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Early Jurassic Trigoniida (Bivalvia) from Argentina

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Abstract.—Bivalves of the Order Trigoniida were abundant and diverse in the Andean Early Jurassic shallow-marine paleoenvironments. Based on extensive collections with detailed stratigraphic information from 40 localities in central-western Argentina, we describe 20 species (4 new) belonging to 11 genera (3 new) and 5 families (Groeberellidae, Trigoniidae, Prosogyrotrigoniidae, Frenguelliellidae, and Myophorellidae). The abundant material allows the description of ontogenetic development and intraspecific variability, highlighting the likely phylogenetic significance of previously underestimated features. Within Frenguelliellidae, we show that the stratigraphic range of *Frenguelliella* Leanza in the region is restricted to the Sinemurian–Pliensbachian. We propose *Poultoniella* new genus for some late Pliensbachian–Toarcian species. *Jaworskiella* Leanza is limited to its type species, whereas for certain convergent forms we propose *Moerickella* new genus (most likely the oldest Myophorellidae). *Pseudovaugonia* new genus likely descended from *Moerickella* n. gen., rather than from the highly diverse *Promyophorella* Kobayashi and Tamura, and is unrelated to *Vaugonia* Crickmay. *Frenguelliella chubutensis* (Feruglio) and *Promyophorella basoaltorum* new species are the most frequently occurring species. Some species were probably endemic (e.g., *Promyophorella*? *sanjuanina* new species), although a few (such as *Frenguelliella eopacifica* new species and *Poultoniella jaworskii* new genus new species) had a wide paleolatitudinal range and occur throughout the Pacific coasts and terranes of the Americas, revealing a significant faunal interchange among marine basins during Hettangian–Pliensbachian times. The well-documented Argentinian Early Jurassic record shows a rapid recovery and radiation of the Trigoniida after the Triassic/Jurassic extinction. Many of the new taxa that evolved in America eventually dispersed worldwide by Toarcian and Middle Jurassic times.

UUID: http://zoobank.org/82c0d95e-f147-4736-a417-ebc252911181.

Introduction

The order Trigoniida arose in the late Silurian, maintaining a low diversity until the Permian when it experienced a radiation (Newell and Boyd, 1975). It was highly successful during Mesozoic times, when it was the most conspicuous and diverse group of shallow-burrowing bivalves (Stanley, 1977). It was considered a highly resilient taxon (Ros and Echevarría, 2011) that swiftly recovered after being strongly affected by the end-Permian and end-Triassic mass extinctions. On the other hand, after the end-Cretaceous extinction event, trigoniids were confined to epicontinental seas of Australia and New Guinea, where they are nowadays represented by a single genus (Darragh, 1986).

During most of the Early Jurassic the Trigoniida seems to have been largely restricted to the Pacific coast of the Americas and to Japan (Ziegler, 1971; Aberhan, 2002, appendices 1, 2; Francis and Hallam, 2003; Ros Franch et al., 2014, fig. 41; Echevarría and Ros Franch, 2019); although some authors mentioned the presence of lower Early Jurassic trigoniids elsewhere (e.g., Deecke, 1925; Hallam, 1977, appendix, p. 72). By the late Early Jurassic–early Middle Jurassic they experienced a wide dispersion, reaching the European Tethys (Francis, 2000; Francis and Hallam, 2003) and South East Asian Tethys (Wandel, 1936; Hayami, 1972) by the Toarcian, the high latitudes of Antarctica by the Pliensbachian–Toarcian (Kelly, 1995), New Zealand by the Aalenian (Fleming, 1987), and eastern Africa by the Bajocian (Cox, 1965). After the Triassic/Jurassic extinction event, the Trigoniida are well recorded and relatively abundant in South American Early Jurassic deposits (Leanza, 1942; Pérez and Reyes, 1977; Ishikawa et al., 1983; Leanza, 1993; Pérez et al., 2008). The present paper deals with this particularly interesting place and time-span for the study of Trigoniida systematics and evolution, and documents the rapid radiation of the group.

The systematics of the group has been variably treated, but a stable taxonomic framework has remained elusive. The genus *Trigonia* was first described by Bruguière (1789) and characterized mostly by its particular hinge; soon, several species were recognized within it and the genus was subdivided into sections (Agassiz, 1840; Lycett, 1872–1879), which were the base for the recognition of many new genera (Bayle, 1878; van Hoepen, 1929; Crickmay, 1930; Dietrich, 1933). Cox (1952, see also Cox et al., 1969) differentiated the family Trigoniidae from the family Myophoriidae on the basis of hinge characters, particularly the broad and prominent median tooth of the left valve with transverse ridges on both occluding surfaces in the

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former. Later authors (Kobayashi, 1954; Saveliev, 1958; Poulton, 1979; Leanza, 1993; Francis, 2000) maintained that scheme of a single family, subdividing it into several subfamilies. Although Newell and Boyd (1975) suggested a polyphyletic origin for trigoniid hinge characters, few authors followed their scheme. Boyd and Newell (1997) themselves returned to the distinction between Myophoriidae and Trigoniidae.

Cooper (1991) considered that, given the high variability within the Trigoniida, the systematic scheme was inadequate. He proposed two suborders within the order Trigoniida: Trigoniina and Myophorellina. The first one included the superfamilies Myophoriacea (equivalent to Myophoriidae sensu Cox, 1952) and Trigoniacea. The second one included the superfamilies Myophorellacea and Megatrigoniacea. Many of the subfamilies were raised in rank to families.

Because the Early Jurassic stock is the basis for the main Mesozoic radiation of the group, the detailed study of the faunas here presented is fundamental in order to understand the evolution (and, as a consequence, the systematics) of the order. To infer evolutionary relationships among the studied species we employed a stratophenetic approach (Gingerich, 1979) whenever possible, based mostly on a qualitative assessment of characters. We tried to maintain a phylogenetic criterion on supraspecific taxa, avoiding polyphyletic groups. In contrast, since ancestor-descendant relationships were inferred in some cases, paraphyly could not be avoided.

The systematics of Early Jurassic Trigoniida still needs to be supported by a phylogenetic analysis of the Triassic representatives (work in progress, but out of the scope of this contribution). The systematic arrangement followed here is thus tentative, and is based on Bieler et al. (2010) and Carter et al. (2011), with some modifications. We accept the superfamily Trigonioidea in the sense of Bieler et al. (2010) and Carter et al. (2011), including, among others, the families Groeberellidae, Trigoniidae, and Prosogyrotrigoniidae, and the family Myophoriidae as the ancestral stock for the others. The superfamily Myophorelloidea includes, in this report, the families Frenguelliellidae and Myophorellidae. We regard Frenguelliellidae as ancestral to Myophorellidae. Since we were not able to thoroughly analyze the later diversification of the suprageneric taxa here included, we refrained from providing proper diagnoses for them. The subfamily category sometimes has been used in excess in this group, resulting in lots of monogeneric subfamilies. Therefore, we prefer to avoid the use of subfamilies until further systematic revision is carried out.

The oldest paleontological papers describing Early Jurassic marine macrofossils from Argentina contain records of Trigoniida (Behrendsen, 1891; Burckhardt, 1902; Jaworski, 1915), even though a few of the earliest described species were erroneously assigned stratigraphically to the Early Cretaceous (Jaworski, 1915) or the Late Triassic (Groeber, 1924). Further descriptions were included in papers dealing with diverse invertebrate faunas (Weaver, 1931; Feruglio, 1934; Carral-Tolosa, 1942; Leanza, 1942), and later in papers specifically concerning the Trigoniida (Lambert, 1944; Levy, 1966, 1967; Leanza and Garate-Zubillaga, 1987; Leanza et al., 1987; Leanza, 1993). Early Jurassic Trigoniida from Chile were recently revised by Pérez et al. (2008).

We present here a comprehensive systematic analysis based on collections gathered during decades, by detailed sampling of a geographically extensive area across the entire Early Jurassic stratigraphy. Specimens from old collections made in Argentina are scattered in several European repositories; these specimens were examined whenever possible. The large amount of material available enabled us to pay particular attention to morphologic variability within many of the taxa described, an aspect somewhat neglected in the past, although its importance has been highlighted by some authors (e.g., Francis, 2000; Schneider et al., 2011).

Geological setting

Marine Lower Jurassic beds in Argentina were widely deposited in the west-center of the country from southern San Juan to Chubut provinces (Fig. 1). Two main basins, probably interconnected, developed (i.e., Neuquén and Chubut). They both contain widespread deposits exhibiting a variety of paleoenvironments. The Aconcagua-Neuquén depocenter (Riccardi, 1983) developed during the Late Triassic–Eocene (Howell et al., 2005; Lanés, 2005) between 30° and 41°S latitude, with an eastward expansion towards the southeast (the Neuquén Embayment) that can be regarded as an epeiric sea. The onset of this basin is related to a rifting phase from the Middle Triassic to the Sinemurian (Ramos, 1992; Manceda and Figueroa, 1995) that led to the evolution of a series of narrow and isolated depocenters (Uliana and Biddle, 1988; Legarreta and Uliana, 1996). Marine sediments of this first stage crop out only in the Atuel River region (southern Mendoza) (Riccardi et al., 1988), close to the so-called Curepto Strait, which was one of the main connections of the basin with the Paleopacific (Vicente, 2005). After that, a sag stage developed from late early Sinemurian to Toarcian, causing the coalescence of the initial depocenters during the late Sinemurian–Pliensbachian, and thus enlargement of the area under marine influence (Legarreta and Gulisano, 1989; Legarreta and Uliana, 1996). From this time on, the Neuquén Basin developed as a back-arc basin related to circum-Pacific convergence (Legarreta and Uliana, 1996), with pyroclastic and volcanic content especially common in Lower Jurassic deposits. During the early Pliensbachian the basin expanded southward, reaching its maximum extension in the late Pliensbachian. Although the basin was partially barred from the open ocean, the well-diversified faunas indicate that free oceanic connections occurred through gaps in the arc (Legarreta and Uliana, 1996). By Middle Jurassic times, proximal deltaic and alluvial facies started to prograde, reducing the depositional area (Legarreta and Uliana, 1999, p. 405).

The Chubut Basin is a NNW-SSE elongated depocenter (Fig. 1) with marine and continental sedimentary deposits of Early Jurassic age, mainly exposed in the western region of Chubut Province and extending northwards into Río Negro Province (41°00'–46°30′S) (Suárez and Márquez, 2007). The sedimentary succession of the Chubut Basin accumulated under an extensional tectonic regime (Lizuain, 1999; Uliana and Legarreta, 1999), starting with continental deposits overlain by shallow-marine and continental successions. To the east, these marine beds interfinger with mainly pyroclastic continental facies (Franchi et al., 1989). Early Jurassic marine sediments lie unconformably over late Paleozoic rocks, but contrary to Carral-Tolosa's (1942, p. 22, 67) assumption of a complete Early

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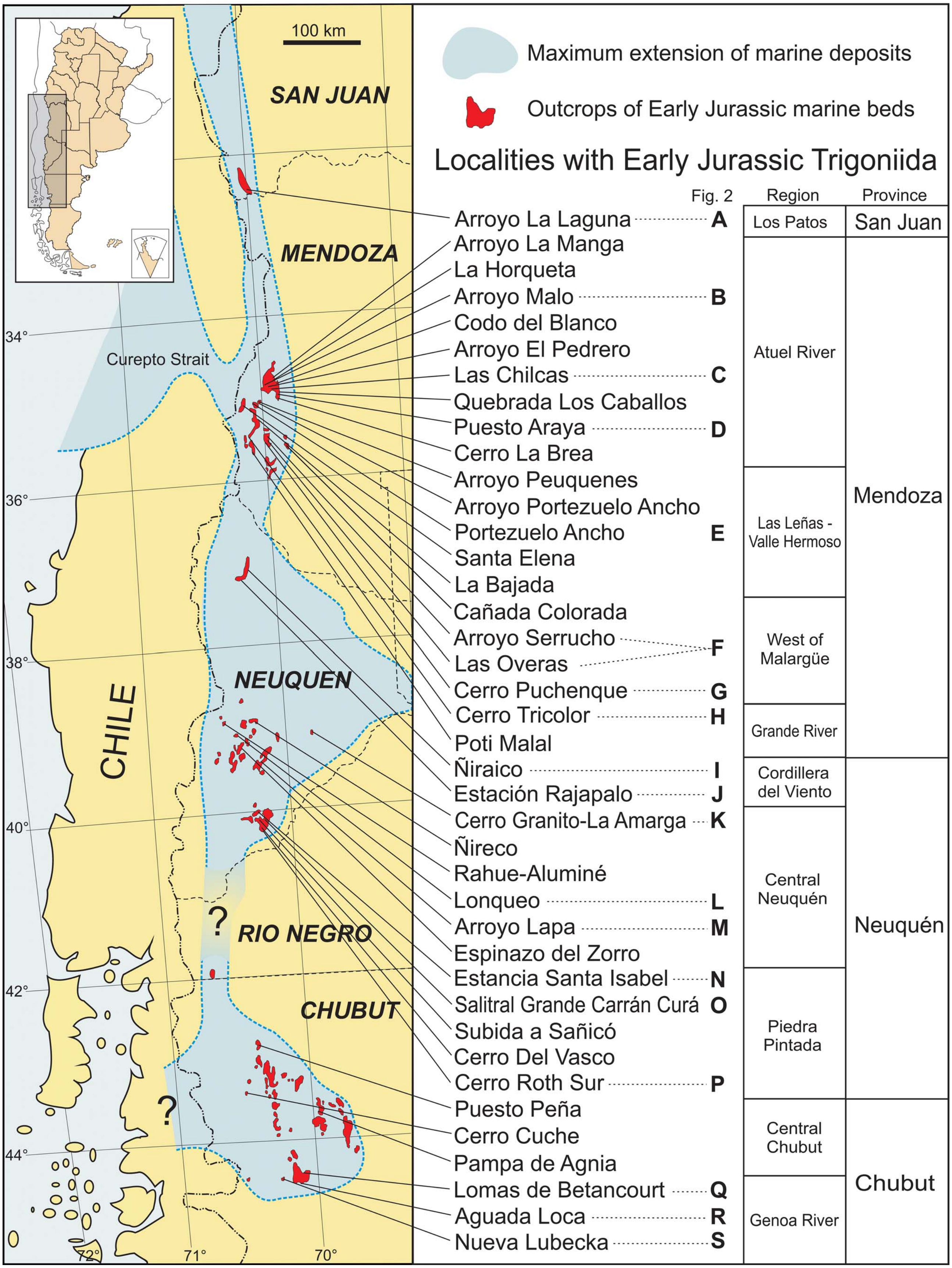

Figure 1. Map of the localities mentioned in the text, in the context of general Pliensbachian–Toarcian paleobiogeography, compiled from various sources, mainly Legarreta and Uliana (1996), and Vicente (2005). Localities are grouped by region and province as used in the text. Stratigraphical sections depicted in Figure 2 are indicated by capital letters.

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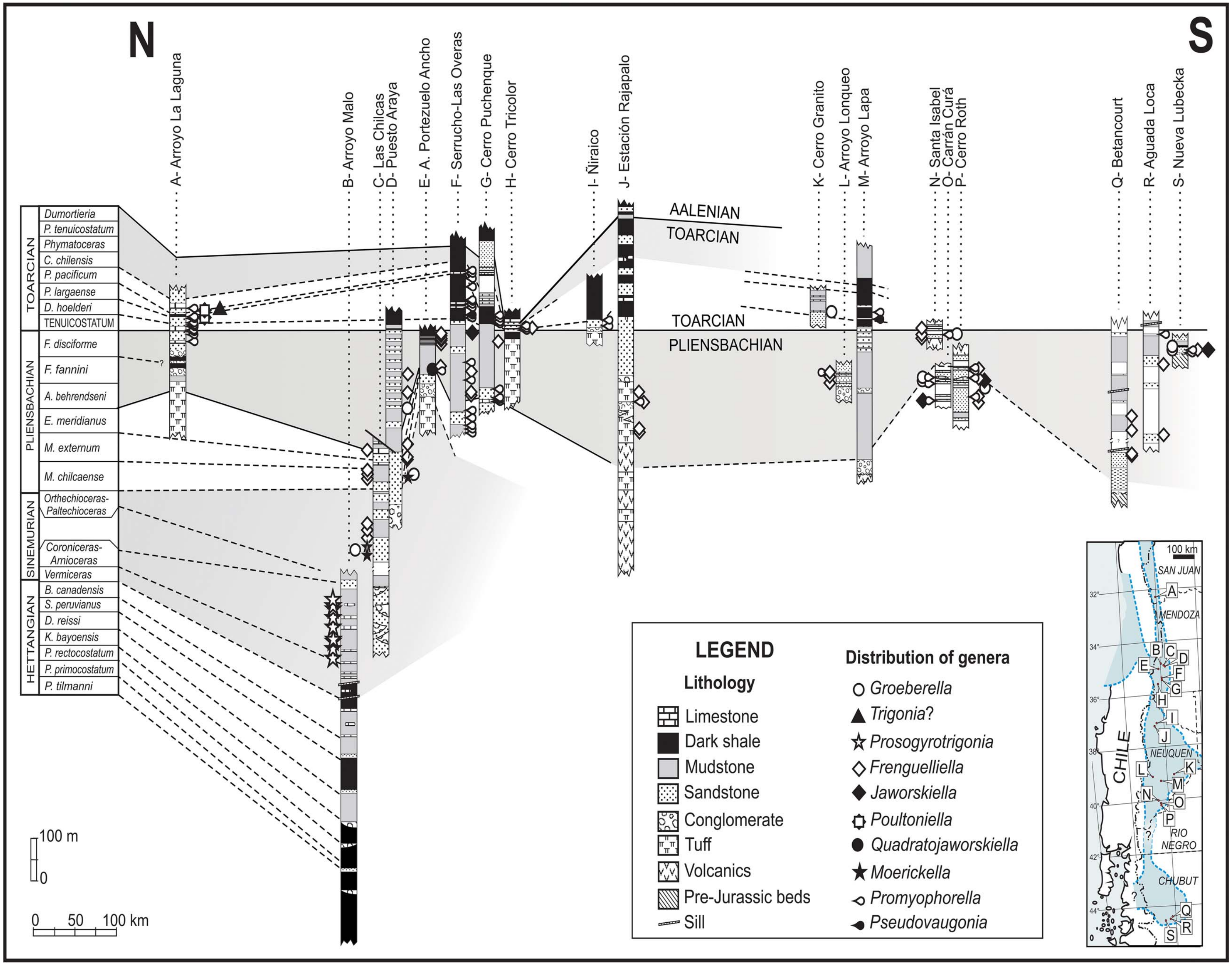

Figure 2. Selected sections arranged from north to south, with the distribution in space and time of the genus-group taxa treated in this paper. Biostratigraphic framework from Riccardi (2008a, b) and Riccardi et al. (2011). All sections sketched to the same scale and leveled to the base of the Toarcian.

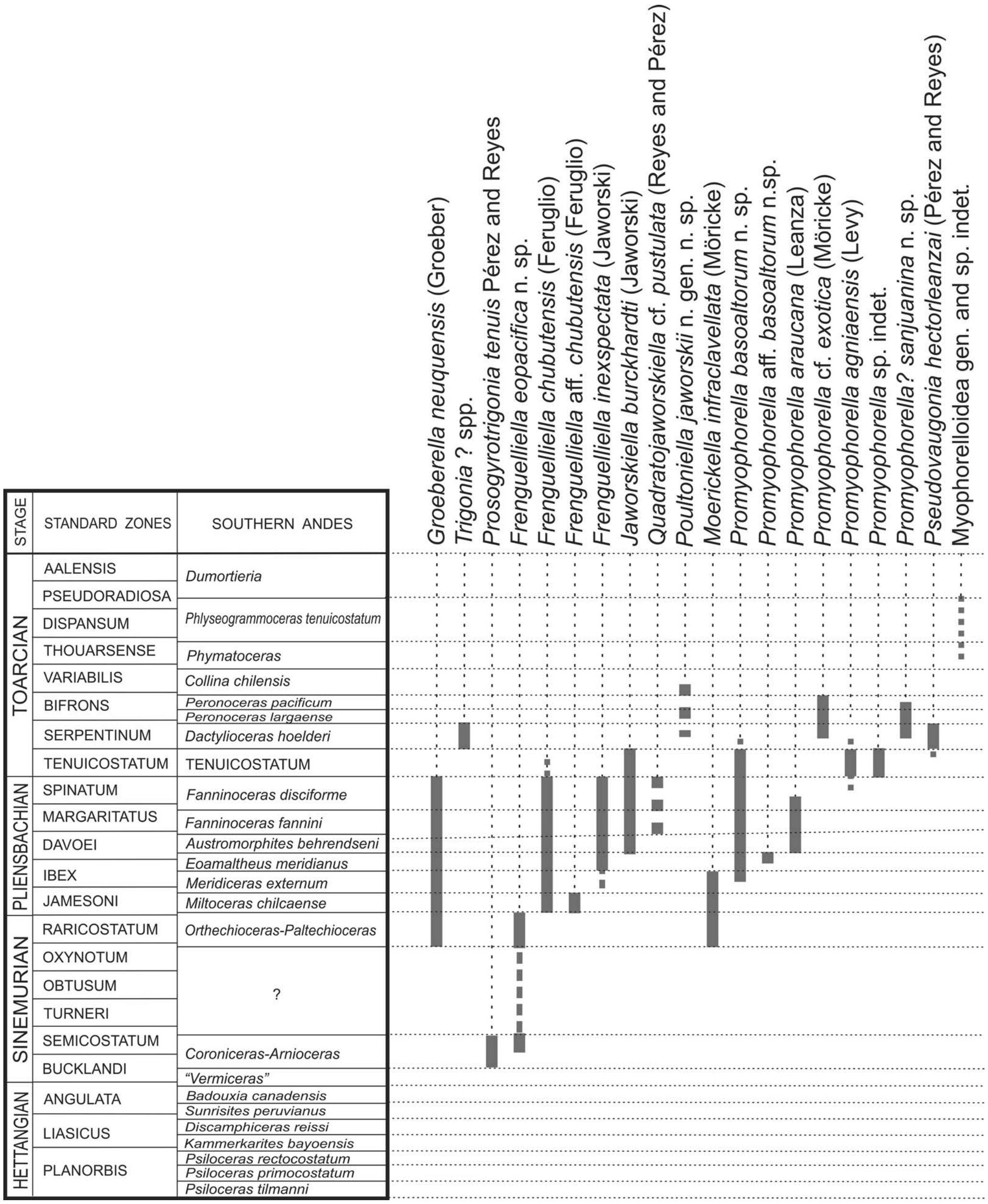

Figure 3. Stratigraphic distribution in Argentina of species described. Local ammonite biozonation and its equivalence to the standard zonation from Riccardi (2008a, b).

Jurassic marine sequence in Chubut, most marine beds seem to have been deposited during the short interval from the late Pliensbachian to the early Toarcian (Riccardi 2008a, b).

Thus, by late Pliensbachian times, there was an elongate marine encroachment with two expanded basins (Neuquén and Chubut) that were connected with the Pacific Ocean (Legarreta and Uliana, 1996). Their sedimentary successions maintained local variations in thickness and lithology due to an uneven basin floor related to active rifting and a variety of depositional environments (Legarreta and Uliana, 1999). The basinal successions are punctuated by turbiditic strata and by shallower water deposits (lowstand wedges). Syntheses of paleogeographic reconstructions for different time intervals were published by Legarreta and Uliana (1996, fig. 9, 1999, figs. 5–7), Vicente (2005, 2012), and Arregui et al. (2011, figs. 5, 6), among others.

Ammonite faunas are abundant and diverse in both the Neuquén and Chubut basins. A detailed local biostratigraphy, which is well correlated to the standard zonation, was developed by Riccardi (2008a, b) and Riccardi et al. (2011). This is the age framework used as reference in this paper (as shown in Figs. 2, 3).

Materials and methods

Stratigraphic sections were logged at most of the localities listed in Figure 1, but only the most relevant to this study are sketched in Figure 2. The entire fauna was recorded and/or sampled at each fossiliferous bed, but only those horizons containing Trigoniida are indicated in the figure. A synthesis of the stratigraphic range for each species is depicted on Figure 3.

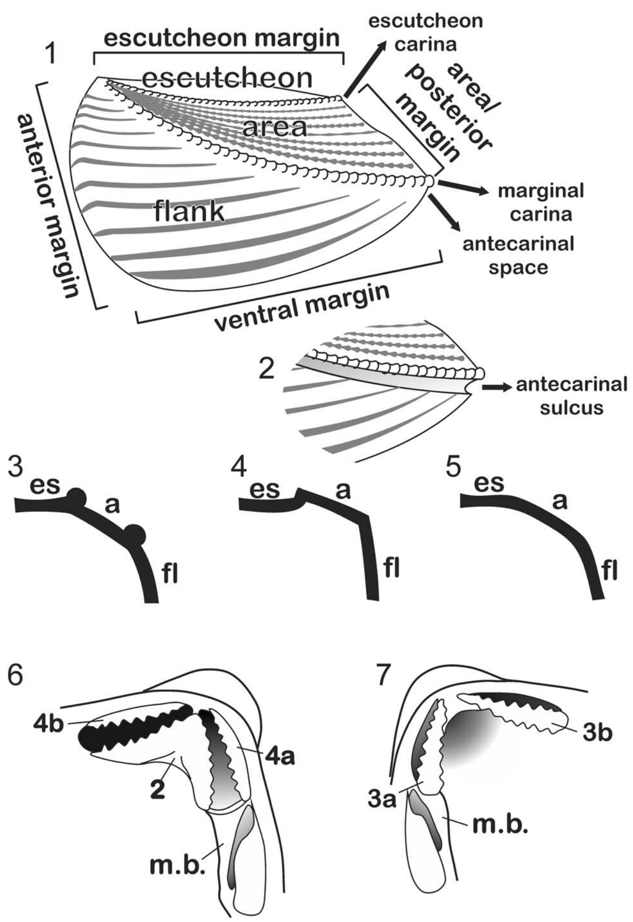

Figure 4. Morphology and terminology. (**1, 2**) Main descriptive terminology for trigoniid shell features; (**3–5**) transverse sections of valve, showing different types of contact between escutcheon (es) and area (a), and between area and flank (fl): (**3**) prominent escutcheon and marginal carinae, (**4**) stepped escutcheon angulation and marginal angulation, (**5**) escutcheon and marginal bends; (**6, 7**) trigonian-grade hinge in left and right valves, showing hinge notation, m.b. = myophoric buttress.

Terminology.—We follow Carter et al. (2012) for general morphologic terminology (Fig. 4). Accordingly, we use "costae" or "ribs" for shell surface ornamentation structures that are not expressed in the interior of the shell, and "folds" for undulations that affect the entire thickness of the shell. Some of the terms used here need explanation. For instance, the marginal and escutcheon carinae are typical characters of the group, to the point that sometimes they have been described even when the shell lacks an actual carina. Because these differences may bear importance in the phylogenetic study of the group, we distinguish and apply the following terms: (1) "carina" when a protruding elevation is developed (Fig. 4.3), sometimes (though not always) as a fold in the shell; (2) "angulation" (sensu Cooper, 1989) when there is a sharp change in orientation between the area and the other surfaces (Fig. 4.4), developing a linear structure equivalent in position to the carina, but not a carina strictly speaking; and (3) "bend" (see Pérez et al., 2008, p. 66 under "Description" for *Prosogyrotrigonia tenuis* Pérez and Reyes in Pérez et al., 2008) for a gentle change in orientation between the area and the other surfaces (Fig. 4.5). The term "stepped angulation" is used when the boundary between the area and the escutcheon is an angulation, but because the escutcheon is depressed, a small step between both surfaces is developed (Fig. 4.4). Similar to the carinae, an antecarinal sulcus occasionally has been described, even when there is no actual depression. Thus, the term "antecarinal sulcus" is restricted to a true depression anterior to the marginal carina, angulation, or bend (Fig. 4.2), and "antecarinal space" is used for flat surfaces (leveled with the flank) showing an abrupt difference in ornamentation relative to the flank (Fig. 4.1).

In addition to the usual kinds of costae orientation in shell ornamentation (e.g., radial, commarginal, and oblique), the term "sub-commarginal" is here used to refer to flank costae where the costal segment on the central part of the flank is commarginal, but on the anterior part, it cuts across growth lines and meets the anterior margin at high angles (see Poulton, 1979, p. 12, text-fig. 4, characterized as "pseudoconcentric"; Fig. 4.1).

Some genera may develop an "internal radial ridge" (sensu Cox, 1952, p. 57–58, under *Prorotrigonia*, and p. 59–60, under *Pterotrigonia*) on the posterior part of the inner surface of the shell, which is approximately coincident with the midline of the area. According to Gould and Jones (1974), this internal radial ridge may have helped these bivalves separate inhalant from exhalant currents.

Dentition notation is the most generally used for the group (Fig. 4.6, 4.7). Trigonian-grade hinge has been characterized by the presence of a prominent, subtriangular, and extremely broad median tooth on the left valve (tooth 2 on Fig. 4.6), with a concave ventral surface giving it a bifid aspect, and with anterior and posterior faces bearing strong transverse ridges or striae (Cox, 1952; Newell and Boyd, 1975; Poulton, 1979; Boyd and Newell, 1997). The two main teeth of the right valve (teeth 3a and 3b; Fig. 4.7) are widely divergent and more or less symmetrically disposed, also with transverse ridges (Cox, 1952; Newell and Boyd, 1975; Poulton, 1979). Other characters usually mentioned are a gap or hiatus in the right valve hinge plate and the presence of a myophoric buttress ("m.b." on Fig. 4.6, 4.7) posterior to the anterior adductor muscle scar. This myophoric buttress is fused with tooth 3a in the right valve and with the hinge plate, which forms the socket for this tooth in the left valve (Cox, 1952; Fleming, 1964; Newell and Boyd, 1975).

In contrast, the myophorian-grade hinge (see Newell and Boyd, 1975, fig. 12.C, 12.D) has been characterized as having a simple (Cox, 1952) or bifid tooth 2, which is not particularly prominent (Cox, 1952; Fleming, 1964; Newell and Boyd, 1975). Teeth 3a and 3b are more unequally and asymmetrically arranged than in the trigonian-grade hinge, and are placed on a hinge plate (Cox, 1952; Fleming, 1964; although Newell and Boyd, 1975, mentioned that some species may have a hiatus). Dental striations are variably developed in the myophorian-grade hinge, although the striation is less conspicuous than that of the trigonian-grade hinge (Cox, 1952; Newell and Boyd, 1975). Newell and Boyd (1975) and Boyd and Newell (1997) also mentioned, as a distinctive character of myophorian-grade hinge, the elongation of the posterior limb of the tooth 2, which functioned as a second inner pseudolateral tooth.

Although the trigonian-grade hinge definition provided above fits well for the hinges of most, if not all, post-Triassic

Trigoniida, that is not the case for Triassic representatives, where the different elements may be variably combined (e.g., Boyd and Newell, 1997; Hautmann, 2003). This mosaic combination of characters may be indicative of a polyphyletic origin for the trigonian-grade hinge, as suggested by Newell and Boyd (1975). Although the subject is beyond the scope of this study, when discussing some Triassic representatives of the group, we follow Boyd and Newell (1997) and consider that the minimum requirements for a hinge to be defined as trigonian-grade are: (1) to have well-developed striation on both surfaces of teeth 2 and 3a (and on the corresponding sockets), and (2) the absence of the elongate posterior limb on tooth 2.

Shell size is characterized by length according to the following scheme: length <20 mm = very small shell; 20 to <40 mm = small shell; 40 to <60 mm = medium-sized shell; 60 to <80 mm = large shell; length ≥80 mm = very large shell. Measurements are given in mm, and the following abbreviations are used: L = length, H = height, W = width of both valves, V = width of a single valve.

Repositories and institutional abbreviations.—Specimens collected by the authors are housed in the following repositories: IANIGLA-PI = Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina; MCF-PIPH = Museo Municipal Carmen Funes, Plaza Huincul, Argentina; MLP = División Paleontología Invertebrados, Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MOZ-PI = Museo Provincial de Ciencias Naturales "Dr. Prof. Juan A. Olsacher", Zapala, Argentina; and MPEF-PI, Museo Paleontológico Egidio Feruglio, Chubut, Argentina. Further specimens examined are housed in: BMNH = Burke Museum of Natural History, Seattle, USA; CPBA = Geology Department, Universidad de Buenos Aires, Buenos Aires, Argentina; SIRAME-SEGEMAR and DNGM = Dirección Nacional de Geología y Minería, Buenos Aires, Argentina; GSC = Geological Survey of Canada, Calgary, Canada; IGPB = Institute of Geosciences, Paleontology Section, Bonn, Germany; NHMB = Naturhistorisches Museum Basel, Basel, Switzerland; SNGM = Servicio Nacional de Geología y Minería, Santiago, Chile; MNHN = Muséum Nationale d' Histoire Naturelle, Paris, France. A list of Argentinian Trigoniida specimens included in this study by species, locality, repository abbreviation, and local zonation is provided in Appendix 1.

The synonymy lists were prepared according to Matthews (1973) to indicate the degree of confidence in allocation of each entry. They include only published records.

Systematic paleontology

Order Trigoniida Dall, 1889
Superfamily Trigonioidea Lamarck, 1819

Remarks.—According to Bieler et al. (2010) and Carter et al. (2011), this superfamily includes members representing the three hinge grades (schizodian-grade, myophorian-grade, and trigonian-grade). Of interest for this report are the families Groeberellidae, Trigoniidae, and Prosogyrotrigoniidae, all with a trigonian-grade hinge, and the family Myophoriidae, with a myophorian-grade hinge and without any Jurassic representatives, but probably ancestral to the other three.

Family Groeberellidae Pérez, Reyes, and Damborenea, 1995

Remarks.—The family Groeberellidae was characterized by Pérez et al. (1995) as having a myophoriform shell (i.e., subquadrate, inflated, orthogyrate to slightly prosogyrate), trigonian-grade hinge and a flank ornamentation dominated by radial costae. They inferred an origin from myophorid ancestors independent from that of other trigoniids.

General shell morphology in *Groeberella* corresponds well to that of some Triassic species with myophorian-grade hinges, and for this reason Groeber (1924) assigned a Triassic age to the beds bearing the type material. *Costatoria*, for example, is characterized by the presence of well-developed radial costation, in some species with wide concave interspaces (see Hautmann, 2001, figs. 26.10, 26.11, 27.1–27.11 for some examples). Although being most abundant in the Tethys and in Japan (Ros Franch et al., 2014, p.120, fig. 42), there are also a few mentions from the American Pacific margin (Chong and Hillebrandt, 1985, *Costatoria* sp., Norian or Rhaetian from Quebrada San Juan, Antofagasta Region, North Chile; Damborenea and González-León, 1997, *Costatoria*? sp., Upper Triassic, probably Norian, of Sierra del Álamo, Sonora, Mexico). The record from Mexico shows poorly developed striation on hinge teeth not covering the entire occluding surfaces, but, as in *Groeberella*, striation does not develop on the posterior face of 3b (Damborenea and González-León, 1997, p. 192, fig. 8.3, 8.4).

In contrast, some authors (e.g., Levy, 1967; Leanza, 1993) related *Groeberella* to the Minetrigoniinae, with a trigonian-grade hinge, flank sculpture of intersecting radial and commarginal costae, and trellised ornament on the area (Kobayashi, 1954; Fleming, 1987).

Genus *Groeberella* Leanza, 1993

Type species.—*Myophoria neuquensis* Groeber, 1924, Pliensbachian, Neuquén, Argentina.

Diagnosis.—Subquadrangular, inequivalve, palmate shell. Orthogyrate to slightly prosogyrate umbos. Prominent escutcheon and marginal carinae, and few widely spaced radial costae on the flank. Intercostal (and intercarinal) spaces concave. Trigonian-grade hinge.

Remarks.—The diagnosis of the genus is adapted from Pérez et al. (1995). Besides the type species, early Sinemurian material from Chile was referred to *Groeberella* sp. (Pérez et al., 1995). Also, an early Pliensbachian left valve from Mexico was described as *Groeberella* sp. A (Scholz et al., 2008), and a fragmentary specimen from Neuquén referred to the Bajocian was likewise left in open nomenclature as *Groeberella* sp. by Leanza (1993, p. 19).

Groeberella neuquensis (Groeber, 1924)
Figure 5.1–5.8

v* 1924 *Myophoria neuquensis* Groeber, p. 92, pl. 1, figs. a, b.
v 1931 *Myophoria neuquensis*; Windhausen, p. 179, fig. 71. [reproduced from Groeber, 1924]

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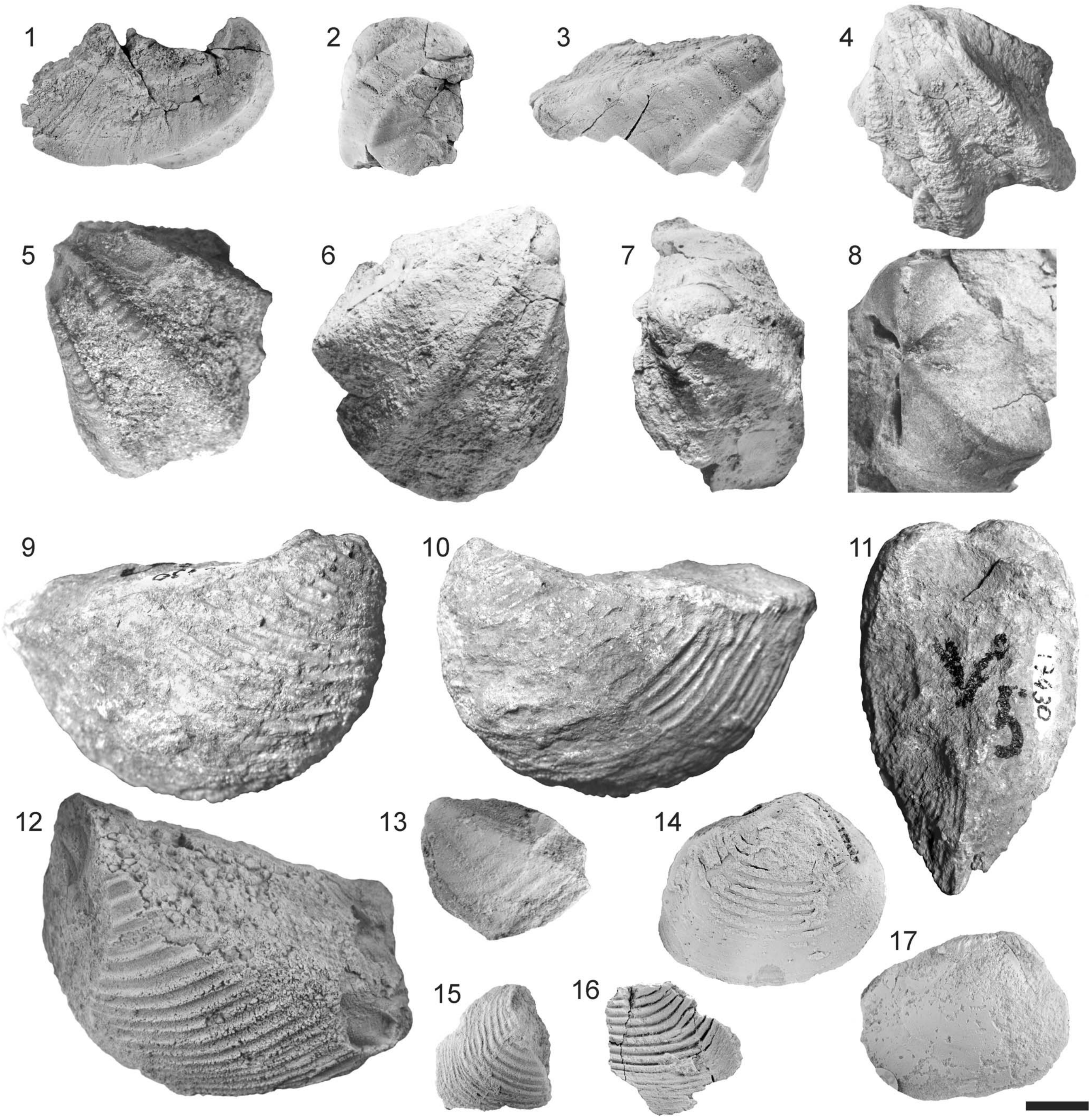

Figure 5. Trigoniida from the Early Jurassic of Argentina. Scale bar = 10 mm. (**1–8**) *Groeberella neuquensis* (Groeber): (**1–3**) holotype, DNGM 7337, right valve, dorsal, anterior and right lateral views, Pliensbachian, Puruvé-Pehuén; (**4**) DNGM 7340a, left valve, lateral view, Pliensbachian, Nueva Lubecka; (**5**) MPEF-PI 6401, left valve, Pliensbachian, Nueva Lubecka; (**6, 7**) DNGM 7339, right valve, lateral and dorsal views, Pliensbachian, Nueva Lubecka; (**8**) MLP 27844, internal molds of both valves open in butterfly position, early Pliensbachian, Puesto Araya; (**9–11**) *Trigonia*? sp. 2, CPBA 17430, right lateral, left lateral and dorsal views, early Toarcian, Arroyo La Laguna; (**12, 13**) *Trigonia*? sp. 1, early Toarcian, Arroyo La Laguna: (**12**) MLP 36312a, left valve; (**13**) MLP 36311, juvenile? left valve; (**14–17**) *Prosogyrotrigonia tenuis* Pérez and Reyes, early Sinemurian, Arroyo Malo: (**14**) MLP 32789, composite mold with shell remains, right lateral view; (**15**) MLP 32802, postero-ventral fragment of right valve composite mold; (**16**) MLP 32828, postero-ventral fragment of right valve external mold; (**17**) MLP 32805, internal mold, right lateral view.

v 1942 *Myophoria neuquensis*; Carral-Tolosa, p. 59, pl. 6, figs. 3a–c.
v 1967 *Myophorigonia neuquensis*; Levy, p. 14, figs. 1a–f.
1981 *Myophorigonia neuquensis*; Hillebrandt and Schmidt-Effing, p. 10.
1982 *Myophorigonia* aff. *M*. *neuquensis*; Pérez, p. 40, pl. 15, figs. 2–5, appendix 1.
v 1992 ‘*Myophorigonia*’ *neuquensis*; Damborenea and Manceñido, p. 134, pl. 1, fig. 5a.
v 1992 *Myophorigonia neuquensis*; Damborenea et al., pl. 115, fig. 14.

1993 *Groeberella neuquensis*; Leanza, p. 18, pl. 1, figs. 2, 3.
1995 *Groeberella neuquensis*; Pérez et al., p. 147, pl. 1, figs. 1–3, 5–13, 15, 16, 18–22.
1997 *Groeberella neuquensis*; Pérez and Reyes, p. 573.
v 2008 *Groeberella neuquensis*; Pérez and Reyes in Pérez et al., p. 58, pl. 1, figs. 1–13, 15, 17–18.
v 2011 *Groeberella neuquensis*; Riccardi et al., fig. 7.3.

Type materials.—Holotype: DNGM 7337 (= casts SNGM 7366, MLP 24324); right valve from the Pliensbachian of Puruvé-Pehuén, Neuquén Province, Argentina. Figured by Groeber (1924, pl. 1, figs. a, b), Damborenea and Manceñido (1992, pl. 1, fig. 5a), Damborenea et al. (1992, pl. 115, fig. 14), Pérez et al. (1995, pl. 1, fig. 1), and Figure 5.1–5.3 herein.

Occurrence.—The type locality is Puruvé-Pehuén (somewhere between Ñireco and Lonqueo in central Neuquén). Also recorded from: Las Chilcas, Puesto Araya, Quebrada de los Caballos (Atuel River region); La Bajada, Portezuelo Ancho (Las Leñas/ Valle Hermoso region); Estancia Santa Isabel, Salitral Grande Carrán Curá, Cerro Roth Sur (Piedra Pintada region); and Nueva Lubecka (Genoa River region). Leanza (1993, p. 10) mentioned the presence of this species at La Amarga, near Rincón del Águila (central Neuquén), but he listed neither this locality when describing the species (p. 19) nor this species among the fauna from that locality (p. 68). In Argentina, its stratigraphical range is late Sinemurian to late Pliensbachian (Fig. 3). This species seems to have had a wider stratigraphical range in Chile, extending at least to early Aalenian according to Pérez et al. (2008, p. 55).

Description.—Medium-sized, subquadrangular, orthogyrate to slightly prosogyrate shell. Umbos anteriorly located, slightly displaced from each other (Fig. 5.8). Escutcheon margin feebly convex; posterior margin slightly concave. Ventral margin palmate due to the presence of two radial ribs (Fig. 5.4). Anterior margin slightly convex. Escutcheon wide, smooth or with growth lines; escutcheon carina prominent. Area smooth (or with growth lines), slightly concave (Fig. 5.1, 5.4); prominent marginal carina. Area and flank meet at an angle of ~90°. Flank with two prominent radial ribs; spaces between the ribs (and marginal carina) wide and concave. Flank ribs and carinae as folds of the shell, shell thicker on the costae than on the interspaces. Costae and carinae on the left valve with transverse crenulations (Fig. 5.4, 5.5); intercostal spaces on the flank with thin commarginal costellae, more densely arranged than the crenulations. Costae sharper on the right valve (Fig. 5.1–5.3), lacking transverse ornamentation.

Trigonian-grade hinge (sensu Boyd and Newell, 1997). Tooth 2 broad and conspicuous, ventrally bifid; teeth 4a and 4b relatively short. Tooth 3a thicker than tooth 3b. Few strong ridges on both occluding surfaces of 2 and 3a, on the anterior face of 3b, and on the posterior face of 4a. Nymph short.

Materials.—Thirty-five specimens were examined: the holotype and DNGM 7338–7340, MLP 16387, 17478, 17724, 27246–27253, 27844, 27931, 28683, 36194; MPEF-PI 2913, 2918, 2993, 3392, 6397, 6435; IANIGLA-PI 3344; plus the specimen MOZ-PI 4060 figured by Leanza (1993).

Measurements.—Holotype (DNGM 7337): L = 42 mm (broken ventrally); DNGM 7339: L = 47 mm, H = 44 mm; DNGM 7340: H = 47 mm.

Remarks.—The species is endemic to South America (Damborenea et al., 2013).

Family Trigoniidae Lamarck, 1819

Remarks.—The Trigoniidae were described by Cooper (1991) as having a trigonal to rhomboidal shell shape, a trigonian-grade hinge, subcommarginal flank ornamentation, a prominent marginal carina, and an area with radial ornamentation (at least on early stages). Some previous authors (e.g., Kobayashi, 1954; Poulton, 1979), provided a similar characterization for the subfamily Trigoniinae.

The earliest representatives of this family are included in the genus *Primatrigonia* (defined as a subgenus of *Trigonia* by Repin in Paevskaya et al., 2001; see Echevarría et al., 2018 for a nomenclatural revision of this taxon). All the species included in *Primatrigonia* share a subdued ornamentation pattern, with weak radial costellae on the area and very subtle commarginal costellae or prominent growth lines on the flank (nearly smooth in some cases). *Trigonia tabacoensis* Barthel, 1958 (see also Pérez and Reyes, 2008, fig. 1) from the Anisian of Chile, and *Trigonia* n. sp. A of Fleming (1987), from the Anisian of New Zealand, may well be included in *Primatrigonia*. The Chilean species is the oldest within the order with a recognizable trigonian-grade hinge. Other Late Triassic species are *Primatrigonia yunnanensis* (Guo, 1985), from southwestern China, *Primatrigonia zlambachiensis* (Haas, 1909), from Austria, Iran, and Vietnam (Hautmann, 2001), and *Primatrigonia gaytani* (von Klipstein, 1843) from Austria. The hinge shows some variability among these species (Hautmann, 2001, p. 120–122). The genus *Trigonia* probably evolved from *Primatrigonia* by the development of a stronger ornamentation pattern.

Genus *Trigonia* Bruguière, 1789

Type species.—*Venus sulcata* Hermann, 1781, pl. 4, figs. 2–4, 9, 10 (see ICZN, 1955), late Early Jurassic (Toarcian), Gundershoffen, Alsace, France.

Diagnosis.—Shell trigonal to trigonally ovate, inequilateral, opisthogyrate. Area bipartite, with reticulate ornament, composed of radial and commarginal costellae. Prominent marginal carina; antecarinal sulcus present on the left valve. Flank with sub-commarginal costae. Escutcheon smooth or with striae.

Remarks.—The diagnosis of the genus was compiled from Crickmay (1932), Leanza (1993), and Francis (2000). If *Primatrigonia* is regarded as a different genus, then the oldest *Trigonia* representative is the species *Trigonia senex* Kobayashi and Mori, 1954, from the Hettangian of Japan. During most of the Early Jurassic, the genus occurred in the Pacific (Kobayashi and Mori, 1954; Poulton, 1976, 1979, Ishikawa et al., 1983; Pérez and Reyes, 1991; Pérez et al., 2008). By the Toarcian it reached the European Tethys (Hermann, 1781; Agassiz, 1840; Fürsich et al., 2001, Francis and Hallam, 2003).

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Trigonia? sp. 1
Figure 5.12, 5.13

Occurrence.—Arroyo La Laguna (Los Patos region), San Juan Province. Early Toarcian (*D. hoelderi* Biozone [≈ Serpentinum Biozone]) (Fig. 3).

Description.—Medium-sized, slightly opisthogyrate shell. Escutcheon poorly preserved, apparently wide. Area wide, ~1/3 of shell surface (Fig. 5.12), with mid radial stepped angulation and thin radial costellae intersected by thin commarginal costellae (Fig. 5.12, 5.13). Marginal carina poorly preserved, prominent (at least in juvenile stages). Flank with sharp sub-commarginal costae, more densely arranged as shell grows.

Materials.—Three left valves, MLP 36311, 36312a, 36313.

Measurements.—MLP 36311, composite mold: L = 25 mm, H = 24 mm; MLP 36313, composite mold: L = 28 mm, H = 23 mm; MLP 36312a, single valve: L = 55 mm, H = 45 mm, V = 18 mm.

Remarks.—Poor preservation of the material prevents a specific taxonomic assignment. *Neuquenitrigonia* Leanza and Garate-Zubillaga, 1987 was distinguished from *Trigonia* mainly due to flank ornamentation (oblique to growth lines), but Pérez et al. (2008) later included material with sub-commarginal flank costae. Unfortunately, they did not discuss the diagnosis for the genus. Yet, based on the material they included, the main difference from *Trigonia* seems to be the transverse costellae on the escutcheon that occur in *Neuquenitrigonia*. Escutcheon ornamentation is not preserved in our material; hence, an assignment to *Neuquenitrigonia* cannot be ruled out. Only two species of *Neuquenitrigonia* are known: *N. hunickeni* (Leanza and Garate-Zubillaga, 1985), from the Bajocian of Neuquén, Argentina, and middle Toarcian–early Aalenian of Atacama, Chile; and *N. plazaensis* Pérez and Reyes in Pérez et al., 2008, from the middle Toarcian of Atacama, Chile. The second one seems closer in morphology to the material here described. However, *Trigonia*? sp. 1 is larger, has a wider area, and is somewhat more elongate. *Trigonia* sp. 1 in Pérez et al. (2008), from the middle Toarcian of Atacama (Chile), is also similar in morphology, although it is smaller and with middle flank costae more densely arranged; the area ornamentation pattern, on the other hand, is strikingly similar in both taxa. The Toarcian unfigured material from northern Chile referred to *Trigonia* aff. *T. bella* Lycett, 1877 (Möricke, 1894, p. 48; see also Pérez and Reyes, 1977, p. 11) may be related to this record, according to that broad description. *Trigonia* sp. B of Ishikawa et al. (1983), from the Lower Jurassic of south central Perú, is a rather fragmentary specimen, but the observable characters agree with those of *Trigonia*? sp. 1.

Most Middle Jurassic *Trigonia* species from the Neuquén Basin can be distinguished easily from *Trigonia*? sp. 1. *Trigonia stelzneri* Gottsche, 1878, has a narrower area, a more clearly opisthogyrate shell, and is relatively shorter. *Trigonia corderoi* Lambert, 1944, is larger, much more opisthogyrate, and with stronger and blunter flank costae. *Trigonia mollensis* Lambert, 1944, is more similar to *Trigonia*? sp. 1 in general shell shape, but the flank costae show some undulations that are absent in the Toarcian material. *Trigonia losadai* Leanza, 1993 has stronger and more sparsely arranged flank costae.

Trigonia senex from the Hettangian of Japan (Kobayashi and Mori, 1954) bears a large area and an ornamentation pattern similar to that in *Trigonia*? sp. 1. According to its original description, the Japanese species is particular in having an insignificant marginal carina; unfortunately, the marginal carina is not preserved in any of our specimens. *Trigonia* sp. described by Poulton (1976), based on probably Pliensbachian material from south-western British Columbia (Canada), is similar in general shell shape (though slightly smaller); the most noticeable differences are a closer spacing of flank costae and a coarser commarginal ornamentation on the area in the North American taxon. The type species, *Trigonia sulcata* (Hermann, 1781), and its probable synonym, *Trigonia similis* Agassiz, 1840 (see also Bayle 1878, pl. 119, figs. 3–5, as *Lyriodon simile*; Cox et al., 1969, fig. D66.1), both from the late Early Jurassic of Alsace, are similar in general ornamentation pattern, but they differ from *Trigonia*? sp. 1 by their more opisthogyrate shell shape.

Trigonia? sp. 2
Figure 5.9–5.11

Occurrence.—Arroyo La Laguna (San Juan Province), early Toarcian (*D. hoelderi* ? Biozone [≈ Serpentinum Biozone]) (Fig. 3).

Description.—Large, clearly opisthogyrate shell. Escutcheon wide, poorly preserved. Area narrow, ~1/4 of shell surface (Fig. 5.11), and almost at right angles to the flank; with thin radial costellae intersected by thin commarginal costellae. Mid radial stepped angulation on the area. Marginal carina poorly preserved, seemingly prominent. Antecarinal sulcus narrow. Semicircular flank margin, though in one of the shells the ventral margin is clearly longer than the anterior one. Flank with sub-commarginal sharp costae, less closely spaced as shell grows (8–9 costae/cm on umbonal region, 3–5 costae/cm in middle flank), in late growth stages dense again (6 costae/cm).

Materials.—Two shells, CPBA 17430, 17478.

Measurements.—CPBA 17430; L = 65 mm, H = 44 mm, W = 36 mm.

Remarks.—Although similar to *Trigonia*? sp. 1, *Trigonia*? sp. 2 shows some differences that suggest a different species. In *Trigonia*? sp. 2, the shell is larger and more opisthogyrate; besides, the area is narrower, and area and flank surfaces are almost perpendicular. Both taxa share a pattern of flank costae growing closer at later growth stages; anyhow, this is an age-related character.

As in *Trigonia*? sp. 1, the assignment to *Neuquenitrigonia* cannot be ruled out. *Trigonia*? sp. 2 is similar to *Neuquenitrigonia plazaensis*, but larger and more opisthogyrate. *Trigonia* sp. 1 in Pérez et al. (2008), from the middle Toarcian of Atacama (Chile), is smaller and less opisthogyrate.

Trigonia stelzneri Gottsche, 1878, from the Bajocian of Paso del Espinacito (San Juan Province), seems close to *Trigonia*? sp. 2, though it has a subtriangular flank; it is also relatively shorter. Besides, flank costae in *T. stelzneri* tend to bend ventrally at their anteriormost portion. *Trigonia corderoi* Lambert, 1944, also has a subtriangular flank with stronger and blunter costae. *Trigonia mollesensis* Lambert, 1944, bears flank costae with some undulations absent in the Toarcian material. The two species described by Lambert also have a relatively narrower area with stronger radial costellae. *Trigonia losadai* Leanza, 1993, has stronger and more sparsely spaced flank costae.

This taxon seems close to *Trigonia sulcata*, although it appears to have a narrower area and, if the illustrations of the European species (Hermann, 1781, pl. 4, figs. 2–4, 9, 10) are to be trusted, *Trigonia*? sp. 2 differs also by its area orthogonal to the flank. The specimen from Normandy illustrated by Hermann (1781, pl. 4, figs. 13, 14) as intermediate between *T. sulcata* and *T. dubia* (Hermann, 1781) is quite similar to *Trigonia*? sp. 2.

Family Prosogyrotrigoniidae Kobayashi, 1954

Remarks.—Kobayashi (1954) characterized the Prosogyrotrigoniidae as lacking a prominent marginal carina and having smooth shell or ornamented by commarginal costae. Cooper (1991) also considered the prosogyrate umbo and rounded posterior margin as characteristic of the family, and he assumed an origin from the Trigoniidae. Nevertheless, other authors (e.g., Kobayashi and Tamura, 1968, p. 129–130, table 7) considered the possibility of an independent origin from myophorid genera.

Genus *Prosogyrotrigonia* Krumbeck, 1924

Type species.—*Prosogyrotrigonia timorensis* Krumbeck, 1924, p. 245, by monotypy. Late Triassic, Timor.

Diagnosis.—Subovate shell with prosogyrate beaks, trigonian-grade hinge, commarginal ornamentation throughout the shell surface, and with marginal bend, usually associated with a change in costae density between the flank and the area.

Remarks.—The diagnosis is modified from Cox (1952) and Cox et al. (1969). The type species, *Prosogyrotrigonia timorensis*, was recorded from the Late Triassic of Timor (late Norian, according to Hasibuan, 2010); it shows the typical prosogyrate shell shape, commarginal ornamentation, and marginal bend of other species (Kobayashi and Mori, 1954). *Prosogyrotrigonia iranica* Fallahi et al., 1983, from the Norian–Rhaetian of Iran and Late Triassic of Yunnan in China (Hautmann, 2001, fig. 11), has a subtriangular shell shape, thin and dense commarginal costae, and a rounded marginal bend.

Early Jurassic species included in *Prosogyrotrigonia* show few differences from Triassic representatives. In this sense, *Prosogyrotrigonia* can be considered a conservative lineage during the Triassic/Jurassic transition. Early Jurassic records include the species *P. tenuis* Pérez and Reyes in Pérez et al., 2008, from southern South America, and *P. inouyei* (Yehara, 1921), from the Hettangian or early Sinemurian of Japan (Kobayashi and Mori, 1954). Frebold and Poulton (1977) and Poulton (1991, p. 45, 48) also reported *P.*? cf. *P. inouyei* from the early Hettangian of Yukon, in northern Canada. From the early Sinemurian of Sonora, Mexico, Scholz et al. (2008, p. 292–293, figs. 10.L, 10.M) illustrated *Prosogyrotrigonia* sp. A, comparable to both species mentioned above. Pérez et al. (2008) also mentioned three other undetermined species of *Prosogyrotrigonia*, mostly from the Sinemurian of Chile, two of which have the commarginal costae broken into irregular tubercles. Considering this appearance of tubercles in the genus, the unusual Hettangian *Quadratojaworskiella acarinata* Pérez and Reyes in Pérez et al., 2008, p. 78, from Chile, is here referred to *Prosogyrotrigonia* (see Remarks under *Quadratojaworskiella*).

Prosogyrotrigonia tenuis Pérez and Reyes in Pérez et al., 2008
Figure 5.14–5.17

	1997	*Prosogyrotrigonia* sp.; Pérez and Reyes, p. 574.
*v	2008	*Prosogyrotrigonia tenuis* Pérez and Reyes in Pérez et al., p. 64, pl. 3, figs. 1–3, 5–7, 11, 12, pl. 4, figs. 1–12, 14, 15, pl. 5, figs. 2, 5.
v	2015	*Prosogyrotrigonia tenuis*; Damborenea and Echevarría, appendix 2.
v	2017	*Prosogyrotrigonia tenuis*; Damborenea et al., p. 101, fig. 4, table 2.

Type material.—Holotype: SNGM 486 (Pérez et al., 2008, pl. 4, figs. 11, 12), right valve with ventral margin incomplete; hinge partly visible. From Cerros de Cuevitas, northern Chile.

Occurrence.—Arroyo Malo section (Atuel River region), Mendoza Province. Early Sinemurian (*Coroniceras-Arnioceras* Biozone [≈ Bucklandi-Semicostatum Biozone]) (Fig. 3). The species was first described from Chile, where it occurs in the late Hettangian west of Quillagua and late Hettangian and earliest Sinemurian of Cerros de Cuevitas, Antofagasta (Pérez et al., 2008).

Description.—Poorly preserved material. Small, weakly inflated, orthogyrate to slightly prosogyrate shell (Fig. 5.14). Escutcheon margin straight to slightly convex, at an obtuse angle with the anterior margin (~117–118°). Anterior margin strongly convex, gradually merging with the convex ventral margin. Postero-ventral angle rounded; posterior margin straight to slightly convex. Rounded marginal bend separating flank from area (Fig. 5.15, 5.16). Area occupying 1/4–1/3 of shell surface (Fig. 5.14).

Shell ornamented with commarginal costae, continuous through flank and area (escutcheon not preserved). Intercostal spaces similar in width to costae, sometimes slightly wider; ~6–7 costae/cm at mid-flank. Costae sometimes thinner on the area than on the flank (Fig. 5.15). Area occasionally with bifurcated or extra costellae (Fig. 5.15, 5.16). Costae end abruptly at the escutcheon edge. Costae thinner, more densely packed, and somewhat irregular at late growth stages (Fig. 5.15, 5.16).

Crenulated tooth 3a poorly preserved in one internal mold (Fig. 5.14). Adductor muscle scars very slightly impressed; continuous pallial line (Fig. 5.17).

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Materials.—Five fragmentary and sometimes strongly corroded shells, one composite mold, one internal mold, and one external mold: MLP 32711, 32786, 32789, 32802, 32803, 32805, 32815, and 32828.

Measurements.—MLP 32786: L = 38 mm, H = 31 mm; MLP 32789: L = 39 mm, H = 31 mm; MLP 32805: L = 34 mm, H = 27 mm.

Remarks.—The characters observed on the studied specimens show no significant differences from the material described by Pérez et al. (2008) from Chile. The shell seems to be less rectangular in some Argentinian specimens, with the anterior margin slightly more protruding (Fig. 5.14) and narrower area, but such differences are here regarded as intraspecific. Although Pérez et al. (2008) described thin flank costae separated by much wider intercostal spaces, some of their figured specimens (e.g., pl. 4, figs. 9, 15, pl. 5, fig. 2) show costae as wide as the intercostal spaces. Within the bounds of intraspecific variability accepted by Pérez et al. (2008), the material from west of Quillagua (late Hettangian) is remarkable: shells are orthogyrate to slightly prosogyrate, with a relatively large area (1/3–2/5 of shell surface) and flank costae are densely spaced (8 or more costae/cm). In these shells, area costae are thinner than those from the flank, they are more frequently dichotomous, and the flank costae tend to swell over the marginal bend (Pérez et al., 2008, pl. 4, fig. 3). All these characters closely resemble the genus *Frenguelliella*, hinting to a possible phylogenetic relationship between both genera, as suggested by Poulton (1979, p. 18; see also Remarks under *Frenguelliella*).

Prosogyrotrigonia tenuis has been recorded from the late Hettangian–early Sinemurian of southern South America (Pérez et al., 2008; this paper). The contemporary species, *Prosogyrotrigonia* sp. A, is smaller than *P. tenuis* and more variable in elongation/shell shape (Scholz et al., 2008, figs. 10L, 10M), with costae thinner and more densely packed. Shells of *P.*? cf. *P. inouyei* in Frebold and Poulton (1977, pl. 2, figs. 5–9) are somewhat larger and coarser, with a somewhat narrower area. The only known specimen of *Prosogyrotrigonia* sp. 1 of Pérez and Reyes in Pérez et al., 2008, is very similar to *P. tenuis*, and was found in the same locality where the Hettangian record of that species appeared; the main difference between both taxa is the breaking up of commarginal costae into irregular tubercles in *P.* sp. 1.

Superfamily Myophorelloidea Kobayashi, 1954

Remarks.—Cooper (1991) described the superfamily Myophorelloidea as having posteriorly produced shells with nodate marginal and escutcheon carinae. He characterized the area as broad, with transverse ornamentation and a longitudinal groove. According to his description, flank costae are subcommarginal and entire in primitive forms, but strongly oblique and nodate in more derived forms. The species we describe here share as a distinctive character an area with transverse costellae and a radial median groove (replaced by a row of pustules in certain derived forms, such as *Poultoniella* new genus).

Family Frenguelliellidae Nakano, 1960

Remarks.—Frenguelliellinae has been regarded as a subfamily of the Laevitrigoniidae (Bieler et al., 2010; Carter et al., 2011). The subfamily Laevitrigoniinae includes mainly genera characterized by weak sculpture, being most likely a polyphyletic group (see Fleming, 1987, p. 37–38 for a discussion on the Laevitrigoniinae). For the time being, we prefer to maintain Frenguelliellidae and Laevitrigoniidae as two different families. The Frenguelliellidae are characterized by shells ornamented with subcommarginal costae (occasionally nodate and oblique), interrupted or attenuated at the antecarinal space (Cooper, 1991).

Genus *Frenguelliella* Leanza, 1942

Type species.—*Trigonia inexspectata* Jaworski, 1915, p. 377–380. Pliensbachian, Piedra Pintada (Neuquén, Argentina).

Diagnosis.—Shell orthogyrate to clearly opisthogyrate. Well-defined sharp angulations bordering the area, slightly protruding marginal carina in early growth stages. Area with fine commarginal costellae, usually densely spaced. Flank with sub-commarginal costae reaching anterior margin, usually stronger but fewer than in the area. Antecarinal space smooth or delicately ornamented. Escutcheon smooth or with commarginal costellae crossing from the area (though in fewer numbers).

Remarks.—Leanza (1942, p. 164–166) proposed *Frenguelliella* as a subgenus of *Trigonia*, and this status was maintained by Cox (1952, p. 54) and Cox in Cox et al. (1969, p. N478). Tamura (1959) regarded it as a different genus, and this was followed by most subsequent authors. The original diagnosis by Jaworski (1915, 1925) for *Trigonia inexspectata* and by Leanza (1942) for the genus is here amended to encompass the observed range of morphological variability displayed in this genus. *Frenguelliella* was considered a survivor from the Triassic by Tamura (1959), who described the subgenus *Frenguelliella* (*Kumatrigonia*) Tamura, 1959, based on *F.* (*K.*) *tanourensis* Tamura, 1959, from the Upper Triassic of Japan. He distinguished it from *Frenguelliella* s.s. by the continuity of flank and area costae in the former. Later, Kobayashi and Tamura (1968, p. 107) found shells with more numerous costae on the area than on the flank, and hence considered *Frenguelliella* and *Kumatrigonia* as synonyms. Nevertheless, there are some differences between *Frenguelliella* (*Kumatrigonia*) *tanourensis* and the Early Jurassic representatives of *Frenguelliella*. In *Kumatrigonia*, there is a prominent marginal carina and an antecarinal sulcus (both as folds of the shell surface, Tamura 1959, pl. 2, figs. 1, 4, discernible even on the internal mold, Tamura 1959, pl. 2, fig. 3). Conversely, Early Jurassic *Frenguelliella* species bear a prominent carina in the earliest juvenile stages, which is replaced by a sharp marginal angulation and a flat antecarinal space in late juvenile and adult stages. Also, the area in the Triassic species is strongly concave, while in the Jurassic species it is flat. Furthermore, according to Poulton (1979), there is a transition in the Early Jurassic from *Prosogyrotrigonia* to *Frenguelliella* species in North America, expressed as a progressive differentiation of area, flank, marginal angulations,

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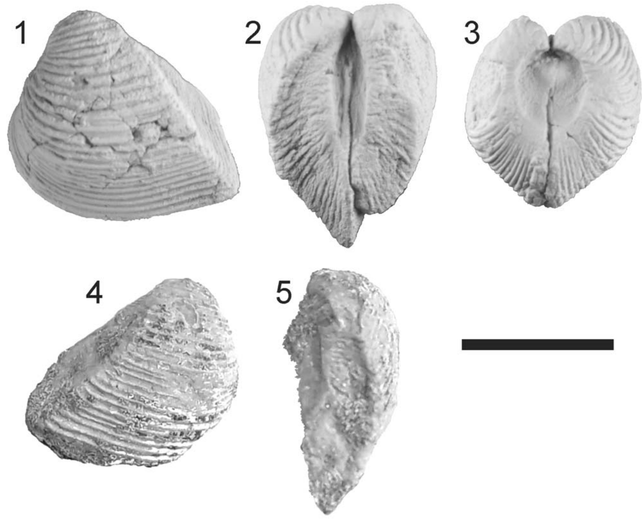

Figure 6. *Trigonastarte perezreyesi* (Leanza) n. comb., early Bajocian, Barda Negra Sur. Scale bar = 10 mm. (**1–3**) MLP 36314, complete specimen left lateral, dorsal, and anterior views; (**4, 5**) paratype, MOZ-PI 3030/2, incomplete right valve right lateral and dorsal views (photographs courtesy of B. Boilini).

and antecarinal space in *Frenguelliella*, as well as the development of finer commarginal ornament on the area. According to this view, the distinction of *Frenguelliella* from the probably ancestral *Prosogyrotrigonia* is arbitrary and mainly based on the prosogyrate umbos, the simple ovate outline, and the absence of marginal carina or angulation in the types species of *Prosogyrotrigonia* (Poulton, 1979, p. 18).

On the other hand, the species included in *Frenguelliella* have an internal radial ridge on the posterior part of the inner surface of the shell. This ridge is not present in *Prosogyrotrigonia tenuis*, but it seems to occur in *Kumatrigonia nemtinovi* (Bychkov, 1985, p. 14–15, pl. 4, fig. 8). Given this uncertainty, *Kumatrigonia* is regarded here as a different genus, containing only Triassic species (*K. tanourensis* [Tamura, 1959], *K. nemtinovi* Bychkov, 1985, and probably *Frenguelliella*? sp. of Newton et al., 1987), and *Frenguelliella* is considered to have appeared during the Early Jurassic.

Frenguelliella seems to have been restricted to the Pacific coast of the Americas during the Early Jurassic (Feruglio, 1934; Leanza, 1942; Lambert, 1944; Poulton, 1979; Ishikawa et al., 1983; Leanza, 1993; Pérez et al., 2008). The earliest representatives appeared during the Sinemurian and were widely distributed. According to Leanza (1993, 1996), the genus extended to the early Bajocian in the Andes, but records younger than Toarcian proved to be doubtful. The species *Frenguelliella perezreyesi* Leanza (1993, p. 27, pl. 2, figs. 1, 2, 7, 8) was described based on two incomplete specimens from early Bajocian beds at Barda Negra Sur, Neuquén. The morphology of the paratype (Fig. 6.4, 6.5; MOZ-PI 3030/2) and of well-preserved topotypic material personally collected at that locality (Fig. 6.1–6.3; MLP 36314) reveals that this species has prosogyrate umbos, a large smooth lunule, and crenulated margin. This is clearly not a trigoniid, and instead is here referred to the crassatelloidean genus *Trigonastarte* Bigot, 1895.

Frenguelliella eopacifica new species
Figure 7

- 1934 *Trigonia* aff. *T. costatula*; Lees, p. 42, pl. 4, fig. 6.
- 1964 *Trigonia* aff. *T. costatula*; Frebold, p. 14, pl. 5, fig. 6.
- 1979 *Frenguelliella* sp. B; Poulton, p. 18, pl. 1, fig. 10.
- v 2007 *Frenguelliella* cf. *F. poultoni*; Damborenea and Lanés, p. 78, table 3.B, 3.C.
- v 2008 *Frenguelliella poultoni*; Pérez and Reyes in Pérez et al., p. 72, pl. 5, figs. 6–8.
- p ?2008 *Frenguelliella poultoni*; Scholz et al., p. 291, fig.10I, 10J.
- v 2015 *Frenguelliella poultoni*; Damborenea and Echevarría, appendix 2.
- v 2017 *Frenguelliella* cf. *F. poultoni*; Damborenea et al., p. 101, fig. 4, table 2.

Type materials.—Holotype: SNGM 541 from Quebrada Pan de Azúcar, 10 km SW of Las Bombas, Atacama Region, Chile; Sinemurian (probably Obtusum Biozone, Pérez et al., 2008), figured here in Figure 7.5. Paratypes SNGM 561 from Quebrada Pan de Azúcar, 10 km SW of Las Bombas, Atacama Region, Chile, Sinemurian (Fig. 7.1), and MLP 32837 from Las Chilcas, Atuel River region, Mendoza Province, late Sinemurian (Fig. 7.7).

Diagnosis.—Small, subtriangular to subrectangular, orthogyrate to slightly opisthogyrate shell. Escutcheon smooth; escutcheon angulation stepped. Area with commarginal costellae; shallow radial groove interrupting them. Prominent marginal carina in early growth stages; sharp angulation in later growth stages. Antecarinal space flat, widening posteriorly. Flank with densely spaced sub-commarginal costae.

Occurrence.—Las Chilcas, Arroyo El Pedrero and Codo del Blanco (Atuel River region), Mendoza Province. Sinemurian (≈ Bucklandi–Raricostatum biozones): one specimen (Fig. 7.8) from *Coroniceras-Arnioceras* Biozone?; all other specimens from *Orthechioceras-Paltechioceras* Biozone (Fig. 3). The species is also recorded from the early Sinemurian of Yukon, Canada (Poulton, 1979), early Sinemurian of Sierra del Álamo, Mexico (Scholz et al., 2008, figs. 10.I, 10.J), and late Sinemurian of Atacama, Chile (Pérez et al., 2008).

Description.—Very small to small, subtriangular (Fig. 7.4) to subrectangular (Fig. 7.3); orthogyrate to slightly opisthogyrate shell. Escutcheon angulation stepped; escutcheon rarely preserved, smooth (Fig. 7.6). Area, ~1/3–1/4 of general shell surface, with fine commarginal costellae, densely spaced (14–19 costae/cm), separated into two sets by a shallow radial groove; costellae dorsal and ventral to the groove may alternate (Fig. 7.4). Prominent marginal carina at early growth stages (Fig. 7.8); a sharp angulation at late growth stages, though highlighted by tubercles corresponding to the costellae on the area (Fig. 7.4, 7.5). Antecarinal space flat, widening posteriorly; somewhat depressed in some shells (Fig. 7.7), most likely a preservational artifact. Antecarinal space barely invaded by area ornamentation (Fig. 7.4), some costellae

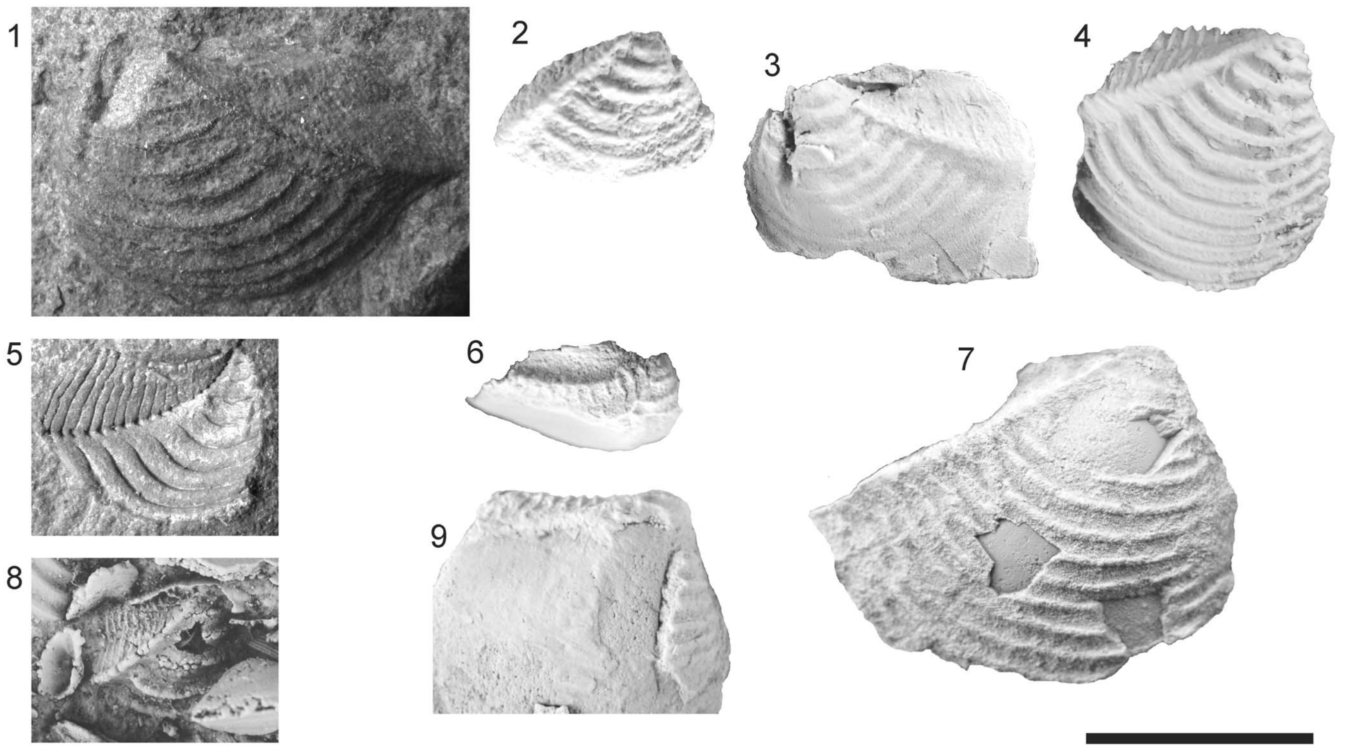

Figure 7. *Frenguelliella eopacifica* n. sp., Sinemurian of Argentina and Chile. Scale bar = 10 mm. (**1**) Paratype, SNGM 561, composite mold of left valve, Sinemurian, Quebrada Pan de Azúcar, Chile; (**2**) MLP 32864a, right valve, late Sinemurian, Las Chilcas; (**3**) MLP 32875, composite mold of left valve, late Sinemurian, Las Chilcas; (**4**) MLP 32848, rubber cast of right valve, late Sinemurian, Las Chilcas; (**5**) holotype, SNGM 541, external mold of left valve, Sinemurian, Quebrada Pan de Azúcar, near Las Bombas, Atacama, Chile; (**6, 9**) MLP 32864c, fragmented right valve and internal mold, dorsal and right lateral views, late Sinemurian, Las Chilcas; (**7**) paratype, MLP 32837, right valve, late Sinemurian, Las Chilcas; (**8**) MLP 32823, rubber cast of right valve, early Sinemurian, Arroyo El Pedrero.

continuous with the costae of the flank. Flank with densely spaced subcommarginal costae (8–10 or more costae/cm). Flank costae departing from the antecarinal sulcus at right to slightly acute angles (Fig. 7.2).

Etymology.—The Greek prefix *eo-* (from *eos* = dawn), implying both the eastern horizon and earliness, and *-pacifica* for the Paleopacific Ocean: "early *Frenguelliella* from the Eastern Pacific."

Materials.—MLP 18387a, 18389, 32823, 32834, 32843, 32848, 32850, 32851, 32860, 32864, 32875, 32881, 32891: 10 right valves, 7 left valves, and one specimen with both valves, preserved as composite, external, or internal molds, one specimen (Fig. 7.6, 7.9) with shell fragments preserved.

Measurements.—Holotype (SNGM 541): L = 11 mm, H = 8 mm. Paratypes: SNGM 561: L = 17 mm, H = 12 mm, and MLP 32837: L = 19 mm, H = 15 mm. MLP 18387a: L = 20 mm, H = 14 mm; MLP 32851: L = 23 mm, H = 17 mm; MLP 32875: L = 13 mm, H = 9 mm; MLP 32881: L = 19 mm, H = 15 mm.

Remarks.—*Frenguelliella eopacifica* n. sp. differs from other *Frenguelliella* species by its: (1) small size, (2) smooth escutcheon, (3) relatively large area, and (4) orthogyrate to slightly opisthogyrate shell shape. Material assigned to this new species was often referred to as *F. poultoni* or *F.* cf. *F. poultoni* in the literature. *Frenguelliella poultoni* Leanza, 1993, is regarded here as a junior synonym of *Frenguelliella chubutensis* (Feruglio, 1934) (see Remarks under *F. chubutensis*). The main differences here recognized between *F. eopacifica* n. sp. and *F. chubutensis* are the lack of ornamentation on the escutcheon in *F. eopacifica* n. sp. together with its smaller size. The species is rather homogeneous with regard to these characters throughout the eastern margin of the Paleopacific, from NW Canada to Neuquén. *Frenguelliella eopacifica* n. sp. differs from *F. inexspectata* by its much smaller size and proportionally larger area; also, the type species is strongly opisthogyrate.

Although *F. eopacifica* n. sp. clearly occurs in Argentina, it is more abundant and better preserved in Chile (Pérez et al., 2008). Specimens from Chile show a smooth escutcheon (Fig. 7.5), a wide area (∼1/3 of general shell surface, Fig. 7.1, 7.5), with a shallow radial groove dorsally displaced. Their marginal carina is slightly protruding at the beginning, developing in later growth stages as a sharp angulation, sometimes highlighted by small tubercles arising from the swelling of each area costella (Fig. 7.5). Area costellae and flank costae are closely spaced (16–24 costellae/cm and 9–12 costae/cm, respectively). Area costellae are usually interrupted by the radial groove, and the ventral and dorsal portions of the costellae may alternate (Fig. 7.5). Shell elongation is variable within the species; interestingly, in longer shells the anterior angle between flank costae and antecarinal space tends to be acute, while in short ones it is almost 90°.

Frenguelliella sp. B described by Poulton (1979) from the early Sinemurian of Yukon (NW Canada) shows no significant differences with the South American specimens. Material referred to *Frenguelliella poultoni* was also recorded from lower Sinemurian to lower Pliensbachian beds in Sonora (NW Mexico) by Scholz et al. (2008). Their figured specimens (Scholz et al., 2008, fig. 10.I, 10.J, from lower Sinemurian of Sierra del Álamo) agree in shape and size with the material here described. Nevertheless, they considered their specimens as "apparently identical" (Scholz et al., 2008, p. 291) to *Trigonia* cf. *T. inexspectata* Jaworski, 1929, which shows significant differences with the material they illustrated (see Remarks under *Poultoniella* new genus). Since they also included some larger shells up to 45 mm long (Scholz et al., 2008, fig. 11), an unusual size for *F. eopacifica* n. sp., we only refer the two specimens figured by Scholz et al. (2008, fig. 10.I, 10.J) to *F. eopacifica* n. sp. The assignment of the remaining specimens will depend on further study.

Frenguelliella chubutensis (Feruglio, 1934)
Figure 8

p 1915 *Trigonia inexspectata* Jaworski, p. 377 (part; not pl. 5, fig. 2).
p 1925 *Trigonia inexpectata* [sic]; Jaworski, p. 79 (part; not pl. 1, fig. 2).
1926a *Trigonia inexspectata* var. *densecostata* Jaworski, p. 396 (not *Trigonia densicostata* Röder, 1882; nec *Trigonia densicostata* Marshall, 1919).
1926b *Trigonia inexspectata* var. *densecostata*; Jaworski, p. 180.
1931 *Trigonia inexspectata* var. *densecostata*; Weaver, p. 233.
*v 1934 *Trigonia chubutensis* Feruglio, p. 34, pl. 4, figs. 9, 11.
1934 *Trigonia* sp.; Feruglio, p. 36, pl. 4, figs. 10a, b.
1944 *Trigonia tapiai* Lambert, p. 358, pl. 13, fig. 1.
1977 *Trigonia* (*Frenguelliella*) *tapiai*; Pérez and Reyes, p. 12, pl. 1, fig. 2. [reproduced from Lambert, 1944]
1978b *Trigonia* (*Frenguelliella*) sp.; Volkheimer et al., p. 212 (table 2).
v 1980 *Frenguelliella tapiai*; Hillebrandt, pl. 2, figs. 8a, b.
v 1982 *Frenguelliella tapiai*; Cuerda et al., p. 331.
v 1987 *Frenguelliella tapiai*; Leanza and Garate-Zubillaga, p. 210, pl. 1, fig. 5.
v 1990 *Frenguelliella tapiai*; Leanza and Blasco, p. 163.
v 1992 *Frenguelliella chubutensis*; Damborenea et al., pl. 116, fig. 17.
v 1992 *Frenguelliella tapiai*; Damborenea et al., pl. 116, fig. 18.
1993 *Frenguelliella tapiai*; Leanza, p. 26, pl. 1, fig. 8.
v 1993 *Frenguelliella poultoni* Leanza, p. 26, pl. 2, figs. 3–6.
1997 *Frenguelliella tapiai*; Pérez and Reyes, p. 574.
v 2008 *Frenguelliella tapiai*; Pérez and Reyes in Pérez et al., p. 70, pl. 5, figs. 1, 3, 4, 9–13.
v 2011 *Frenguelliella tapiai*; Riccardi et al., fig. 7.14.
v 2012 *Frenguelliella* sp.; Pagani et al., p. 413, fig. 3c.

Type materials.—Lectotype: MLP 3729. Riccardi and Martín (1987, p. 61) listed this specimen as "Holotipo"; yet, since Feruglio (1934, p. 34, pl. 4, figs. 9, 11) had established the taxon based on two specimens, their action may be regarded as fixation of lectotype by inference of holotype (ICZN, 1999, Art. 74.6.1.2). The specimen is a composite mold of a right valve, collected by Piatnizky in the Genoa River region (Chubut Province), "lote 20" (most likely the locality now known as Aguada Loca). This is undoubtedly one of Feruglio's syntypes, illustrated by Feruglio (1934, pl. 4, fig. 11), by Damborenea et al. (1992, pl. 116, fig. 17), and here (Fig. 8.2). The whereabouts of Feruglio's second specimen (paralectotype) is unknown.

Holotype of *Trigonia inexspectata* var. *densecostata* Jaworski.—An external mold of a right valve at the Institute of Geosciences, Paleontology Section, Bonn (Germany), IGPB-Jaworski-74, from Cerro Puchenque, Mendoza Province (Figure 8.1).

Type of *Trigonia tapiai* Lambert.—DNGM 43-109, from a bend of arroyo Pichi Picún Leufú, east of Cerro Chachil, Neuquén Province, figured by Lambert (1944, pl. 13, fig. 1).

Holotype of *Frenguelliella poultoni* Leanza.—MOZ-PI 5315, from Ñireco, east of Cerro Chachil, Neuquén, figured by Leanza (1993, pl. 2, fig. 3) and here (Fig. 8.3).

Diagnosis.—Ovate-subquadrangular to ovate-subrectangular shell, slightly opisthogyrate to orthogyrate. Escutcheon with commarginal costellae crossing from the area. Area wide, with costellae densely arranged, with a submedian radial groove dorsally displaced and sometimes interrupting the costellae. Flank with densely but evenly spaced fine and sharp sub-commarginal costae (up to 20–25 in adult shells), fewer than area costellae (usually about half). Escutcheon angulation stepped; prominent marginal carina at early growth stages, sharp angulation at later ones.

Occurrence.—Arroyo La Laguna (Los Patos region) San Juan Province; La Horqueta, Codo del Blanco, Las Chilcas, Quebrada Los Caballos, Puesto Araya, Cerro La Brea (Atuel River region), Arroyo Peuquenes, Arroyo Portezuelo Ancho (Las Leñas/Valle Hermoso region), Arroyo Serrucho, Cerro Puchenque (west of Malargüe region), Mendoza Province; Estación Rajapalo (Cordillera del Viento region), Ñireco, Rahue-Aluminé (Cuerda et al., 1982), Lonqueo (Central Neuquén region), Estancia Santa Isabel (Piedra Pintada region), Neuquén Province; Puesto Peña (central Chubut region), Lomas de Betancourt, Aguada Loca, Nueva Lubecka (Genoa River region), Chubut Province. Early Pliensbachian to late Pliensbachian (*M. chilcaense*–*F. disciforme* biozones [≈ Jamesoni–Spinatum biozones]) (Fig. 3), early Toarcian? (Tenuicostatum Biozone).

Description.—Small to medium-sized, subquadrangular (Fig. 8.18, 8.19) to subrectangular (Fig. 8.2, 8.15, 8.20) shell. Slightly opisthogyrate to orthogyrate, with umbo anteriorly located. Escutcheon margin slightly convex (Fig. 8.7, 8.19). Area margin long, gently convex or almost straight (Fig. 8.14, 8.19), ventral portion sometimes projected posteriorly (Fig. 8.10, 8.12). Area margin generating right to slightly obtuse angles with escutcheon and ventral margins (Fig. 8.1,

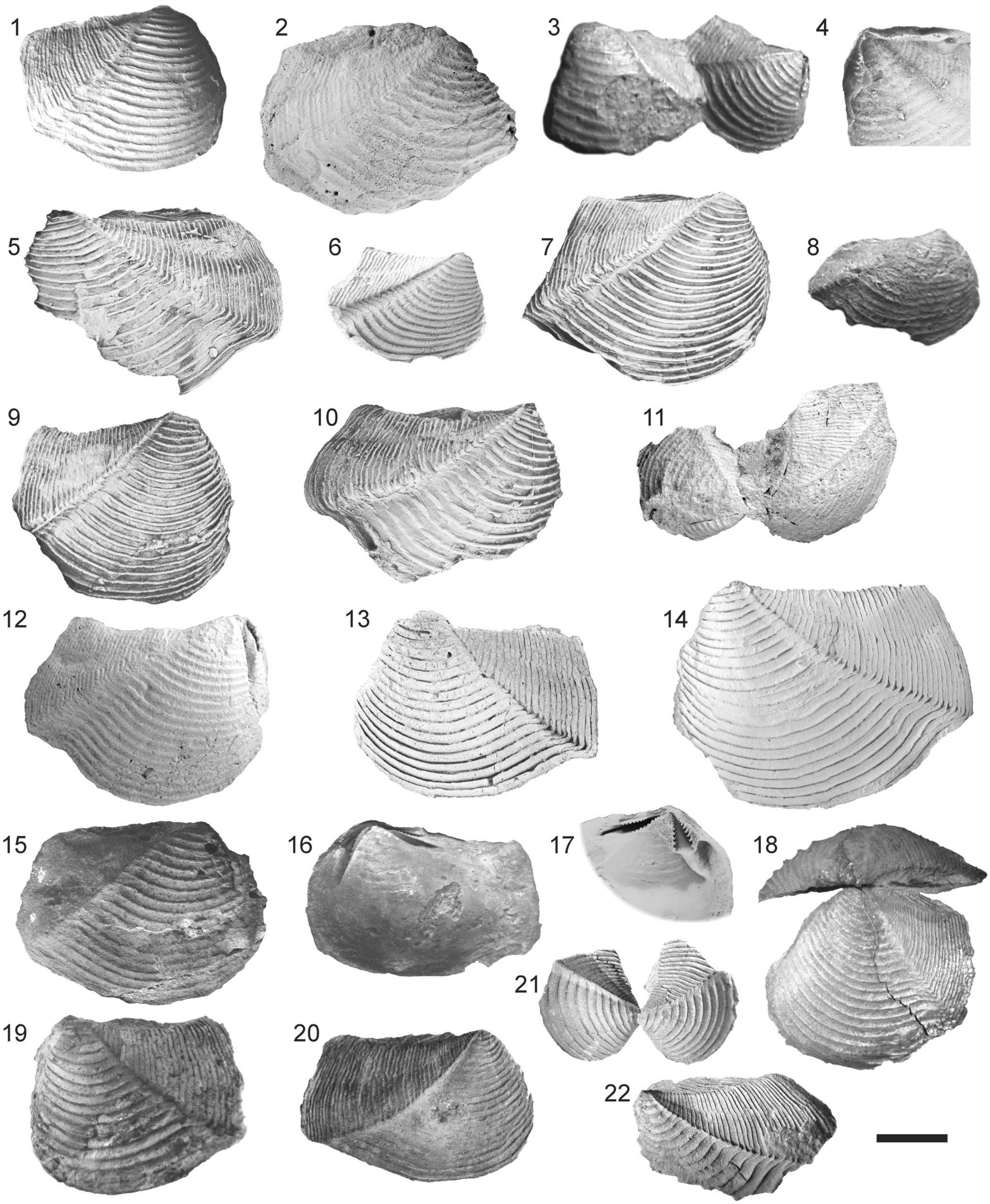

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Figure 8. *Frenguelliella chubutensis* (Feruglio), Pliensbachian to early Toarcian of Argentina. Scale bar = 10 mm. (**1**) Cast of IGPB-Jaworski-74 (photograph courtesy of G. Heumann), holotype for *Trigonia inexspectata* var. *densecostata* Jaworski, an external mold of right valve, Pliensbachian, Cerro Puchenque; (**2**) MLP 3729, lectotype for *Trigonia chubutensis* Feruglio, composite mold of right valve, Pliensbachian, Genoa River region; (**3**) MOZ-PI 5315, holotype for *Frenguelliella poultoni* Leanza, composite mold of right valve (in association with a left valve), Pliensbachian, Ñireco; (**4**) rubber cast of MLP 36165, composite mold of right valve with a detail of the hinge, Pliensbachian, Arroyo Serrucho; (**5**) rubber cast of MLP 36164, external mold of left valve, Pliensbachian, Arroyo Serrucho; (**6**) MLP 33187c, external mold of left valve, Pliensbachian, Las Chilcas; (**7**) rubber cast of MLP 36161, external mold of right valve, Pliensbachian, Arroyo Serrucho; (**8**) MOZ-PI 5316, paratype for *Frenguelliella poultoni* Leanza, composite mold of right valve, Pliensbachian, Ñireco; (**9**) rubber cast of MLP 36159a, external mold of right valve, Pliensbachian, Arroyo Serrucho; (**10**) rubber cast of MLP 28671, external mold of right valve, Pliensbachian, Quebrada Los Caballos; (**11**) MLP 36179, composite mold of both valves open in butterfly position, Pliensbachian, Lonqueo; (**12**) MLP 36181, composite mold of right valve, Pliensbachian, Lonqueo; (**13**) MLP 36172, external mold of right valve, Pliensbachian, Estación Rajapalo; (**14**) MLP 24468, external mold of right valve, Pliensbachian, Ñireco; (**15**) MPEF-PI 5861, composite mold of right valve, late Pliensbachian–early Toarcian, Lomas de Betancourt; (**16, 17**, **20**) MPEF-PI 6383, left valve, late Pliensbachian–early Toarcian, Lomas de Betancourt; (**16**) internal mold; (**17**) rubber cast of the hinge of **16** (photograph courtesy of A. Pagani); (**20**) external mold; (**18**) MPEF-PI 3295, external mold of shell with valves gaping, late Pliensbachian–early Toarcian, Aguada Loca; (**19**) MPEF-PI 6379, external mold of right valve, late Pliensbachian–early Toarcian, Lomas de Betancourt; (**21**) MPEF-PI 3390, external mold of juvenile shell open in butterfly position, late Pliensbachian–early Toarcian, Aguada Loca; (**22**), MPEF-PI 3043, external mold of right valve, late Pliensbachian–early Toarcian, Aguada Loca.

8.2, 8.15, 8.19, 8.20). Ventral margin convex, at a slightly obtuse angle with anterior convex margin. Escutcheon with commarginal costellae crossing from the area (sometimes two area costellae joining into one escutcheon costella; Fig. 8.22); escutcheon margin slightly raised. Escutcheon angulation stepped. Area wide (~1/3–2/5 of general shell surface), with barely impressed radial groove; ventral part slightly wider. Area with fine commarginal costellae, very densely spaced (7–20 costellae/cm; most values 10–16 costellae/cm); sometimes interrupted by the radial groove; dorsal and ventral costellae often alternating (Fig. 8.22); ventral costellae frequently more numerous. Prominent marginal carina at initial growth stages, later as a sharp angulation. Area costellae slightly swollen over the angulations, and most conspicuously tending to bend posteriorly, rendering a pustulose appearance to the marginal angulation (Fig. 8.5, 8.7, 8.9, 8.21, 8.22), which even resembles a prominent carina (Fig. 8.7, 8.10). Antecarinal space widening posteriorly, frequently with flank costae conspicuously weakening; posterior portion usually invaded by area costellae (especially in later growth stages). Costae occasionally deviating when crossing the antecarinal space (Fig. 8.10). Antecarinal space slightly concave in early growth stages, flat in later stages, yet forming a slight angle with the flank (some molds with truly concave sulcus; Fig. 8.10, 8.12, 8.13). Flank with thin, densely spaced (5–15 costae/cm; most values 6–10 costae/cm), sub-commarginal costae (Fig. 8.7, 8.9). Costae sometimes with a rounded posterior bend (Fig. 8.6); most frequently, anterior angle between costa and antecarinal space nearly right (Fig. 8.3, 8.6, 8.12) to slightly acute (Fig. 8.2, 8.5, 8.15, 8.20).

Internal radial ridge in the posterior part of the inner surface, perpendicular to area margin (Fig. 8.12, 8.16). Trigonian-grade hinge (Fig. 8.4, 8.17); densely arranged ridges on both occluding surfaces of 2, 3a, and 3b, on the anterior face of 4b, and on the posterior face of 4a. Muscle scars typical for the group, including the umbonal pedal retractor insertion (Fig. 8.16).

Materials.—The type specimens already mentioned above, plus ~220 specimens, MLP: 15321, 15326, 15422, 15428, 15438, 21076, 24467, 24468, 25047, 27821, 27855, 27873, 27877, 27902, 27951, 28671, 28693, 28696, 28698, 28704, 28738, 28985, 28986, 31135, 33185, 33187, 33188, 33191, 33203, 33205, 33267, 36150–36193, 36212, 36310; IANIGLA-PI: 3254–3259, 3264, 3288, 3305–3317, 3319–3343A, 3345–3349, 3352–3354; MPEF-PI: 2911 (part), 2940, 2947, 2957, 3041, 3043, 3048–3051, 3061, 3064, 3293, 3295, 3390, 5787, 5796, 5861, 5875, 6178, 6376–6380, 6382, 6383, 6403–6408, 6410–6416, 6420, 6421; MOZ-PI: 5316, 5317. Specimens from Chile SNGM 501–507.

Measurements.—Lectotype (MLP 3729): L = 37 mm, H = 26 mm; largest shell (IANIGLA-PI 3346): L = 61 mm, H = 40 mm; all measurements are plotted in Figure 9.

Remarks.—*Frenguelliella chubutensis* is widely distributed in south-western South America; it seems to be more frequent in the south (Chubut Province), but it is a common component of bivalve faunas from Mendoza and Neuquén provinces as well. A few shells from Chile were also referred to the species (Pérez et al., 2008, p. 70–72, pl. 5, figs. 1, 3, 4, 9–13, as *F. tapiai*). This taxon is difficult to characterize due to the wide range of morphological variation of the shells. One of the most obvious aspects of intraspecific variability involves elongation: while some shells are subquadrangular (Fig. 8.18, 8.19, 8.21), others are more elongate (Fig. 8.2, 8.5, 8.20). This is evident in H/L ratios, ranging between 0.69–0.92. Allometry analysis of length and height showed an isometric relationship between both variables (slope for log values of height vs. length = 1.03; $p_{(slope=1)} = 0.41$; Fig. 9), so an ontogenetic variability for the character can be ruled out.

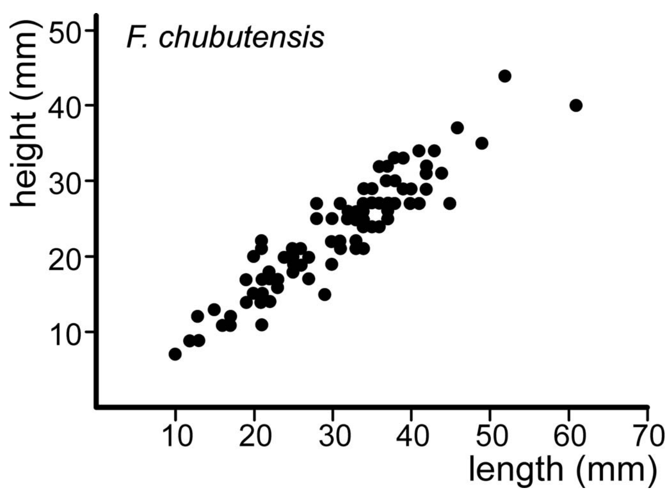

Figure 9. Scatter plot of height vs. length for *Frenguelliella chubutensis* (Feruglio).

Costae density is also highly variable. For area costellae, the minimum value is 7 costellae/cm, and the maximum is 20 costellae/cm. For the flank, the minimum value is 5 costae/cm (Fig. 8.5, 8.10) and the maximum is 15 costae/cm (Fig. 8.6, 8.8). The main variation shows no clear geographical pattern. On the other hand, much of this variability may actually be a preservational artifact, as illustrated by the material depicted in Figure 8.11: this represents the composite mold of a shell in butterfly position, but due to differential deformation the left valve looks more elongate and with flank costae more densely arranged than the right valve.

The morphology observed in Chilean specimens falls within the variation displayed by the Argentinian material; but there is a single difference: flank costae are interrupted anteriorly by a smooth surface, tapering towards the dorsal and ventral ends, and the costae reach that surface at right angles (although this last feature could be recognized in some Argentinian specimens as well). The material from the Lower Jurassic of Peru described by Ishikawa et al. (1983, p. 40–41, pl. 1, fig. 7) as *Frenguelliella* sp. agrees with main shell characters of *F. chubutensis* (escutcheon "concentric" —commarginal— costellae are mentioned), although its preservation is not good enough to assign it to Feruglio's species with certainty.

Jaworski (1926a, p. 396, 1926b, p. 180) recognized this taxon as new, and named it as a variety of his previously described species, *T. inexspectata*. He based his detailed description on one external mold of a right valve from Cerro Puchén (= Cerro Puchenque, west of Malargüe region, Mendoza Province, IGPB-Jaworski 74; Fig. 8.1). He also referred two specimens from Arroyo Blanco (Atuel River region) to this variety, which is part of the material he had previously (Jaworski, 1915) included in *T. inexspectata*. He did not figure any of the specimens, which has hindered identification of the taxon. Only Weaver (1931), who had seen Jaworski's specimen at Bonn, used the name *T. inexspectata* var. *densecostata* again to refer to specimens from Arroyo Blanco in the Atuel River region, Mendoza, but he did not figure them.

Specimens from central Patagonia (Chubut Province) were described as *Trigonia chubutensis* by Feruglio (1934). Lambert (1944), in his revision of trigonioids from Neuquén Province, described the new species *Trigonia tapiai* and distinguished it from *T. chubutensis* by the higher density of flank costae and lower density of area costellae in the former. Later, Leanza (1993, p. 2) described the species *F. poultoni*, based on small shells from central Neuquén, diagnosing it as "finely sculptured and more nearly rectangular in outline than any other known species of *Frenguelliella*." He also mentioned, among other characters, the presence of no more than 18 very regular, equally spaced, sub-commarginal costae.

The comprehensive analysis performed here shows that there is a continuous variability of these characters in *F. chubutensis* (with collections including material from the type localities of all the nominal species involved). Therefore, *F. densecostata* (Jaworski), *F. chubutensis* (Feruglio), *F. tapiai* (Lambert), and *F. poultoni* Leanza are here regarded as subjective synonyms. *Trigonia densecostata* Jaworski is a primary junior homonym of *Trigonia densicostata* Röder, 1882 and *Trigonia densicostata* Marshall, 1919, according to ICZN (1999, Art. 58.12—use of different connecting vowels in compound words). Thus, the next oldest available name (ICZN, 1999, Art. 23.1) for this species is *Frenguelliella chubutensis* (Feruglio).

As previously discussed (see Remarks under *F. eopacifica* n. sp.) all the Sinemurian material referred in the literature to *F. poultoni* (including *Frenguelliella* sp. B of Poulton, 1979) is here referred to *F. eopacifica* n. sp.

The diagnosis of *Frenguelliella chubutensis* is here emended to include the observed variability, which encompasses the type material of the nominal species described by Jaworski (1926a), Feruglio (1934), Lambert (1944), and Leanza (1993). *Frenguelliella chubutensis* differs from other *Frenguelliella* species by its: (1) commarginally ornamented escutcheon, (2) relatively large area, and (3) orthogyrate to slightly opisthogyrate shell shape. *Frenguelliella inexspectata* is more opisthogyrate and has a smooth escutcheon and narrower area. *Frenguelliella chubutensis* is most likely descended from *F. eopacifica* n. sp., with which it shares many characters, the main differences being the larger adult size and the presence of escutcheon costellae in *F. chubutensis*.

Frenguelliella aff. *F. chubutensis* (Feruglio, 1934)
Figure 10.1–10.3

Occurrence.—Codo del Blanco and Quebrada Los Caballos (Atuel River region), Mendoza Province. Lowermost Pliensbachian, *M. chilcaense* Biozone (≈ Jamesoni Biozone) (Fig. 3).

Description.—Medium-sized, orthogyrate shell. Escutcheon margin straight or slightly convex (Fig. 10.1). Posterior margin wide, area representing ∼1/3–2/5 of shell surface (Fig. 10.1, 10.2). Ventral margin convex; anterior margin gently convex. Umbo anteriorly located. Escutcheon not preserved. Area with commarginal costellae, closely spaced (9–11 costellae/cm), less densely spaced at early growth stages. With marginal angulation. Antecarinal space dominated by attenuated flank costae. Flank costae sub-commarginal, gradually increasing in spacing (Fig. 10.1–10.3) from 6 costae/cm (at early growth stages) to 4 costae/cm (in mature stage). Flank costae slightly converging anteriorly.

Materials.—MLP 28676, 28684, 28994 (three left valves, preserved as composite molds).

Measurements.—MLP 28994: L = 52 mm, H = 44 mm; MLP 28684: L = 46 mm, H = 37 mm.

Remarks.—This taxon might represent an extreme variety of *F. chubutensis*, but it differs from typical shells of the species by the increase in spacing of flank costae during ontogeny, the larger size, and the orthogyrate shell shape. *Frenguelliella inexspectata* is similar in size, but strongly differs by its narrower area, its opisthogyrate shell, and its relatively regular costae spacing on the flank.

Trigonia costatula Lycett, 1850, as illustrated by Lycett (1872–1879, p. 81, pl. 15, figs. 8–10) shows some affinities with *Frenguelliella* aff. *F. chubutensis*. The main difference lies in the absence of ornamentation on the area and antecarinal space, and some irregularities on the posterior portion of the last-formed flank costae in the European species.

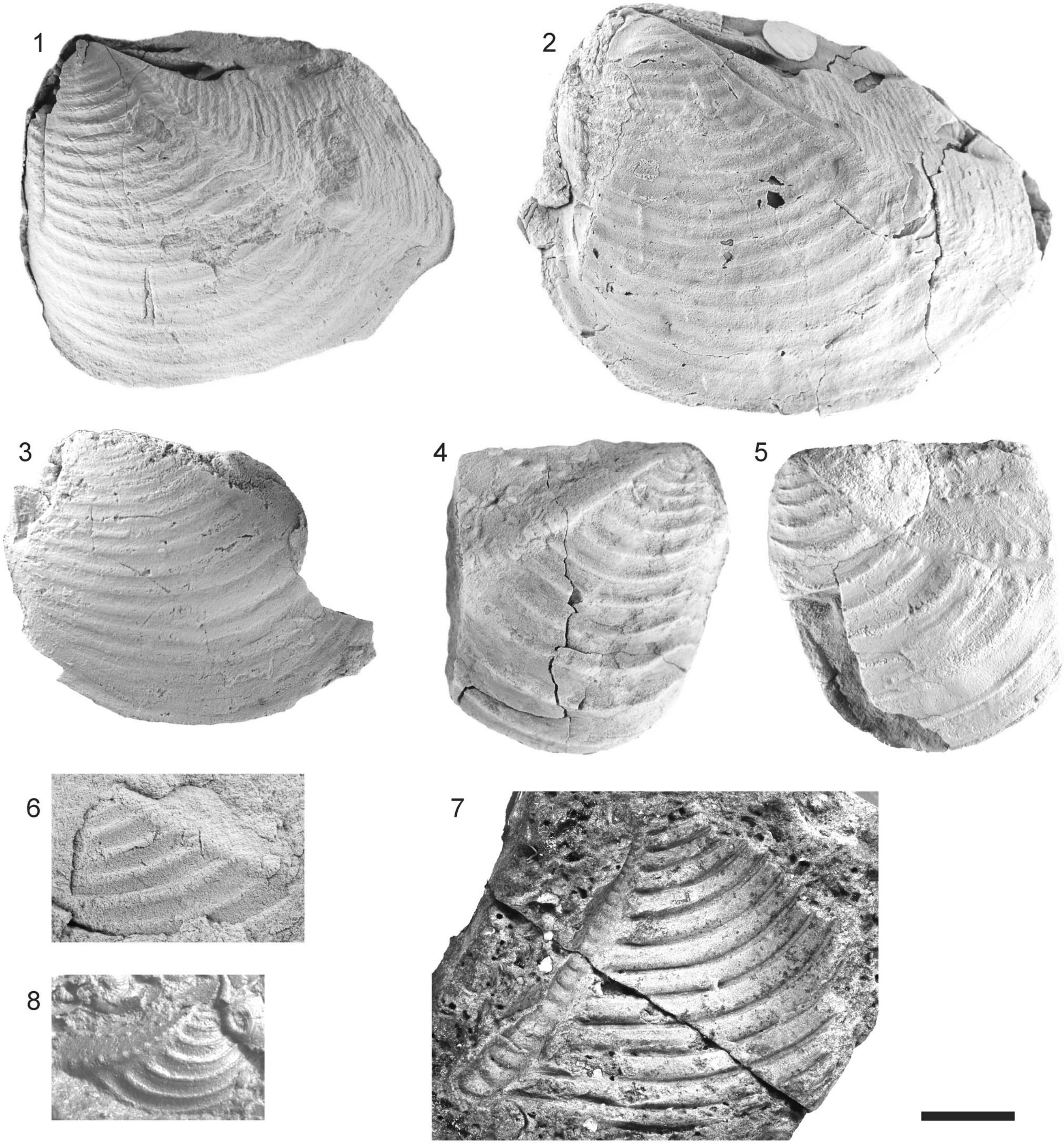

Figure 10. Trigoniida from the Early Jurassic of Argentina and North America. Scale bar = 10 mm. (**1–3**) *Frenguelliella* aff. *F. chubutensis*, Pliensbachian: (**1**) MLP 28684, composite mold of a left valve, Quebrada Los Caballos; (**2**) MLP 28994, composite mold of a left valve, Codo del Blanco; (**3**) MLP 28676, composite mold of a left valve, Quebrada Los Caballos; (**4–8**) *Poultoniella jaworskii* n. gen. n. sp.; (**4, 5**) holotype, MLP 36315, fragmentary shell, right and left lateral views, Toarcian, Arroyo La Laguna; (**6**) MLP 36317, composite mold of left valve, Toarcian, Arroyo La Laguna; (**7**) NHMB 28/9/77, n° 52[7] (photograph courtesy of S. Kühni), external mold of a left valve, Early Jurassic, Sonora, Mexico; (**8**) SNGM 7281, cast of an external mold of a right valve, late Pliensbachian, Vancouver Island, Canada.

Frenguelliella inexspectata (Jaworski, 1915)
Figure 11.1–11.10

*p 1915 *Trigonia inexspectata* Jaworski, p. 377, pl. 5, figs. 2a, b (part; see remarks under *F. chubutensis*).

p 1925 *Trigonia inexpectata* [sic]; Jaworski, p. 79, pl. 1, fig. 2. (part; see remarks under *F. chubutensis*).

1931 *Trig. inexpectata* [sic]; Windhausen, pl. 2, fig. 5. [reproduced from Jaworski, 1915]

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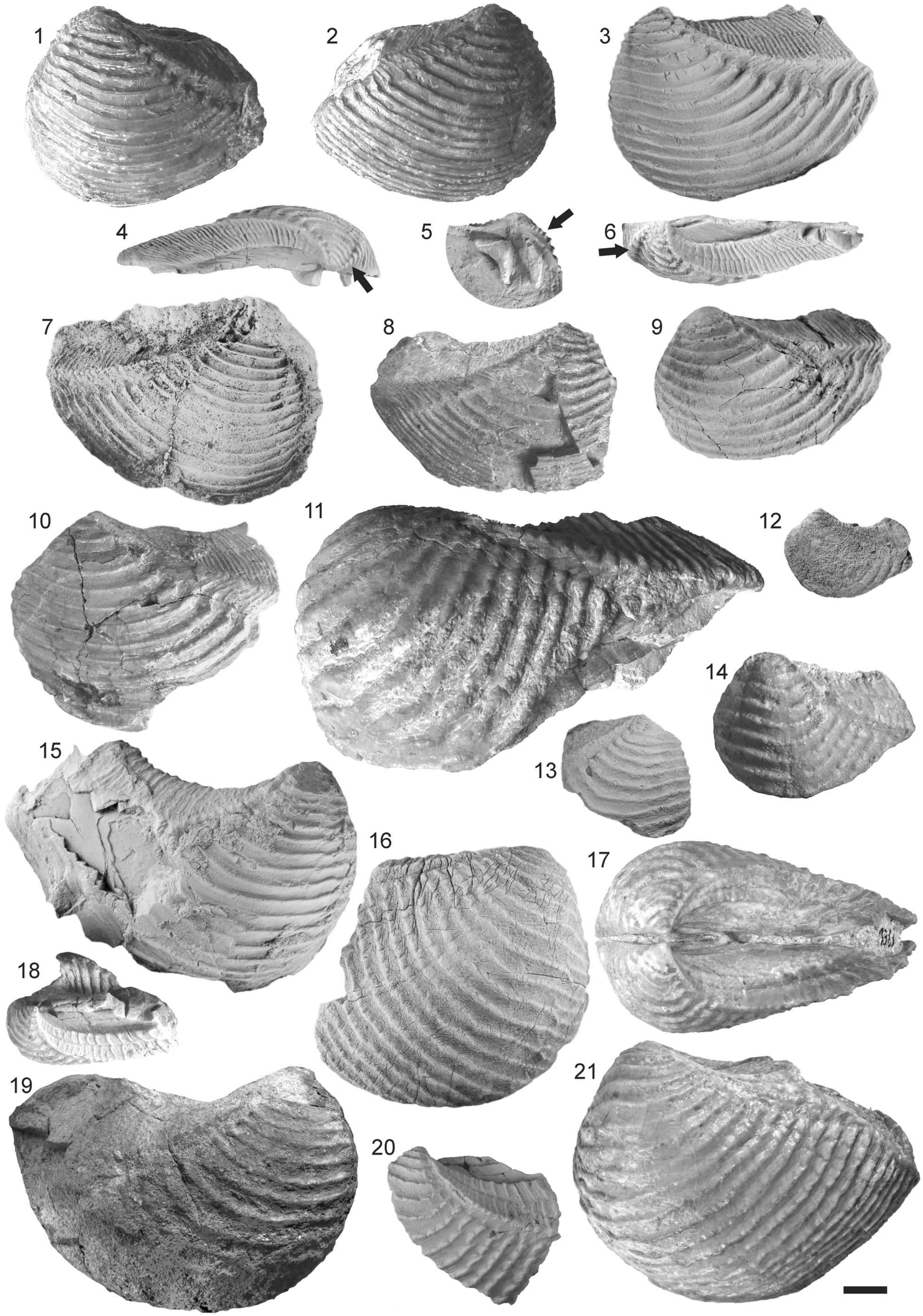

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Figure 11. Trigoniida from the Early Jurassic of Argentina. Scale bar = 10 mm. (**1–10**) *Frenguelliella inexspectata* (Jaworski) from the Pliensbachian, arrows show the anterior radial ruga: (**1, 2**) lectotype, IGPB-Jaworski-6 (photograph courtesy of G. Heumann), shell, left and right lateral views, Piedra Pintada region; (**3**, **6**) MLP 13008a, left valve, lateral and dorsal views, Cerro Roth Sur; (**4, 5**) MLP 36204, left valve, dorsal view and detail of the hinge, Cerro Roth Sur; (**7**) rubber cast of MLP 36201, external mold of right valve, Subida a Sañicó; (**8**) MLP 6726, right valve, Cerro Roth; (**9**) MLP 36198, left valve, Salitral Grande Carrán Curá; (**10**) MLP 6139, left valve, Cerro Roth; (**11–14, 16–21**) *Jaworskiella burckhardti* (Jaworski): (**11**) holotype, IGPB Jaworski-7 (photograph courtesy of G. Heumann), a fragmentary left valve, Pliensbachian, Piedra Pintada region; (**12**) BMNH1039-104, holotype for *Trigonia catanlilensis* Weaver, a weathered shell, left lateral view, Pliensbachian, Catan Lil; (**13**) MLP 36309 a fragmentary right valve, Pliensbachian, Cerro Roth Sur; (**14**) MOZ-PI 1064, juvenile left valve retrieved from growth lines on an adult specimen, Pliensbachian, Cerro Roth; (**16**) MLP 6261, fragmentary right valve, Pliensbachian, Cerro Roth; (**17**) MLP 36307 shell, dorsal view, Pliensbachian, North of Cerro Roth; (**18**, **20**) MCF-PIPH 503a, fragmentary left valve, dorsal and lateral view, Pliensbachian, Cerro Roth Sur; (**19**) MPEF-PI 6389, right valve, late Pliensbachian–early Toarcian, Nueva Lubecka; (**21**) MLP 36306 shell, left lateral view, Pliensbachian, North of Cerro Roth. (**15**) MLP 36303, probably *Jaworskiella burckhardti*, right valve, Pliensbachian, Salitral Grande Carrán Curá.

v 1942 *Trigonia* (*Frenguelliella*) *inexpectata* [sic]; Leanza, p. 165, pl. 7, fig. 1.
vp 1942 *Trigonia* cf. *T. inexpectata* [sic]; Carral-Tolosa, p. 57 (non pl. 6, fig. 2).
1969 *Trigonia* (*Frenguelliella*) *inexspectata*; Cox in Cox et al., fig. D66.3. [reproduced from Jaworski, 1915]
v 1992 *Frenguelliella inexspectata*; Damborenea et al., pl. 116, fig. 16.
1993 *Frenguelliella inexspectata*; Leanza, p. 26, pl. 2, fig. 9.
v 2008 *Frenguelliella inexspectata*; Pérez and Reyes in Pérez et al., p. 74, pl. 6, figs. 1, 3, 4, 7.
v 2008 *Frenguelliella inexspectata*; Camacho et al., fig. 14.22.D.
v 2011 *Frenguelliella inexspectata*; Riccardi et al., p. 453, fig. 7.8.
2015 *Frenguelliella* aff. *F. inexspectata*; Ferrari and Bessone, p. 353, fig. 2.M.

Type material.—The lectotype (here designated) is a complete shell with conjoined valves, figured by Jaworski (1915, pl. 5, figs. 2a, b), and here (Fig. 11.1, 11.2), from the Pliensbachian of Piedra Pintada region, held at the Institute of Geosciences, Paleontology Section, Bonn, IGPB-Jaworski-6.

Diagnosis.—Medium-sized to large, ovate-subtriangular shell; clearly opisthogyrate. Escutcheon smooth, depressed. Area narrow, with closely spaced commarginal costellae. Flank with strong, sharp, sub-commarginal, and widely spaced costae. Anterior radial ruga on the flank separating the commarginal portion of the costae from the oblique one. Antecarinal space bordered by swellings of flank costae, carrying a more subtle ornamentation than the flank.

Occurrence.—Salitral Grande Carrán Curá, Estancia Santa Isabel, Subida a Sañicó, Cerro del Vasco, Cerro Roth Sur (Piedra Pintada region), Neuquén Province; Nueva Lubecka (Genoa River region), La Casilda (in Ferrari and Bessone, 2015), Chubut Province. Latest early Pliensbachian to late Pliensbachian (*E. meridianus*–*F. disciforme* biozones [≈ Davoei–Spinatum biozones]) (Fig. 3), early Toarcian? (Tenuicostatum Biozone). The species is also recorded from Quebrada Asientos (Atacama, Chile) from the early/late Pliensbachian (Pérez et al., 2008).

Description.—Medium-sized to large, opisthogyrate shells. Straight escutcheon margin, but with the umbo and the posterodorsal angle slightly projecting dorsally (Fig. 11.3). Area margin narrow, area representing ∼1/4–1/5 of shell surface. Ventral margin gently convex; anterior margin convex and somewhat projecting anteriorly (umbo located at ∼1/4 of shell length). Escutcheon excavated, smooth (some shells with commarginal costellae or striae; Fig. 11.4); escutcheon angulation stepped. Area with sub-median groove, with commarginal costellae (Fig. 11.6), loosely arranged in early growth stages (6 costellae/cm), more closely spaced later on (10–11 costellae/cm); dorsal and ventral portions normally meeting at an angle. Prominent marginal carina in early growth stages, turning into a sharp angulation later. Antecarinal sulcus present at very early growth stages, widening and shallowing posteriorly (antecarinal space), usually dominated by attenuated flank costae; otherwise, posterior half invaded by area costellae (especially at late growth stages). Flank costae extending across the antecarinal space without attenuation at late growth stages. Flank costae strong, widely spaced (3–4 costae/cm), sub-commarginal, reaching the anterior margin nearly at right angles; sometimes, denser costae arrangement at late growth stages (Fig. 11.1, 11.2, 11.8); subtle swelling of flank costae bordering the antecarinal space. Anterior radial ruga on the shell, generating a prominence on the costae (Fig. 11.4–11.6); better developed at early growth stages, fading at later ones.

Trigonian-grade hinge (Fig. 11.5). Nymph short (Fig. 11.4, 11.6).

Materials.—About 30 specimens. The lectotype mentioned above, plus MLP 6139, 6726, 13008 (part), 36195–36210, MCF-PIPH 502 (part), 631; MPEF-PI 2911 (part), 6385, 6387, 6400; and DNGM 8851 and 8863. Specimens from Chile SNGM 562, 563.

Measurements.—Lectotype: L = 56 mm, H = 46 mm (G. Heumann, personal communication, 2019); MLP 13008a: L = 61 mm, H = 45 mm; MLP 36202: L = 48 mm, H = 37 mm; MLP36201: L = 59 mm, H = 39 mm.

Remarks.—In his original description, Jaworski (1915) included material from southern Neuquén and also some specimens from southern Mendoza, but the latter were subsequently separated by him as part of his new variety *Trigonia inexspectata* var. *densecostata* (see Remarks under *F. chubutensis*), thus restricting *F. inexspectata* s.s. to the material from Piedra Pintada region.

The shells from Chile, described by Pérez et al. (2008), show all the main features of the species, but with smaller

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shell size and more densely spaced flank costae (5–6 costae/cm, or even denser at final growth stages).

This taxon is easily differentiated from other *Frenguelliella* species from the region by its: (1) larger size, (2) more opisthogyrate shell shape, (3) narrower area, (4) stronger and less densely spaced flank costae, and (5) anterior radial ruga. It has a fairly limited geographic distribution, restricted to certain facies, such as biofacies A in Damborenea et al. (1975), which corresponds to shallow-water, well-lit environments.

Genus *Jaworskiella* Leanza, 1942

Type species.—*Trigonia burckhardti* Jaworski, 1915, p. 380–382. Pliensbachian, Piedra Pintada (Neuquén Province, Argentina).

Diagnosis.—Shell opisthogyrate, with well-defined sharp angulations. Escutcheon smooth and slightly excavated. Area with fine commarginal costellae, usually densely spaced. Antecarinal space developed. Flank ornamentation variable, but always beginning with sub-commarginal sharp costae. Posterior segment of later costae broken up into irregular tubercles (not always developed); anterior segment oblique to growth lines and sharp. Anterior radial ruga variably developed on the flank.

Remarks.—The diagnosis is slightly modified from the original one by Leanza (1942, p. 166–168), when he proposed *Jaworskiella* as a subgenus of *Trigonia*. Cox (1952) regarded *Jaworskiella* as a subgenus of *Myophorella*, but later considered it as a separate genus (Cox et al., 1969, p. N481), an interpretation that was followed by most subsequent authors.

The type species for the genus, *T. burckhardti* from the Pliensbachian of Piedra Pintada, seems to be closely related to *F. inexspectata* (type species of *Frenguelliella*, described above). Escutcheon and area sculptures are the same in both species, and they both share an anterior radial ruga on the flank. The main differences seem to lie in the development of the anterior flank and of the ornamentation. The anterior margin in *J. burckhardti* is more extended (compared to the ventral margin) and more convex than in *F. inexspectata*, resulting in a more opisthogyrate shell; inflation is also stronger in *Jaworskiella*. Besides, the flank in *J. burckhardti* is dominated by oblique ornamentation, a pattern already developed on the anteriormost portion of flank costae in *F. inexspectata* and related to the anterior margin. The tubercles in *J. burckhardti* (more or less developed) are fairly irregular. Furthermore, there seems to be a gradation in morphologies (Fig. 11.1–11.21) between those typical of *F. inexspectata* and the extreme forms of *J. burckhardti*. So, both species are closely related (most likely sister species, or even a single species with a high degree of variation). The two species frequently occur in the same localities and even the same beds. At this time we prefer to maintain the specific and generic distinction, but we regard *Jaworskiella* as monotypic, other proposed species being referred to different genera.

Taking into account that most of the remaining species that were previously included in *Jaworskiella* (Pérez and Reyes, 1977; Poulton, 1979; Pérez et al., 2008) show some meaningful morphological differences and/or are Sinemurian in age, we consider unlikely that they could have been genetically related to *J. burckhardti*. Cox (1952) also referred to this genus the species *Trigonia freixialensis* Choffat, 1885, and *T. kobyi* Choffat, 1885, from the Upper Jurassic in Portugal. Even though flank ornamentation in both Portuguese species is reminiscent of that of *J. burckhardti*, the lack of an antecarinal space and of area ornamentation (except for earliest growth stages) precludes their assignment to the genus.

Jaworskiella burckhardti (Jaworski, 1915)
Figure 11.11–11.21

v 1902 *Trigonia gryphitica* Steinm. [sic]; Burckhardt, p. 245, pl. 4, fig. 4.
* 1915 *Trigonia burckhardti* Jaworski, p. 380, pl. 5, fig. 3.
1925 *Trigonia burckhardti*; Jaworski, p. 81, pl. 1, fig. 3.
v 1931 *Trigonia catanlilensis* Weaver, p. 233, pl. 20, fig. 98.
1931 *Trigonia Burckhardti*; Windhausen, pl. 20, fig. 4. [reproduced from Jaworski, 1915]
1931 *Trigonia gryphytica* Stein. [sic]; Windhausen, pl. 22, fig. 7. [reproduced from Burckhardt, 1902]
v 1942 *Trigonia* (*Jaworskiella*) *burckhardti*; Leanza, p. 166, pl. 4, figs. 2, 3.
v 1942 *Trigonia* aff. *T. Burckhardti*; Carral-Tolosa, p. 58, pl. 6, fig. 2 (as *Trigonia* cf. *T. inexpectata* [sic] in plate caption).
1969 *Jaworskiella burckhardti*; Cox in Cox et al., fig. D68.6. [reproduced from Jaworski, 1915]
v 1977 *Jaworskiella burckhardti*; Pérez and Reyes, p. 14, pl. 2, figs. 1, 3, 6. [figs. 1, 3 reproduced from Leanza, 1942; fig. 6 reproduced from Jaworski, 1915]
v 1980 *Jaworskiella burckhardti*; Hillebrandt, pl. 2, figs. 5a, b.
v 1987 *Jaworskiella burckhardti*; Leanza and Garate-Zubillaga, p. 210, pl. 1, figs. 1, 2.
v 1993 *Jaworskiella burckhardti*; Leanza, p. 28, pl. 1, figs. 1, 6, 7, 10.
1997 *Jaworskiella burckhardti*; Pérez and Reyes, p. 574.
v 2008 *Jaworskiella burckhardti*; Pérez and Reyes in Pérez et al., p. 75, pl. 6, figs. 2, 8, 9, pl. 7, figs. 1–3, 6, 7, pl. 8, fig. 3.

Type materials.—Holotype: IGPB Jaworski-7, an incomplete left valve from the Pliensbachian of Piedra Pintada (Neuquén Province), wrongly attributed originally to the Upper Jurassic. Jaworski's (1915) original description was based on this single left valve (illustrated in his pl. 5, fig. 3; Fig. 11.11).

Holotype of *Trigonia catanlilensis* Weaver.—A weathered juvenile shell at the Burke Museum of Natural History, Seattle (USA), BMNH1039-104 (a cast at Museo de La Plata under collection number MLP 22356), from the late Early Jurassic of Catan Lil (Piedra Pintada region), Neuquén Province (Fig. 11.12).

Diagnosis.—Large to very large opisthogyrate shell, ovate-subtriangular to semicircular, anteriorly inflated. Escutcheon smooth, depressed. Area narrow, with closely disposed commarginal costellae. Flank ornamentation beginning with sub-commarginal sharp costae; later costae with posterior segment broken up into irregular tubercles (not always developed), and anterior segment oblique and sharp. Anterior radial ruga on the flank. Antecarinal space more subtly ornamented than the flank.

Occurrence.—Salitral Grande Carrán Curá, Cerro del Vasco, Cerro Roth Sur (Piedra Pintada region), Neuquén Province; Nueva Lubecka (Genoa River region), Chubut Province; doubtful specimen from La Bajada (Las Leñas/Valle Hermoso region), Mendoza Province. Latest early Pliensbachian (*A. behrendseni* Biozone) to early Toarcian (Tenuicostatum Biozone?; Fig. 3). The species is also recorded from the late Pliensbachian and Toarcian in Quebrada Asientos (Atacama) and Punilla Oriental (Coquimbo) in Chile (Pérez et al., 2008).

Description.—Very large opisthogyrate shell, strongly inflated anteriorly. Straight and short escutcheon margin, with the umbo and the posterodorsal angle projecting dorsally (Fig. 11.15, 11.19, 11.21). Posterior margin not preserved in the known specimens; short and slightly convex according to growth lines. Convex ventral margin, passing gradually to the strongly convex anterior margin (Fig. 11.19, 11.21). Umbos prominent, anteriorly situated. Escutcheon narrow, slightly excavated, smooth (Fig. 11.17, 11.18) or with strong growth lines. Escutcheon angulation stepped. Area narrow, ∼1/4 –1/5 (or less) of general shell surface, though hard to estimate due to fragmentation; somewhat wider on the shells closest to *F. inexspectata* (Fig. 11.15). Submedian radial groove developed; ventral portion of the area wider than dorsal portion. Area with commarginal, somewhat irregular costellae, less densely spaced in late ontogenetic stages, widening when crossing both angulations; ventral portion with some extra costellae interrupted at the groove. Marginal carina slightly protruding in early growth stages, changing gradually to a sharp angulation (sometimes with tubercles enhancing it). Antecarinal space flat, widening posteriorly, smooth, or, more frequently, with thin costellae (weakened continuation of flank costae) perpendicular to marginal angulation (especially in early growth stages) or commarginal (mostly in late growth stages). Flank ornamentation highly variable; strong and sharp commarginal costae developed in early growth stages, with a bend on the posterior portion, at right angles with marginal carina/angulation. Flank costae oblique in late growth stages, with the posterior segment weakened, giving rise to the antecarinal space. Some shells with flank costae similar to those of *Frenguelliella inexspectata*, although always at right angles with the antecarinal space (Fig. 11.13, 11.15). Maximum costae separation at the point of maximum shell inflation (Fig. 11.11, 11.16, 11.21), resulting in costae with a diverging posterior segment and a converging anterior one (recognized by Jaworski, 1925). Costae posterior segment usually fragmented into irregular tubercles (Fig. 11.11, 11.14, 11.16, 11.20, 11.21), but not always (e.g., Fig. 11.13). Costae anterior segment continuous, frequently with irregularities and bifurcations (Fig. 11.16, 11.21). Anterior radial ruga developed in early stages, fading later on.

Trigonian-grade hinge (Fig. 11.18). Nymph short and wide (Fig. 11.17).

Materials.—More than 30 specimens were examined: MLP 6257, 6261, 36213, 36302, 36304–36309, and probably 17145, 36303; MOZ-PI 1064, 3043, 3044; DNGM 8684 (cast = MLP 19080); MPEF-PI 2910, 2997, 6388, 6389, 6391, 6401, and probably 6398; MCF-PIPH 502 (part), 503. The specimen from Piedra Pintada illustrated by Burckhardt (1902, pl. 4, fig. 4) as *Trigonia gryphitica* was examined at Basel (Switzerland): NHMB-G 16636. Specimens from Chile SNGM 568–572.

Measurements.—Holotype (IGPB Jaworski-7): L = 110 mm, H = 65 mm (G. Heumann, personal communication, 2019), though the ventral margin is broken; few shells are complete enough to be measured: MLP 36306: L = 82 mm, H = 60 mm, W = 49 mm; MLP 36307: L = 79 mm, H = 59 mm, W = 46 mm; MPEF-PI 6389: L = 73 mm, H = 50 mm, V = 20 mm.

Remarks.—The strong resemblance of this species to *F. inexspectata*, from which it differs mostly in shell size and anterior inflation, strongly suggests a sister-species relationship. Some differences in ornamentation seem to be the result of alterations of the shell. For example, in some shells of *J. burckhardti* (Fig. 11.21), it is clear that posterior portions of costae (at least in latest growth stages) are still commarginal, and their anterior portions are oblique, as is actually the case in *F. inexspectata*. It is also strongly suggestive that both species frequently occur together. These similarities sometimes make the distinction of both taxa difficult. The specimen on Figure 11.15, for example, shows many characters typical of *F. inexspectata*, such as the continuous and sharp flank costae, the relatively large area and the less-inflated anterior flank; in contrast, the strongly opisthogyrate shell shape, the slightly irregular costellae on the area, and the anterior irregularities on flank costae are characteristic of *J. burckhardti*.

As correctly suggested by Poulton (1979, p. 19), the type material shows tubercles on the posterior portion of flank costae (Fig. 11.11), unlike Jaworski's drawing (1915, pl. 5, fig. 3), which shows smooth flank costae. The wide but continuous variability in shell ornamentation (Fig. 11.11–11.21) allows for the inclusion of specimen BMNH1039-104 (Fig. 11.12) within the species. This heavily weathered material is the holotype for *Trigonia catanlilensis* Weaver, 1931, and hence this last species is considered as a junior synonym of *Jaworskiella burckhardti*. This specimen is a small juvenile, comparable to other juvenile shells included within the species (e.g., Fig. 11.14).

Genus *Poultoniella* new genus

Type species.—*Poultoniella jaworskii* new species, by original designation herein. Late Pliensbachian–early Toarcian of the Pacific coast of the Americas.

Other species.—*Trigonia malladae* Choffat, 1885, from the late Toarcian of Portugal, may be tentatively referred to *Poultoniella* n. gen.

Diagnosis.—Orthogyrate to opisthogyrate. Prominent marginal carina with transversely elongate tubercles on top. Area smooth except for a median radial row of well-spaced, round, small pustules. Very narrow antecarinal space. Flank with sharp sub-commarginal costae.

Occurrence.—Late Pliensbachian and Toarcian from the Pacific coast of the Americas and maybe Western Europe.

Etymology.—The genus is dedicated to Terence P. Poulton, Canadian paleontologist and specialist on fossil Trigoniida.

Remarks.—Although the material of the type species was referred to *Frenguelliella* or related to species now included in it (Jaworski, 1929; Poulton, 1979), area ornamentation and marginal carina morphology prevent its assignment to that genus, as here understood. Furthermore, previous characterizations of *Frenguelliella* emphasized the absence of any trace of radial ornament on the area (Cox in Cox et al., 1969, p. N478; Poulton, 1979, p. 18). Yet, we consider it unlikely that the single radial row of pustules along the area midline would relate this genus to *Trigonia*, which has well-developed radial costae over the entire area.

Instead, *Poultoniella* n. gen. is here interpreted as a descendant of *Frenguelliella*, with the rows of elongate tubercles on the marginal carina and escutcheon angulation, and the central row of pustules representing thickened remains of former transverse costellae across the area. The prominent marginal carina would be another innovation of this taxon. The abrupt appearance of these features hinders relating it to any particular species of *Frenguelliella*.

The description and figure of *Trigonia malladae* Choffat (1885, pl. 9, fig. 23, 1888, p. 37) suggest the presence of *Poultoniella* n. gen. in the late Toarcian of Portugal.

Poultoniella jaworskii new species
Figure 10.4–10.8

v 1929 *Trigonia* cf. *T. inexspectata* Jaw.; Jaworski, p. 7, pl. 1, fig. 4.
p 1979 *Frenguelliella* sp. A; Poulton, p. 18, pl. 1, figs. 4, 5, 22, non figs. 6–8.

Type material.—Holotype: MLP 36315, a posteriorly broken shell (Fig. 10.4, 10.5).

Diagnosis.—Orthogyrate and trigonally elongate shell. Escutcheon carina as a row of spaced, very small, and transversely elongate tubercles. Area ∼1/3 of shell surface, smooth except for a median radial row of well-spaced, round, small pustules. Prominent marginal carina with regular transversely elongate tubercles; very narrow antecarinal space. Flank costae sub-commarginal, gradually increasing in spacing, sharp, with a sudden downward bend anteriorly.

Occurrence.—Arroyo La Laguna (Los Patos region), San Juan Province. Early Toarcian (somewhere between late *D. hoelderi* Biozone and early *C. chilensis* Biozone [≈ Serpentinum Biozone or, more likely, Bifrons Biozone]) (Fig. 3). Material assignable to this species was recorded from the late Pliensbachian of Vancouver Island, British Columbia (Canada) by Poulton (1979) and the Early Jurassic of Sonora (Mexico) by Jaworski (1929).

Description.—Medium-sized, orthogyrate, and apparently trigonally elongate shell (all materials fragmentary). Anterior and ventral margins slightly convex, meeting at nearly right angles (Fig. 10.4, 10.5). Escutcheon poorly preserved, with some tuberculate costellae. Escutcheon carina as a row of very small, spaced, transversely elongate tubercles. Area ∼1/3 of shell surface, smooth; without median groove, but with a radial row of small, well-spaced, and round pustules. Prominent marginal carina with regular transverse ridge-like tubercles. Antecarinal space present as an interruption of flank costae, very narrow but widening posteriorly. Flank with sharp sub-commarginal costae showing gradually increasing spacing (Fig. 10.4, 10.5), from 7 costae/cm on the umbonal region to 2–3 costae/cm in final growth stages. Flank costae with a sudden downward bend near the anterior margin, becoming somewhat irregular (Fig. 10.4) and meeting the margin at high angles.

Etymology.—The species is dedicated to the memory of Erich Jaworski, German paleontologist, who first described material referable to this taxon.

Materials.—The holotype, plus eight isolated valves and some fragments, MLP 36312b, 36316–36320, mostly recrystallized shells and composite molds. The specimen from Mexico described by Jaworski (1929) is housed in the Naturhistorisches Museum Basel (Switzerland): NHMB 28/9/77, n° 52[7] (Fig. 10.7). Casts of the material described by Poulton (1979) as *Frenguelliella* sp. A are housed at the SERNAGEOMIN in Santiago (Chile) under catalog numbers SNGM 7280–7283 (one of them illustrated in Fig. 10.8).

Measurements.—Holotype, MLP 36315 (broken posteriorly): L = 30 mm (the whole shell was longer), H = 33 mm. MLP 36317: L = 28 mm, H = 19 mm. Jaworski's (1929) specimen from Mexico: L = 45 mm, H = 36 mm (though shell margins are not well preserved).

Remarks.—The material from Argentina is strikingly similar to that found in North America. Both the description and the figure by Jaworski (1929, p. 7, pl. 1, fig. 4; Fig. 10.7) agree with *P. jaworskii* n. gen. n. sp. Likewise, *Frenguelliella* sp. A (Fig. 10.8) described by Poulton (1979, p. 18, pl. 1, figs. 5, 22 and potentially fig. 4, from Geological Survey of Canada, GSC locality 93587, but not figs. 6–8, from the GSC locality 89090) shows the same characters as the Argentinian material, although the antecarinal space is broader in the specimens from Vancouver Island. This material was initially regarded as of controversial age (specimens either Sinemurian or Toarcian, according to Poulton, 1979); subsequently, Aberhan (1998, appendix I) listed the locality involved as late Pliensbachian in age (*Kunae* Biozone [≈ Margaritatus Biozone]).

As highlighted by Poulton (1979), the most noticeable character of this species is the lack of commarginal costellae on the area. Jaworski (1929) described some faint transverse costellae in initial growth stages that later fade, although he considered that their absence might be also due to a preservational bias.

Flank costae somewhat resemble those of *F. inexspectata*. Although this last species usually has a sharp marginal angulation, on some shells there seems to be an incipient carina similar to that of *Poultoniella jaworskii* n. gen. n. sp. In contrast, the progressive spacing of flank costae in *Poultoniella jaworskii* n. gen. n. sp. is similar to the pattern found in *Frenguelliella* aff. *F. chubutensis*, but the Toarcian species is more elongate, with a narrower area and a better-defined nodose carina.

Poultoniella? *malladae* (Choffat, 1885) n. comb., from the late Toarcian of Portugal, differs from *Poultoniella jaworskii* n. gen. n. sp. in being higher and shorter and with closer spacing of flank costae.

Genus *Quadratojaworskiella* Reyes and Pérez, 1980

Type species.—*Jaworskiella* (*Quadratojaworskiella*) *pustulata* Reyes and Pérez, 1980, p. 87–93. Early Pliensbachian, northern Chile.

Diagnosis.—Very large subquadrate shell, slightly opisthogyrate. Area wide, divided by a shallow median groove; ornamented by commarginal costae. Marginal carina blunt, slightly overhanging a narrow antecarinal sulcus. Flank ornamented with sharp sub-commarginal costae in early growth stages, changing gradually during development to rows of tubercles.

Remarks.—*Quadratojaworskiella* was proposed by Reyes and Pérez (1980) as a subgenus of *Jaworskiella*; the diagnosis here presented is modified from their original one. Subsequently, Pérez and Reyes (1991) and Pérez et al. (2006, 2008) regarded *Quadratojaworskiella* as a distinct genus. Its early development suggests a direct derivation from *Frenguelliella* rather than a close relationship to *Jaworskiella* or *Moerickella* n. gen. (see below). *Quadratojaworskiella* is endemic of southern South America (Chile and Argentina).

Quadratojaworskiella acarinata Pérez and Reyes in Pérez et al., 2008, from the Hettangian and late Sinemurian of Chile, was diagnosed as having a "shell without marginal carina and antecarinal sulcus…" (Pérez et al., 2008, p. 80). These authors also described the Sinemurian species *Prosogyrotrigonia* sp. 1 and *Prosogyrotrigonia* sp. 2, both characterized by commarginal flank costae, which in late ontogeny break up into rows of tubercles. Because *Prosogyrotrigonia* lacks a true carina (the genus is characterized by a marginal bend) and already shows an early tendency to generate tubercles on the flank, we refer *Q. acarinata* Pérez and Reyes in Pérez et al., 2008, to *Prosogyrotrigonia*. *Quadratojaworskiella* is thus regarded as monotypic.

Quadratojaworskiella cf. *Q. pustulata* (Reyes and Pérez, 1980)
Figure 12

cf. 1977 *Jaworskiella* (*Quadratojaworskiella*) *pustulata* Pérez and Reyes, p. 15, pl. 2, figs. 2, 4, 5 (nom. nud.)
*v cf. 1980 *Jaworskiella* (*Quadratojaworskiella*) *pustulata* Reyes and Pérez, p. 89, pl. 1, 2.
cf. 1980 *Quadratojaworskiella pustulata*; Hillebrandt, pl. 2, fig. 9.

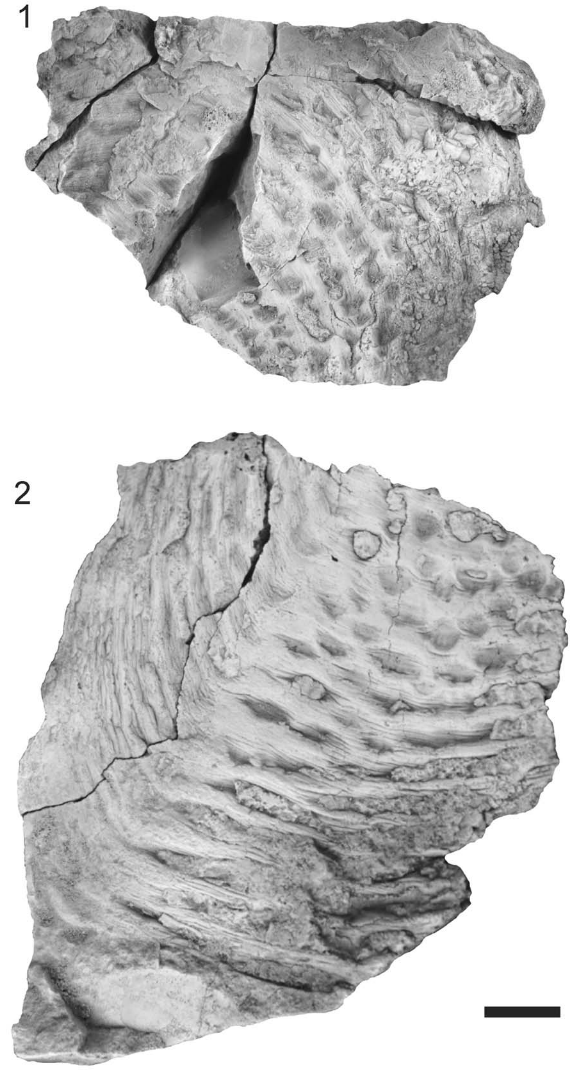

Figure 12. *Quadratojaworskiella* cf. *Q. pustulata* (Reyes and Pérez), Pliensbachian, Arroyo Portezuelo Ancho. Scale bar = 10 mm. (**1, 2**) IANIGLA-PI 3263, external mold of the shell; (**1**) right and (**2**) left valves.

cf. 1982 *Jaworskiella* (*Quadratojaworskiella*) *pustulata*; Pérez, pl. 15, figs. 7–10, appendix 1.
cf. 1997 *Quadratojaworskiella pustulata*; Pérez and Reyes, p. 574.
v cf. 2008 *Quadratojaworskiella pustulata*; Pérez et al., p. 76, pl. 11, figs. 2–4, 6, 7.
v cf. 2008 *Quadratojaworskiella pustulata*; Pérez and Reyes, p. 28.

Occurrence.—Arroyo Portezuelo Ancho (Las Leñas-Valle Hermoso region), Mendoza Province. Latest early Pliensbachian–late Pliensbachian (*Fanninoceras* s.l. Biozone; Fig. 3). The species *Q. pustulata* is found in Quebrada Asientos (Atacama, Chile) in the early/late Pliensbachian (Pérez et al., 2008).

Description.—Fragmentary single specimen preserved as external mold of the ventroposterior portion of a left valve and

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a portion of a right flank. Very large shell (probably >100 mm long). Area and flank surfaces gently sloping away, separated by a straight marginal angulation or marginal bend. Area wide, bearing commarginal strong and irregular rugae (Fig. 12.2), sometimes fragmented into tubercles. Flank with commarginally aligned strong tubercles, somewhat elongate (parallel to growth lines) in late growth stages (Fig. 12).

Material.—External mold of a shell (in butterfly position), IANIGLA-PI 3263.

Remarks.—The few observable characters agree well with those described for *Q. pustulata*. Although marginal carina and antecarinal sulcus were described and illustrated by Reyes and Pérez (1980), these features lose prominence as growth proceeds (e.g., Pérez et al., 2008, pl. 8, fig. 6, pl. 9, fig. 1, pl. 10, fig. 4). Their absence in our material might well be a preservational bias (it is an incomplete fragment preserved as external mold). Because the umbonal part of the shell is missing, the specific assignment remains uncertain. This is the first record of the genus for Argentina.

Family Myophorellidae Kobayashi, 1954

Remarks.—The family Myophorellidae was characterized as having conspicuously nodate flank costae, sub-commarginal near the umbo, but becoming strongly oblique in maturity (Cooper, 1991). Because those characters may develop in some Frenguelliellidae (such as *Jaworskiella*), and taking into account the inferred evolutionary relationships of the species discussed here, we only include in Myophorellidae those species that are likely descendants of *Moerickella* n. gen.

Genus *Moerickella* new genus

Type species.—*Trigonia infraclavellata* Möricke, 1894, p. 46–48, pl. 2, fig. 3, from the Early Jurassic of Las Amolanas, Chile.

Other species.—*Jaworskiella siemonmulleri* Poulton, 1979; *Jaworskiella supleiensis* Poulton, 1979.

Diagnosis.—Shell opisthogyrate with slightly protruding carinae, usually rounded angulations in late growth stages. Escutcheon slightly depressed. Area with fine commarginal costellae, usually densely spaced. Antecarinal space variably developed. Flank with oblique costae, subparallel, anteroventrally sloping, and orthogonal to the antecarinal space. Flank costae sometimes sharp and continuous on the anteriormost segment; otherwise formed by small tubercles, frequently elongate along growth lines.

Occurrence.—Sinemurian and Pliensbachian from the Pacific coast of the Americas.

Etymology.—The genus is dedicated to Wilhelm Möricke, German paleontologist who described the type species.

Remarks.—*Moerickella* n. gen. is established based on *Trigonia infraclavellata* Möricke, 1894; the species *Trigonia gryphitica* Möricke, 1894 is here regarded as synonym of *T. infraclavellata*. The characters shared with *J. siemonmulleri* Poulton, 1979, from the late Sinemurian of Nevada (USA) and Early Jurassic of British Columbia (Canada), and with *J. supleiensis* Poulton, 1979, probably from the late Pliensbachian of Oregon (USA), allow for assignment of the North American species to *Moerickella* n. gen. Previously discussed characters relating *J. burckhardti* to *F. inexspectata* preclude assigning the species here included in *Moerickella* n. gen. to *Jaworskiella*.

When discussing the genus *Jaworskiella*, Poulton (1979, p. 19–20) provided an emended diagnosis that was partly considered here for the diagnosis of *Moerickella* n. gen. According to his interpretation, *Jaworskiella* and the species now included under *Moerickella* n. gen. show a gradual rotation of the costae over a major part of the flank, while in *Myophorella* Bayle, 1878 (including *Promyophorella*) only the posteriormost segments of costae were rotated. This results in subparallel smoothly curved costae departing from the antecarinal space at right angles in *Moerickella* n. gen., and diverging costae, usually increasing curvature during development, and departing from the antecarinal space at obtuse anterior angles in *Promyophorella*.

Moerickella n. gen. differs from *Jaworskiella* by having a much more regular ornamentation pattern (also recognized by Poulton, 1979, p. 20, for *M. siemonmulleri* n. comb.), with subparallel flank costae bearing well-developed and elongate tubercles on their posterior segments. The presence of an anterior radial ruga in *Jaworskiella* is the main distinctive character separating it from *Moerickella* n. gen. and other morphologically convergent forms.

Moerickella infraclavellata (Möricke, 1894) new combination
Figure 13

*	1894	*Trigonia infraclavellata* Möricke, p. 46, pl. 2, fig. 3.
	1894	*Trigonia gryphitica* Möricke, p. 45, pl. 3, fig. 5.
non v	1902	*Trigonia gryphitica*; Burckhardt, p. 245, pl. 4, fig. 4.
non	1931	*Trigonia gryphytica*; Windhausen, pl. 22, fig. 7. [reproduced from Burckhardt, 1902]
	1977	*Jaworskiella infraclavellata*; Pérez and Reyes, p. 15, pl. 3, fig. 5. [reproduced from Möricke, 1894]
	1977	*Jaworskiella gryphitica*; Pérez and Reyes, p. 15, pl. 3, fig. 4. [reproduced from Möricke, 1894]
	1997	*Jaworskiella infraclavellata*; Pérez and Reyes, p. 574.
	1997	*Jaworskiella gryphitica*; Pérez and Reyes, p. 574.
v	2008	*Jaworskiella gryphitica*; Pérez and Reyes in Pérez et al., p. 74, pl. 6, figs. 5, 6, 10, 11.

Type materials.—Möricke (1894) based his description on two specimens collected by G. Steinmann from beds referred to the Early Jurassic at Las Amolanas, Chile; he only figured an incomplete right valve (Möricke, 1894, pl. 2, fig. 3). We could not trace the whereabouts of his syntypes.

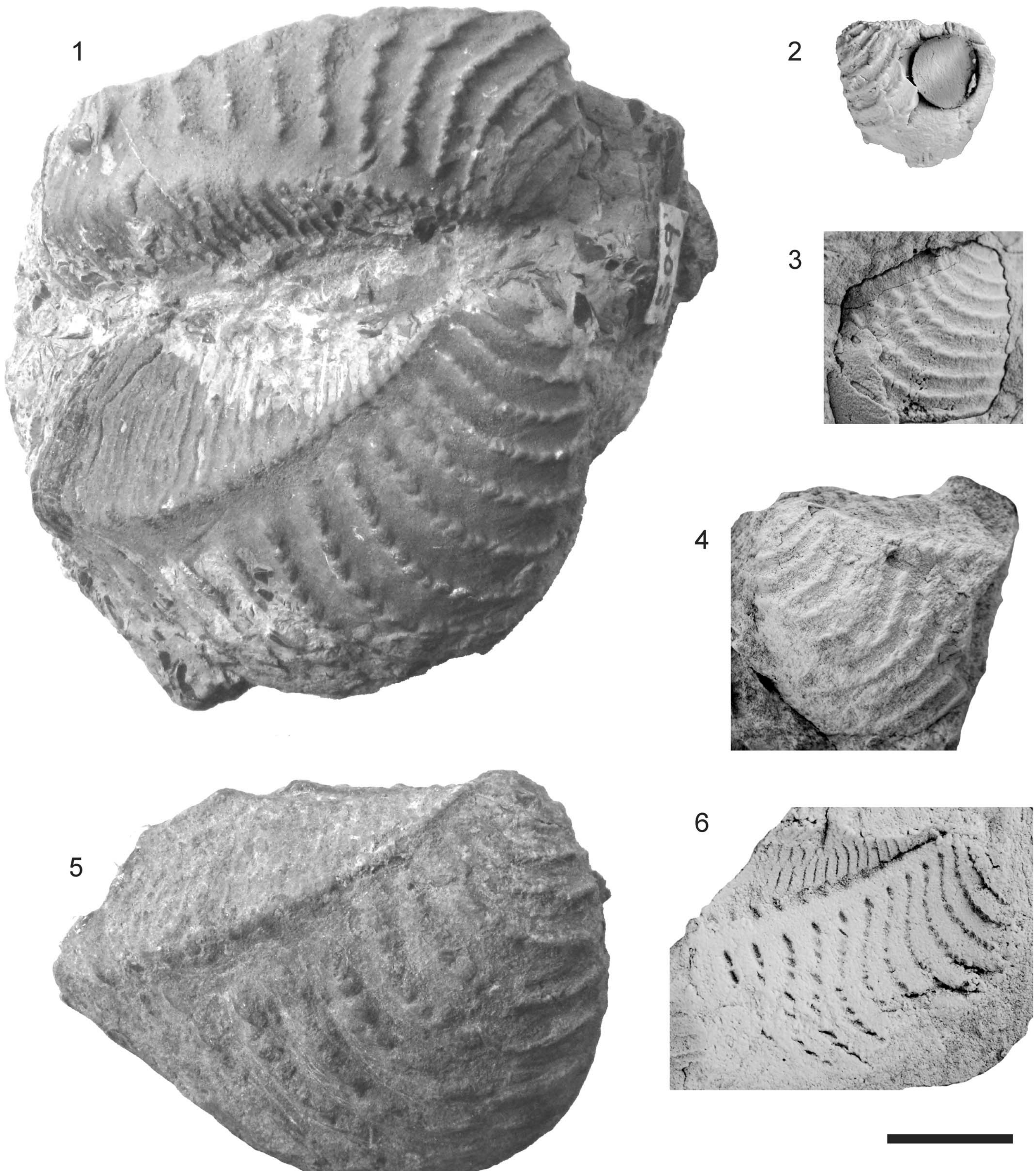

Figure 13. *Moerickella infraclavellata* (Möricke) n. comb. from the Early Jurassic of Argentina and Chile. Scale bar = 10 mm. (**1**) SNGM 779, shell in butterfly position, Sinemurian, Sierra Muñiz, Chile; (**2**) MLP 18387b, fragmentary left valve, Sinemurian, Codo del Blanco; (**3**) MLP 32846, fragmentary right valve, Sinemurian, Las Chilcas; (**4**) MLP 31153, fragmentary left valve, Sinemurian, Las Chilcas; (**5**) SNGM 778, right valve, Sinemurian, Sierra Muñiz, Chile; (**6**) MLP 31119a, external mold of a left valve, earliest Pliensbachian, La Horqueta.

Diagnosis.—Small opisthogyrate shell. Escutcheon smooth, with a stepped escutcheon angulation. Large area with commarginal, densely spaced costellae; with submedian groove. Marginal carina tuberculate, slightly protruding at early growth stages, later as a rounded angulation. Antecarinal space smooth and well developed, widening posteriorly. Flank

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semicircular, with oblique, subparallel costae fragmented into very small and elongate tubercles. Delicate sculpture throughout the shell.

Occurrence.—La Horqueta, Codo del Blanco, Las Chilcas, Puesto Araya (Atuel River region), Mendoza Province. Late Sinemurian (*Orthechioceras-Paltechioceras* Biozone [≈ Raricostatum Biozone]) to early Pliensbachian (*M. externum* Biozone [≈ Ibex Biozone]; Fig. 3). In Chile, this species occurs in late Sinemurian beds at Río Manflas, Quebrada del Pobre, Sierra de Muñiz, Quebrada de Las Vizcachas, Sierra de la Ternera (Pérez et al., 2008).

Description.—Small, slightly opisthogyrate shell. Escutcheon not preserved in Argentinian specimens, smooth in Chilean material; with slightly protruding escutcheon carina to stepped angulation. Area ~1/3 of general shell surface in Chilean samples (Fig. 13.1, 13.5). Area with commarginal costellae, densely spaced (~12 costellae/cm), sometimes interrupted by a faint groove; costellae on the ventral and dorsal sides of the groove sometimes alternate (Fig. 13.6). Chilean specimens with a submedian groove on the area; dorsal and ventral surfaces of the area converging at the groove. Marginal carina slightly protruding at early growth stages, a rounded angulation later; with well-developed tubercles, usually related to an area costella (only half of the costellae with tubercles; Fig. 13.1). Antecarinal space smooth and well developed, widening posteriorly. Flank semicircular, with oblique, subparallel costae fragmented into very small and elongate tubercles.

Materials.—Fifteen specimens; from Argentina: MLP 13354, 18387b, 31118, 31119, 31153, 32846, 32885, 33235; from Chile: SNGM 564–566, 778, 779.

Measurements.—MLP 31153: L = 23 mm, H = 21 mm. Some Chilean specimens are more complete; SNGM 778: L = 35, H = 26 mm; SNGM 779: L = 39 mm, H = 29 mm.

Remarks.—*Moerickella infraclavellata* n. comb. differs from other species of *Moerickella* n. gen. by its: (1) smooth and widening antecarinal space, (2) delicate sculpture, and (3) small size. We regard *T. gryphitica* Möricke as a subjective synonym of *T. infraclavellata* Möricke. Because relative page position is not a mandatory criterion when choosing between simultaneously published names, in accordance with ICZN 1999 (Art, 24.2.2 and Rec. 24A), precedence over *T. gryphitica* is given to *T. infraclavellata*. Such action best serves nomenclatural stability because the material originally referred to the latter species by Möricke (1894) is described more accurately (it was probably better preserved, too), providing the diagnostic features recognized here. Pérez and Reyes (1977) and Pérez et al. (2008) considered both species as distinct and valid; they distinguished them by the presence of more widely spaced flank costae in *T. gryphitica* (Pérez et al., 2008, p. 75). When describing both species, Möricke (1894) related *T. gryphitica* to the old "section Undulatae," which is characterized by the presence of a bend in the flank costae, although this character in *T. gryphitica* was not as sharp as in the typical "Undulatae" (Möricke, 1894, p. 45). According to our analysis of the Argentinian and Chilean material, such differences are here regarded as part of the intraspecific variation of a single species.

Moerickella siemonmulleri (Poulton, 1979) n. comb. and *M. supleiensis* (Poulton, 1979) n. comb. from North America have larger shells with stronger sculpture than *M. infraclavellata* n. comb., both characters more developed in *M. supleiensis* n. comb. *Moerickella siemonmulleri* n. comb. also has an ornamented antecarinal space. In both North American species, flank costae have continuous anterior segments.

Möricke (1894, p. 46) already recognized *M. infraclavellata* n. comb. as the oldest species of the "section Clavellatae," characterized by flanks with nodate curved costae. The transitional character of this species is quite remarkable. The Sinemurian samples seem close to *F. eopacifica* n. sp., bearing tubercles mostly on the posterior segment of flank costae; the anterior segment being sharp and continuous, like in *Frenguelliella* (Fig. 13.3). Part of the material illustrated by Pérez et al. (2008, pl. 6, figs. 5, 10, 11) closely resembles these samples. On the other hand, Pliensbachian samples (Fig. 13.6), together with Chilean material under collection numbers SNGM 778, 779 (Fig. 13.1, 13.5), resemble *Promyophorella basoaltorum* n. sp., with tubercles well developed along the whole costa, but they bear subparallel flank costae orthogonal to the antecarinal space, while *P. basoaltorum* n. sp. shells have diverging flank costae departing from antecarinal space at markedly obtuse angles anterior to the costae.

Genus *Pseudovaugonia* new genus

Type species.—*Vaugonia hectorleanzai* Pérez and Reyes in Pérez et al., 2008, p. 91–92, from the late Sinemurian–early Toarcian of Antofagasta and Atacama Regions, Chile.

Other species.—*Vaugonia vancouverensis* Poulton, 1976; *Vaugonia oregonensis* Poulton, 1979.

Diagnosis.—Elongate, opisthogyrate shell; with slightly protruding carinae at early growth stages, rounded angulations at late growth stages. Escutcheon slightly depressed, smooth. Area with fine commarginal costellae, usually densely spaced; costellae wavy or irregular at late growth stages. Sub-median groove developed on the area. Antecarinal space barely developed or absent. Flank with oblique costae, in three sets: posterior one subparallel, anteroventrally sloping and orthogonal to marginal angulation; medium set sub-horizontal to slightly anterodorsally directed; anterior set short and orthogonal to anterior margin. Posterior and median sets of costae meeting towards mid-flank; median and anterior sets of costae meeting along a radial anterior line. Anterior and median sets of costae replaced by thin commarginal costae at late growth stages. Flank costae (especially the posterior set) with small, irregular tubercles, sometimes barely developed or fading away.

Occurrence.—Sinemurian to Toarcian from the Pacific coast of the Americas.

Etymology.—The Greek prefix *pseudo-* meaning false, and *-vaugonia* for the morphologically similar genus: "False *Vaugonia*."

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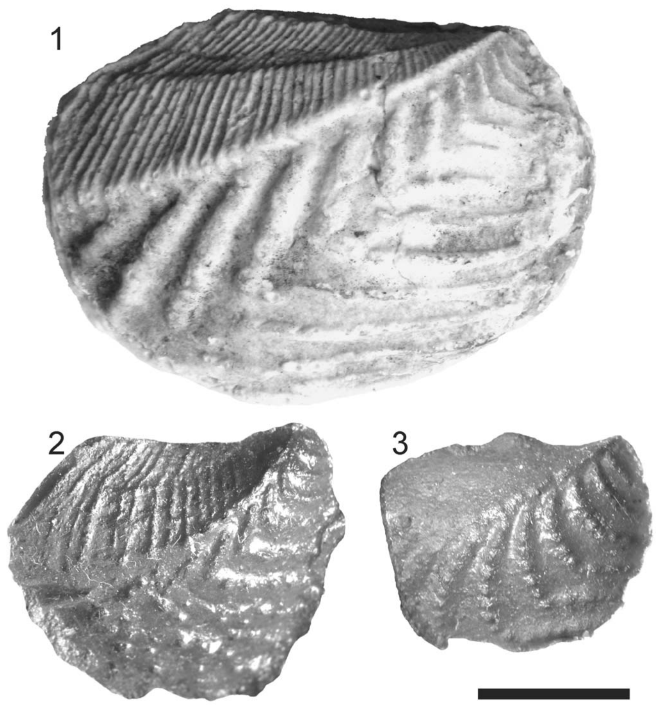

Figure 14. *Vaugonia* species from Japan and North America. Scale bar = 10 mm. (**1**) *Vaugonia veronica* Crickmay, cast of the holotype (SNGM 7530), Middle Jurassic, British Columbia, Canada; (**2**) *Vaugonia yokoyamai* var. *gracilis* Kobayashi and Mori, external cast of a left valve (SNGM 7535), Hettangian, Shizukawa area, Japan; (**3**) *Vaugonia niranohamensis* Kobayashi and Mori, external cast of the holotype, a left valve (SNGM 7523), Hettangian, North coast of Bentenzaki, Japan.

Remarks.—Pseudovaugonia hectorleanzai n. comb. shares with other Myophorelloidea the area ornamentation pattern, with commarginal costellae and a sub-median radial groove. The posterior set of flank costae, orthogonal to the marginal angulation, relates it to *M. infraclavellata* n. comb. *Vaugonia oregonensis*, from late Pliensbachian beds of Oregon (Poulton 1979, p. 23, figs. 10.14–10.19), shows strong affinities with *P. hectorleanzai* n. comb., as already recognized by Pérez et al. (2008), and hence it is included in the new genus. *Vaugonia vancouverensis*, from the Pliensbachian? of Vancouver Island, British Columbia (Poulton 1976, p. 48, pl. 8, figs. 13–20), shows most of the characters of *Pseudovaugonia* n. gen. (area with submedian groove, posterior set of costae coarser, with tubercles and almost perpendicular to the antecarinal space). There is no clear indication of an anterior set of costae at early growth stages, but Poulton (1979, p. 23) stated that juveniles of *V. oregonensis* and *V. vancouverensis* may be indistinguishable.

The species included in *Pseudovaugonia* n. gen. were originally referred to the genus *Vaugonia* (Poulton, 1976, 1979; Pérez et al., 2008) due to the V-shape of flank costae. We regard this shared character as convergent and consider *Pseudovaugonia* n. gen. as closely related to *Moerickella* n. gen., and thus a member of the Myophorellidae.

The genus *Vaugonia* Crickmay, 1930 was assigned to the old "section Undulatae," which includes most species with a V or L pattern of flank costae (e.g., Kobayashi and Mori, 1955, p. 77). The holotype of the type species of *Vaugonia*, *V. veronica* Crickmay, 1930, from the Middle Jurassic of British Columbia (GSC27715, a cast of which, under number SNGM 7530, was studied at the SERNAGEOMIN, Chile; Fig. 14.1), has a commarginally ornamented area divided in two, although instead of a groove, the division is formed by a small step, with the dorsal part at a lower level than the ventral part. This step is what Crickmay (1930), in his original diagnosis for *Vaugonia*, characterized as a median carina with a median furrow along the dorsal side. No tubercles are found on flank costae in *V. veronica*; umbonal costae are sub-commarginal, later developing a bend, which finally results in a subdivision of costae into two sets: a sub-vertical posterior one and a sub-horizontal to sub-commarginal anterior one. These two sets meet at right angles on the central to posterior flank, generating an L pattern rather than a V pattern (Fig. 14.1).

The oldest known species assigned to *Vaugonia* are *V. niranohamensis* Kobayashi and Mori, 1955 (Fig. 14.3), *V. yokoyamai* Kobayashi and Mori, 1955 (including its variety *gracilis*; Fig. 14.2), *V. namigashira* Kobayashi and Mori, 1955, and *V. kojiwa* Kobayashi and Mori, 1955, from the Hettangian of Japan. *Vaugonia niranohamensis* bears a smooth area (Fig. 14.3), while the remaining three species bear commarginal costellae, like in *V. veronica* (Fig. 14.1, 14.2). All of them bear a radial sub-median step in the area, like the one found in *V. veronica*, but most of them (with the exception of *V. kojiwa*) also bear small rounded tubercles (Fig. 14.2, 14.3).

The shared characters of *V. veronica* with the Hettangian Japanese species suggest a true phylogenetic relationship among them. Consequently, we consider as diagnostic features of the genus *Vaugonia* (1) a V or L flank costae pattern together with (2) a radial sub-median step in the area, with the dorsal part depressed relative to the ventral part. Its area can be smooth or commarginally ornamented. A thorough revision of the genus, far beyond the scope of this paper, would be necessary to determine if such variations represent two evolutionary lineages or else iterative features. The presence of tubercles and a widening antecarinal space seem to be primitive characters within *Vaugonia*, both subsequently lost in the type species.

Considering this characterization, the genus *Vaugonia* seems to be absent from the Lower Jurassic of South America. Specimens attributed to *V. niranohamensis* and *V. yokoyamai* were mentioned and described from the Batá Formation from Colombia (Geyer, 1973, p. 77–79), originally thought to be Jurassic in age, but were later assigned to the genus *Syrotrigonia* Cox, 1952 (Etayo-Serna et al., 2003; Echevarría et al., 2015), and their age was established as Valanginian–Hauterivian (Etayo-Serna et al., 2003). *Vaugonia* sp. 1 and *Vaugonia* sp. 2 described by Pérez et al. (2008), from the Toarcian (sp. 1) and Pliensbachian (sp. 2) of Atacama, have a flat area, suggesting they are not genuine representatives of *Vaugonia* sensu stricto. Some of the species described by Pérez et al. (2008) within *Vaugonia* may be better placed in *Promyophorella* (see Remarks under *Promyophorella*). Kobayashi (in Kobayashi and Mori, 1955, p. 74), when revising the Vaugoniinae, considered *Vaugonia* and *Myophorella* as belonging to two independent lineages. Such a claim is strongly supported by the diverse Hettangian record of *Vaugonia* in Japan (Kobayashi and Mori, 1955) on one hand, and, on the other, by the Sinemurian–Pliensbachian phylogenetic series presented here, comprising *Frenguelliella*

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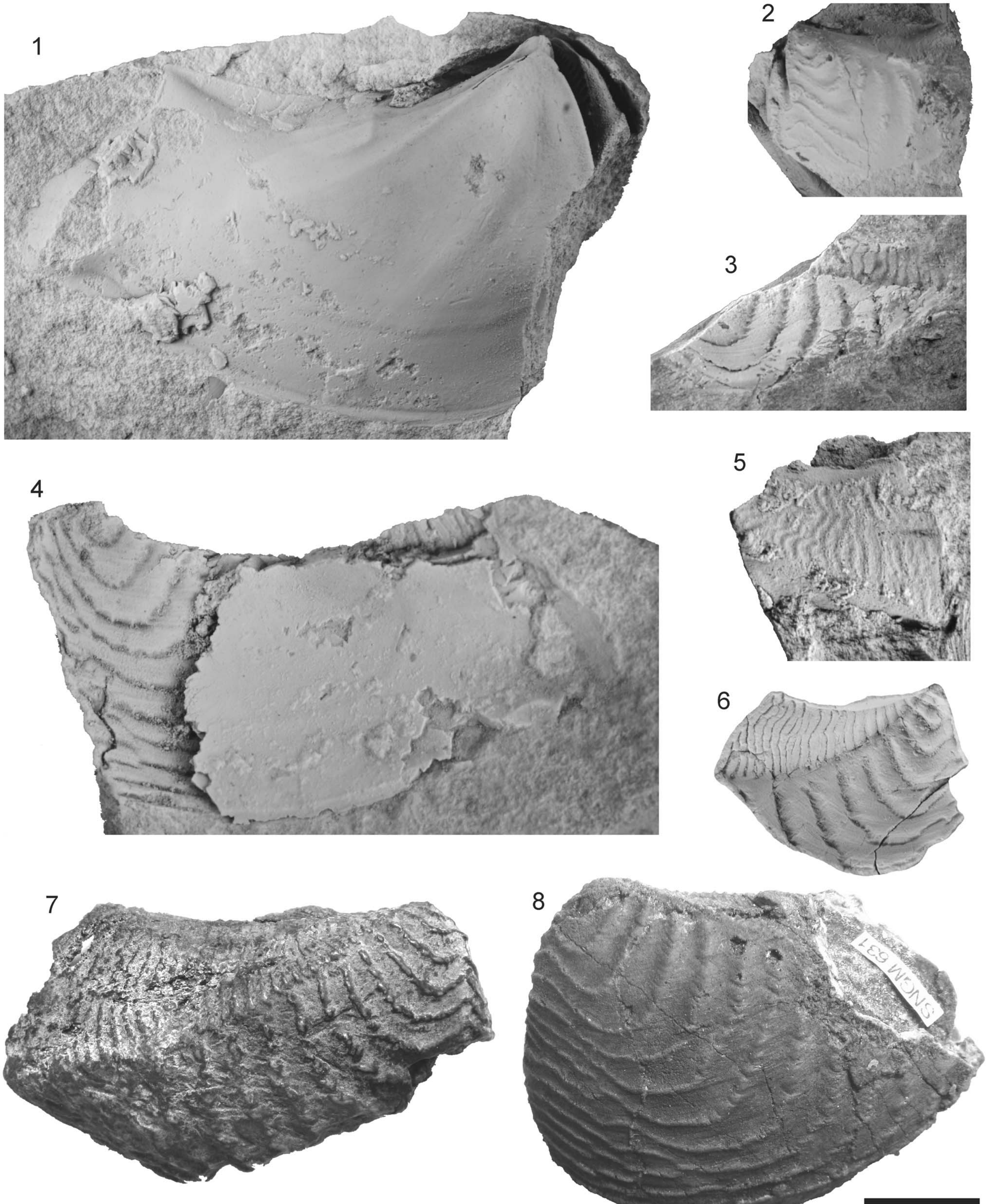

Figure 15. *Pseudovaugonia hectorleanzai* (Pérez and Reyes in Pérez et al.) n. comb. from the Early Jurassic of Argentina and Chile. Scale bar = 10 mm. (**1, 4**) MLP 36322, right valve preserved as internal mold and external mold with shell remains, Toarcian, Arroyo Lapa; (**2, 3, 5**) MLP 36321a–c, Toarcian, Arroyo Lapa; (**2**) fragmentary composite mold of left valve; (**3**) fragmentary external mold of right valve; (**5**) fragmentary composite mold of left valve; (**6**) MLP 36324, external mold of a left valve, Toarcian, Las Overas; (**7**) SNGM 644, right valve, Sinemurian, Sierra Limón Verde, Chile; (**8**) holotype, SNGM 631, shell, left lateral view, Toarcian, Quebrada Chanchoquín, Chile.

eopacifica n. sp., *Moerickella infraclavellata* (Möricke, 1894) n. comb., and *Promyophorella basoaltorum* n. sp.

Pseudovaugonia n. gen. and *Moerickella* n. gen. share many characters (compare Fig. 15.7 with Fig. 13.1, 13.5): the escutcheon is smooth; the area bears commarginal costellae and a median groove (instead of a step); the posterior set of costae departs from the antecarinal space almost at right angles (whereas this angle is obtuse in *Vaugonia*, Fig. 14.1–14.3); flank costae carry similar irregular elongate tubercles, suggesting that the former evolved from the latter rather than being closely related to *Vaugonia*. The main morphological changes from *Moerickella* n. gen. to *Pseudovaugonia* n. gen. are: (1) development of the anterior and median sets of flank costae, resulting in the V pattern; (2) the reduction of the antecarinal space; and (3) the wavy or irregular costellae on the posterior part of the area (Fig. 15.7).

Pseudovaugonia hectorleanzai (Pérez and Reyes in Pérez et al., 2008)
Figure 15

v 1980 *Vaugonia* n. sp.; Hillebrandt, pl. 2, fig. 1.
*v 2008 *Vaugonia hectorleanzai* Pérez and Reyes in Pérez et al., p. 91, pl. 13, fig. 9, pl. 15, figs. 3, 5–11, pl. 16, figs. 1, 3, 8, 9, 11, 12, 14, 15.
v 2008 *Vaugonia hectorleanzai*; Pérez and Reyes, p. 28.

Type material.—Holotype: SNGM 631, from the early Toarcian of Quebrada Chanchoquín/Paitepén, Atacama, Chile, figured by Hillebrandt (1980, pl. 2, fig. 1), Pérez et al. (2008, pl. 15, fig. 7), and Figure 15.8.

Diagnosis.—Medium-sized, opisthogyrate, elongate shell. Area narrow with commarginal costellae, irregular or geniculate towards the posterior end; submedian groove coincident with the inflection of posterior costellae. Antecarinal space barely developed. Anterior radial ruga developed on flank. Flank costae added from the antecarinal space (posterior set of strong, tuberculate costae) and the anterior radial ruga (anterior and median sets of smooth, narrow costae). Posterior and median sets meeting at mid-flank in a V pattern at early stages (more pronounced at late juvenile stages), or in an L pattern (adult stages).

Occurrence.—Las Overas (West of Malargüe region), Mendoza Province; Arroyo Lapa, central Neuquén Province; early Toarcian (*D. hoelderi* Biozone [≈ Serpentinum Biozone]) (Fig. 3). Also probably at Arroyo La Laguna (Los Patos region), San Juan Province; Pliensbachian or Toarcian. The species is also found in beds referred to the late Sinemurian and early Toarcian of Antofagasta and Atacama in Chile (Pérez et al., 2008).

Description.—Medium-sized, opisthogyrate, elongate shell. Escutcheon not preserved. Area narrow, with transverse commarginal costellae, somewhat irregular or geniculated towards the posterior end (Fig. 15.5); with a submedian groove coincident with the inflection of posterior costellae. Marginal carina slightly protruding at early growth stages (Fig. 15.2, 15.6), an angulation at late stages (Fig. 15.5, 15.6), with small tubercles at the intersection with area costellae (Fig. 15.3). Flank with narrow, barely developed antecarinal space (Fig. 15.3, 15.6). Flank with oblique costae showing a V-shaped pattern. New flank costae added from two radial elements: the antecarinal space and the anterior radial ruga (Fig. 15.2, 15.6, 15.7). Two branches added on the anterior radial ruga during shell growth: one anteroventrally directed (anterior set), the other posteroventrally (median set). Ventrally directed branch (posterior set) added adjacent to antecarinal space. Costae of posterior and median sets meeting at mid-flank. Anterior and median sets sub-commarginal and continuous in late growth stages.

Materials.—One right valve preserved as internal and external molds with shell fragments: MLP 36322; fragmented composite and external molds MLP 36321, 36323, 36324. MLP 36398, a poorly preserved shell, most likely belonging to this species. Specimens from Chile SNGM 630–644, 673.

Measurements.—MLP 36322: L = 51 mm, H = 32 mm; holotype (SNGM 631; slightly broken posteriorly): L = 40 mm, H = 28 mm.

Remarks.—The main characteristics of the Argentinian material agree with those described and illustrated by Pérez et al. (2008) as *Vaugonia hectorleanzai* from the late Sinemurian–early Toarcian of Chile. *Pseudovaugonia hectorleanzai* n. comb. can be distinguished from other *Pseudovaugonia* n. gen. species by: (1) the presence of a radial anterior ruga, and (2) the presence of tubercles on the posterior set of flank costae. As pointed out by Pérez et al. (2008), the species *Pseudovaugonia oregonensis* (Poulton, 1979) n. comb. from the late Pliensbachian of Oregon (USA) is very similar to *P. hectorleanzai* n. comb., but differs by lacking tubercles on the posterior set of flank costae. *Pseudovaugonia vancouverensis* (Poulton, 1976) n. comb., from the (probable) Pliensbachian of Vancouver Island (Canada), is only incipiently tuberculate and has a more delicate sculpture. No anterior radial ruga is mentioned for any of the North American species.

Trigonia substriata Giebel in Burmeister and Giebel, 1861, from the Early–Middle Jurassic of Juntas, Chile, shares with *Pseudovaugonia hectorleanzai* n. comb. an early development of V-shaped flank costae. Nevertheless, according to the figure provided in Burmeister and Giebel (1861, pl. 2, fig. 4), the posterior set of flank costae departs from the antecarinal space at obtuse anterior angles (like in *Promyophorella*), and according to his descriptions, the area in *T. substriata* is smooth or with very fine transverse wrinkles, unlike the costellae observed in *P. hectorleanzai* n. comb.

Genus *Promyophorella* Kobayashi and Tamura, 1955

Type species.—*Myophorella* (*Promyophorella*) *sigmoidalis* Kobayashi and Tamura, 1955, pl. 5, figs. 1–3; Hayami, 1975, pl. 5, fig. 9. Bajocian, Miyagi Prefecture (Japan).

Diagnosis.—Slightly to clearly opisthogyrate shell; typically crescentic. Well-defined prominent tuberculate carinae at early

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growth stages, sharp tuberculate angulations at late growth stages. Area surface variably developed, with thin commarginal costellae, sometimes fading at late growth stages; with median groove. Flank with narrow oblique and diverging costae carrying small numerous regular tubercles aligned along their tops; costae generating a clearly obtuse anterior angle with the antecarinal space. Antecarinal space smooth. Escutcheon smooth or with transverse pustulose costellae.

Remarks.—When analyzing the variability within the genus *Myophorella* Bayle, 1878 (pl. 120), Kobayashi and Tamura (1955) defined the subgenus *Promyophorella* for those species with narrow slender costae bearing numerous small tubercles on top. *Myophorella* s.s. differs from *Promyophorella* by its subtriangular, slightly opisthogyrate to orthogyrate, large shell, and its stout flank costae with large button-like tubercles. Kobayashi and Tamura (1955) considered *Promyophorella* as ancestral to *Myophorella* s.s., but they did not regard them as different genera because they recognized numerous intermediate forms. This transition might have occurred iteratively by heterochrony, with the general morphology characteristic of *Myophorella* s.s. representing a paedomorphic state (Echevarría, 2016). The diagnosis provided here is a modification from that of Kobayashi and Tamura (1955), stressing the main differences from *Myophorella* s.s., but also from *Moerickella* n. gen., which differs from *Promyophorella* by its subparallel smoothly curved flank costae orthogonal to the antecarinal space.

Fleming (1987) followed Kobayashi and Tamura (1955), who listed *Scaphogonia argo* Crickmay, 1930, type species of *Scaphogonia*, as a species of *Myophorella* (*Promyophorella*), and considered *Promyophorella* as a junior synonym of *Scaphogonia*.

We regard *Scaphogonia* as a separate genus, related to *Promyophorella*, but differing from it by its flank ornamentation pattern formed by two sets of ornamentation: a main set formed by nodate costae departing from the area at obtuse anterior angles and roughly orthogonal to the ventral margin; and an anterior set of nodate costae orthogonal to the anterior margin that do not meet the costae of the posterior set.

When characterizing the genus *Scaphogonia*, Crickmay (1930, p. 51) also defined the genus *Haidaia* Crickmay, with *Trigonia dawsoni* Whiteaves, 1878, as type species. Kobayashi and Tamura (1955) considered *Haidaia* as a third subgenus in their conception of *Myophorella*, being characterized by narrow ridges extending ventrally from tubercles on flank costae (*Haidaia*-like ornamentation in the sense of Leanza, 1993, p. 60). Although we regard this particular kind of ornamentation as a significant character within the Myophorellidae, we consider it unlikely to characterize a particular phylogenetic lineage within the family because in some of the early species here described it seems to be already outlined. Poulton (1979, p. 33–34), when describing *Trigonia dawsoni* based on new, abundant, and well-preserved material, found that the discrepant anterior ornamentation may also be present in many shells of this species, so we regard *Haidaia* as junior synonym of *Scaphogonia*.

As remarked under *Pseudovaugonia hectorleanzai* n. comb., the L or V patterns of flank costae might have appeared within *Promyophorella* convergently with that observed in *Vaugonia*. We consider that the material assigned by Pérez et al., 2008 to *Vaugonia* cf. *V. gottschei* (Möricke, 1894) from Atacama (Pliensbachian?) would be better placed under *Promyophorella*, close to *P. exotica*. *Vaugonia* cf. *V. substriata* (Burmeister and Giebel, 1861) Pérez et al. (2008), from Atacama (middle Toarcian), is also assigned to *Promyophorella*, showing a similar ornamentation pattern to that of *P. reginae* (Pérez and Reyes in Pérez et al., 2008). In both cases, the flank ornamentation pattern is relatively simple, and the area shows characters typical of early species of *Promyophorella* (commarginal area ornamentation with a submedian groove, tuberculate marginal angulation and a widening antecarinal space). Most of the Jurassic species described as *Vaugonia* (*Vaugonia*) from Antarctica (*V.* [*V.*] *orvillensis*, *V.* [*V.*] sp.; Kelly, 1995) and New Zealand (*V.* [*V.*] *spedeni*, *V.* [*V.*] *kawhiana, V.* [*V.*] sp. A, *V.* [*V.*] sp. B; Fleming, 1987) are actually better placed within the *Promyophorella* lineage, revealing the strong southern diversification of the group during the Middle and Late Jurassic. The exception is *Vaugonia kahuika* Fleming, 1987, from the lower Temaikan (≈ Aalenian) from New Zealand, which is actually referable to *the Vaugoniidae*.

The genus *Orthotrigonia* Cox, 1952, originally proposed as a subgenus of *Myophorella* and later (Cox in Cox et al., 1969) considered a subgenus of *Vaugonia*, is close to *Promyophorella*, sharing with it the area with commarginal ornamentation and a submedian groove, and tuberculate marginal carina/angulation. *Orthotrigonia* differs from *Promyophorella* by its flank ornamentation pattern, with V-shaped or L-shaped costae at early growth stages and steep, straight costae bifurcating anteriorly at late growth stages.

The genus *Scaphorella* Leanza, Pérez, and Reyes, 1987, also shows affinities with *Promyophorella*, both sharing an area with thin commarginal costellae and a median groove, and flank costae with small tubercles on top. The species *S. susanae* Pérez and Reyes in Pérez et al., 2008, from the latest Toarcian and early Aalenian of Atacama, Chile, even has a smooth antecarinal space, widening posteriorly, although this character is absent in the type species, *S. leanzai* (Lambert, 1944). *Scaphorella* differs from *Promyophorella* by its two sets of flank costae: a posterior one of almost straight costae, orthogonal to the ventral margin, and an anterior one of arcuate costae, reaching the anterior margin at right angles; both sets meet at the mid-anterior flank, frequently with two anterior costae meeting a posterior one (bifurcating flank costae). This ornamentation pattern is very similar to that found in *Scaphogonia*, being the only difference the continuity of anterior and posterior costae in *Scaphorella*. A revision of the Middle Jurassic species involved is beyond the scope of this paper; for the time being, we tentatively consider them as separated taxa.

Promyophorella basoaltorum new species
Figure 16.1–16.24, 16.27, 16.28

? 1891 *Trigonia substriata* Giebel; Behrendsen, p. 387.
? 1922 *Trigonia substriata* Giebel; Behrendsen, p. 172.
v 1942 *Trigonia exotica* Steinmann [sic]; Carral Tolosa, p. 56, pl. 6, figs. 1a–c.
v 1978a *Myophorella* cf. *M. araucana* (Leanza); Volkheimer et al., p. 304.

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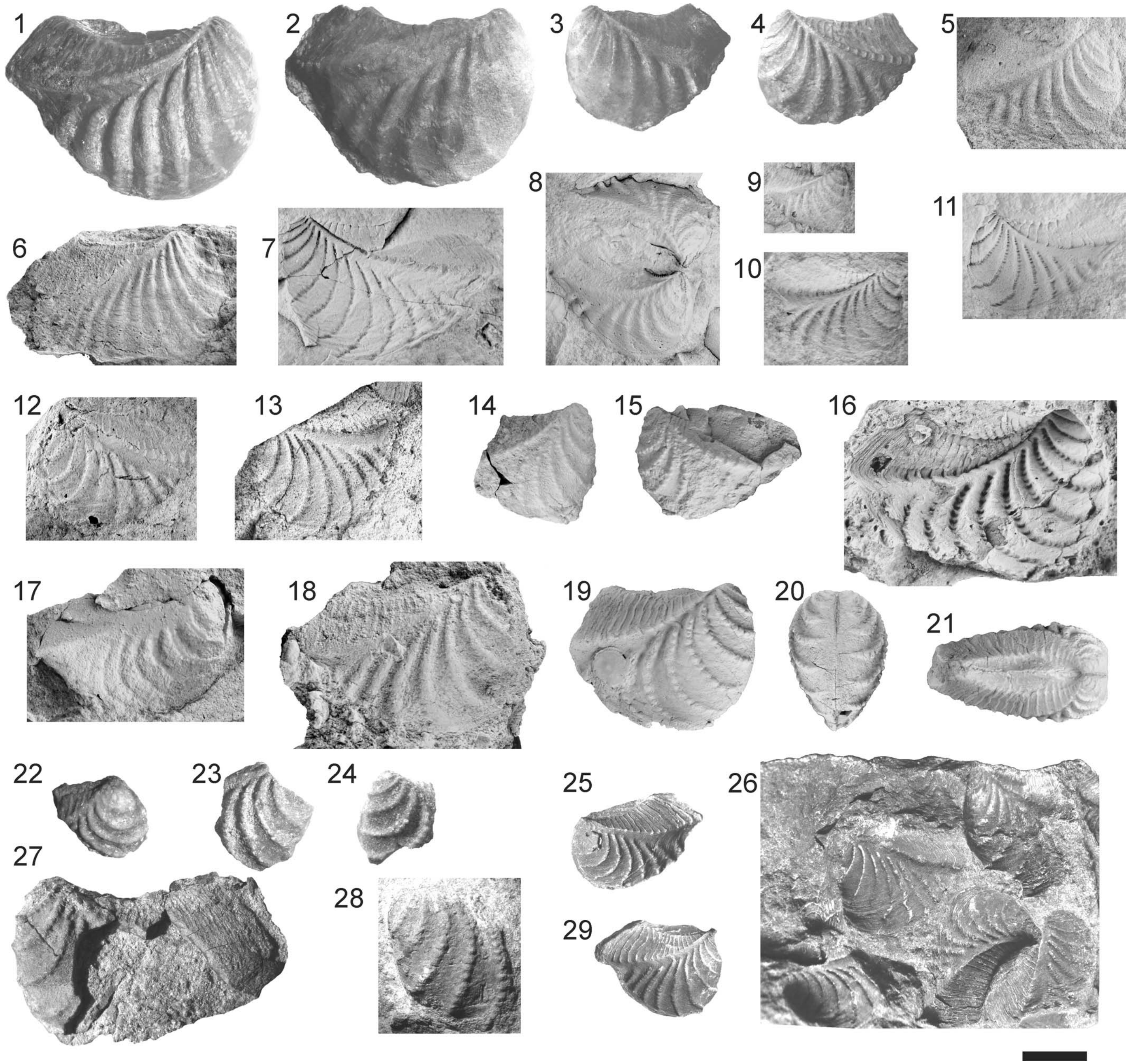

Figure 16. *Promyophorella* species from the Early Jurassic of Argentina and Chile. Scale bar = 10 mm. (**1–24, 27, 28**) *Promyophorella basoaltorum* n. sp. (**1**) SNGM 609, right valve, Pliensbachian, Quebrada Asientos, Chile; (**2**) SNGM 600, right valve, Pliensbachian, Quebrada Asientos, Chile; (**3**) SNGM 604, shell, left lateral view, Pliensbachian, Quebrada Asientos, Chile; (**4**) SNGM 605, left valve, Pliensbachian, Quebrada Asientos, Chile; (**5**) MLP 36370, composite mold of right valve, Pliensbachian, Arroyo La Laguna; (**6**) MLP 28761a, composite mold of right valve, Pliensbachian, Arroyo Serrucho; (**7**) IANIGLA-PI 3273, external mold of right valve, Pliensbachian, Arroyo Serrucho; (**8**) IANIGLA-PI 3276, composite mold of shell in butterfly position, Pliensbachian, Arroyo Serrucho; (**9**) IANIGLA-PI 3250, composite mold of right valve, Pliensbachian, Arroyo Serrucho; (**10**) IANIGLA-PI 3235, external mold of left valve, Pliensbachian, Arroyo Serrucho; (**11**) holotype, IANIGLA-PI 3230, external mold of a right valve, Pliensbachian, Arroyo Serrucho; (**12**) MLP 28761b, composite mold of left valve, Pliensbachian, Arroyo Serrucho; (**13**) MLP 36383, composite mold of left valve, Pliensbachian, Cerro Puchenque; (**14**) MLP 36388a, right valve, Pliensbachian, Cerro Tricolor; (**15**) MLP 36388b, left valve, Pliensbachian, Cerro Tricolor; (**16**) MLP 15322, external mold of left valve, Pliensbachian, South from Rahue-Aluminé; (**17**) MLP 36389, composite mold of right valve, Pliensbachian, Arroyo Lonqueo; (**18**) MLP 36394, composite mold of right valve, Subida a Sañicó; (**19–21**) paratype, MLP 6725, complete shell, right lateral, anterior and dorsal views, Pliensbachian, Cerro Roth; (**22, 23**) MPEF-PI 6386a, b, fragmentary right valves, late Pliensbachian–early Toarcian, Nueva Lubecka; (**24**) MPEF-PI 6399, fragmentary left valve, late Pliensbachian–early Toarcian, Nueva Lubecka; (**27**) MPEF-PI 6392, left valve, late Pliensbachian–early Toarcian, Nueva Lubecka; (**28**) MPEF-PI 6390, anterior part of left valve, late Pliensbachian–early Toarcian, Nueva Lubecka; (**25, 26, 29**) *Promyophorella* aff. *P. basoaltorum* n. sp., CPBA 19657, external molds preserved on a single slab, early Pliensbachian, Cerro Cuche: (**25**) CPBA 19657c, detail of an external mold of right valve; (**26**) rock surface showing several external molds; (**29**) CPBA 19657a, detail of an external mold of left valve.

v 1978b *Myophorella* cf. *M*. *araucana* (Leanza); Volkheimer et al., p. 212 (table 2).

v 1978b *Myophorella*? sp.; Volkheimer et al., p. 212 (table 2).

v 1980 *Myophorella catenifera* (Hupé); Hillebrandt, pl. 2, fig. 4.

v 1981 *Myophorella catenifera* (Hupé); Hillebrandt and Schmidt-Effing, p. 10.

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	1982	*Myophorella* (*Myophorella*) *araucana* (Leanza); Pérez, pl. 14, fig. 9.
v	1982	*Myophorella araucana* (Leanza); Cuerda et al., p. 331.
?	1983	*Myophorella* (*Promyophorella*) sp. indet.; Ishikawa et al., p. 41, pl. 1, fig. 8.
vp	1987	*Myophorella* (*Myophorella*) *araucana* (Leanza); Leanza and Garate-Zubillaga, p. 211, pl. 1, figs. 6, 7, but not fig. 8.
v	1993	*Myophorella* (*Myophorella*) *catenifera* (Hupé); Leanza, p. 29, pl. 2, figs. 10, 11.
	1993	*Myophorella* (*Myophorella*) cf. *M. tuberculata* (Agassiz); Leanza, p. 29, pl. 1, fig. 9.
v	2008	*Myophorella* (*Myophorella*) *araucana* (Leanza); Pérez and Reyes in Pérez et al., p. 82, pl. 11, figs. 1, 4, 5, 8, pl. 12, figs. 2–7, 9, 11, 12, pl. 13, figs. 1, 7.
v	2016	*Myophorella araucana*? (Leanza); Echevarría, p. 179, figs. 1d, e, m, 3a, 6d, 10.

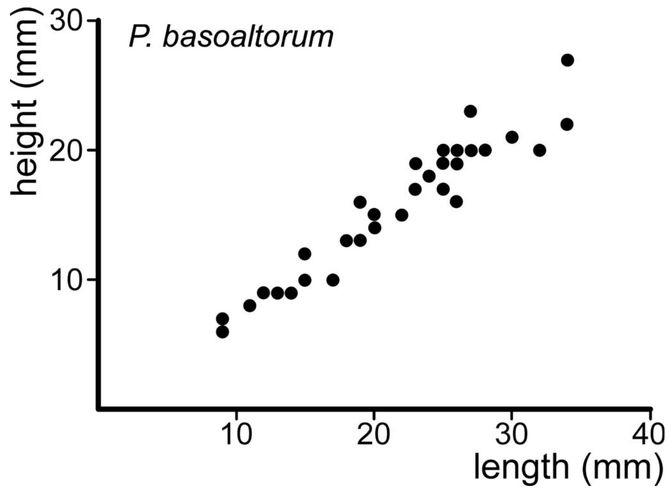

Figure 17. Scatter plot of height vs. length for *Promyophorella basoaltorum* n. sp.

Type materials.—Holotype: IANIGLA-PI 3230, right valve external mold from the Pliensbachian of Arroyo Serrucho (Fig. 16.11); paratype MLP 6725, a well-preserved shell with both valves from the Pliensbachian of Cerro Roth (Fig. 16.19–16.21).

Diagnosis.—Opisthogyrate, crescentic, slightly rostrate shell, with semicircular anteroventral margin. Escutcheon with transverse costellae (oblique to growth lines) variably developed. Area wide with commarginal costellae. Both carinae prominent at early growth stages, sharp angulations at late stages. Flank with arcuate diverging costae with small tubercles along their tops.

Occurrence.—Arroyo La Laguna (Los Patos region), San Juan Province; Puesto Araya (Atuel River region), Arroyo Peuquenes, Arroyo Portezuelo Ancho, Portezuelo Ancho, Santa Elena, La Bajada (Las Leñas/Valle Hermoso region), Arroyo Serrucho, Cerro Puchenque (west of Malargüe region), Cerro Tricolor (Grande River region), Mendoza Province; Ñiraico, Estación Rajapalo (Cordillera del Viento region), 13.5 km south of Rahue-Aluminé, Lonqueo (Central Neuquén region), Estancia Santa Isabel, Subida a Sañicó, Cerro Roth Sur (Piedra Pintada region), Neuquén Province; Nueva Lubecka (Genoa River region), Chubut Province. Early Pliensbachian (*M. externum* or *E. meridianus* Biozone [≈ Jamesoni/Ibex Biozone]) to early Toarcian (Tenuicostatum Biozone; dubious specimens in *D. hoelderi* Biozone [≈ Serpentinum Biozone]) (Fig. 3). In Chile, the species was found in Quebrada Asientos, Atacama (Pérez and Reyes, 1977; Pérez, 1982; Pérez et al., 2008 under *Myophorella* [*Myophorella*] *araucana* Leanza, 1942) in the late Pliensbachian. A very small shell from the Early Jurassic of southern Peru (Ishikawa et al., 1983) agrees in most general characters with this species.

Description.—Small, clearly opisthogyrate shell; crescentic, sometimes slightly rostrate. Semicircular antero-ventral margin; straight and wide posterior margin, with area occupying ∼1/3 of shell surface. Escutcheon margin slightly concave, with the umbo and the posterodorsal angle slightly projecting dorsally. Escutcheon with transverse costellae (oblique to growth lines) (Fig. 16.11, 16.21) continuous with those on the area. Escutcheon carina prominent at early growth stages, later becoming a sharp angulation, with small pustules at its intersection with costellae (Fig. 16.7, 16.10, 16.11, 16.21). Area with commarginal costellae, evenly arranged (8–14 costellae/cm) in early growth stages, later replaced by irregular and fine ridgelets (Fig. 16.13, 16.18, 16.19). Sub-median groove (slightly displaced dorsally) in the area (Fig. 16.11, 16.21), sometimes barely impressed. Prominent marginal carina at early growth stages, sharp angulation at late stages; with small pustules at its intersection with costellae (swellings of the costellae at late growth stages) (Fig. 16.4, 16.10–16.12, 16.16). Antecarinal space smooth, widening posteriorly (Fig. 16.1–16.13, 16.16), crossed by flank costae at very early growth stages. First two flank costae sub-commarginal, later on, oblique to growth lines, evenly curving anteriorwards; in some specimens, initial segment of the costae slightly curved, increasing curvature during ontogeny (Fig. 16.5–16.7). Flank costae bearing small tubercles along top. Flank costae departing from the antecarinal space at obtuse anterior angles and diverging during growth.

Internal radial ridge in the posterior part of the inner surface, perpendicular to area margin (Fig. 16.17). Posterior adductor muscle scar rounded, dorsally located towards mid-length, half underneath the area, and half underneath the escutcheon. Nymph short (Fig. 16.21).

Etymology.—Dedicated to the Basoalto family from Arroyo Serrucho (type locality of the species), for their warm hospitality and invaluable help to geologists and paleontologists through many years.

Materials.—The types plus ∼125 specimens: IANIGLA-PI 3216–3253, 3262, 3265–3271, 3272A, 3273–3285, 3286A, 3287, 3289–3291, 3292A, 3293–3296, 3303, 3304, 3318, 3350, 3351; MPEF-PI 2907, 2909, 2965, 3158, 3375, 6386,

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6390, 6392, 6394, 6396, 6399; MLP 6253 (part), 15322, 15437, 15535, 15554, 17148, 17503, 28761, 33221, 36368–36394; MOZ-PI 1487, 2682. Specimens from Chile: SNGM 596–616.

Measurements.—Holotype (IANIGLA-PI 3230): L = 25 mm, H = 21 mm; paratype (MLP 6725): L = 29 mm, H = 23 mm, W = 16 mm; MLP 36370: L = 25 mm, H = 20 mm; MLP 15322: L = 42 mm, H = more than 27 mm; MLP 36394: L = 34 mm, H = 27 mm; MLP 28761: L = 28 mm, H = 20 mm; the remaining measurements are plotted on Figure 17.

Remarks.—*Promyophorella basoaltorum* n. sp. is the earliest species of *Promyophorella* and is most likely the ancestral stock of all younger species, but the genus is in need of a revision in order to understand its later diversification. Some of the variability within this species relates to flank ornamentation. Most specimens bear evenly curved costae (Fig. 16.5, 16.11, 16.19), while in others, the costae have an almost straight initial portion and a sudden increase in curvature (J pattern) (Fig. 16.2, 16.6). Usually costae are widely spaced (Fig. 16.11, 16.19, 16.28), whereas some shells show closely spaced costae (Fig. 16.6). Shells are typically small, on occasion, medium-sized (Fig. 16.1, 16.2, 16.16). Elongation is also variable within the species. Although the more typical form has a semicircular antero-ventral margin (Fig. 16.3, 16.4, 16.12, 16.13, 16.19), some shells are more elongate (Fig. 16.6–16.8, 16.17), with the ventral margin longer and slightly less convex than the anterior margin.

The specimens referred by Pérez and Reyes (in Pérez et al., 2008) to *Myophorella araucana* are included here in *P. basoaltorum* n. sp. That material is also highly variable; some shells are semicircular in their antero-ventral margin, while others are more elongate and somewhat rostrate. Flank costae may show a variable pattern (of homogeneous curvature or more J-shaped), but they always diverge clearly. Escutcheon usually has transverse costellae variably developed: from small thorn-like projections developing from the escutcheon carina pustules, to well-developed costellae through entire escutcheon surface.

This taxon is one of the most common trigonioids from the Lower Jurassic of southern South America, having been frequently assigned to closely related but significantly different species. Behrendsen (1891, 1922) referred (but did not figure) some Early Jurassic material from Portezuelo Ancho to *T. substriata*, which may belong here based on specimens collected at the same locality.

Material referable to *P. basoaltorum* n. sp. was referred by Carral-Tolosa (1942) to *Trigonia exotica* Möricke, 1894 (she erroneously cited Steinmann as author), but *T. exotica* differs from *P. basoaltorum* n. sp. by having strongly bent flank costae, usually with anteriorly elongate tubercles on the ventral portion. Many specimens referred in the literature to "*Myophorella araucana* (Leanza, 1942)" (e.g., Pérez et al., 2008), belong in *P. basoaltorum* n. sp. It should be noted that specimen MLP 6725 (now paratype of *P. basoaltorum* n. sp.) was labelled as *Trigonia exotica* in the MLP collection, and though it was available to Leanza, it was excluded from the type series of *P. araucana*. Early Jurassic material from many localities in Chile and Argentina (Hillebrandt, 1980; Hillebrandt and Schmidt-Effing, 1981; Leanza, 1993) referred to *Trigonia catenifera* Hupé, 1854, is here included in *P. basoaltorum* n. sp.

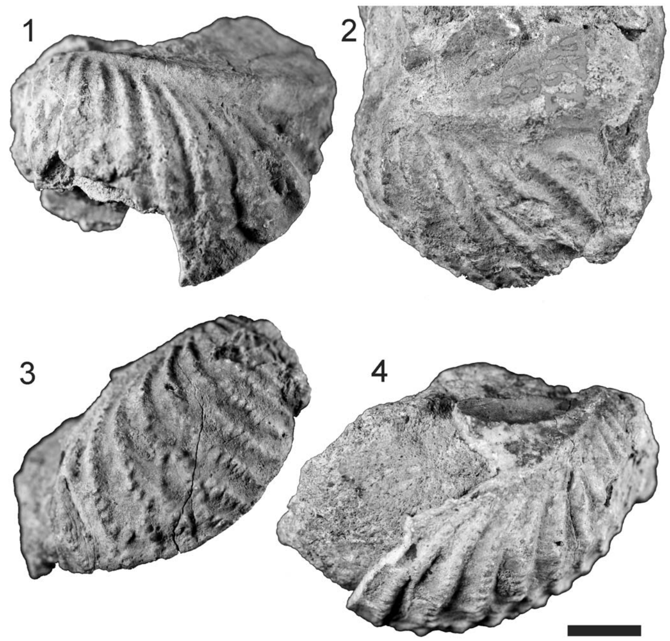

Figure 18. *Promyophorella*? *catenifera* (Hupé), MNHN-GG2005-16393 (photographs courtesy of C. Noyes), Lower Jurassic, Coquimbo, Chile. Scale bar = 10 mm. (**1**) Lectotype, MNHN-GG2005-16393b, left valve (antero-ventrally broken); (**2**) MNHN-GG2005-16393a, left valve; (**3, 4**) MNHN-GG2005-16393c, right valve, antero-ventral and lateral views.

Promyophorella basoaltorum n. sp. differs from other *Promyophorella* species by its: (1) clearly opisthogyrate shell shape, (2) relatively large area surface, and (3) simple (without bifurcations or disruptions) flank costae, evenly curving anteriorwards or with increasing curvature, but never bending.

Promyophorella? *catenifera* (Hupé, 1854) was first described from Coquimbo, Chile, from beds then referred to the Middle Jurassic (Hupé, 1854, p. 328), but later assigned to the Early Jurassic (Pérez and Reyes, 1977, annex I, p. 45). The material described and figured by Hupé is deposited in the Museum National d'Histoire Naturelle in Paris: MNHN-GG2005-16393 (Fig. 18.1–18.4). No holotype was fixed by Hupé (1854), so specimen GG2005-16393b (Fig. 18.1) is here designated as lectotype. The species differs from *P. basoaltorum* n. sp. by having bifurcated costae towards the anteroventral margin (Pérez et al., 2008, p. 86, under remarks for *Myophorella reginae*; Fig. 18.3), sometimes even bifurcating twice (e.g., Fig. 18.3). This character was not mentioned in Hupé's description of the species and is poorly rendered in his figure (Hupé, 1854, p. 328, pl. 5, fig. 8), and may also relate it to the genus *Scaphorella* (see Remarks under *Promyophorella*? *sanjuanina* n. sp.). Pérez and Reyes (1977, p. 12–13, table 4) and Reyes and Pérez (1979, p. 18, table 2) considered that *P.*? *catenifera* was present in the Pliensbachian–Toarcian of Atacama and Coquimbo regions of Chile. Pérez et al. (2008) maintained this temporal and geographical distribution (and they assigned the material from the type locality, Doña Ana, to the Toarcian), but they neither discussed nor illustrated the species.

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Trigonia signata Agassiz var. *keideli* Weaver, 1931, from Early Jurassic deposits of Catan Lil, in Neuquén, seems most likely related to, if not synonymous with, *P. basoaltorum* n. sp. The area/flank surface ratio, the diverging flank costae, the broad, smooth antecarinal space, are all well described by Weaver (1931, p. 235–236), being the main difference the apparently less opisthogyrate shell shape (subquadratic shell with almost straight escutcheon margin, according to Weaver), together with the larger size (Weaver's specimen is 53 mm long and 34 mm high). Unfortunately, Weaver (1931) did not illustrate it, and the type specimen for the variety could not be found (E. Nesbitt, personal communication, 2019). Moreover, in the same work, Weaver also established and figured *Trigonia literata* Young and Bird var. *keideli* Weaver (1931, p. 239–240, pl. 20, fig. 102), which is a primary homonym (ICZN 1999, Art, 57.2), and comes from the Middle Jurassic of central Neuquén. Since both species-group names "*keideli*" were published exactly on the same date, Art. 24.2.2 applies to solve this previously unnoticed homonym conflict. As first revisers, we consider that precedence should be given to *Trigonia literata* var. *keideli* for the sake of nomenclatural stability. Notice that this Middle Jurassic taxon was redescribed by Leanza and Garate-Zubillaga (1983) as *Anditrigonia keideli* (Weaver, 1931), and was subsequently designated as type species of the subgenus *Eoanditrigonia* Leanza (1993, p. 46). Therefore, the species-group name *keideli* Weaver (1931, p. 235) becomes permanently invalid and should not be used for this Early Jurassic myophorelloid species.

Further, the description provided by Weaver (1931, p. 238–239) for other material from the lower Middle Jurassic of southern Mendoza assigned to *Trigonia signata*, suggests a taxon closely related to *P. basoaltorum* n. sp.; unfortunately, no figure was provided.

Promyophorella araucana (Leanza, 1942, p. 162–164, pl. 6, figs. 4–6), from the late Pliensbachian of Neuquén and Chubut provinces, differs from this species by its less opisthogyrate shell shape and relatively smaller area. *Promyophorella exotica* (Möricke, 1894, p. 49, pl. 1, fig. 9, pl. 6, fig. 9), from the Aalenian and Bajocian of Atacama and Valparaíso, Chile (Pérez and Reyes, 1977) differs from *P. basoaltorum* n. sp. by the presence of an inflection in flank costae at late growth stages, resulting in an anterior portion of the costae being commarginal and with weak and elongate tubercles. *Promyophorella reginae* (Pérez and Reyes in Pérez et al., 2008, p. 86–88, pl. 12, fig. 8, pl. 14, figs. 1, 3–6, 8), from the middle and late Toarcian of Atacama, Chile, differs from *P. basoaltorum* n. sp. by its less opisthogyrate shell shape and an anterior bending developed on flank costae at late growth stages.

The type species, *P. sigmoidalis* from the late Aalenian–early Bajocian of Japan, differs from *P. basoaltorum* n. sp. in having a denser ornamentation on the flank, and flank costae bending downwards close to the anterior margin (a sigmoidal pattern). *Promyophorella orientalis* Kobayashi and Tamura, 1955, from the Callovian–Berriasian of Japan (Hayami, 1975) and the Callovian of Alaska (Poulton, 1979), also has denser flank ornamentation, with the anterior part of the flank costae more strongly curved.

The European late Toarcian *P. spinulosa* (Young and Bird, 1828) differs from *P. basoaltorum* n. sp. by having more elongate (sometimes subhorizontal) distal portions of flank costae, and the presence of a plicated median carina on the area (Francis, 2000). According to the figures by Lycett (1872–1879, pl. 3, figs. 4–6), area costellae seem to be more densely spaced in *P. spinulosa*.

Promyophorella hokonuiensis (Fleming, 1987), from the lower Temaikan (≈ Aalenian) of New Zealand, differs from *P. basoaltorum* n. sp. by its more elongate and less opisthogyrate shell, and a narrower antecarinal space. A similar elongate morphology is also found in *Myophorella* sp. B of Poulton, 1979, from the "early Bajocian" (now Aalenian) or late Toarcian of Yukon, Canada, although this last species also differs from *P. basoaltorum* n. sp. by the presence of incipient reticulate ornamentation on the escutcheon.

Promyophorella aff. *P. basoaltorum* new species
Figure 16.25, 16.26, 16.29

1984 *Myophorella* sp.; Pezzuchi and Takigawa, p. 490.
v 2001 *Myophorella* (*Myophorella*) cf. *M. araucana* Leanza; Massaferro, p. 244, figs. 3d, f.

Occurrence.—Cerro Cuche, Chubut Province, early Pliensbachian (*E. meridianus*? Biozone [≈ Ibex/Davoei Biozone]) (Fig. 3) according to Massaferro, 2001, p. 246, based on material referred to *Polymorphites*? sp.

Description.—Very small to small, opisthogyrate, rostrate shell. Slightly convex anterior margin, gradually passing to the convex ventral margin; posterior margin relatively wide (area ∼1/3 of shell surface). Escutcheon excavated, with small transverse costellae variably developed. Escutcheon angulation stepped, a prominent carina at early growth stages. Area with

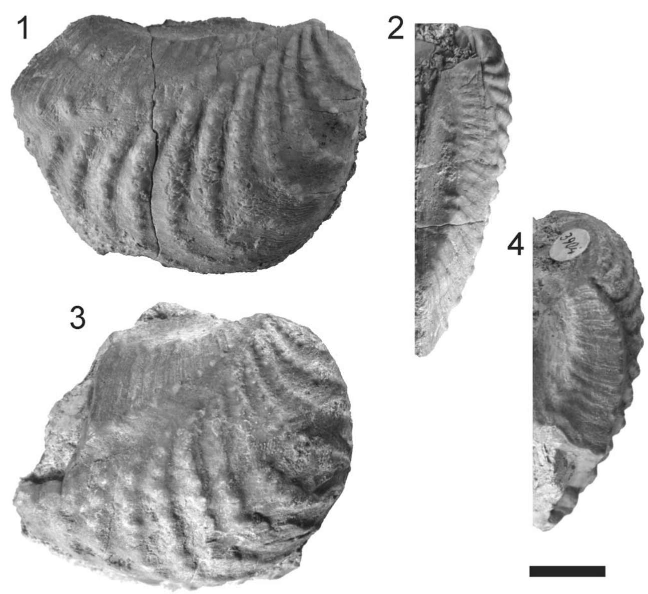

Figure 19. *Promyophorella araucana* (Leanza) from the Pliensbachian of Argentina. Scale bar = 10 mm. (**1, 2**) Lectotype, MLP 6724, shell, right lateral and right dorsal views, Piedra Pintada; (**3, 4**) paralectotype, MLP 3904, fragmentary right valve, lateral and dorsal views, Piedra Pintada.

commarginal costellae, increasing in spacing; sometimes posterior half with closely arranged irregular ridgelets. Antecarinal space smooth and widening posteriorly. Prominent marginal carina at early growth stages, sharp marginal angulation at late stages; area costellae swelling on the angulation. Flank costae oblique to growth lines, anteriorly curved, and diverging, sometimes bearing small, feeble, and closely spaced pustules along top.

Materials.—CPBA 19657 (= cast MLP 20712), a slab with 20 isolated valves.

Measurements.—MLP 20712a: L = 19 mm, H = 15 mm; MLP 20712b: L = 22 mm, H = 16 mm.

Remarks.—This taxon differs from *P. basoaltorum* n. sp. by its smaller shell with finer and more densely arranged ornamentation. It also has a slightly rostrate shell shape. Otherwise, it is similar to *P. basoaltorum* n. sp., with which it is probably closely related if not conspecific.

Promyophorella araucana (Leanza, 1942)
Figure 19

v 1902 *Trigonia* aff. *T. angulata* Sow.; Burckhardt, p. 246, pl. 4, figs. 5, 6.
v 1931 *Trigonia angulata* Sow.; Windhausen, pl. 2, fig. 5. [reproduced from Burckhardt, 1902]
v* 1942 *Trigonia* (*Clavitrigonia*) *araucana* Leanza, p. 162, pl. 6, figs. 4–6.
1977 *Myophorella* (*Myophorella*) *araucana*; Pérez and Reyes, p. 13, pl. 3, figs. 1–3. [reproduced from Leanza, 1942]
v 1992 *Myophorella* (*Myophorella*) *araucana*; Damborenea et al., pl. 116, fig. 12.

Type materials.—Lectotype (here designated): MLP 6724 (Fig. 19.1, 19.2); paralectotypes: some of the other specimens from Leanza's (1942) extant syntypes, MLP 3904 (Fig. 19.3, 19.4), 6253 (part), and 6735. From the type series, we exclude the smallest specimen in MLP 6253.

Diagnosis.—Opisthogyrate, elongate shell, with subtriangular flank. Escutcheon slightly impressed, smooth. Area narrow, with commarginal costellae. Escutcheon bounded by stepped angulation; marginal angulation sharp (stepped in early growth stages). Antecarinal space smooth, widening posteriorly. Flank with oblique, slightly diverging costae bearing small tubercles along top; costae typically with an initial almost straight segment and a sudden anteriorwards inflection towards the anteroventral margin (J pattern).

Occurrence.—Estancia Santa Isabel, Salitral Grande Carrán Curá, Cerro del Vasco, Cerro Roth Sur (Piedra Pintada region), Neuquén Province; possibly Nueva Lubecka (Genoa River region), Chubut Province. Late early Pliensbachian (*A. behrendseni* Biozone [≈ Davoei Biozone]) to late Pliensbachian (*F. fannini* Biozone [≈ Margaritatus Biozone]) (Fig. 3).

Description.—Medium-sized, opisthogyrate, somewhat elongate shell. Subtriangular flank in the most typical forms (Fig. 19.1, 19.3); anterior and ventral margins slightly convex, with a strongly curved transition between them. Area margin narrow; area ∼1/4 of shell surface. Dorso-posterior angle obtuse and slightly projecting dorsally (Fig. 19.1). Escutcheon slightly impressed, with escutcheon margin slightly raised; escutcheon smooth, sometimes with short irregular costellae crossing from the area (Fig. 19.2, 19.4). Both angulations stepped, at least in early growth stages, with pustules at their intersection with area costellae (Fig. 19.3, 19.4). Area with commarginal costellae, evenly arranged (∼8 costellae/cm) and regular anteriorly; in late growth stages irregular and less closely spaced (4 costellae/cm) or fading (Fig. 19.1, 19.2). Mid-area radial groove barely developed and slightly displaced dorsally (Fig. 19.1). Antecarinal space smooth, and widening posteriorly. Flank with oblique costae bearing small tubercles on top; in some shells, small narrow ridges extending posteroventrally from tubercles (*Haidaia*-like ornamentation). Flank costae slightly diverging, with an initial almost straight segment and a sudden anteriorwards inflection towards the anteroventral margin (J pattern; Fig. 19.1, 19.3).

Materials.—The types plus 15 specimens: MLP 13008 (part), 31011, 31573?, 36334–36337; MPEF-PI 6393?, 6395?.

Measurements.—Lectotype (MLP 6724): L = 45 mm, H = 33 mm.

Remarks.—*Promyophorella araucana* can be distinguished from other *Promyophorella* species by its: (1) larger size, (2) less opisthogyrate shell, (3) (almost) smooth escutcheon, (4) narrower area, (5) subtriangular flank, and (6) J pattern in flank costae. Although *P. basoaltorum* n. sp. specimens may show some of the features described above, this combination of characters is only found in shells from southern Neuquén Province (and maybe northern Chubut), suggesting an endemic taxon derived from *P. basoaltorum* n. sp. Many of the shells from elsewhere referred in the literature to *P. araucana* actually belong to *P. basoaltorum* n. sp.

The materials from Cerrito Roth (= Cerro Roth Sur) described and figured by Leanza and Garate-Zubillaga (1987, pl. 1, fig. 8) and from La Amarga (Neuquén) described and figured by Leanza (1993, pl. 1, figs. 4, 5), in both cases as *M. araucana*, most likely belong to a different species, because they differ from both *P. araucana* and *P. basoaltorum* n. sp. in their: (1) larger size, (2) relatively large area, (3) narrow antecarinal space that does not expand posteriorly, and (4) strong flank costae bifurcating towards their distal end. These large, subtriangular, slightly opisthogyrate shells, with large areas, resemble juveniles of *P. basoaltorum* n. sp., and may even suggest a first step along the paedomorphic trends within the group (see Echevarría, 2016). The bifurcating costae resemble those of *Promyophorella*? *sanjuanina* n. sp. and *P.*? *catenifera*.

Promyophorella cf. *P. exotica* (Möricke, 1894)
Figure 20

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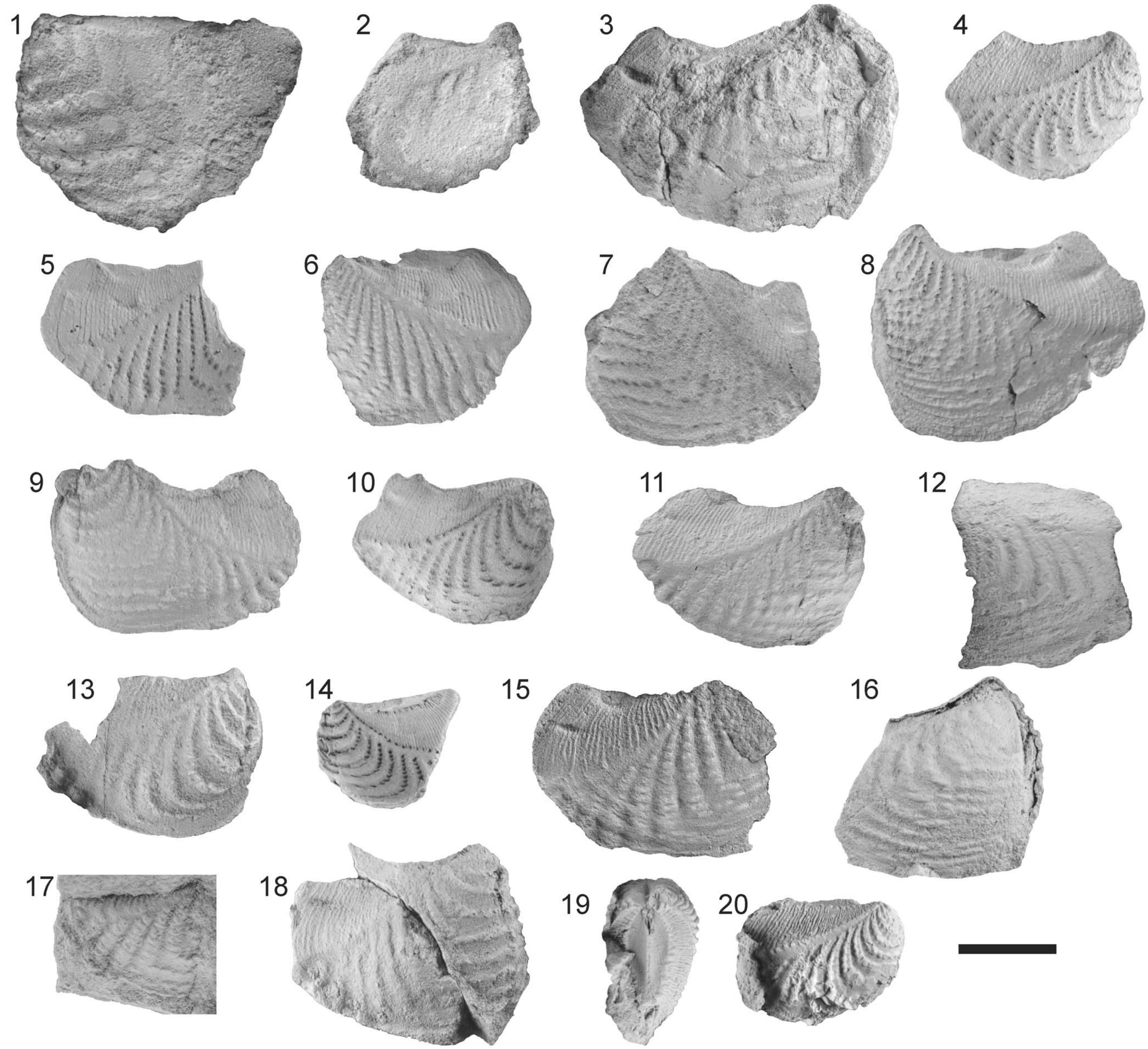

Figure 20. *Promyophorella* cf. *P. exotica* (Möricke) from the Toarcian of Argentina. Scale bar = 10 mm. (**1**) MLP 36338, composite mold of left valve, Arroyo La Laguna; (**2**) MLP 36339, composite mold of right valve, Arroyo La Laguna; (**3**) MLP 36340, composite mold of right valve, Arroyo La Laguna; (**4**) MLP 36346, external mold of left valve, Arroyo Serrucho; (**5, 6**) MLP 36354a, composite mold of a left valve over external and internal mold surfaces, Arroyo Serrucho; (**7**) MLP 36347a, composite mold over the external mold surface of right valve, Arroyo Serrucho; (**8**) MLP 36348a, composite mold over the external mold surface of right valve, Arroyo Serrucho; (**9**) MLP 36349, composite mold of left valve, Arroyo Serrucho; (**10**) MLP 36350, composite mold on the external mold surface of left valve, Arroyo Serrucho; (**11**) MLP 36399a, composite mold of right valve, Arroyo Serrucho; (**12**) MLP 36351a, composite mold of left valve, Arroyo Serrucho; (**13**) MLP 36352a, composite mold of right valve, Arroyo Serrucho; (**14**) MLP 36400a, external mold of right valve, Arroyo Serrucho; (**15**) MLP 36355a, composite mold of right valve, Arroyo Serrucho; (**16**) MLP 36364a, composite mold of right valve, Cerro Puchenque; (**17**) MLP 36365a, composite mold of right valve, Cerro Puchenque; (**18**) MLP 36366a, composite mold, right lateral view, Cerro Puchenque; (**19, 20**) MLP 15547a, shell, dorsal and right lateral views, Estación Rajapalo.

*cf. 1894 *Trigonia exotica* Möricke, p. 49, pl. 1, fig. 9, pl. 6, fig. 9.

cf. 1977 *Vaugonia* (*Vaugonia*) *exotica*; Pérez and Reyes, p. 16, pl. 3, fig. 13. [reproduced from Möricke, 1894]

v 1978b *Vaugonia* sp.; Volkheimer et al., p. 212 (table 2).

Occurrence.—Arroyo La Laguna (Los Patos region), San Juan Province; Arroyo Serrucho, Las Overas, Cerro Puchenque (West of Malargüe region), Mendoza Province; Ñiraico (Cordillera del Viento region), Neuquén Province. Early Toarcian (*D. hoelderi* Biozone [≈ Serpentinum Biozone] to *P. pacificum* Biozone [≈ Bifrons Biozone]) (Fig. 3).

Description.—Small, opisthogyrate, sometimes elongate shell. Semicircular to subtriangular flank; area margin wide (area ∼1/3 of shell surface). Escutcheon smooth (Fig. 20.19). Escutcheon angulation stepped, with pustules, each one linked to several area

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costellae. Area with fine commarginal costellae (Fig. 20.5–20.11, 20.14); umbonal 2 mm with costellae evenly spaced, later very densely spaced ridgelets (up to 30 ridgelets/cm). Mid-area radial groove barely developed, slightly displaced dorsally. Sharp marginal angulation (maybe as prominent carina in initial growth stages), with pustules on every other area costellae (one costella with pustule, one without; Fig. 20.4, 20.5, 20.14, 20.20). Narrow and smooth antecarinal space, widening posteriorly. Flank sculpture variable, with costae oblique to growth lines, bearing small, well-defined tubercles on top. Early costae anteriorly arcuate; late costae with distal extremes projecting anteriorly (usually with tubercles elongate antero-posteriorly; Fig. 20.4–20.7, 20.10, 20.13, 20.14, 20.20). Some shells with a third type of costa, with an almost straight initial segment and a subhorizontal to subcommarginal distal segment ('L' shaped; Fig. 20.1–20.3, 20.8, 20.9, 20.12, 20.15, 20.16). Nymph short (Fig. 20.19). Internal radial ridge in the posterior part of the inner surface, perpendicular to area margin (Fig. 20.3, 20.8, 20.15).

Materials.—Nearly a hundred specimens, MLP 15547, 15548?, 36338–36367, 36399, 36400.

Measurements.—MLP 36340: L = 30 mm, H = 22 mm; MLP 36341: L = 25 mm, H = 20 mm; MLP 36344: L = 24 mm, H = 17 mm; MLP 36366: L = 25 mm, H = 19 mm; MLP 36359: L = 21 mm, H = 16 mm; MLP 15547: L = 16 mm, H = 13 mm.

Remarks.—*Promyophorella* cf. *P. exotica* shows a high degree of variability, mainly in the flank costae pattern. While in some shells the costae show a curved inflection (Fig. 20.4, 20.13, 20.14, 20.20), in others they develop an L-shaped pattern (Fig. 20.1–20.3, 20.7, 20.11, 20.15), and others even show both patterns (Fig. 20.9, 20.10). Costae tubercles can be small and numerous (Fig. 20.4, 20.8, 20.14), or relatively large and stout (Fig. 20.1, 20.3, 20.15). The inflection on flank costae can be developed towards the mid-flank (Fig. 20.7–20.12, 20.16) or somewhat closer to the anteroventral margin (Fig. 20.4–20.6, 20.20). Spacing and degree of development of area costellae can also show some variability (compare Fig. 20.14 with Fig. 20.15).

The species *Trigonia exotica* was described by Möricke (1894) based on shells from the "*Humphriesianus*-Schichten" from Chile, implying a Bajocian age. Pérez and Reyes (1977) assigned an Aalenian–Bajocian range for the species in Chile. The species was later identified by Tornquist (1898) in Bajocian outcrops from Paso del Espinacito (San Juan Province, Argentina), although flank costae show an anterior disruption according to the figured shell. The material studied by Möricke could not be located; nevertheless, he described an anterior bend on flank costae (scarcely indicated in the more umbonal ribs, but very distinct in the anteroventral ones), from which the ribs run in the direction of the growth lines, and tubercles are weakly expressed. This description agrees well with the main pattern of flank ornamentation in our material. Nonetheless, the Toarcian shells described here show more closely spaced flank costae and thinner, more numerous area costellae (at least compared to Möricke's figure), so the taxon is treated as *Promyophorella* cf. *P. exotica*.

Due to its flank costae pattern, *P. exotica* was assigned to the genus *Vaugonia* by previous authors (e.g., Kobayashi and Mori, 1955; Pérez and Reyes, 1977). Nevertheless, the shared characters of the material here described with *P. basoaltorum* n. sp. suggest a closer relationship with it than with any *Vaugonia* species (see Remarks under *Pseudovaugonia* n. gen.). *Promyophorella* cf. *P. exotica* differs from other *Promyophorella* species by its: (1) simple (without bifurcation) strongly bent and/or L-shaped flank costae, (2) densely spaced area costellae, (3) proportionally large area, and (4) smooth antecarinal space that widens posteriorly.

Shell shape in *P.* cf. *P. exotica* is very similar to that of *P. basoaltorum* n. sp., although in the first species it may be less opisthogyrate and sometimes may have a slightly larger area. *Promyophorella* cf. *P. exotica* also differs from *P. basoaltorum* n. sp. by its L-shaped flank costae and more densely spaced area costellae.

The shells identified by Pérez et al. (2008) as *Vaugonia* cf. *V. gottschei* from the late Toarcian and Pliensbachian? share with *P.* cf. *P. exotica* most characters, with the costae always showing an L pattern (even at early growth stages); they differ mainly by having a narrower area with finer and more densely spaced costellae. The Middle Jurassic species *Trigonia chunumayensis* Jaworski, 1915, and *Trigonia argentinica* Jaworski, 1926a, usually assigned to the genus *Vaugonia*, may have evolved from this stock by elongation of the shell.

Vaugonia (*Vaugonia*) *spedeni* Fleming, 1987, from the lower Temaikan (≈ Aalenian) of New Zealand is remarkably similar to *P.* cf. *P. exotica* and is here considered as a *Promyophorella* species. The main differences from *P.* cf. *P. exotica* are the anterior bifurcation of flank costae in some specimens of *V. spedeni* and a slight ventral displacement (i.e., at later growth stages) of the costae main locus of angulation in others, but none of those characters appears in every specimen of the species.

Some of the shells described here (Fig. 20.19, 20.20) are remarkably similar to *P. spinulosa* (Young and Bird, 1828), which, according to Francis and Hallam (2003), is the earliest *Promyophorella* species in central-western Europe (late Toarcian to late Bajocian). The main difference is the presence of a finely tuberculate carina posteriorly bordering the mid-area groove in the European species (Lycett, 1872–1879; Francis, 2000). According to Francis' (2000) description, *P. spinulosa* shows a degree of intraspecific variation similar to that observed in *P.* cf. *P. exotica* described here. *Promyophorella formosa* (Lycett, 1872), figured by Fürsich et al. (2001, fig. 5F) from the Toarcian of Spain, is also very similar to some of the shells from Argentina (e.g., Fig. 20.13), although initial flank costae show more regular curvature and, once again, the European species seems to have a finely tuberculate carina bordering the mid-area groove.

Promyophorella sugayensis Kobayashi and Tamura, 1955, from the Sugaya Formation (= Yamagami Formation, of probable Callovian age; Masatani and Tamura, 1959; Sato, 1992) from Japan is very similar to *P.* cf. *P. exotica*, even showing the same variability, with *P. sugayensis* var. *geniculata* having an angular geniculation on flank costae. It differs from *P.* cf. *P. exotica* by having the costae bending closer to the carina, and the antecarinal space seems to be narrower.

Some of the younger shells included within *P.* cf. *P. exotica* (most likely from *P. pacificum* Biozone) show the late costae

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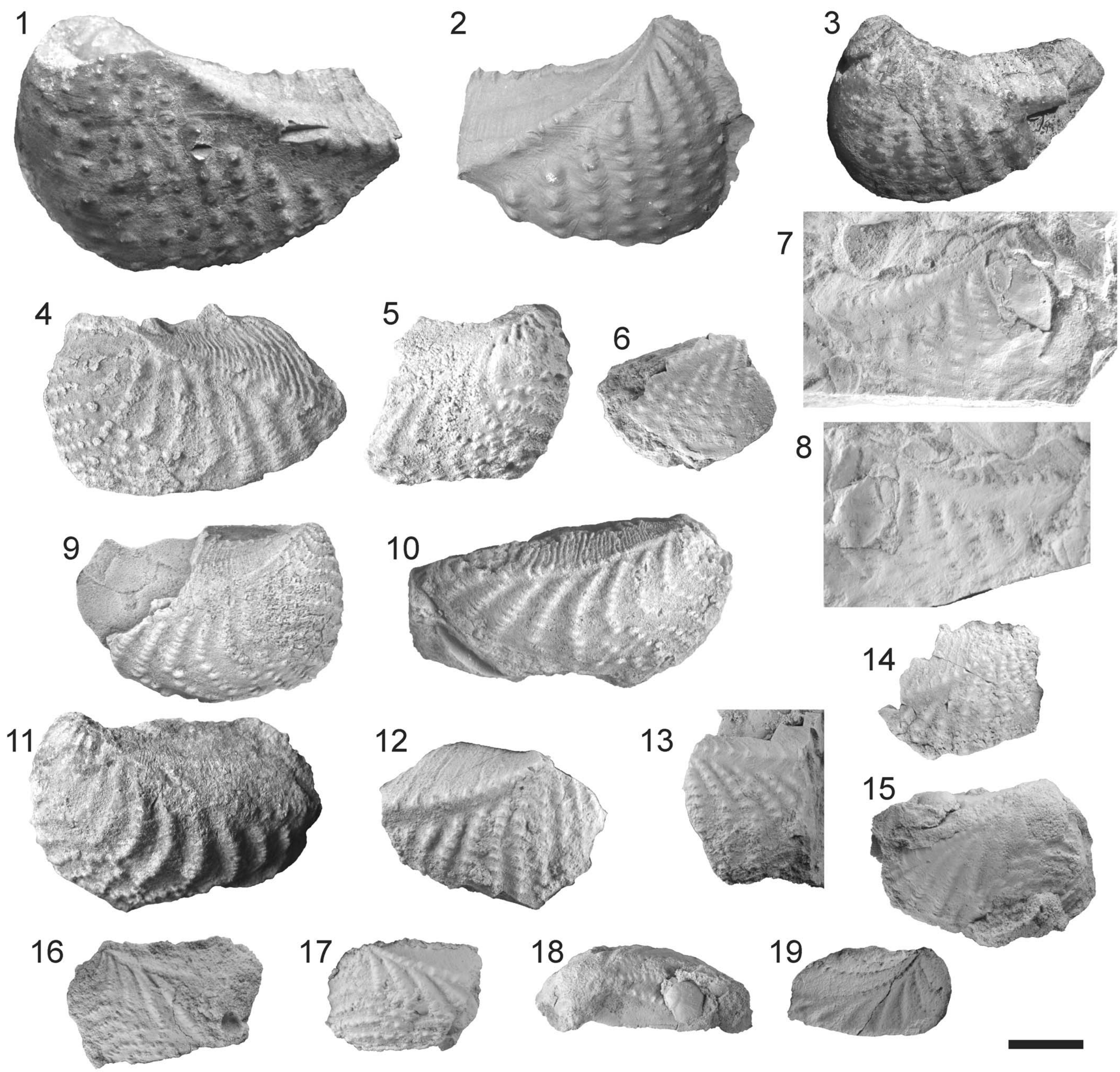

Figure 21. Trigoniida from the Early Jurassic of Argentina. Scale bar = 10 mm. (**1–3, 6–8**) *Promyophorella agniaensis* (Levy): (**1–3**) SIRAME-SEGEMAR 7346, late Pliensbachian–early Toarcian, Pampa de Agnia; (**1**) SIRAME-SEGEMAR 7346a, holotype, left valve; (**2**) SIRAME-SEGEMAR 7346b, cast of an external mold of right valve; (**3**) SIRAME-SEGEMAR 7346c, juvenile left valve; (**6**) MLP 36325, composite mold of right valve, Toarcian, Cerro Tricolor; (**7, 8**) MLP 36326a, composite mold of right valve, internal and external mold surfaces, Toarcian, Cerro Tricolor. (**4, 5, 9–11**) *Promyophorella*? *sanjuanina* n. sp. from the late Pliensbachian to early Toarcian of Argentina: (**4**) paratype, MLP 36330, left valve, Toarcian, Arroyo La Laguna; (**5**) MLP 36331, fragmentary right valve, Toarcian, Arroyo La Laguna; (**9**) holotype, MLP 36329, right valve, Toarcian, Arroyo La Laguna; (**10**) paratype, MLP 36328, right valve, Toarcian, Arroyo La Laguna; (**11**) CPBA 17442, left valve, Arroyo de Las Vegas, late Pliensbachian–early Toarcian; (**12–14**) *Promyophorella* species indet. from the Toarcian of Cerro Tricolor, MLP 36327: (**12**) MLP 36327c, right valve; (**13**) MLP 36327d, fragmentary left valve; (**14**) MLP 36327a, fragmentary right valve. (**15–19**) Myophorelloidea genus and species indet. from the Toarcian of Cañada Colorada: (**15–18**) MLP 36395; (**15**, **18**) MLP 36395a, right valve, lateral and dorsal views; (**16**) MLP 36395b, left valve; (**17**) MLP 36395c, fragmentary left valve; (**19**) MLP 36396, external mold of left valve.

fragmented into tubercles aligned both vertically and horizontally, sometimes rearranged in an en échelon pattern. This kind of ornamentation is reminiscent of some early species included in the genus *Orthotrigonia*, suggesting a close relationship of this last genus to *Promyophorella*. *Orthotrigonia waipahiensis* Fleming, 1987 (from the lower Temaikan of New Zealand) has a similar costation pattern. The New Zealand species differs by its narrower area and more elongate shell. Such an ornamentation pattern is also found in *Orthotrigonia*? *sohli* Poulton, 1979, from the Gypsum Spring Formation

(Aalenian to early Bajocian in age) of Wyoming (USA), though the North American species is smaller. Although some specimens of *P.* cf. *P. exotica* can have L-shaped costae at early growth stages (Fig. 20.1), and some others can have some extra anterior flank costae (Fig. 20.16), the species does not show the combination of characters diagnosing the genus *Orthotrigonia* (see Remarks under *Promyophorella*).

Promyophorella agniaensis (Levy, 1966)
Figure 21.1–21.3, 21.6–21.8

v* 1966 *Myophorella* (*Myophorella*) *agniaensis*; Levy, p. 238, fig. 1a, b.

Type material.—Holotype: DNGM 641a (= SIRAME-SEGEMAR 7346a) from the late Early Jurassic (probably early Toarcian) of Sierra de Pampa de Agnia, Chubut Province, Argentina. Adult shell figured by Levy (1966, p. 239, fig. 1b) and Figure 21.1.

Diagnosis.—Opisthogyrate shell. Flank with tuberculate costae, subcommarginal next to the umbo, then oblique to growth lines and curved, almost perpendicular to the ventral margin at late growth stages. Area with fine commarginal costellae; median groove well defined. Antecarinal space wide and smooth.

Occurrence.—Cerro Tricolor (Grande River region), Mendoza Province; Pampa de Agnia (central Chubut region). Early Toarcian (Tenuicostatum Biozone–*D. hoelderi*? Biozone [≈ Serpentinum Biozone]) (Fig. 3).

Description.—Medium-sized, elongate, opisthogyrate shell. Escutcheon partly observable in the holotype; smooth except for small thorn-like projections from the tubercles on the escutcheon angulation. Area with fine costellae at early growth stages, strong growth lines at late growth stages; sometimes with irregular costellae posteriorly (Fig. 21.1). Marginal angulation rounded, slightly overhanging the antecarinal sulcus, with rounded prominent tubercles. Very shallow antecarinal sulcus, smooth and posteriorly widening (Fig. 21.1, 21.2). Posterior flank costae almost straight, perpendicular to ventral margin, wide and with stout, somewhat elongate tubercles along top (Fig. 21.3, 21.7, 21.8); intercostal spaces barely wider than costae (Fig. 21.1–21.3, 21.6–21.8). Flank costae anteriorly fading, being recognized only by the aligned tubercles (Fig. 21.1, 21.6); anteriormost portion of the flank smooth. Umbonal flank costae oblique to growth lines, curved, surrounding the umbo (Fig. 21.3).

Materials.—Besides the holotype, SIRAME-SEGEMAR 7346 includes an external mold of a right valve (Fig. 21.2) and a left juvenile valve (illustrated by Levy, 1966, p. 239, fig.1a; Fig. 21.3). Three specimens from Mendoza (MLP 36325, 36326) were also studied.

Measurements.—Holotype (SIRAME-SEGEMAR 7346): L = 53 mm, H = 32 mm; juvenile illustrated by Levy: L = 32 mm, H = 20 mm; third specimen from SEGEMAR: L = 37 mm, H = 30 mm; MLP 36326: L = ~40 mm, H = ~24 mm.

Remarks.—*Promyophorella agniaensis* can be distinguished from other *Promyophorella* species by: (1) the stout flank costae perpendicular to the ventral margin and almost as wide as the intercostal spaces, (2) the wide antecarinal sulcus, and (3) the fading of anterior flank costae at late growth stages. The material from Mendoza (Fig. 21.6–21.8) can be assigned with confidence to this species. This new record from Cerro Tricolor reveals a wide geographical distribution for the species within the basin.

Levy (1966) assigned the species to the subgenus *Myophorella* (*Myophorella*) due to the well-developed tubercles, separated by smooth spaces. Nevertheless, we regard the ornamentation pattern in *P. agniaensis* as closer to that of *P. sigmoidalis* than to that of *M. nodulosa*. Tubercles on flank costae in *Myophorella* are much larger and more prominent than the tubercles in *P. agniaensis*.

The species most likely evolved from *P. basoaltorum* n. sp. by developing a stronger ornamentation pattern, with flank costae less anteriorly curved at initial growth stages. Although the straight flank costae on adult shells are comparable to those of the genus *Scaphorella* and to those of some of the species here described (e.g., *P. araucana*), none of these taxa shows a smooth anteriormost flank.

Promyophorella species indet.
Figure 21.12–21.14

Occurrence.—Cerro Tricolor (Grande River region), Mendoza Province. Early Toarcian (Tenuicostatum? Biozone) (Fig. 3).

Description.—Small, orthogyrate to slightly opisthogyrate shell. Large area (Fig. 21.12, 21.14; ~2/5 of shell surface or more); with commarginal costellae at early growth stages, replaced later by strong growth lines (Fig. 21.13). Sharp marginal angulation, with tubercles on top. Antecarinal space smooth, slightly widening posteriorly (Fig. 21.12–21.14). Straight, slightly diverging flank costae and orthogonal to ventral margin at early growth stages, curving anteriorly towards the anteroventral margin (Fig. 21.13). Flank costae with tubercles on top.

Materials.—Fragmentary shells: MLP 36327; probably also part of MLP 17186.

Measurements.—MLP 36327a: L = 23 mm, H = 17 mm; MLP 36327b: L = 23 mm, H = 20 mm.

Remarks.—The material cannot be assigned to any of the *Promyophorella* species already recognized in the basin. Slightly diverging J-shaped flank costae is a character typical of *P. araucana*, but in this last species the costae curve anteriorwards from the beginning. Flank costae on *Promyophorella agniaensis* start their development with a straight portion, but *Promyophorella* species indet. differs from this species (and from *P. araucana*) by having a larger area and orthogyrate shell shape. The straight portion of the flank costae in *Promyophorella* species indet. is like that found on the genus *Scaphorella*, although the former lacks the anterior bifurcating ornamentation observed in the latter.

Promyophorella basoaltorum n. sp. most likely gave rise to this species by a change in flank costae pattern, a widening of the area margin, and development of a less-opisthogyrate shell.

Promyophorella? *sanjuanina* new species
Figure 21.4, 21.5, 21.9–21.11

pv 1978b *Vaugonia* sp.; Volkheimer et al., p. 212 (table 2).
v 1996 *Myophorella* cf. *M*. *araucana*; Álvarez, p. 92, fig. 23h.
v 1997 *Myophorella* cf. *M*. *araucana* (Leanza); Álvarez, p. 231, pl. 1, fig. h.
v 2008 *Myophorella* (*Myophorella*) sp. 2; Pérez and Reyes in Pérez et al., p. 88, pl. 14, fig. 9.

Type materials.—Holotype: MLP 36329, paratypes: MLP 36328, 36330.

Diagnosis.—Small to medium-sized, slightly opisthogyrate, elongate, trapezoidal shell. Escutcheon smooth; escutcheon angulation stepped, with small tubercles on top. Wide area with submedian groove dorsally displaced. Area with commarginal costellae, less dense and slightly stronger at late growth stages. Marginal angulation with tubercles. Antecarinal space feebly developed. Two sets of flank costae, both with well-developed regular tubercles: a sub-vertical regular dorso-posterior set, and a sub-horizontal to sub-commarginal irregular and frequently bifurcated anterior set (sometimes with costae broken up into tubercles).

Occurrence.—Arroyo La Laguna (Los Patos region), San Juan Province; Las Overas (west of Malargüe region), Mendoza Province. Early Toarcian (*D. hoelderi*–*P. largaense* or maybe *P. pacificum* biozones [≈ Serpentinum–Bifrons biozones]) (Fig. 3). The material illustrated by Álvarez (1996) is from late Pliensbachian or early Toarcian (Tenuicostatum Biozone) from Arroyo de Las Vegas (∼7 km north from Arroyo La Laguna), and she mentioned its presence in Arroyo La Laguna, both localities in San Juan Province. The material from Chile (Quebrada Asientos, Atacama Region) is from the late Pliensbachian *F. fannini* Biozone (≈ Margaritatus Biozone).

Description.—Small to medium-sized, slightly opisthogyrate, elongate, trapezoidal shell. Escutcheon excavated, smooth (Fig. 21.9). Escutcheon angulation stepped, with small tubercles on top (projecting slightly towards the escutcheon). Area wide (∼1/3 of shell surface), with submedian groove dorsally displaced. With closely spaced commarginal costellae; dorsal and ventral portions normally meeting at an angle towards the groove. Area costellae densely arranged at early growth stages, increasing spacing and becoming stronger during ontogeny (Fig. 21.4, 21.10). Sharp to rounded marginal angulation; with tubercles, though not as strong as those on the escutcheon angulation. Antecarinal space barely developed, but interrupting flank costae (Fig. 21.4, 21.9, 21.10). Flank costae strong, tuberculate, oblique to growth lines; with a sub-vertical dorso-posterior portion (slightly incurved anteriorwards) and an anterior, irregular, and frequently bifurcated sub-horizontal to sub-commarginal portion; anteroventral costae sometimes fragmented into tubercles, resulting in a reticulate appearance (Fig. 21.4, 21.5). Anteriormost portion of flank costae sharp and continuous, without tubercles in some specimens.

Etymology.—In reference to San Juan Province, from where the type material was collected.

Materials.—Eight specimens, the types plus MLP 36312c, 36331–36333, CPBA 17442 and SNGM 665.

Measurements.—MLP 36329 (holotype): L = 35 mm, H = 23 mm; MLP 36330 (paratype): L = 40 mm, H = 24 mm; CPBA 17442: L = 38 mm, H = 26 mm.

Remarks.—General morphology and ornamentation (including the bifurcation on the anterior portion of flank costae) match those of *Myophorella* sp. 2 of Pérez et al. (2008) from the late Pliensbachian of Chile, and thus is considered here as conspecific, although the Chilean material is relatively shorter and higher. *Promyophorella*? *sanjuanina* n. sp. differs from other species within the Neuquén and Chubut basins by its: (1) bifurcating flank costae, sometimes with a reticulate pattern; (2) reduced antecarinal space, and (3) progressively stronger and more spaced area ornamentation. *Promyophorella*? *catenifera* (Fig. 18.1–18.4), from the Pliensbachian–Toarcian of Chile, shows similar flank ornamentation, although in this last case costae do not bend anteriorwards as markedly as in *Promyophorella*? *sanjuanina* n. sp. Besides, *P.*? *catenifera* bears a well-developed antecarinal space and an almost smooth area. One of the specimens referred to *Myophorella araucana* by Leanza and Garate-Zubillaga (1987, pl. 1, fig. 8, MOZ PI-0937/1) from the early Pliensbachian at Cerrito Roth (Neuquén Province) and the one referred to the same species by Leanza (1993) from the Pliensbachian at La Amarga (Neuquén Province) also share with *Promyophorella*? *sanjuanina* n. sp. the bifurcating flank costae and the reduction of the antecarinal space; the material from Neuquén, nonetheless, is larger and with stronger ornamentation.

Vaugonia (?) *yukonensis* Poulton, 1979 (p. 25–26, pl. 8, figs. 6–11), probably from the "middle Bajocian" (now early Bajocian) of Yukon, shows a similar somewhat irregular anteriorwards costation pattern to that of *Promyophorella*? *sanjuanina* n. sp., even with the reticulate ornamentation. Shell sculpture is much coarser and sometimes more densely spaced in the North American species. Poulton (1979) recognized some affinity of *Vaugonia* (?) *yukonensis* to *Myophorella* (including *Promyophorella*).

The anterior bifurcation and disruption in the flank costae of all these species, including *P.*? *sanjuanina* n. sp., also suggest a relationship to *Scaphorella*. The type species, *Scaphorella leanzai* (Lambert, 1944) bears a posterior set of sub-vertical, tuberculate, nearly straight, narrow costae, with the anteriormost ones strongly curving anteriorly (and some of them bifurcating) to generate the anterior set of sub-horizontal costae. This pattern differs from the one seen in *Promyophorella*? *sanjuanina* n. sp., where the anterior set of costae is much more irregular (especially at late growth stages). *Scaphorella susanae* Pérez and Reyes in Pérez et al., 2008, is the earliest species assigned to the genus (late Toarcian and early Aalenian from Atacama, Chile); the anterior disruption of the ornamentation pattern in this species is similar to that found on *P.*? *sanjuanina* n. sp., but in *S. susanae* there is a wide and well-developed, smooth antecarinal space, and area costellae are thinner than on the new species. Besides, the reticulate pattern on some specimens of *P.*? *sanjuanina* n. sp. does not develop in the known species assigned to *Scaphorella*.

Considering the well-defined regular tubercles on oblique diverging, gently curved, costae departing from antecarinal space at obtuse anterior angles, we include *P.*? *sanjuanina* n. sp. in the genus *Promyophorella*, but using open nomenclature.

Myophorelloidea genus and species indet.
Figure 21.15–21.19

Occurrence.—Cañada Colorada (west of Malargüe region), Mendoza Province. Late Toarcian (Fig. 3).

Description.—Small, slightly opisthogyrate, elongate shell. Escutcheon smooth (Fig. 21.18). Area smooth or bearing very thin ridglets (almost imperceptible); with a median row of tubercles (Fig. 21.17–21.19). Escutcheon and marginal angulations with transverse tubercles. Antecarinal space very narrow (Fig. 21.15–21.17). Flank with oblique, L-shaped costae; posterior branches strong, subradial, and diverging; anterior branches slightly concave ventrally and thinner than posterior ones (Fig. 21.15–21.17). Flank costae with small, round tubercles.

Materials.—MLP 36395–36397.

Measurements.—MLP 36395d: L = 35 mm, H = ~26 mm.

Remarks.—This taxon differs from other Myophorelloidea species by its: (1) smooth area, except for the median radial row of small tubercles; (2) reduced antecarinal space; and (3) oblique, L-shaped flank costae with the anterior branches slightly concave ventrally and with tubercles on top. Area ornamentation is remarkably similar to that of *Poultoniella* n. gen., but the flank costae pattern strongly differs. The taxon here described has a similar ornamentation pattern to that of *Promyophorella*? *sanjuanina* n. sp., as well as a reduced antecarinal space, but, in contrast, the latter has a commarginally ornamented area. Although frenguelliellids may develop oblique costae on the flank, even with tubercles, the regularity in the ornamentation pattern and the flank costae generating a clearly obtuse anterior angle with the antecarinal space suggest a closer affinity with the Myophorellidae.

Trigonia lycetti Gottsche, 1878, from the Bajocian of Paso del Espinacito, San Juan Province (type material housed at the SEGEMAR under collection numbers SIRAME-SEGEMAR 7877, 7981, and 7982), also shares a similar flank ornamentation pattern with this taxon, and it even has a median "carina" on the area with small tubercles. It differs, nonetheless, by having well-developed transverse costellae on the area (finely preserved on SIRAME-SEGEMAR 7877), a well-developed antecarinal space, and a middle step on the area (*Trigonia lycetti* may actually be a species of *Vaugonia*). The material from Cañada Colorada does not show any sign of a middle step on the area, precluding the assignment of the taxon to *Vaugonia*.

Vaugonia sp. cf. *V.* (?) *yukonensis* described by Poulton (1979, p. 26, pl. 8, fig. 12), probably from the Bajocian of southern Yukon Territory, Canada, resembles the material here described, but differs by having a sharper umbo and a median groove in the area. In addition, the Canadian material has flank costae more densely disposed, and posterior and anterior branches are similarly developed and continuous, whereas in the Argentinian material the posterior branches tend to be stronger, and the anterior ones may be more numerous (Fig. 21.15–21.17).

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Appendix 1: List of specimens from Argentina

Specimens of each Trigoniida species listed by locality from North to South. Locality map, repository abbreviations, and local biozonation in text. N = Number of specimens

Species	Collection number	Locality	Age/Biozone	N	Type	Figure
Groeberella neuquensis (Groeber)	MLP 27246a–c	Las Chilcas	*Orthech.–Paltechioc.*	3		
	MLP 27247	Las Chilcas	*Orthech.–Paltechioc.*	1		
	MLP 27248	Las Chilcas	*Orthech.–Paltechioc.*	1		
	MLP 28683	Qda. Los Caballos	*M. chilcaense*	1		
	MLP 27250	Puesto Araya	*M. externum*	1		
	MLP 27249	Puesto Araya	*M. externum*	1		
	MLP 27844	Puesto Araya	*M. externum*	1		Fig. 5.8
	MLP 36194	Puesto Araya	*M. externum*	1		
	IANIGLA-PI 3344	Puesto Araya	Pliensbachian	1		
	MLP 27931	Portezuelo Ancho	Pliensbachian	1		
	MLP 17478	La Bajada	Late Pliensbachian	1		
	DNGM 7337 [= cast MLP 24324]	Puruvé-Pehuén central Neuquén	Pliensbachian	1	Holotype	Fig. 5.1–5.3
	MLP 27251	Ea. Santa Isabel	*F. disciforme*	1		
	MLP 27252	Carrán Curá	*F. disciforme*	1		
	MLP 17724	Carrán Curá	*F. disciforme*	1		
	MLP 27253a, b	Carrán Curá	*F. disciforme*	2		
	MLP 16387	Cerro Roth Sur	*A. beherendseni* ?	1		
	MOZ-PI 4060	Cerro Roth Sur	*A. beherendseni* ?	1		
	MPEF-PI 3392	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 2993	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 2913	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 2918	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6397	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6435	Nueva Lubecka	Late Pliensbachian	1		Fig. 5.5
	DNGM 7338a, b	Nueva Lubecka	Late Pliensbachian	2		
	DNGM 7339	Nueva Lubecka	Late Pliensbachian	1		Fig. 5.6, 5.7
	DNGM 7340a–c	Nueva Lubecka	Late Pliensbachian	3		a: Fig. 5.4
Trigonia? sp. 1	MLP 36311	Arroyo La Laguna	E Toarcian (*hoelderi*)	1		Fig. 5.13
	MLP 36312a	Arroyo La Laguna	E Toarcian (*hoelderi*)	1		a: Fig. 5.12
	MLP 36313	Arroyo La Laguna	E Toarcian (*hoelderi*)	1		
Trigonia? sp. 2	CPBA 17430	Arroyo La Laguna	E Toarcian (*hoelderi*?)	1		Fig. 5.9–5.11
	CPBA 17478	Arroyo La Laguna	E Toarcian (*hoelderi*?)	1		
Prosogyrotrigonia tenuis Pérez and Reyes	MLP 32786	Arroyo Malo	*Coroniceras–Arnioceras*	1		
	MLP 32789	Arroyo Malo	*Coroniceras–Arnioceras*	1		Fig. 5.14
	MLP 32802	Arroyo Malo	*Coroniceras–Arnioceras*	1		Fig. 5.15
	MLP 32803	Arroyo Malo	*Coroniceras–Arnioceras*	1		
	MLP 32805	Arroyo Malo	*Coroniceras–Arnioceras*	1		Fig. 5.17
	MLP 32815	Arroyo Malo	*Coroniceras–Arnioceras*	1		
	MLP 32711	Arroyo Malo	*Coroniceras–Arnioceras*	1		
	MLP 32828	Arroyo Malo	*Coroniceras–Arnioceras*	1		Fig. 5.16
Frenguelliella eopacifica new species	MLP 32823	Arroyo El Pedrero	*Coronic–Arnioceras* ?	1		Fig. 7.8
	MLP 18387a	Codo del Blanco	*Orthech.–Paltechioc.*	1		
	MLP 18389	Codo del Blanco	*Orthech.–Paltechioc.*	1		
	MLP 32834	Las Chilcas	*Orthech.–Paltechioc.*	1		
	MLP 32837	Las Chilcas	*Orthech.–Paltechioc.*	1	Paratype	Fig. 7.7
	MLP 32843	Las Chilcas	*Orthech.–Paltechioc.*	1		
	MLP 32848	Las Chilcas	*Orthech.–Paltechioc.*	1		Fig. 7.4
	MLP 32850	Las Chilcas	*Orthech.–Paltechioc.*	1		
	MLP 32851a, b	Las Chilcas	*Orthech.–Paltechioc.*	2		
	MLP 32860	Las Chilcas	*Orthech.–Paltechioc.*	1		
	MLP 3286 a–d	Las Chilcas	*Orthech.–Paltechioc.*	4		a: Fig. 7.2; c: Fig. 7.6, 7.9
	MLP 32875	Las Chilcas	*Orthech.–Paltechioc.*	1		Fig. 7.3
	MLP 32891	Las Chilcas	*Orthech.–Paltechioc.*	1		
	MLP 32881	Las Chilcas	*Orthech.–Paltechioc.*	1		
Frenguelliella chubutensis (Feruglio)	MLP 36150a, b	Arroyo La Laguna	*F. disciforme*	2		
	MLP 31135a, b	La Horqueta	*E. meridianus* ?	2		
	MLP 28986	Codo del Blanco	*M. chilcaense*	1		
	MLP 28985a, b	Codo del Blanco	*M. chilcaense*	2		
	MLP 33185a, b	Las Chilcas	*M. chilcaense*	2		
	MLP 36151	Las Chilcas	*M. chilcaense*	1		
	MLP 33187a–o	Las Chilcas	*M. chilcaense*	15		c: Fig. 8.6
	MLP 33188a, b	Las Chilcas	*M. chilcaense*	2		

Continued.

Species	Collection number	Locality	Age/Biozone	N	Type	Figure
	MLP 33191	Las Chilcas	*M. chilcaense*	1		
	MLP 27902	Las Chilcas	*M. chilcaense*	1		
	MLP 36310	Las Chilcas	*M. chilcaense*	1		
	MLP 27821	Las Chilcas	*M. externum*	1		
	MLP 28671	Qda. Los Caballos	*M. chilcaense*	1		Fig. 8.10
	MLP 28693	Qda. Los Caballos	*F. fannini*	1		
	MLP 28696	Qda. Los Caballos	*F. fannini*	1		
	MLP 28698	Qda. Los Caballos	*F. disciforme*	1		
	MLP 28704	Qda. Los Caballos	*F. disciforme*	1		
	MLP 36152a–d	Puesto Araya	*M. externum*	4		
	MLP 33203	Puesto Araya	*M. externum*	1		
	MLP 33205a, b	Puesto Araya	*M. externum*	2		
	MLP 27855	Puesto Araya	*M. externum*	1		
	MLP 27877	Puesto Araya	*M. externum*	1		
	MLP 36192	Puesto Araya	Early Pliensbachian	1		
	MLP 36193	Puesto Araya	Early Pliensbachian	1		
	MLP 33267	Puesto Araya	*E. meridianus*	1		
	MLP 27873	Puesto Araya	*E. meridianus*	1		
	MLP 25047	Puesto Araya	*F. disciforme*	1		
	MLP 36153	Puesto Araya	*F. disciforme*	1		
	IANIGLA-PI 3319	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3320	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3321	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3322	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3323	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3324	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3325	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3326	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3327	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3328	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3329	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3330	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3331	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3332	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3333A	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3334	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3335	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3336	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3337A	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3338	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3339	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3340	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3341	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3342	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3343A	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3345	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3346	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3347	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3348	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3349	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3352	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3353	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3354	Arroyo Serrucho	Pliensbachian	1		
	MLP 36212	Cerro La Brea	Pliensbachiano	1		
	MLP 27951	Arroyo Peuquenes	Pliensbachiano	1		
	MLP 36154	Arroyo Peuquenes	Late Pliensbachian	1		
	MLP 36155 a-c	Arroyo Peuquenes	Late Pliensbachian	3		
	MLP 36156 a-d	Arroyo Peuquenes	Late Pliensbachian	4		
	MLP 36157	Arroyo Peuquenes	Late Pliensbachian	1		
	MLP 36190	Arroyo Peuquenes	Late Pliensbachian	1		
	MLP 36191	Arroyo Peuquenes	Late Pliensbachian	1		
	IANIGLA-PI 3259	A. Portezuelo Ancho	Late Pliensbachian	1		
	IANIGLA-PI 3264	A. Portezuelo Ancho	Late Pliensbachian	1		
	IANIGLA-PI 3305A	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3306	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3307	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3308	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3309	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3310	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3311	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3312	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3313	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3314	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3315	A. Portezuelo Ancho	Pliensbachian	1		

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Species	Collection number	Locality	Age/Biozone	N	Type	Figure
	IANIGLA-PI 3316	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3317	A. Portezuelo Ancho	Pliensbachian	1		
	MLP 36158	Arroyo Serrucho	Early Pliensbachian	1		
	MLP 36159a, b	Arroyo Serrucho	Late Pliensbachian	2		a: Fig. 8.9
	MLP 36189a–c	Arroyo Serrucho	Late Pliensbachian	3		
	MLP 36160	Arroyo Serrucho	Late Pliensbachian	1		
	MLP 36161	Arroyo Serrucho	Late Pliensbachian	1		Fig. 8.7
	MLP 36162	Arroyo Serrucho	Late Pliensbachian	1		
	MLP 36163	Arroyo Serrucho	Late Pliensbachian	1		
	MLP 36164	Arroyo Serrucho	Late Pliensbachian	1		Fig. 8.5
	MLP 36165	Arroyo Serrucho	Late Pliensbachian	1		Fig. 8.4
	MLP 36166a–c	Arroyo Serrucho	Late Pliensbachian	3		
	MLP 36167a, b	Arroyo Serrucho	Late Pliensbachian	2		
	MLP 36168	Arroyo Serrucho	Late Pliensbachian	1		
	MLP 28738	Arroyo Serrucho	Late Pliensbachian	1		
	IANIGLA-PI 3254	Arroyo Serrucho	Late Pliensbachian	1		
	IANIGLA-PI 3255	Arroyo Serrucho	Late Pliensbachian	1		
	IANIGLA-PI 3256A	Arroyo Serrucho	Late Pliensbachian	1		
	IANIGLA-PI 3257	Arroyo Serrucho	Late Pliensbachian	1		
	IANIGLA-PI 3258	Arroyo Serrucho	Late Pliensbachian	1		
	IANIGLA-PI 3288	Arroyo Serrucho	Late Pliensbachian	1		
	MLP 24467	Cerro Puchenque	Latest Pliensbachian	1		
	MLP 36169	Cerro Puchenque	Latest Pliensbachian	1		
	MLP 36170	Cerro Puchenque	Latest Pliensbachian	1		
	IGPB-Jaworski 74	Cerro Puchenque	Pliensbachian	1	*T. densecostata* J. type	Fig. 8.1
	MLP 36171	Estación Rajapalo	Latest Pliensbachian	1		
	MLP 36172	Estación Rajapalo	Late Pliensbachian	1		Fig. 8.13
	MLP 36173	Estación Rajapalo	Late Pliensbachian	1		
	MLP 36174	Estación Rajapalo	Late Pliensbachian	1		
	MLP 15422a–f	Estación Rajapalo	Late Pliensbachian	6		
	MLP 15428	Estación Rajapalo	Late Pliensbachian	1		
	MLP 15438	Estación Rajapalo	Late Pliensbachian	1		
	MLP 36185a, b	Ñireco	Late Pliensbachian	2		
	MLP 24468	Ñireco	Late Pliensbachian	1		Fig. 8.14
	MLP 21076	Ñireco	Late Pliensbachian	1		
	MOZ-PI 5315a, b	Ñireco	Late Pliensbachian	2	*F. poultoni* holotype	Fig. 8.3
	MOZ-PI 5316	Ñireco	Late Pliensbachian	1	*F. poultoni* paratype	Fig. 8.8
	MOZ-PI 5317	Ñireco	Pliensbachian	1		
	MLP 36175	Lonqueo	Late Pliensbachian	1		
	MLP 36176	Lonqueo	Late Pliensbachian	1		
	MLP 36177	Lonqueo	Late Pliensbachian	1		
	MLP 36178	Lonqueo	Late Pliensbachian	1		
	MLP 36179	Lonqueo	Late Pliensbachian	1		Fig. 8.11
	MLP 36180	Lonqueo	Late Pliensbachian	1		
	MLP 36181	Lonqueo	Late Pliensbachian	1		Fig. 8.12
	MLP 36182	Lonqueo	Late Pliensbachian	1		
	MLP 36183a–e	Lonqueo	Late Pliensbachian	5		
	MLP 36184	Lonqueo	Late Pliensbachian	1		
	MLP 15321	Rahue-Aluminé	Pliensbachian	1		
	MLP 15326	Rahue-Aluminé	Pliensbachian	1		
	MLP 36186a, b	Ea. Santa Isabel	Late Pliensbachian	2		
	MLP 36187	Ea. Santa Isabel	Late Pliensbachian	1		
	MLP 36188a, b	Ea. Santa Isabel	Late Pliensbachian	2		
	MPEF-PI 6420	Puesto Peña	Late Pliensbachian	1		
	MPEF-PI 6421	Puesto Peña	Late Pliensbachian	1		
	MPEF-PI 2940	Betancourt	Late Pliensbachian	1		
	MPEF-PI 2947	Betancourt	Late Pliensbachian	1		
	MPEF-PI 2957	Betancourt	Late Pliensbachian	1		
	MPEF-PI 5787	Betancourt	Late Pliensbachian	1		
	MPEF-PI 5796	Betancourt	Late Pliensbachian	1		
	MPEF-PI 5861	Betancourt	Late Pliensbachian	1		Fig. 8.15
	MPEF-PI 5875	Betancourt	Late Pliensbachian	1		
	MPEF-PI 6178	Betancourt	Late Pliensbachian	1		
	MPEF-PI 6376	Betancourt	Late Pliensbachian	1		
	MPEF-PI 6377	Betancourt	Late Pliensbachian	1		
	MPEF-PI 6378	Betancourt	Late Pliensbachian	1		
	MPEF-PI 6379	Betancourt	Late Pliensbachian	1		Fig. 8.19
	MPEF-PI 6380	Betancourt	Late Pliensbachian	1		
	MPEF-PI 6382	Betancourt	Late Pliensbachian	1		
	MPEF-PI 6383	Betancourt	Late Pliensbachian	1		Fig. 8.16, 8.17, 8.20
	MLP 3729	Genoa (= A. Loca?)	Late Pliensbachian	1	Lectotype	Fig. 8.2

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Species	Collection number	Locality	Age/Biozone	N	Type	Figure
	MPEF-PI 3041	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 3043	Aguada Loca	Late Pliensbachian	1		Fig. 8.22
	MPEF-PI 3048	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 3049	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 3050	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 3051	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 3161	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 3164	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 3293	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 3295	Aguada Loca	Late Pliensbachian	1		Fig. 8.18
	MPEF-PI 3390	Aguada Loca	Late Pliensbachian	1		Fig. 8.21
	MPEF-PI 6403	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6404	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6405	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6406	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6407	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6408	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6410	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6411	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6412	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6413	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6414	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6415	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 6416	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 2911a	Nueva Lubecka	Late Pliensbachian	1		
Frenguelliella aff. *F. chubutensis*	MLP 28994	Codo del Blanco	*M. chilcaense*	1		Fig. 10.2
	MLP 28676	Qda. Los Caballos	*M. chilcaense*	1		Fig. 10.3
	MLP 28684	Qda. Los Caballos	*M. chilcaense*	1		Fig. 10.1
Frenguelliella inexspectata (Jaworski)	MLP 36195a, b	Ea. Santa Isabel	*F. disciforme*	2		
	MLP 36196	Ea. Santa Isabel	*F. disciforme*	1		
	MLP 36198	Carrán Curá	*F. disciforme*	1		Fig. 11.9
	MLP 36199	Carrán Curá	*F. disciforme*	1		
	MLP 36200	Subida Sañicó	Pliensbachian	1		
	MLP 36201	Subida Sañicó	Pliensbachian	1		Fig. 11.7
	MLP 36202	Subida Sañicó	Pliensbachian	1		
	MLP 36197a, b	Cerro del Vasco	Pliensbachian	2		
	MLP 6139	Cerro Roth	*A. beherendseni* ?	1		Fig. 11.10
	MLP 6726	Cerro Roth	*A. beherendseni* ?	1		Fig. 11.8
	MLP 13008a	Cerro Roth Sur	*A. beherendseni* ?	1		Fig. 11.3, 11.6
	MLP 36203	Cerro Roth Sur	*A. beherendseni* ?	1		
	MLP 36204	Cerro Roth Sur	*A. beherendseni* ?	1		Fig. 11.4, 11.5
	MLP 36205	Cerro Roth Sur	*A. beherendseni* ?	1		
	MLP 36206	Cerro Roth Sur	*A. beherendseni* ?	1		
	MLP 36207	Cerro Roth Sur	*A. beherendseni* ?	1		
	MLP 36208	Cerro Roth Sur	*A. beherendseni* ?	1		
	MLP 36209	Cerro Roth Sur	*A. beherendseni* ?	1		
	MLP 36210	Cerro Roth Sur	*A. beherendseni* ?	1		
	MCF-PIPH 631	Cerro Roth Sur	*A. beherendseni* ?	1		
	MCF-PIPH 502a	Cerro Roth Sur	*A. beherendseni* ?	1		
	IGPB-Jaworski-6	Piedra Pintada	Late Pliensbachian	1	Lectotype	Fig. 11.1, 11.2
	DNGM 8851	Nueva Lubecka	Late Pliensbachian	1		
	DNGM 8863	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 2911b	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6385	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6387	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6400	Nueva Lubecka	Late Pliensbachian	2		
Jaworskiella burckhardti (Jaworski)	(?) MLP 17145	La Bajada	Late Pliensbachian	1		
	BMNH 1039-104 (cast MLP 22356)	Catán Lil (Piedra Pintada region)	Late Pliensbachian?	1	*T. catanlilensis* type	Fig. 11.12
	IGPB Jaworski-7	Piedra Pintada	Late Pliensbachian	1	Holotype	Fig. 11.11
	NHMB-G 16636	Piedra Pintada	Late Pliensbachian	1		
	MLP 36302	Carrán Curá	Late Pliensbachian	1		
	(?) MLP 36303	Carrán Curá	Late Pliensbachian	1		Fig. 11.15
	MLP 36304	Carrán Curá	Late Pliensbachian	1		
	MLP 36305a, b	Carrán Curá	Late Pliensbachian	2		
	MLP 36213a–d	Cerro del Vasco	Late Pliensbachian	4		
	MLP 6257	Cerro Roth	Late Pliensbachian	1		
	MLP 6261	Cerro Roth	Late Pliensbachian	1		Fig. 11.16
	MLP 36306	Cerro Roth Sur	Late Pliensbachian	1		Fig. 11.21
	MLP 36307	Cerro Roth Sur	Late Pliensbachian	1		Fig. 11.17
	MLP 36308	Cerro Roth Sur	Late Pliensbachian	1		
	MLP 36309	Cerro Roth Sur	Late Pliensbachian	1		Fig. 11.13
	MCF-PIPH 502b–d	Cerro Roth Sur	Late Pliensbachian	3		
	MCF-PIPH 503a, b	Cerro Roth Sur	Late Pliensbachian	2		a: Fig. 11.18, 11.20

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Species	Collection number	Locality	Age/Biozone	N	Type	Figure
	MOZ-PI 1064	Cerro Roth	Late Pliensbachian	1		Fig. 11.14
	MOZ-PI 3043	Cerro Roth	Late Pliensbachian	1		
	MOZ-PI 3044	Cerro Roth	Late Pliensbachian	1		
	DNGM 8684 (cast MLP 19080)	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 2910	Nueva Lubecka	Late Pliensbachian	13		
	MPEF-PI 2997	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6388	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6389	Nueva Lubecka	Late Pliensbachian	1		Fig. 11.19
	MPEF-PI 6391	Nueva Lubecka	Late Pliensbachian	1		
	(?) MPEF-PI 6398	Nueva Lubecka	Late Pliensbachian	3		
	MPEF-PI 6401	Nueva Lubecka	Late Pliensbachian	12		
Poultoniella jaworskii new species	MLP 36315	Arroyo La Laguna	Toarcian (*D. hoelderi-C. chilensis*)	1	Holotype	Fig. 10.4, 10.5
	MLP 36312b	Arroyo La Laguna	Toarcian (*D. hoelderi-C. chilensis*)	1		
	MLP 36316	Arroyo La Laguna	Toarcian (*D. hoelderi-C chilensis*)	1		
	MLP 36317	Arroyo La Laguna	Toarcian (*D. hoelderi-C chilensis*)	1		Fig. 10.6
	MLP 36318	Arroyo La Laguna	Toarcian (*D. hoelderi-C. chilensis*)	1		
	MLP 36319a, b	Arroyo La Laguna	Toarcian (*D. hoelderi-C chilensis*)	2		
	MLP 36320a–c	Arroyo La Laguna	Toarcian (*D. hoelderi-C chilensis*)	3		
Q. cf. *Q. pustulata*	IANIGLA-PI 3263	A. Portezuelo Ancho	Pliensbachian	1		Fig. 12.1, 12.2
Moerickella infraclavellata (Möricke)	MLP 31118a, b	La Horqueta	*M. externum*	2		
	MLP 31119a, b	La Horqueta	*M. externum*	2		Fig. 13.6
	MLP 18387b	Codo del Blanco	*Orthech.–Paltechioc.*	1		Fig. 13.2
	MLP 13354a–e	Codo del Blanco	*Orthech.–Paltechioc.*	5		
	MLP 32846	Las Chilcas	*Orthech.–Paltechioc.*	1		Fig. 13.3
	MLP 32885	Las Chilcas	*Orthech.–Paltechioc.*	1		
	MLP 31153	Las Chilcas	*Orthech.–Paltechioc.*	1		Fig. 13.4
	MLP 33235a, b	Puesto Araya	*M. externum*	2		
Pseudovaugonia hectorleanzai (Pérez and Reyes)	(?) MLP 36398	Arroyo La Laguna	Pliesb/Toarcian	1		
	MLP 36323	Las Overas	E Toarcian (*hoelderi*)	1		
	MLP 36324	Las Overas	E Toarcian (*hoelderi*)	1		Fig. 15.6
	MLP 36321a–c	Arroyo Lapa	E Toarcian (*hoelderi*)	3		a: Fig. 15.2; b: Fig. 15.3; c: Fig. 15.5
	MLP 36322	Arroyo Lapa	E Toarcian (*hoelderi*)	1		Fig. 15.1, 15.4
Promyophorella basoaltorum new species	MLP 36368	Arroyo La Laguna	*F. disciforme*	1		
	MLP 36369	Arroyo La Laguna	*F. disciforme*	1		
	MLP 36370	Arroyo La Laguna	*F. disciforme*	1		Fig. 16.5
	MLP 36371	Arroyo La Laguna	*F. disciforme*	1		
	MLP 36372	Arroyo La Laguna	*Tenuicostatum*	1		
	MLP 36373	Arroyo La Laguna	*Tenuicostatum*	1		
	IANIGLA-PI 3318	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3350	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3351	Puesto Araya	Pliensbachian	1		
	IANIGLA-PI 3262	A. Portezuelo Ancho	Pliensbachian	1		
	IANIGLA-PI 3265	A. Portezuelo Ancho	Pliensbachian	1		
	MLP 36374	Portezuelo Ancho	Late Pliensbachian	1		
	MLP 36375	Portezuelo Ancho	Late Pliensbachian	1		
	MLP 36376	Portezuelo Ancho	Late Pliensbachian	1		
	MLP 36377	Santa Elena	Late Pliensbachian	1		
	MLP 17148	La Bajada	Late Pliensbachian	1		
	MLP 17503	La Bajada	Late Pliensbachian	1		
	MLP 36378	Arroyo Serrucho	*A. beherendseni* ?	1		
	MLP 36379	Arroyo Serrucho	*A. beherendseni* ?	1		
	MLP 36380	Arroyo Serrucho	*A. beherendseni* ?	1		
	MLP 36381	Arroyo Serrucho	*A. beherendseni* ?	1		
	MLP 28761a, b	Arroyo Serrucho	Late Pliensbachian	2		a: Fig. 16.6; b: Fig. 16.12
	MLP 36382	Arroyo Serrucho	*F. fannini*	1		
	IANIGLA-PI 3216	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3217	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3218	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3219	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3220	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3221	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3222	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3223	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3224	Arroyo Serrucho	Pliensbachian	1		

Continued.

Species	Collection number	Locality	Age/Biozone	N	Type	Figure
	IANIGLA-PI 3225	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3226	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3227	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3228	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3229	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3230	Arroyo Serrucho	Pliensbachian	1	Holotype	Fig. 16.11
	IANIGLA-PI 3231	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3232	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3233	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3234	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3235	Arroyo Serrucho	Pliensbachian	1		Fig. 16.10
	IANIGLA-PI 3236	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3237	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3238	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3239	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3240	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3241	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3242	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3243	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3244	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3245	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3246	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3247	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3248	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3249	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3250	Arroyo Serrucho	Pliensbachian	1		Fig. 16.9
	IANIGLA-PI 3251	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3252	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3253	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3266	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3267	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3268	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3269	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3270	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3271	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3272A	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3273	Arroyo Serrucho	Pliensbachian	1		Fig. 16.7
	IANIGLA-PI 3274	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3275	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3276	Arroyo Serrucho	Pliensbachian	1		Fig. 16.8
	IANIGLA-PI 3277	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3278	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3279	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3280	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3281	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3282	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3283	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3284	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3285	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3286A	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3287	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3289	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3290	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3291	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3292A	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3293	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3294	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3295	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3296	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3303	Arroyo Serrucho	Pliensbachian	1		
	IANIGLA-PI 3304	Arroyo Serrucho	Pliensbachian	1		
	MLP 36383	Cerro Puchenque	*E. meridianus*	1		Fig. 16.13
	MLP 36384	Cerro Puchenque	*E. meridianus*	1		
	MLP 36385	Cerro Puchenque	*E. meridianus*	1		
	MLP 36386	Cerro Puchenque	*A. beherendseni* ?	1		
	MLP 36387	Cerro Puchenque	*A. beherendseni* ?	1		
	MLP 36388a, b	Cerro Tricolor	Early Toarcian	2		a: Fig. 16.14; b: Fig. 16.15
	MLP 15535	Ñiraico	*Tenuicostatum*	1		
	MLP 15554	Ñiraico	*Tenuicostatum*	1		
	MLP 15437	Estación Rajapalo	*F. fannini*	1		
	MOZ-PI 1487	Cerro Granito	Pliensbachian	2		
	MLP 15322	Rahue-Aluminé	Pliensbachian	1		Fig. 16.16
	MLP 36389	Lonqueo	*F. fannini*	1		Fig. 16.17

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Species	Collection number	Locality	Age/Biozone	N	Type	Figure
	MLP 36390	Ea. Santa Isabel	*F. disciforme*	1		
	MLP 36391	Ea. Santa Isabel	*F. disciforme*	1		
	MLP 36392	Ea. Santa Isabel	*F. disciforme*	1		
	MLP 36393	Subida a Sañicó	*A. beherendseni* ?	1		
	MLP 36394	Subida a Sañicó	*A. beherendseni* ?	1		Fig. 16.18
	MLP 6253a	Cerro Roth	Pliensbachian	1		
	MLP 6725	Cerro Roth	Pliensbachian	1	Paratype	Fig. 16.19–16.21
	MOZ-PI 2682	Cerro Roth	Pliensbachian	1		
	MPEF-PI 3158	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 3375	Aguada Loca	Late Pliensbachian	1		
	MPEF-PI 2907	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 2909	Nueva Lubecka	Late Pliensbachian	6		
	MPEF-PI 2965b	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6386a–c	Nueva Lubecka	Late Pliensbachian	3		a: Fig. 16.22; b: Fig. 16.23
	MPEF-PI 6390	Nueva Lubecka	Late Pliensbachian	1		Fig. 16.28
	MPEF-PI 6392	Nueva Lubecka	Late Pliensbachian	1		Fig. 16.27
	MPEF-PI 6394	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6396	Nueva Lubecka	Late Pliensbachian	1		
	MPEF-PI 6399	Nueva Lubecka	Late Pliensbachian	1		Fig. 16.24
Promyophorella aff. *P. basoaltorum* n. sp.	CPBA 19657a–l [= cast MLP 20712a–l]	Cerro Cuche	Early (?) Pliensbachian	12		Fig. 16.26; a: Fig. 16.29; c: Fig. 16.25
Promyophorella araucana (Leanza)	MLP 6724	Piedra Pintada	Pliensbachian	1	Lectotype	Fig. 19.1, 19.2
	MLP 3904	Piedra Pintada	Pliensbachian	1	Paralectot.	Fig. 19.3, 19.4
	MLP 6253b	Piedra Pintada	Pliensbachian	1	Paralectot.	
	MLP 6735	Piedra Pintada	Pliensbachian	1	Paralectot.	
	MLP 13008b	Piedra Pintada	Pliensbachian	1		
	MLP 31011	Piedra Pintada	Pliensbachian	1		
	MLP 36336a, b	Cerro del Vasco	Pliensbachian	2		
	(?) MLP 36337a–f	Cerro del Vasco	Pliensbachian	6		
	MLP 36334a–d	Cerro Roth Sur	Pliensbachian	4		
	(?) MLP 36335	Cerro Roth Sur	Pliensbachian	1		
	(?) MLP 31573	Nueva Lubecka	Late Pliensbachian	1		
	(?) MPEF-PI 6393	Nueva Lubecka	Late Pliensbachian	1		
	(?) MPEF-PI 6395	Nueva Lubecka	Late Pliensbachian	1		
Promyophorella cf. *exotica* (Möricke)	MLP 36338	Arroyo La Laguna	E Toarcian (*hoelderi*)	1		Fig. 20.1
	MLP 36339	Arroyo La Laguna	E Toarcian (*hoelderi*)	1		Fig. 20.2
	MLP 36340	Arroyo La Laguna	E Toarcian (*hoelderi*)	1		Fig. 20.3
	MLP 36341a–h	Arroyo La Laguna	E Toarcian (*hoelderi*)	8		
	MLP 36342a–o	Arroyo La Laguna	E Toarcian (*hoelderi*)	15		
	MLP 36343	Arroyo Serrucho	E Toarcian (*hoelderi*)	1		
	MLP 36344a–h	Arroyo Serrucho	E Toarcian (*hoelderi*)	8		
	MLP 36345a–e	Arroyo Serrucho	E Toarcian (*hoelderi*)	5		
	MLP 36346	Arroyo Serrucho	E Toarcian (*hoelderi*)	1		Fig. 20.4
	MLP 36347a, b	Arroyo Serrucho	E Toarcian (*hoelderi*)	2		a: Fig. 20.7
	MLP 36348a, b	Arroyo Serrucho	E Toarcian (*hoelderi*)	2		a: Fig. 20.8
	MLP 36349	Arroyo Serrucho	E Toarcian (*hoelderi*)	1		Fig. 20.9
	MLP 36350	Arroyo Serrucho	E Toarcian (*hoelderi*)	1		Fig. 20.10
	MLP 36351a, b	Arroyo Serrucho	E Toarcian (*hoelderi*)	2		a: Fig. 20.12
	MLP 36352a–c	Arroyo Serrucho	E Toarcian (*hoelderi*)	3		a: Fig. 20.13
	MLP 36353	Arroyo Serrucho	E Toarcian	1		
	MLP 36354a, b	Arroyo Serrucho	E Toarcian	2		a: Fig. 20.5, 20.6
	MLP 36355a, b	Arroyo Serrucho	E Toarcian (*hoelderi*)	2		a: Fig. 20.15
	MLP 36356a, b	Arroyo Serrucho	E Toarcian	2		
	MLP 36399	Arroyo Serrucho	E Toarcian (*hoelderi*)	2		a: Fig. 20.11
	MLP 36400	Arroyo Serrucho	E Toarcian (*hoelderi*)	6		a: Fig. 20.14
	MLP 36357	Las Overas	E Toarcian (*hoelderi*)	1		
	MLP 36358a–d	Las Overas	E Toarcian (*hoelderi*)	4		
	MLP 36359a–d	Las Overas	E Toarcian (*hoelderi*)	4		
	MLP 36360	Las Overas	E Toarcian (*hoelderi*)	1		
	MLP 36361a–d	Las Overas	E Toarcian (*largaense*)	4		
	MLP 36362	Las Overas	E Toarcian (*largaense*)	1		
	MLP 36363a, b	Las Overas	E Toarcian (*hoelderi*)	2		
	MLP 36364a–e	Cerro Puchenque	E Toarcian (*hoelderi*)	5		a: Fig. 20.16
	MLP 36365a, b	Cerro Puchenque	E Toarcian (*hoelderi*)	2		a: Fig. 20.17
	MLP 36366a, b	Cerro Puchenque	E Toarcian (*hoelderi*)	2		a: Fig. 20.18
	MLP 36367a–d	Cerro Puchenque	E Toarcian (*pacificum*)	4		
	MLP 15547a–d	Ñiraico	E Toarcian (*hoelderi*)	4		a: Fig. 20.19, 20.20
	(?) MLP 15548	Ñiraico	E Toarcian (*hoelderi*)	1		
Promyophorella agniaensis (Levy)	MLP 36325	Cerro Tricolor	E Toarcian (Tenuicostatum?)	1		Fig. 21.6
	MLP 36326a, b	Cerro Tricolor	E Toarcian (*hoelderi*)	2		a: Fig. 21.7-21.8

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Species	Collection number	Locality	Age/Biozone	N	Type	Figure
	DNGM 641a–c (= SIRAME-SEGEMAR 7346a–c)	Pampa de Agnia	Early Toarcian	3	Holotype (a)	a: Fig. 21.1; b: Fig. 21.3; c: Fig. 21.2
Promyophorella species indet.	MLP 36327a–d	Cerro Tricolor	E Toarcian (Tenuicostatum?)	4		a: Fig. 21.14; c: Fig. 21.12; d: Fig. 21.13
	(?) MLP 17186a–d	Cerro Tricolor	Early Toarcian	4		
Promyophorella? sanjuanina new species	CPBA 17442	Arroyo Las Vegas (N of A. La Laguna)	L Pliens-E Toarcian	1		Fig. 21.11
	MLP 36328	Arroyo La Laguna	E Toarcian (*hoelderi*)	1	Pratype	Fig. 21.10
	MLP 36329	Arroyo La Laguna	E Toarcian (*hoelderi*)	1	Holotype	Fig. 21.9
	MLP 36330	Arroyo La Laguna	E Toarcian (*hoelderi*)	1	Paratype	Fig. 21.4
	MLP 36331	Arroyo La Laguna	E Toarcian (*hoelderi*)	1		Fig. 21.5
	MLP 36312c	Arroyo La Laguna	E Toarcian (*hoelderi*)	1		
	MLP 36332	Las Overas	E Toarcian (*largaense*)	1		
Myophorelloidea genus and species indet.	MLP 36395a–d	Cañada Colorada	Late Toarcian	4		a: Fig. 21.15, 21.18; b: Fig. 21.16; c: Fig. 21.17
	MLP 36396	Cañada Colorada	Late Toarcian	1		Fig. 21.19
	MLP 36397	Cañada Colorada	Late Toarcian	1		