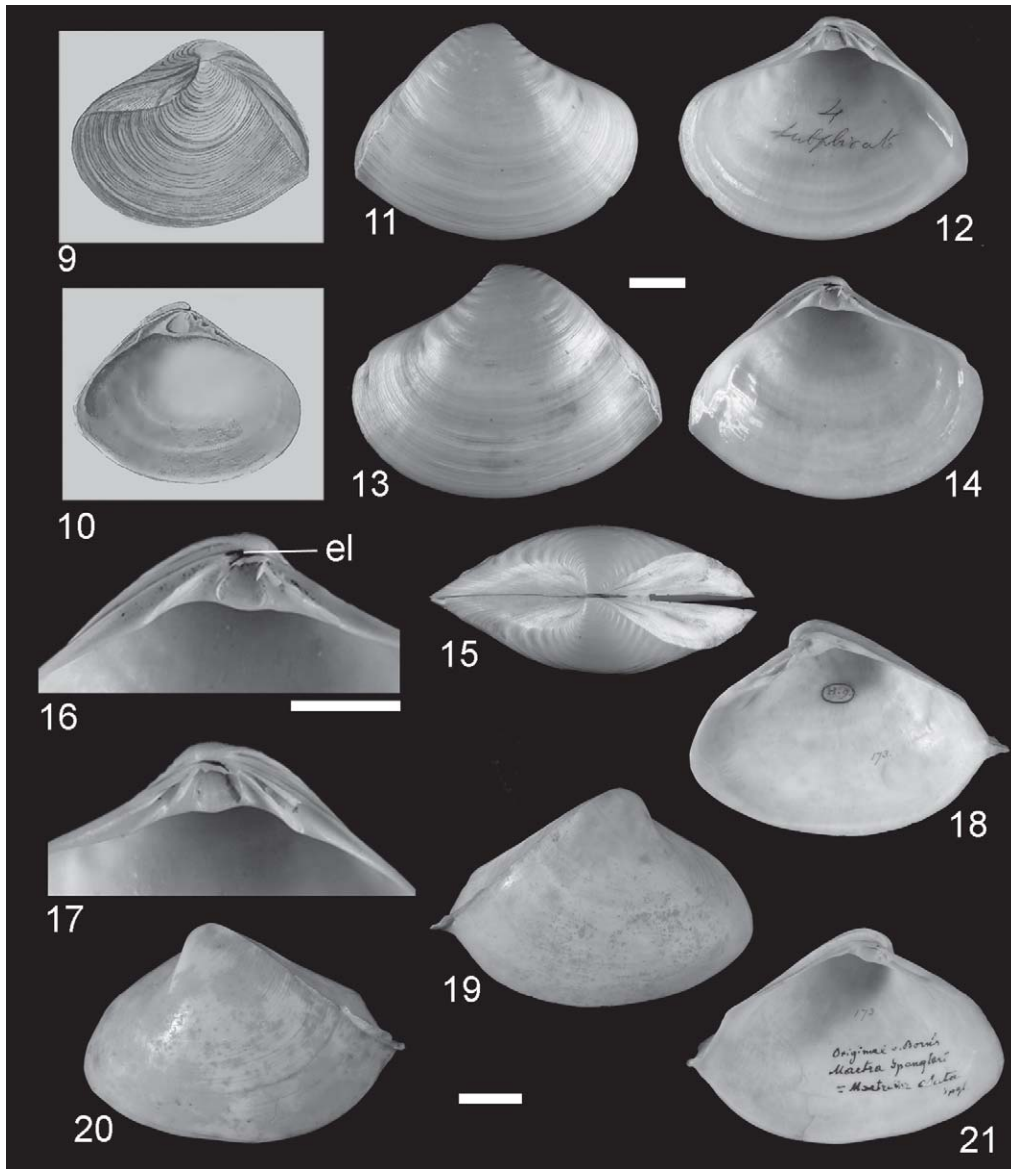
Diagnosis: Valves concentrically plicate, inequilateral; posterior slope set off by ridge; resilifer large and narrow, hinge teeth not concentrated, cardinal in left valve reinforced by apophysis with accessory lamella in front.

Distribution: Indian and Pacific oceans.

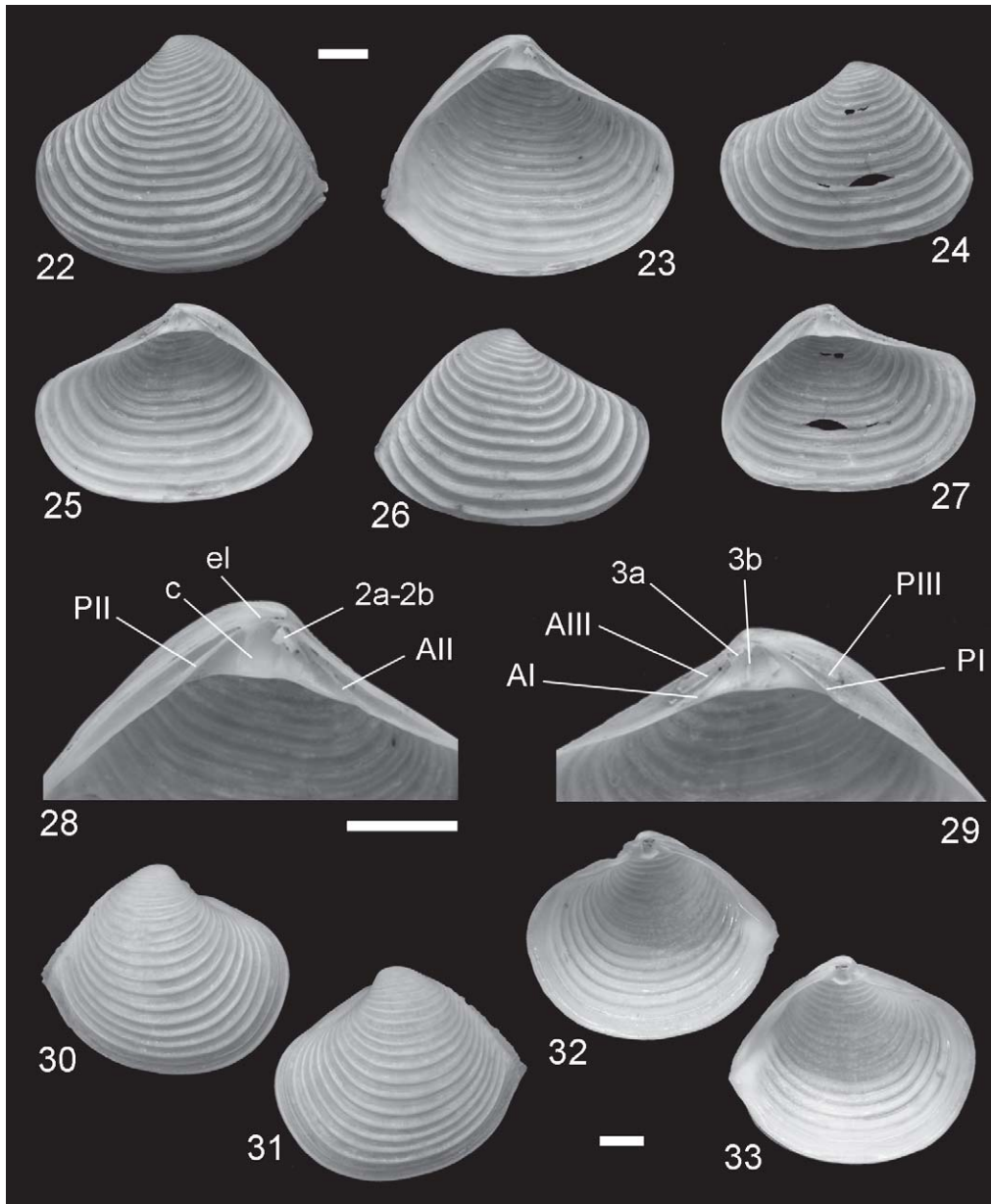
Mactrinula plicataria Linnaeus, 1767
(Figs. 22–29)

Mactra plicataria Linnaeus, 1767: 1125; Chemnitz, 1782: 213, pl. 20, figs. 202–204; Gmelin, 1791: 3257; Spengler, 1802: 98; Lamarck, 1818: 476; Bory de Saint Vincent, 1827, in Bruguière et al., 1791–1827: 151; Deshayes, 1830: 396; Deshayes & Milne Edwards, 1835, 102; Gray, 1837: 372, fig. 31; Hanley, 1842: 30; Reeve, 1854: fig. 26; Mörch, 1870: 122; Weinkauff, 1884, in Küster & Weinkauff, 1841–1884: 7, pl. 2, figs. 4–6; Hedley, 1910: 351; Lamy, 1914: 134.

Mactrinula plicaria Gray, 1853: 41, misspelling of *M. plicataria* Linnaeus.



FIGS. 9–21. Shells of *Mactra* spp. FIGS. 9, 10: *Mactra laevis* Chemnitz, 1782 (work rejected), original illustration; FIGS. 11–17: *Mactra subplicata* Lamarck, 1818, syntype MNHN 24189, el: external ligament. Scale bar = 1 cm; FIGS. 18–21: *Mactra spengleri* Born, 1780 (*non* Linnaeus, 1767), original material from Born collection, NHMW 14050. Scale bar = 2 cm.



FIGS. 22–33. Shells of Mactridae. FIGS. 22–29: *Mactrinula plicataria* (Linnaeus, 1767), syntypes LSL 77; FIGS. 22–27: General aspect; FIGS. 28, 29: Detail of hinge plate, el: external ligament, c: condrophore; FIGS. 30–33: *Harvella elegans* (Sowerby, 1825), syntypes deposited at NHMUK (without number). Scale bars = 2 cm.

Mactrinula plicataria Linnaeus. H. Adams & A. Adams, 1856: 377, pl. 99, fig. 2, 2a; Chenu, 1862: 55, fig. 226; Conrad, 1868: 35; Melvill & Standen, 1907: 828.

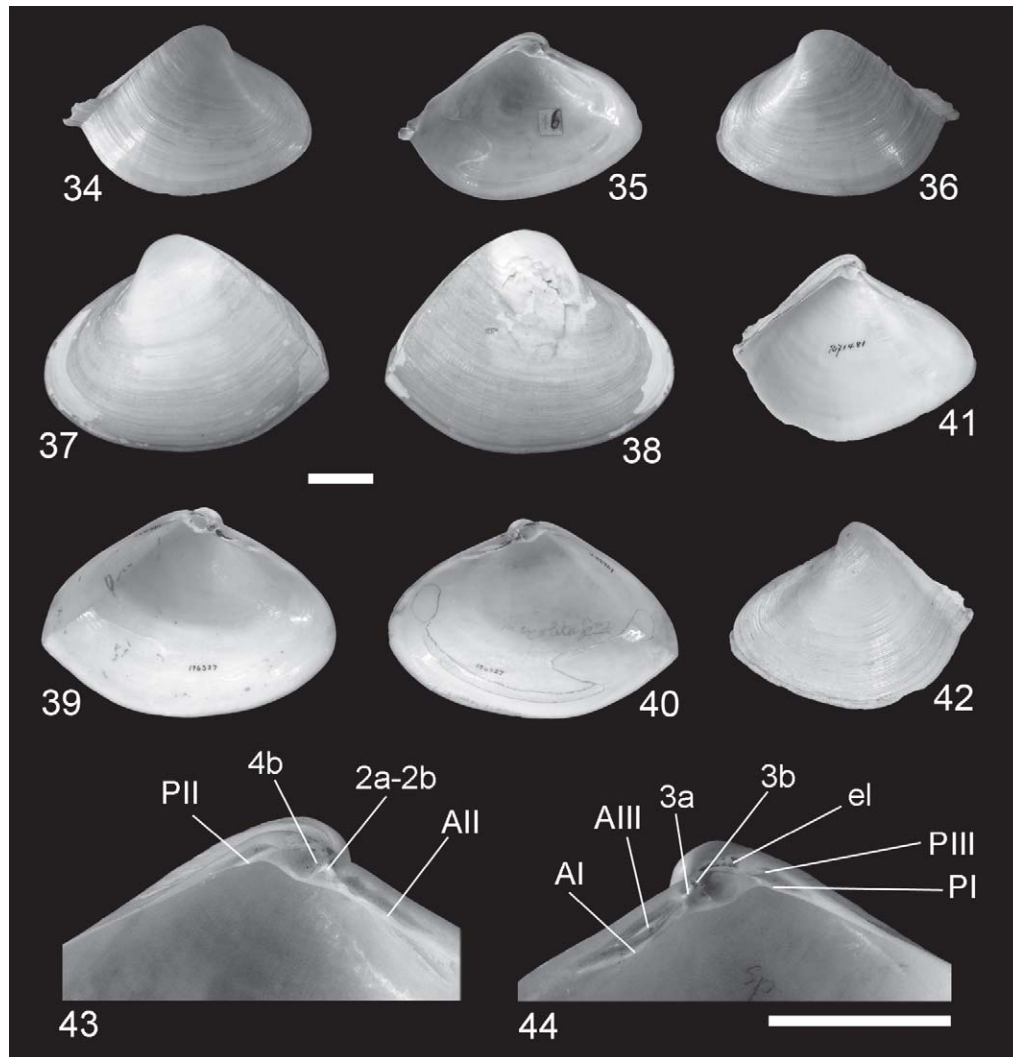
Mactra (*Mactrinula*) *plicataria* Linnaeus. Tryon, 1884: 157, pl. 109, fig. 1; E. A. Smith, 1885: 57; 1914: 117; Lamy, 1917: 268; Keen, 1969: N598, figs. E92–94.

Mactrella plicataria Linnaeus. Dall, 1895: 211; 1898: 877.

Harvella plicataria Linnaeus. Abbott & Dance, 1986: 335; Dharma, 1992: 92, pl. 24, fig. 4.

Diagnosis: Shell trigonal, fragile with external surface plicate; posterior end defined by a keel-like carina.

Description: Shell thin and fragile, trigonal, elongate, inequilateral, external surface with com-marginal ridges; anterior margin round, mod-



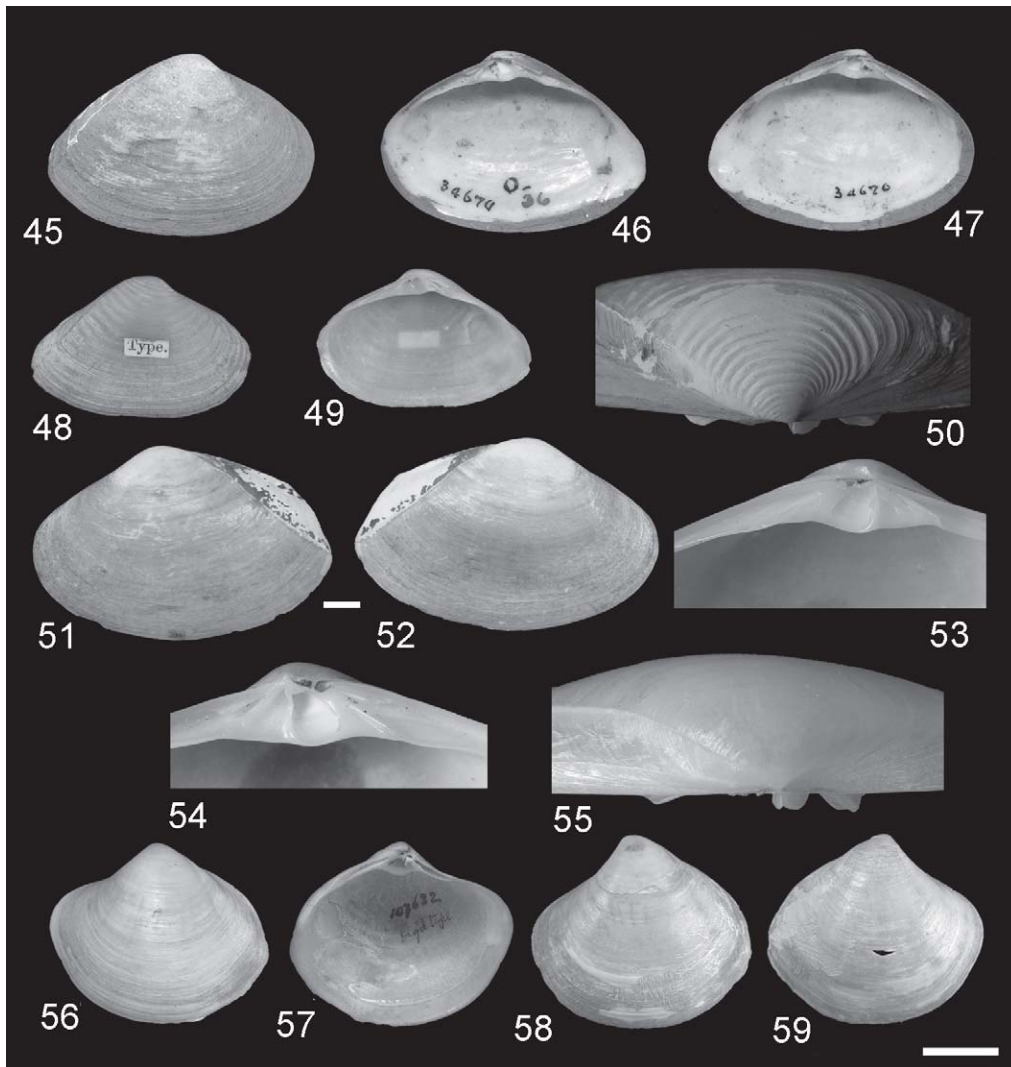
FIGS. 34–44. Shells of *Mactrellona* spp. FIGS. 34–36: *Mactrellona alata* Spengler (Spengler, 1802) holotype, ZMUC unnumbered); FIGS. 37–40: *Mactrellona clisia* (Dall, 1915) holotype, USNM 271481; FIGS. 41, 42: *Mactrellona exoleta* (Gray, 1837), syntype, NHMUK 196327; FIGS. 43, 44: Detail of hinge plate of *M. alata*, el: external ligament. Scale bars = 2 cm.

erately concave, longer than posterior margin; anterior end rounded, posterior end defined by a keel-like carina on which the concentric lines are closely spaced; umbones small, prosogyrous; escutcheon deep; periostracum brownish; internally pellucid with external ornamentation visible due to the shell thinness; left hinge with inverted V-shaped cardinal tooth (2a–2b), the single tooth 2a longer, one anterior and one

posterior lateral tooth (All & PII) elongate, with the dorsal ends close to cardinals; right hinge with two anterior and two posterior lateral teeth, equal in size and shape and less elongate than left laterals, pallial sinus moderate, round.

Type Material: LSL 77.

Type Locality: Java Sea, Indonesia.



FIGS. 45–59. Shells of Mactridae. FIGS. 45–47: *Mactrella californica* (Conrad, 1837), AMNH (34670); FIGS. 48–50: *Mactrella janeiroensis* (Smith, 1915), syntype, NHMUK 1915.4.18.489; FIGS. 51–55: *Standella fragilis* (Gmelin, 1791), AMNH 34063; FIGS. 56–59: *Trinitasia iheringi* (Dall, 1897); FIGS. 56, 57: Holotype of *Mactrella iheringi* (USNM 107632); FIGS. 58, 59: *Mulinia kempfi* Cauquoïn, 1969, two syntypes (MNHN unnumbered). Scale bars = 1 cm.

Distribution: Indian and Pacific oceans, Malaysia, Thailand, Indonesia, India, Australia.

Remarks: Although the generic position of *Macrinula plicataria* has varied among authors (e.g., Lamy, 1917; Abbott & Dance, 1986), this species was proposed as the type species of *Macrinula* by Gray (1853). The inclusion of *M. plicataria* in the genus *Harvella*, as some authors have proposed, is not accepted. Although the morphology of the external surface could suggest this assignment, the hinge morphology observed in this Linnean species significantly differs from that of *Harvella elegans* G. B. Sowerby I, 1825, type species of *Harvella* (Figs. 30–33). The lateral teeth are longer, and the resilifer is less ventrally projecting in *Macrinula*. In addition, the anterior dorsal edge is rounded and dorsally prolonged in *Harvella*, whereas in *Macrinula*, it is straight and inclined anteriorly. *Mactra subplicata* Lamarck of W. Wood (1828), *non M. subplicata* Lamarck, 1818, was considered a synonym of *M. plicataria* (Lamy, 1917); however, the illustration in Wood is extremely rudimentary and does not allow a taxonomic conclusion to be drawn.

DISCUSSION

A study of the type species of *Macrinula* and *Mactrella* reveals the presence of two different and valid groups. A complete comparison of diagnostic characters of the genera treated here is given in Table 1. The introduction of *Mactrellona* Marks clarifies the taxonomic status of *Mactrella*. Marks (1951) described his new genus to provide a name for a group of species that includes *M. alata* Spengler, 1802, *M. clisia* Dall, 1915, and *M. exoleta* Gray, 1837 (Figs. 34–44), previously placed in *Mactrella*. The congeneric relationship of *Mactra plicataria* (type species of *Macrinula*) and *Mactra striatula* (type species of *Mactrella*) mentioned by Marks (1951) is incorrect. The shell morphology of the type specimens reveals two distinguishable genera (Figs. 1–8 vs. Figs. 22–29). The external ornamentation of *Macrinula plicataria* plus the hinge morphology suggest a generic position different from the species included in *Mactrella*. In addition, Marks (1951) erroneously cited both taxa from the Indo-Pacific region; however, *Mactra striatula* Linnaeus was described from European waters.

The inclusion of species closely related to *Mactra alata* Spengler in the genus *Mactrella*

was based on the diagnosis given by Gray (1853). The characters of *M. striatula* mentioned by Gray fit better with those observed in *M. alata* (Marks, 1951). In addition, in the “*Mactra* B” section of Gray (1837), he mentioned *M. carinata* Lamarck, 1818, as synonymous with *M. striatula*. However, this nominal species is, in fact, the same as *Mactrellona alata* (e.g., Dall, 1894; Lamy, 1917). Evidently, Gray misidentified the specimens considered by him as *M. striatula*. These facts allowed Marks (1951) to introduce the new genus *Mactrellona* for the *M. alata* group and to keep *M. striatula* as type species of *Mactrella*. Marks based his decision on Opinion 168 (ICZN, 1945), which considered that a species designed as type of a genus must be accepted assuming that the original author of a genus correctly identified the species assigned by him in the absence of evidence to the contrary.

The genus *Micromactra* described as a section of *Mactra* by Dall (1894) is here added to the synonymy of *Mactrella*. This genus was included in the synonymy of *Mactrotoma* Dall, 1894, by Coan & Valentich-Scott (2012). In addition, Petit (2012) noted that the genus *Standella* Gray, 1853, is a senior objective synonym of *Mactrotoma* because they have the same type species (*M. fragilis* Gmelin, 1791). The type species of *Standella*, *Micromactra*, and *Mactrella* all have commarginal ribs on their umbones. However, *M. striatula* and *M. californica* present additional similarities that suggest a congeneric condition (Figs. 45–47). These are a trigonal shell with concentric wrinkles on the posterior umbonal area, a hinge plate with elongate lateral teeth not concentrated in the cardinal area, and a sharply rounded posterior end without a siphonal gape. These similarities were pointed out by Hanley (1855). However, *M. fragilis* is characterized by a less inflated and oval shell with a smooth posterior umbonal external surface, and the hinge plate is fragile, with short lateral teeth close to the cardinals. The posterior end of *M. fragilis* is truncate and gaping (Figs. 51–55).

The synonymy, proposed here, expands the geographic distribution of *Mactrella* along the western Atlantic Ocean from the southern coast of the United States to northern Patagonia in Argentina and to the Pacific coast of North America (Abbott, 1986; Signorelli & Pastorino, 2012a). *Mactrella californica* (Conrad, 1837) and *Mactrella janeiroensis* (Smith, 1915) are new combinations of two valid species (Figs. 48–50). The genus *Papyrina* introduced by Mörch in April 1853 grouped several species

TABLE 1. Diagnostic characters to differentiate the treated valid genera.

Genus	Type species	Shell shape	Hinge plate	Sculpture	Revised species included
<i>Harvella</i> Gray, 1853	<i>M. elegans</i> G. B. Sowerby I, 1825	Ovate, thin, translucent, with a posterior keel	Lateral teeth close to the cardinals, external ligament separated from resilium by a ridge	With heavy commarginal undulations	<i>Harvella elegans</i> (G. B. Sowerby I, 1825)
<i>Mactrella</i> Gray, 1853 (= <i>Micromactra</i> Dall, 1894, type <i>M. californica</i> Conrad, 1837)	<i>M. striatula</i> Linnaeus, 1767	Trigonal shell, posterior end sharply rounded without siphonal gap	Hinge plate with elongate lateral teeth not concentrated on the cardinal area	With concentric wrinkles on the postumbonal area of the external surface	<i>Mactrella striatula</i> (Linnaeus, 1767) <i>Mactrella californica</i> (Conrad, 1837) <i>Mactrella janeiroensis</i> (Smith, 1915)
<i>Mactrellona</i> Marks, 1951	<i>M. alata</i> Spengler, 1802	Large with a posterior area defined by keel	Hinge plate inclined anteriorly, with short lateral teeth	With commarginal striae, external surface smooth	<i>Mactrellona alata</i> (Spengler, 1802) <i>Mactrellona exoleta</i> (Gray, 1837) <i>Mactrellona clisia</i> (Dall, 1915)
<i>Mactrinula</i> Gray, 1853	<i>M. plicataria</i> Linnaeus, 1767	Trigonal, elongate, thin, inequilateral; external ornamentation evidenced due to shell thinness	Hinge teeth not concentrated, cardinal in left valve reinforced by apophysis with accessory lamella in front; resilifer large, narrow	Widely spaced concentrically plicate; posteriorly, with a pronounced keel.	<i>Mactrinula plicataria</i> (Linnaeus, 1767)
<i>Standella</i> Gray 1853 (= <i>Macrotoma</i> Dall, 1894)	<i>M. fragilis</i> Gray (= <i>M. fragilis</i> Gmelin, 1791)	Trigonal to oval, inequilateral, posterior end truncate and gaped, posterior dorsal area defined by a conspicuous line	Fragile with short lateral teeth close to the cardinals	With the postumbonal external surface totally smooth	<i>Standella fragilis</i> (Gmelin, 1791)
<i>Trinitasia</i> Maury, 1928	<i>Thyasira sanctiandreae</i> Maury, 1925	Shell trigonal to sub-circular, lunule well defined, anterior end round and high	Lateral teeth short, close to cardinals, anterior ones almost fused with anterior cardinal tooth, accessory lamella strong	External surface smooth	<i>Trinitasia iheringi</i> (Dall, 1897)

that currently represent more than one genus. He included both *M. striatula* and *M. plicataria* Linnaeus in this genus. The type species of *Papyrina* was designated by Keen (1969) as *Mactra plicataria* Linnaeus, and it must be considered an objective synonym of *Mactrinula*, published in January 1853 (Dall, 1915; Keen, 1969).

Finally the types of *Trinitasia iheringi* (Dall, 1897) and its synonym *Mulinia kempfi* Cauquoin, 1969, are illustrated (Figs. 56–59). This species was historically included in the genus *Mactrella*; however, its shell morphology suggests better placement in *Trinitasia*. A complete taxonomic and morphological review of *T. iheringi* was given by Signorelli & Pastorino (2012b).

ACKNOWLEDGEMENTS

Special thanks to Kathie Way (NHMUK), Virginie Heros and P. Maestrati (MNHN), Anita Eschner and A. Schumacher (NHMW), and Ilya Temkin (USNM) for their assistance in the revision of the type material and additional examined specimens. To Eugene V. Coan and two anonymous reviewers, who made very useful comments that improved an early version of the manuscript. Many thanks to Greg Herbert, André F. Sartori and Guido Pastorino for their considerable suggestions. To “Idea Wild” for contributing with a 60-mm Nikkor micro lens. JHS acknowledges CONICET of Argentina, to which he belongs as a researcher. This work was partially supported by the following projects: PICT-R 01869 and PICT-0323 of Agencia Nacional de Promoción Científica y Tecnológica, Argentina.

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Revised ms. accepted 4 June 2012