

Early Jurassic Trochotomidae (Vetigastropoda, Pleurotomarioidea) from the Neuquén Basin, Argentina

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Abstract.—Trochotomidae is a small but distinctive extinct family of pleurotomarioidean gastropods characterized by trochiform shells with an elliptical trema. Two new species of trochotomids are described from Pliensbachian deposits in the Neuquén Basin, Argentina. The new genus-group name *Placotoma* is proposed to replace the pre-occupied name *Discotoma* Haber non Mulsant. The record of *Trochotoma* (*Trochotoma*) *protonotalis* new species and *Trochotoma* (*Placotoma*) *neuquensis* new species in the early Jurassic of Argentina extends the paleobiogeographical distribution of the genus (and the family) to the Southern Hemisphere. The new taxa reported here represent a component of the pleurotomarioidean adaptive radiation that took place in the Tethyan region during the earliest Jurassic. They are related to local patch coral reefs of shallow, open-marine paleoenvironments, agreeing with the known habitat of most species of this family. The group was well represented in the Tethyan region during the Mesozoic, especially during the Jurassic, and the new species represent its southernmost occurrence.

Introduction

Pleurotomarioidean gastropods were abundant and diverse in marine Paleozoic and Mesozoic shallow waters, but during the Cenozoic they became rare, and now tend to be limited to deep-water environments (Harasewych, 2002). The very distinctive late Triassic–Jurassic family Trochotomidae Cox, 1960 is included in the superfamily Pleurotomarioidea Swainson, 1840 by most authors (see discussion below), but its phylogenetic affinities are in fact problematic. This group includes trochiform shells with an elongate elliptical trema that have been grouped into the genus-group taxa *Trochotoma* Eudes-Deslongchamps, 1843, *Discotoma* Haber, 1934 non Mulsant, 1850 (here renamed *Placotoma*), *Valfinia* Cox, 1958, and *Legayella* Fischer, 1969. *Urkutitoma* Szabó, 1984 is another taxon tentatively included in the family by Szabó (2009). Almost 120 species names have been referred to this group, most of them instituted in the nineteenth century, with many figured solely by drawings and only poorly characterized, and a few were never figured (Table 1 and Supplementary Data). The family needs a thorough revision to elucidate its phylogenetic relationships with other vetigastropod groups, such as Scissurelloidea Gray, 1847 and Halioidea Rafinesque, 1815.

Early Jurassic marine gastropods from South America were studied by Bayle and Coquand (1851), Behreidsen (1891, 1922), Mörcke (1894), Burckhardt (1900, 1902), Jaworski (1925, 1926a, 1926b), Weaver (1931), Feruglio (1934), Wahnish (1942), Gründel (2001), and Damborenea and Ferrari (2008). Ferrari (2009, 2011, 2012, 2013, 2014) and Ferrari et al. (2014) recently provided new data on the taxonomic

composition of early Jurassic marine gastropod faunas from west-central Patagonia. Ferrari (2009) pointed out that some genera are cosmopolitan, being known from the Southern Hemisphere and other regions of the world (i.e., Europe), and are represented by some endemic species in west-central Patagonia and other localities in Argentina and Chile. Ferrari (2011, 2012, 2013, 2014) reported 13 gastropod families from the early Jurassic (Pliensbachian–Toarcian) marine deposits of Chubut Province. These include 20 genera, two subgenera, and 36 species. Most of these genera were recorded for the first time in the Argentinean Jurassic, and at least nine new species seem to be endemic to the Patagonian region.

Nevertheless, early Jurassic gastropods from the Neuquén Basin are still poorly known, despite being widely distributed and locally diverse (see synthesis of previous knowledge in Ferrari, 2009; Riccardi et al., 2011). Their potential use in paleobiogeography and paleoecology awaits updated systematic revisions. At least 15 gastropod species were preliminarily reported from the uppermost lower Pliensbachian beds at Piedra Pintada (southern Neuquén) by Damborenea et al. (1975). This paper deals with two of these species from the Piedra Pintada area and nearby localities. The two new species are the first Trochotomidae to be described from the Southern Hemisphere.

Geological setting

The Neuquén Basin is a well-known back-arc basin developed on the eastern margin of the Paleo-Pacific (or Panthalassa) Ocean, which had a rich depositional history spanning most of the Mesozoic. The late Triassic and early Jurassic extensional

Table 1. List of nominal species once referred to Trochotomidae, with an indication of their updated generic affinities. Those discussed in this paper (including supplementary data) are in bold type. Taxa doubtfully related to this family are indicated with question marks.

| Species name | Author and reference | First figure | Genus (Subgenus) | Originally referred to | Distribution | Age | This paper |
|-------------------------------|--|---|------------------------|------------------------|---------------|----------------|--|
| <i>acuminata</i> | E.-Deslongchamps, 1843, p. 108 | pl. 8, figs. 11-15 | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | France | Bathonian | Suppl. Fig. 1.B |
| <i>affinis</i> | E.-Deslongchamps, 1843, p. 106 | pl. 8, figs. 8-10 | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | Europe | Baj-Bathonian | Fig. 5.5-6 |
| <i>amata</i> | d'Orbigny, 1850b, p. 9 | d'Orbigny 1853, pl. 343, figs. 3-8 | <i>T. (Placotoma)</i> | <i>Ditremaria</i> | France | Late Jurassic | Suppl. Fig. 5.C |
| <i>angulata</i> | Münster in Goldfuss, 1844, p. 56 | pl. 180, fig. 7 | <i>Trochotoma?</i> | <i>Trochus</i> | Germany | Unter Oolithe | |
| <i>auris</i> | von Zittel, 1873, p. 347-348 | pl. 51, figs. 3-4 | <i>Trochotoma s.l.</i> | <i>Trochotoma</i> | Europe | Late Jurassic | Suppl. |
| <i>barremica</i> | Cossmann, 1916, p. 29 | pl. 2, figs. 30-33 | <i>T. (Placotoma)?</i> | <i>Trochotoma</i> | France | Barremian | |
| <i>bartkoi</i> | Szabó, 1984, p. 70-71 | fig. 3 | <i>Urkutitoma</i> | <i>Urkutitoma</i> | Hungary | Sinemurian | |
| <i>bellampensis</i> | Haber, 1934, p. 329 | Gemmellaro 1879, pl. 5, figs. 69-70 | <i>Trochotoma</i> (T.) | <i>Ditremaria</i> | Sicily | Early Jurassic | Suppl., see <i>meneghini</i> |
| <i>bicarinata</i> | d'Orbigny, 1843, p. 276-277 | d'Orbigny 1853, pl. 340, figs. 8-11 | <i>Trochotoma</i> (T.) | <i>Ditremaria</i> | France | Early Jurassic | Fig. 5.7 |
| <i>blaschkei</i> | Haber, 1934, p. 388-389 | Blaschke 1911, pl. 5, figs. 7a-b | <i>Valfinia</i> | <i>Didymodon</i> | Czech Rep. | Tithonian | |
| <i>brocastellensis</i> | Moore, 1867, p. 267 | pl. 15, fig. 29 | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | Great Britain | Early Jurassic | Suppl. Fig. 2.C |
| <i>calix</i> | Phillips, 1829, p. 157 | pl. 11, fig. 30 | <i>Trochotoma</i> (T.) | <i>Solarium</i> | Great Britain | Aalenian | Fig. 5.1-2 |
| <i>canaliculata</i> | Pictet, 1855, p. 180 | Error pro <i>carinata</i> | <i>Trochotoma</i> | <i>Trochotoma</i> | Great Britain | Bathonian | Suppl. |
| <i>carinata</i> | Lycett, 1850, p. 417 | Lycett 1857, pl. 4, fig. 5 | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | Great Britain | Bathonian | Fig. 5.4 |
| <i>carinata</i> | von Zittel, 1873, p. 341 | pl. 50, fig. 9 | <i>Valfinia?</i> | <i>Ditremaria</i> | Czech Rep. | Late Jurassic | |
| <i>carpatica</i> | Kochanová in Kollárová & Kochanová, 1973, p. 198 | pl. 10A, fig. 3 | <i>Trochotoma?</i> | <i>Trochotoma</i> | Slovakia | Norian | |
| <i>chanoise</i> | Henry, 1875, p. 441 | pl. 4, figs. 33-34 | ? | <i>Trochotoma</i> | France | Hettangian | |
| <i>chordulata</i> | Haber, 1934, p. 373 | Morris & Lycett 1851, pl. 10, fig. 10 | <i>T. (Placotoma)</i> | <i>Ditremaria</i> | Great Britain | Bathonian | Suppl. Fig. 6.D, see <i>funiculosa</i> |
| <i>clypeus</i> | Terquem, 1855, p. 268 | pl. 16, figs. 9-9a | <i>Trochotoma?</i> | <i>Trochotoma</i> | Europe | Hettangian | Suppl. |
| <i>conica</i> | Rollier, 1918, p. 57 | Cossmann 1885, pl. 13, fig. 14 | <i>Trochotoma</i> (T.) | <i>Ditremaria</i> | France | Bathonian | Suppl. Fig. 1.C, see <i>acuminata</i> |
| <i>conuloides</i> | E.-Deslongchamps, 1843, p. 109 | pl. 8, figs. 16-19 | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | France | Bathonian | Suppl. Fig. 1.A |
| <i>cossmanni</i> | Rollier, 1918, p. 59 | Cossmann 1900, pl. 16, figs. 3-5 | <i>T. (Placotoma)</i> | <i>Ditremaria</i> | France | Bathonian | Suppl. Fig. 6.F |
| <i>cotteauana</i> | Haber, 1934, p. 335 | Cossmann 1885, pl. 8, figs. 13-14 | <i>Trochotoma</i> (T.) | <i>Ditremaria</i> | France | Bathonian | Suppl., see <i>extensa</i> |
| <i>croisei</i> | de Folin, 1869 in de Folin & Périer, p. 144 | pl. 22, fig. 6 | <i>Sinezona</i> | <i>Trochotoma</i> | Cap Vert | living | |
| <i>deffneri</i> | Fraas, 1882, p. 144 (nom. nud.) | | ? | <i>Ditremaria</i> | Germany | Kimmeridgian? | |
| <i>depressa</i> | Gioli, 1889, p. 9-10 | pl. 1, fig. 9 | <i>T. (Placotoma)?</i> | <i>Ditremaria</i> | Italy | Aalenian | |
| <i>depressiuscula</i> | Lycett, 1850, p. 417 | Hudleston 1896, pl. 41, fig. 10 | <i>T. (Placotoma)</i> | <i>Trochotoma</i> | Great Britain | Bathonian | Suppl. Fig. 6.C |
| <i>desoriana</i> | Cotteau, 1854, p. 36 | | <i>Trochotoma</i> (T.) | <i>Ditremaria</i> | France | Bathonian | Suppl. |
| <i>discoidea</i> | Roemer, 1836, p. 150 | pl. 11, fig. 12 | <i>Trochotoma?</i> | <i>Trochus</i> | France | Kimmeridgian | Suppl. Fig. 4.E |
| <i>discoidea</i> | Buvignier, 1852, p. 39 | pl. 25, figs. 10-11 | <i>T. (Placotoma)</i> | <i>Trochotoma</i> | Europe | Bathonian | Suppl. Fig. 5.D |
| <i>distefanoi</i> | Scalia, 1903, p. 37 | Fucini 1913, pl. 1, figs. 1-2 | <i>Trochotoma?</i> | <i>Trochotoma</i> | Sicily | Early Jurassic | Suppl. |
| <i>elegans</i> | Gemmellaro, 1889, p. 152 | pl. 15, figs. 27-29 | ? | <i>Trochotoma</i> | Sicily | Permian | |
| <i>elegans</i> | Favre in Joukowsky & Favre, 1913, p. 425 | pl. 25, figs. 18-20 | <i>Valfinia?</i> | <i>Ditremaria</i> | France | Portlandian | |
| <i>elongata</i> | Nalivkin & Akimov, 1917, p. 27-28 | pl. 3, fig. 10 | <i>Valfinia?</i> | <i>Ditremaria</i> | | | |
| <i>extensa</i> | Morris & Lycett, 1851, p. 83 | pl. 10, figs. 19a-b | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | Europe | Bathonian | Suppl. Fig. 2.A |
| <i>funata</i> | Lycett, 1850, p. 417 | Hudleston 1896, pl. 41, figs. 5a-b | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | Great Britain | Bathonian | Suppl. |
| <i>funiculosa</i> | Cossmann, 1885, p. 309 | pl. 10, figs. 36-37 | <i>T. (Placotoma)</i> | <i>Trochotoma</i> | Europe | Bathonian | Suppl. Fig. 6.D-E |
| <i>gansuensis</i> | Tong & Erwin, 2001, p. 15 | pl. 2, figs. 5-10 | <i>Trochotoma ?</i> | <i>Trochotoma</i> | China | Anisian | |
| <i>gemmellaro</i> | Haber, 1934, p. 340 | Gemmellaro 1879, pl. 6, figs. 18-19 | <i>Trochotoma?</i> | <i>Ditremaria</i> | Sicily, Italy | Sinemurian | |
| <i>gigantea</i> | von Zittel, 1873, p. 345-346 [463] | pl. 51, figs. 1-2 | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | Czech Rep. | Late Jurassic | Suppl. |
| <i>globulus</i> | E.-Deslongchamps, 1843, p. 109 | pl. 8, figs. 20-22 | <i>Valfinia?</i> | <i>Trochotoma</i> | France | Bathonian | |
| <i>gracilis</i> | von Zittel, 1873, p. 343 | pl. 50, figs. 11, 13 | <i>Valfinia</i> | <i>Trochotoma</i> | Czech Rep. | Late Jurassic | |
| <i>gradata</i> | Gemmellaro, 1879, p. 198 | pl. 6, fig. 17 | <i>Trochotoma</i> (T.) | <i>Ditremaria</i> | Sicily | Early Jurassic | Suppl. |
| <i>gradus</i> | E.-Deslongchamps, 1843, p. 106 | pl. 8, figs. 4-7 | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | France | Toarcian | Fig. 5.8-9 |
| <i>granulifera</i> | von Zittel, 1873, p. 342 | pl. 50, figs. 10, 12 | <i>Valfinia?</i> | <i>Ditremaria</i> | Czech Rep. | Late Jurassic | |
| <i>hamptonensis</i> | Haber, 1934, p. 344-345 | Morris & Lycett 1851, pl. 10, figs. 18a, 20 | <i>Trochotoma</i> (T.) | <i>Ditremaria</i> | Great Britain | Bathonian | Suppl. Fig. 1.D, see <i>obtusata</i> |
| <i>haueri</i> | Hörnnes in von Hauer, 1853, p. 763 | | <i>Trochotoma</i> (T.) | <i>Trochotoma</i> | Germany | Sin-Pliensbach | Suppl. |
| <i>hermitei</i> | Gemmellaro, 1879, p. 196 | pl. 5, figs. 65-68 | <i>Trochotoma</i> | <i>Trochotoma</i> | Sicily | Early Jurassic | Suppl. Fig. 3.D |
| <i>hermitei</i> | de Loriol, 1887, p. 208 | pl. 23, figs. 6-7 | <i>Valfinia</i> | <i>Ditremaria</i> | France | Oxfordian | |

| | | | | | | | |
|---|--|--|--|--|--|--|---|
| <i>hudlestoni</i> <i>humbertina</i> | Rollier, 1918, p. 55 Buvignier, 1852, p. 39 | Hudleston 1896, pl. 41, figs. 1a-b pl. 25, figs. 12-13 | <i>Trochotoma</i> (T.) <i>Valfinia</i> | <i>Ditremaria</i> <i>Trochotoma</i> | Great Britain France, Germany | Aalenian Late Jurassic | Suppl. |
| <i>imbricata</i> <i>infundibulum</i> <i>ingens</i> <i>intermedia</i> <i>kimmeridgiensis</i> <i>lamberti</i> <i>legayi</i> <i>lindonensis</i> <i>lorioli</i> <i>lycetti</i> <i>lycetti</i> | Cossmann, 1885, p. 308 Étallon, 1862, p. 114 Rollier, 1918, p. 52 Münster in Goldfuss, 1844, p. 70 Maire, 1927, p. 102-104 de Loriol, 1893, p. 74 Cossmann, 1885, p. 304 Hudleston, 1896, p. 449 Cossmann, 1902, p. 97 Moore, 1867, p. 565 Hermite, 1877, p. 693 | pl. 8, fig. 18 pl. 43, figs. 4a-c pl. 185, figs. 1-2 pl. 6, figs. 19-21 pl. 5, figs. 11, 11a-c pl. 15, figs. 27-29 pl. 41, fig. 8 de Loriol 1887, pl. 23, figs. 6-7 pl. 15, figs. 27-28 Morris & Lycett 1851, pl. 10, figs. 16, 20 | <i>Trochotoma</i> (T.) <i>Trochotoma</i> (T.) <i>Trochotoma</i> ? <i>Legayella</i> ? <i>Legayella</i> ? <i>Trochotoma</i> ? <i>Trochotoma</i> ? <i>Legayella</i> <i>Valfinia</i> <i>Valfinia</i> <i>Trochotoma</i> ? <i>Trochotoma</i> (T.) | <i>Trochotoma</i> <i>Ditremaria</i> <i>Ditremaria</i> <i>Pleurotomaria</i> <i>Trochotoma</i> <i>Trochotoma</i> ? <i>Trochotoma</i> <i>Trochotoma</i> <i>Trochotoma</i> <i>Trochotoma</i> <i>Trochotoma</i> | France France France Germany France France France Great Britain France Great Britain Great Britain | Bathonian Middle Jurassic Hett-Sinemur? Kimmeridgian Oxfordian Bathonian Aalenian? Late Jurassic Early Jurassic Bathonian | Suppl. Fig. 2.D Suppl. Suppl. Fig. 4.F Suppl. Fig. 1.D-E, see <i>conuloides</i> Fig. 5.3 |
| <i>magnifica</i> <i>mantochensis</i> <i>marbachensis</i> <i>mastoidea</i> | Cossmann, 1885, p. 305 Étallon, 1864, p. 454 Hermite, 1877, p. 691 Étallon in Thurmann & Étallon, 1861, p. 131 | pl. 14, figs. 9-11 pl. 12, fig. 108 | <i>Trochotoma</i> (T.) <i>Trochotoma</i> ? <i>Valfinia</i> <i>Trochotoma s.l.</i> | <i>Trochotoma</i> <i>Ditremaria</i> <i>Trochotoma</i> <i>Ditremaria</i> | France France France France | Bathonian Portlandian Aalenian Oxfordian | Suppl. Fig. 4.A-C |
| <i>maubertense</i> <i>meneghini</i> <i>metzertensis</i> <i>morieri</i> | Terquem & Piette, 1865, p. 55 Gemmellaro, 1879, p. 195 Terquem & Piette, 1865, p. 60 Eudes-Deslongchamps, 1864, p. 177 | pl. 4, figs. 20, 21 pl. 6, figs. 11-12 pl. 4, fig. 28 | <i>Trochotoma</i> ? <i>Trochotoma</i> (T.) ? <i>Trochotoma</i> (T.) | <i>Trochotoma</i> <i>Trochotoma</i> <i>Pleurotomaria</i> <i>Trochotoma</i> | Luxembourg Sicily, Italy Luxembourg France | Hettangian Sinemurian Hettangian Early Jurassic | Suppl. Suppl. Fig. 1.F Suppl. |
| <i>multicincta</i> <i>multiplœura</i> <i>neuquensis</i> | Schübler in von Zieten, 1832, p. 45 Pan, 1977, p. 97 Ferrari et al., here | pl. 34, fig. 1 pl. 2, figs. 13a-c Fig. 2.8-2.9 | <i>T. (Placotoma)</i> ? <i>T. (Placotoma)</i> ? <i>T. (Placotoma)</i> | <i>Trochus</i> <i>T. (Discotoma)</i> <i>T. (Placotoma)</i> | Germany Yunnan, China Neuquén, Argentina | Early Jurassic Carnian Pliensbachian | Suppl. Fig. 6.H Fig. 2.8-2.9 |
| <i>nucleus</i> <i>obtusa</i> <i>orbita</i> <i>orientalis</i> <i>ornata</i> | Terquem, 1855, p. 270 Morris & Lycett, 1851, p. 83 Pan, 1982, p. 168 Kiparisova, 1952, p. 22 Münster in Goldfuss, 1844, p. 101 | pl. 16, fig. 5 pl. 10, figs. 15a-b pl. 2, figs. 1-7 pl. 6, figs. 1, 3, 4 pl. 195, fig. 6 | <i>Trochotoma</i> ? <i>Trochotoma</i> (T.) <i>Trochotoma</i> ? <i>Trochotoma</i> (T.) <i>Valfinia</i> | <i>Pleurotomaria</i> <i>Trochotoma</i> <i>Trochotoma</i> <i>Ditremaria</i> <i>Monodonta</i> | France Europe Ghizou, China East Russia Germany, France | Hettangian Bathonian Middle Triassic Early Jurassic Callovian | Suppl. Fig. 5.10 Fig. 5.14 |
| <i>oxfordiana</i> <i>pachyspira</i> | Étallon, 1864, p. 304 E.-Deslongchamps, 1868, p. 216 | pl. 4, figs. 1a-c | <i>Valfinia</i> ? <i>Trochotoma</i> (T.) | <i>Ditremaria</i> <i>Trochotoma</i> | France France, Morocco | Oxfordian Pliens-Toarc | Suppl. Fig. 2.E |
| <i>petrariae</i> <i>picteti</i> <i>planoconvexa</i> <i>portlandica</i> <i>praecursor</i> <i>prisca</i> <i>protonotialis</i> | Bigot, 1935, p. 719 von Zittel, 1873, p. 347 Yu, Pan & Wang, 1974, p. 322 Étallon, 1864, p. 454 Stoppani, 1857, p. 364-365 Gemmellaro, 1889, p. 153 Ferrari et al., here | pl. 39, figs. 4, 4a pl. 50, fig. 16 pl. 171, figs. 1-3 Stoppani 1861, pl. 2, figs. 17-19 pl. 18, figs. 12-14 Figs. 2.1-2.9 | <i>T. (Placotoma)</i> <i>Trochotoma</i> ? <i>T. (Placotoma)</i> ? <i>Valfinia</i> <i>Trochotoma</i> ? <i>Trochotoma</i> (T.) | <i>Trochotoma</i> <i>Trochotoma</i> <i>Trochotoma</i> <i>Ditremaria</i> <i>Ditremaria</i> <i>Trochotoma</i> <i>Trochotoma</i> (T.) | France Czech Rep. China France Italy Sicily Neuquén, Argentina | Bathonian Late Jurassic Middle Triassic Portlandian Rhaetian Permian Pliensbachian | Suppl. Fig. 6.G Fig. 2.1-2.9 |
| <i>putealis</i> <i>quenstedti</i> <i>quinquecincta</i> <i>ranvilliana</i> <i>rathieriana</i> | Cossmann, 1885, p. 310 Rollier, 1918, p. 56 von Zieten, 1832, p. 46 Rollier, 1918, p. 60 d'Orbigny, 1850b, p. 9 | pl. 15, figs. 25-26 Quenstedt 1858, pl. 57, fig. 20 pl. 35, fig. 2 Cossmann 1885, pl. 11, figs. 24-25 d'Orbigny 1853, pl. 342, figs. 6-8, pl. 343, figs. 1.2 | <i>Trochotoma</i> (T.) <i>Trochotoma</i> (T.) <i>Valfinia</i> <i>Trochotoma</i> (T.) <i>Trochotoma</i> (T.) | <i>Trochotoma</i> <i>Ditremaria</i> <i>Trochus</i> <i>Ditremaria</i> <i>Ditremaria</i> | France Germany France France France, Germany | Bathonian Bajocian Late Jurassic Bathonian Callovian- Oxfordian | Suppl. Fig. 1.G Suppl. Fig. 1.H Suppl. Fig. 5.11 |
| <i>recondita</i> <i>rota</i> <i>salevensis</i> | Lycett, 1863, p. 106 E.-Deslongchamps, 1843, p. 105 Favre in Joukowsky & Favre, 1913, p. 424 | pl. 45, fig. 7 pl. 8, figs. 1-3 pl. 1 | <i>Trochotoma</i> (T.) <i>T. (Placotoma)</i> <i>Valfinia</i> ? | <i>Pleurotomaria</i> <i>Trochotoma</i> <i>Trochotoma</i> | Great Britain France France | Bathonian Bathonian Portlandian | Suppl., see <i>obtusa</i> Suppl. Fig. 5.A-B |
| <i>scalaris</i> | d'Orbigny, 1850b, p. 9 | d'Orbigny 1853, pl. 344, figs. 1-3 | <i>Trochotoma</i> (T.) | <i>Ditremaria</i> | France, Germany | Late Jurassic | Suppl. |

Table 1. (Continued)

| Species name | Author and reference | First figure | Genus (Subgenus) | Originally referred to | Distribution | Age | This paper |
|--|--|---|--|---|---|---|--|
| <i>scansilis schlosseri</i> | Ammon, 1892, p. 188-189 Haber, 1934, p. 383 | tex-fig- 20 (p. 189) Schlosser 1882, pl. 13, fig. 17 | <i>Trochotoma?</i> <i>T. (Placotoma)</i> | <i>Pleurotomaria</i> <i>Ditremaria</i> | Germany Germany | Early Jurassic Kimmeridgian | Suppl., see <i>discoidea</i> Buv. |
| <i>schlumbergeri secans sequanica</i> | E.-Deslongchamps, 1868, p. 219 Dubar, 1948, p. 137 Haber, 1934, p. 381-382 | pl. 8, fig. 5 pl. 11, figs. 12a.c de Lorioi 1887, pl. 23, fig. 10-11 | <i>Trochotoma (T.)</i> <i>Trochotoma (T.)</i> <i>Trochotoma</i> | <i>Trochotoma</i> <i>Ditremaria</i> <i>Ditremaria</i> | France Morocco France | Aalenian Pliensbachian? Late Jurassic | Fig. 5.13 Suppl. Fig. 2.F Suppl. Fig. 4.B, see <i>mastoidea</i> |
| <i>siciliana solarium somertonensis strambergensis striata</i> | Haber, 1934, p. 360 Koch, 1848, p. 174 Rollier, 1918, p. 55 Remeš, 1909 Hörnes in von Hauer, 1853, p. 762-763 | Gemmellaro 1879, pl. 5, figs. 71.72 pl. 25, figs. 17-19 Hudleston 1896, pl. 41, figs. 2-3 Stoliczka 1861, pl. 5, figs. 2a-b | <i>Trochotoma (T.)</i> <i>T. (Placotoma)?</i> <i>Trochotoma (T.)</i> <i>Valfinia?</i> <i>Trochotoma</i> | <i>Ditremaria</i> <i>Pleurotomaria</i> <i>Ditremaria</i> <i>Ditremaria</i> <i>Trochotoma</i> | Sicily (Italy) Germany Great Britain Czech Rep. Europe, Turkey | Sinemurian Early Jurassic Aalenian Late Jurassic Sinemurian- Pliensbachian | Suppl., see <i>pachyspira</i> Suppl. Suppl. |
| <i>striata suevica tabulata terquemi tethys thurmanni</i> | von Zittel, 1873, p. 344 Quenstedt, 1884, p. 373 Morris & Lycett, 1851, p. 83 Deshayes, 1865, p. 236 d'Orbigny, 1850a, p. 301 de Lorioi, 1890, p. 162 | pl. 50, figs. 14-15 pl. 199, figs. 48-49 pl. 10, fig. 17, 17a pl. 7, fig. 1 d'Orbigny 1853, pl. 404, figs. 14-19 pl. 18, figs. 5-6 | <i>Trochotoma?</i> <i>Trochotoma s.l.</i> <i>Trochotoma (T.)</i> <i>Sinezona</i> <i>Trochotoma?</i> <i>Valfinia</i> | <i>Ditremaria</i> <i>Ditremaria</i> <i>Trochotoma</i> <i>Trochotoma</i> <i>Pleurotomaria</i> <i>Ditremaria</i> | Czech Rep. Germany Europe France France France, Switzerland | Late Jurassic Kimmeridgian Bathonian Miocene Bathonian Kimmeridgian | Suppl. Fig. 4.D Fig. 5.12 |
| <i>tornatilis / tornata trocheata trochoides valfinensis vetusta</i> | Phillips, 1829, p. 188 Terquem, 1855, p. 271 Gemmellaro, 1879, p. 197 Haber, 1934, p. 386 Terquem, 1855, p. 267 | pl. 4, fig. 16 pl. 16, figs. 15, 15a pl. 6, figs. 13-16 de Lorioi 1887, pl. 23, figs. 8-9 pl. 16, figs. 10-10a | <i>T. (Placotoma)</i> <i>Trochotoma?</i> <i>Trochotoma</i> <i>Trochotoma s.l.</i> <i>Trochotoma (T.)</i> | <i>Trochus</i> <i>Pleurotomaria</i> <i>Ditremaria</i> <i>Ditremaria</i> <i>Trochotoma</i> | Great Britain France Sicily France Europe, Morocco? | Bathonian Hettangian Early Jurassic Late Jurassic Hett-Sinem | Suppl. Fig. 6.A-B Suppl. Fig. 3.B Suppl. Fig. 3.C Suppl., see <i>auris</i> Suppl. Fig. 2.B |
| <i>yunnanensis zitteli</i> sp. sp. indet. | Pan, 1977, p. 97 Haber, 1934, p. 386-387 Szabó, 2008, p. 53-54 Kiparisova, 1952, p. 23 | pl. 2, figs. 10-12 von Zittel 1873, pl. 51, fig. 5 (only) fig. 47 pl. 5, figs. 3a-b | <i>T. (Placotoma)?</i> <i>Trochotoma s.l.</i> <i>Urkutitoma?</i> <i>Trochotoma?</i> | <i>T. (Discotoma)</i> <i>Ditremaria</i> <i>Urkutitoma?</i> <i>Ditremaria</i> | Yunnan, China Czech Rep. Hungary East Russia | Carnian Tithonian Pliensbachian? Early Jurassic | Suppl., see <i>auris</i> Suppl. Fig. 4.G |

time (Uliana and Biddle, 1988) was followed by the deposition of a thick sedimentary succession in which several sedimentary cycles can be recognized, each with different paleogeographical and temporal extension (Legarreta and Uliana, 1996, 2000). The initial transgression occurred through the Curepto Strait (Vicente, 2005) in southern Mendoza Province, and the first filling was accommodated in pre-existing rift depocenters. During Pliensbachian times, the transgression spread and became generalized, attaining the first of the two largest marine floodings of the basin: the Pliensbachian–Toarcian and the Tithonian–Neocomian (see Gulisano and Gutiérrez-Pleimling, 1995; Arregui et al., 2011).

The material studied here was found in localities near the southern end of the embayment (Fig. 1) in sublittoral deposits of Pliensbachian age. Most specimens were recorded from the classical Piedra Pintada fossil locality discovered near the end of the nineteenth century by an expedition organized by the Museo de La Plata (Roth, 1899). In this particular area, a variety of marginal marine and littoral environments developed (Gulisano and Pando, 1981) within the Cuyo Mesosequence (Legarreta and Gulisano, 1989), which represents the first Mesozoic marine sedimentation in this part of the basin. In the Piedra del Águila–Carrán Curá region, the volcanic influence was quite persistent. Several lithofacies were recognized by Gulisano and Pando (1981, p. 561); the gastropods described here are associated with what they called “light colored sandstones, mudstones and tuffs facies.” These sediments were deposited in a moderate- to high-energy shoreface to foreshore environment, with frequent pyroclastic input, referred by Gulisano and Pando (1981) to the Lajas Formation (Weaver, 1931). Other authors (see Arregui et al., 2011) use the local name Piedra Pintada Formation (Stipanovic et al., 1968) for these deposits. The marine sediments overlie Lower Jurassic volcanic and pyroclastic rocks (Sañicó Formation).

Damborenea et al. (1975) distinguished two main biofacies and seven sub-biofacies in these deposits. The beds bearing the gastropods described here belong to their sub-biofacies A2, characterized by high-diversity systematic and ecological assemblages, dominated by an epifauna with a large percentage of cemented organisms. This sub-biofacies includes coral buildups, which locally form small bioherms. It is associated with the ‘light coloured sandstones, mudstones and tuffs’ lithofacies already mentioned.

Zonal successions spanning the Pliensbachian–Tithonian interval were recognized on the basis of abundant, diverse, and stratigraphically significant cephalopod, bivalve, and brachiopod taxa, which are correlated with the international standard scale (see Riccardi et al., 2011), and are used as the time frame for this study.

Materials and methods

Specimens were collected at three localities (Cerro Roth, Carrán Curá, and Estancia Santa Isabel, Fig. 1), all in southern Neuquén Province. The stratigraphic sections logged there were described by Damborenea et al. (1975, fig. 3) and Damborenea (1987, fig. 5). The accompanying fauna is both abundant and highly diverse, comprising mostly epifaunal bivalves, brachiopods, other gastropods, and corals. The material from Piedra Pintada was found in

uppermost lower Pliensbachian beds (*Austromorphites behrendseni* Zone), according to the local ammonite biozonation (Riccardi, 2008a, 2008b; Riccardi et al., 2011). At Estancia Santa Isabel, ammonites indicate a slightly younger age (*Fanninoceras fannini* or *F. disciforme* Zones), i.e., lower upper Pliensbachian.

The material is housed in the collections of the División Paleozoología Invertebrados, Museo de Ciencias Naturales de La Plata (MLP), and Museo Carmen Funes, Plaza Huincul (MCF-PIPH). Newly collected shells were prepared by technical staff at the Museo Paleontológico “Egidio Feruglio” (MPEF) laboratory. All specimens were coated with ammonium chloride to enhance sculptural details for photography.

Systematic paleontology

Institutional abbreviations.—MLP: Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MCF-PIPH: Museo Carmen Funes, Plaza Huincul, Neuquén, Argentina; MPEF: Museo Paleontológico “Egidio Feruglio”, Trelew, Chubut, Argentina.

Superfamily Pleurotomarioidea Swainson, 1840
Family Trochotomidae Cox, 1960

Remarks.—Although *Ditremariinae* Haber, 1934 (p. 320), available under ICZN Art. 13.2.1 (Bouchet and Rocroi, 2005, p. 66, 176) would hold priority as a family group name (still used by Wang, 1978, p. 399), Trochotomidae Cox (in Knight et al., 1960, p. 220) is to be maintained because it was proposed before 1961 and has gained prevailing usage (ICZN Art. 40.2).

Trochotomids are frequently related to reef environments of the Tethyan region (Europe, northern Africa). Outside of this region they were only mentioned from northern Russia by Kiparisova (1952), and from western Argentina by Damborenea et al. (1975, 2012b). This last record is in fact a preliminary identification of nearly all the material described below. Except for such records, the family was unknown either from the rest of the Americas or other Austral regions.

Genus *Trochotoma* Eudes-Deslongchamps, 1843

Type species.—*Trochotoma conuloides* Eudes-Deslongchamps, 1843, p. 109, pl. 8, figs. 16–19, from the Bathonian of France, subsequent designation by Woodward, 1851, p. 148, pl. 10, fig. 26.

Remarks.—Woodward (1851, p. 148) already regarded *Trochotoma* Eudes-Deslongchamps, 1843 and *Ditremaria* d’Orbigny, 1843 as subjective synonyms, and used the first name as valid. The reasons for preferring the generic name *Trochotoma* over *Ditremaria* were also explained by Pictet (1855, p. 179), Hermite (1877, p. 688), and Fischer and Weber (1997, p. 151). Despite this, some authors used *Ditremaria* as the valid genus name (i.e., Rollier, 1918; Haber, 1934; Dubar, 1948). A few other authors did not regard them as synonyms, and notably, Eudes-Deslongchamps (1868, p. 215) restricted *Ditremaria* to shells with two closely set tremata and *Trochotoma* to shells with a single trema (see also Stoliczka, 1867, p. 384; von Zittel, 1873, p. 341; and Burckhardt, 1897, p. 203).

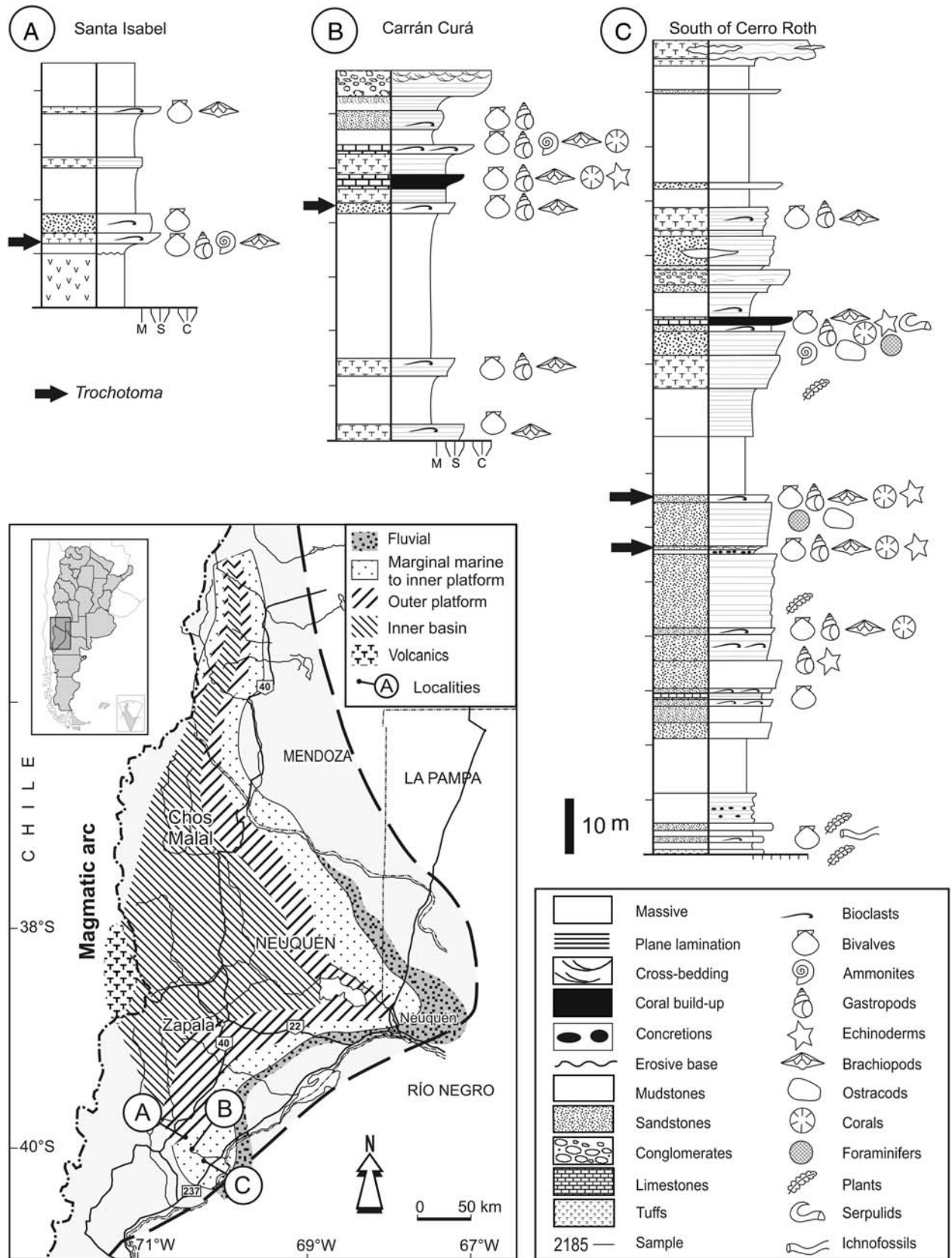


Figure 1. Location map and simplified logged sections at Santa Isabel (A), Carrán Curá (B) and Cerro Roth (C) in southern Neuquén Province, Argentina. Beds with *Trochotoma* indicated with an arrow. Paleogeography after Legarreta and Uliana (2000), sections adapted from Damborenea et al. (1975) and Damborenea (1987).

The genus had a Mesozoic stratigraphic distribution, and greatly diversified very early in Jurassic times. Middle and late Triassic records, mostly from China (Yu et al., 1974; Pan, 1977, 1982; Tong and Erwin, 2001) and Slovakia (Kollárová-Andrusovová and Kochanová, 1973), are few and doubtful. Even some Permian species were referred to *Trochotoma* (Gemmellaro, 1889), but they clearly do not belong to this genus. Similarly, the Miocene species described by Deshayes (1865) as *Trochotoma terquemi* was later referred to the Scissurellidae genus *Sukashitrochus* Habe and Kosuge, 1964 by Lozouet et al. (2001). It is now included in *Sinezona* Finlay, 1926 (Geiger, 2012, p. 593). Likewise, the living species described as *Trochotoma crossei* de Folin (in de Folin and Périer, 1869, p. 144, pl. 22, fig. 6) is now regarded as a species of *Sinezona*. The specific diversity of *Trochotoma* was high until the latest Jurassic, and there is a single record from Lower Cretaceous deposits (*Trochotoma barremica* Cossmann, 1916). These genus names have also been applied to members of *Trochotoma*: *Rimulus* d'Orbigny, 1841, p. 199, (*nom. nud.*), and *Ditremaria* d'Orbigny, 1843, p. 276.

Subgenus *Trochotoma* Eudes-Deslongchamps, 1843
Trochotoma (Trochotoma) protonotalis new species
 Figure 2.1–2.7

Type material.—Holotype MLP 26172; complete teleoconch; paratypes MLP 12168, 26169, two specimens.

Diagnosis.—Shell turbiniform, gradate, broadly pseudomphalous; teleoconch with 5 whorls; ramp and outer face slightly concave; suture visible in a narrow furrow; spiral elements on the shell surface predominant; three to four cords between two peripheral angulations on mature whorls; elliptical trema on the adapical angulation; peristome prosocline and discontinuous in mature growth stages, but with deep notch in juvenile growth stages; base flat to slightly excavated, with spiral threads intercepted by fine prosocline growth lines.

Type locality and horizon.—Estancia Santa Isabel, Neuquén Province, Argentina. Early Jurassic (lower upper Pliensbachian, *Fanninoceras fannini* or *F. disciforme* Zones), Piedra Pintada Formation.

Description.—Dextral, turbiniform, gradate, broadly pseudomphalous shell. Protoconch not preserved. Teleoconch consisting of five whorls. Juvenile whorls slightly convex, with narrow, flat subsutural ramp. Sutural ramp abaxially delimited by rounded angulation. Outer face of juvenile whorls also flat. Ramp and outer face slightly concave on mature teleoconch. Width of ramp gradually increasing with growth. Angulation sharp on penultimate whorl; surface well rounded between the adapertural end of trema and outer lip. Suture visible in very narrow but distinct furrow. Ornament consisting of clearly visible spiral elements; three to four spiral cords developed on outer face between two peripheral angulations. Elongate elliptical trema situated on adapical angulation a short distance behind aperture. Adapical angulation not continuing beyond trema; shell surface consequently changing abruptly from sharply angular to gently convex between trema and peristome. Adult peristome

prosocline, discontinuous. Juvenile peristome with deep notch, reflected on shell as selenizone on adapical angulation. Base flat to slightly convex, widely excavated, with broad, funnel-shaped false umbilicus. Spiral threads intercepted by fine prosocline growth lines on base. Figure 3 is a diagram of the variations of height and width of *T. protonotalis* n. sp. See Table 2 for measurements.

Etymology.—Latinized adjective derived from Greek *protos* = first and *notios* = southern, referring to the first Southern Hemisphere occurrence of the genus, in the Jurassic of South America.

Additional material.—Eight almost complete specimens and one internal mold (MLP 12166, 12167, 26170; MCF-PIPH 553, 554, 555, 564, 684) from uppermost lower Pliensbachian (*Austromorphites behrendseni* Zone) to lower upper Pliensbachian (*Fanninoceras fannini* or *F. disciforme* Zones) in the Piedra Pintada area (Cerro Roth, Carrán Curá, and Estancia Santa Isabel), southern Neuquén. All material collected by the authors during several field trips since 1973, as mentioned by Dambořena et al. (1975, table I, #53).

Remarks.—The type species, *Trochotoma conuloides* Eudes-Deslongchamps (1843, p. 109, pl. 8, figs. 16–19; d'Orbigny, 1853, p. 385–386, pl. 341, figs. 14–17; Hermite 1877, pl. 14, figs. 4–5; Cossmann, 1885, pl. 10, figs. 38–39), from the Bathonian of France, can be compared to the Argentinean species; the European form has a more elongate spire, more convex-to-flat teleoconch whorls, finer spiral cords on the shell surface, and an oblique trema. *Trochotoma acuminata* Eudes-Deslongchamps (1843, p. 108, figs. 11–15; d'Orbigny 1853, p. 384–385, pl. 341, figs. 8–13), from the Bathonian of France, and *T. lycetti* Hermite (1877, p. 693; Morris and Lycett 1851, pl. 10, figs. 16, 20, as *T. conuloides* and *T. acuminata* respectively), from the Bathonian of Great Britain, differ from *T. protonotalis* n. sp. in having trochiform shells with flattened whorls and a poorly developed sutural ramp, finer spiral cords, better developed collabral elements, and opisthocyrt lunulae.

Trochotoma calix (Phillips, 1829, pl. 11, fig. 30; Hudleston, 1885, pl. 4, figs. 6a–b; 1896, p. 445, pl. 41, figs. 6–7), from the Middle Jurassic of England, is also similar to the new species; however, it has a single spiral keel and a more depressed aperture. *Trochotoma affinis* Eudes-Deslongchamps (1843, p. 106, pl. 8, figs. 8–10; Eudes-Deslongchamps, 1868, pl. 8, figs. 6a–b; d'Orbigny, 1853, p. 381–383, pl. 341, figs. 1–3; Hudleston 1896, p. 447, pl. 41, fig. 4; including *T. carinata* Lycett 1850, p. 417; 1857, pl. 4, fig. 5), from the Middle Jurassic of the European area, differs from the Argentinean species in having a slightly more concave outer face. Close affinities of *T. (T.) protonotalis* n. sp. can be seen with *Trochotoma gradus* Eudes-Deslongchamps (1843, pl. 8, figs. 4–7; Eudes-Deslongchamps, 1868, pl. 4, figs. 2a–b; d'Orbigny, 1843, p. 276, not figured, as *Ditremaria bicarinata*; Fischer and Weber, 1997; p.150, pl. 24, figs. 5a–c), from the Early Jurassic of France. However, d'Orbigny's species is larger, has nine spiral cords on the spire whorls, the whorl side is almost vertical, and the elliptical trema is widely open. The Argentinean material has only five spiral cords per whorl and the whorl side is slightly

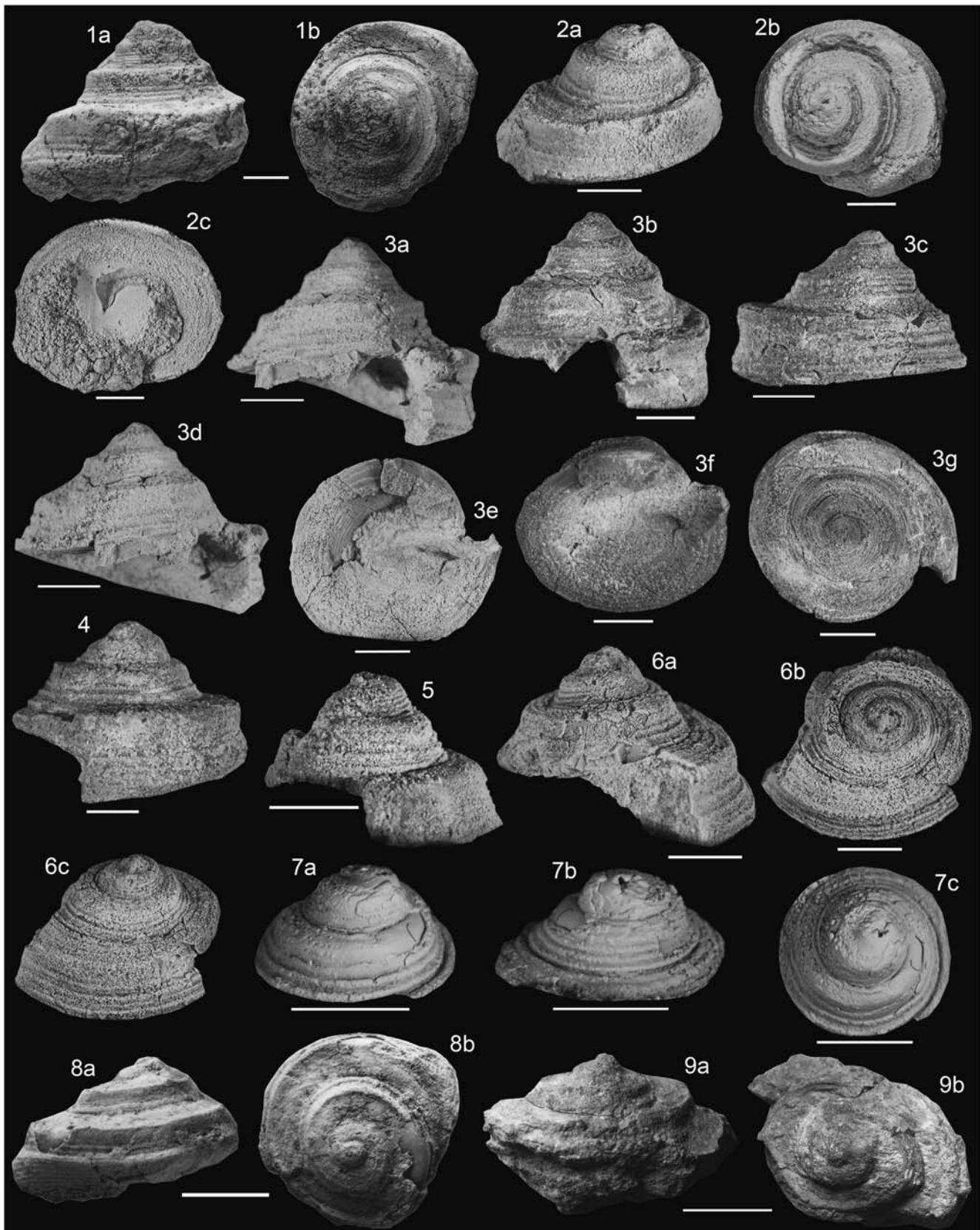


Figure 2. (1–7) *Trochotoma* (*Trochotoma*) *protonotalis* n. sp. (1) MLP 26172, holotype, (1a) lateral view; (1b) apical view. (2) MLP 12168, paratype. (2a) lateral view; (2b) apical view; (2c) basal view. (3) MCF-PIPH 554. (3a, b, c) lateral views; (3d) apertural view; (3e, f) basal and umbilical views; (3g) apical view. (4) MCF-PIPH 553, lateral view. (5) MCF-PIPH 684, lateral view. (6) MCF-PIPH 555. (6a) lateral view; (6b, c) lateral and apical views. (7) MLP 12167. (7a, b) lateral views; (7c) apical view. (8, 9) *Trochotoma* (*Placotoma*) *neuquensis* n. sp. (8) MLP 26171, holotype. (8a) lateral view; (8b) apical view. (9) MLP 26173, paratype. (9a) lateral view; (9b) apical view. Scale bar represents 5 mm.

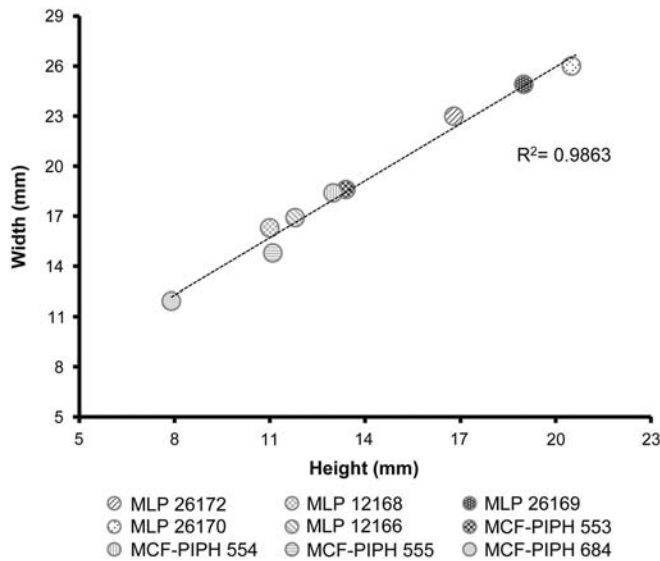


Figure 3. Diagram showing the variations of height/width ratio in *Trochotoma protonotalis* n. sp. Note that R^2 indicates a good correlation between these parameters.

Table 2. Measurements of *Trochotoma (T.) protonotalis* n. sp.

| Specimen number | Material | Height (mm = millimeters) | Width (mm = millimeters) |
|-----------------|----------|---------------------------|--------------------------|
| MLP 26172 | Holotype | 16.8 | 23.0 |
| MLP 12168 | Paratype | 11.0 | 16.3 |
| MLP 26169 | Paratype | 19.0 | 24.9 |
| MLP 26170 | * | 20.5 | 26.0 |
| MLP 12166 | * | 11.8 | 16.9 |
| MCF-PIPH 553 | * | 13.4 | 18.6 |
| MCF-PIPH 554 | * | 13.0 | 18.4 |
| MCF-PIPH 555 | * | 11.1 | 14.8 |
| MCF-PIPH 684 | * | 7.9 | 11.9 |

inclined. The trema in *Trochotoma (T.) protonotalis* n. sp. seems to be slightly more elongate and located on a low but clearly distinct funnel-like elevation of the shell. This elevation appears to be far more reduced or missing in d'Orbigny's and Fischer and Weber's figures. The aperture is only partially visible in our material, but it appears to be somewhat more tangential.

The late Jurassic species most similar to the one described here is *Trochotoma rathieriana* (d'Orbigny, 1850b, p. 9; 1853, pl. 342, figs. 6–8, pl. 343, figs. 1–2), from the Oxfordian of France; but *T. rathieriana* has a teleoconch with more numerous whorls. Another European Bathonian species similar to *T. (T.) protonotalis* n. sp. is *Trochotoma obtusa* Morris and Lycett (1851, p. 83, pl. 10, figs. 15a–b; Fischer 1969, pl. 14, figs. 20–21a–c), from the Middle Jurassic of England and France; however, *T. obtusa* differs from *T. (T.) protonotalis* n. sp. in having more convex whorls, a less conical shell, and a more elliptical trema. *Trochotoma tabulata* Morris and Lycett (1851, p. 83, pl. 10, figs. 17–17a; Cossmann, 1885, pl. 8, figs. 13–14), from the Middle Jurassic (Bathonian) of England, has a narrower apex than in *T. protonotalis* n. sp., and the side of the whorls is nearly flat instead of concave. *Trochotoma magnifica* Cossmann (1885, pl. 8, figs. 15–17; 1900, pl. 14,

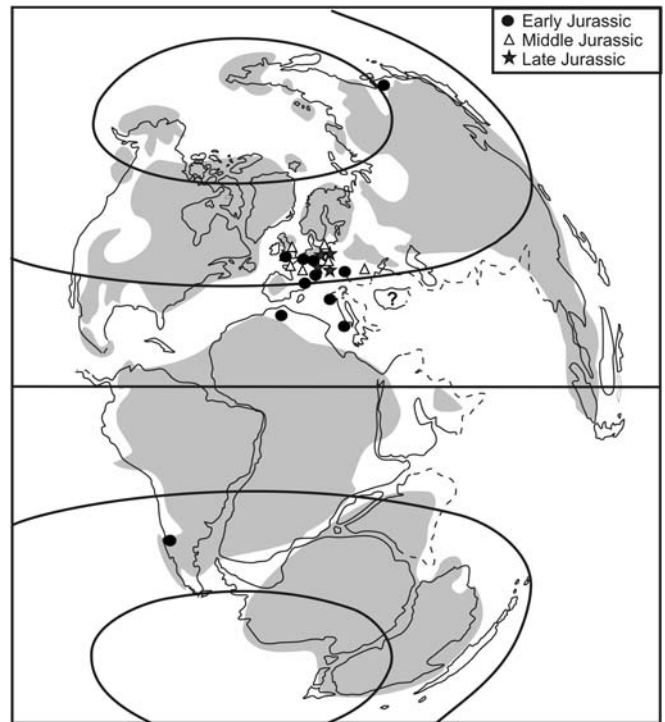


Figure 4. Paleobiogeographical distribution of *Trochotoma* s.l. species. Base map depicting early Jurassic paleogeography compiled from various sources.

figs. 10–11), from the Bathonian of Europe, differs from the Argentinean form in having more teleoconch whorls (seven to eight), a more elongate trema, a concave selenizone, and better-developed collabral elements on the ramp of the whorls and on the base.

Trochotoma extensa Morris and Lycett (1851, p. 83, pl. 10, figs. 19a–b; Fischer 1969, pl. 14, figs. 19a–b), from the Middle Jurassic (Bathonian) of England and France, differs from *T. (T.) protonotalis* n. sp. in having flattened whorls and weaker spiral ornament.

The general shell morphology of the Argentinean Jurassic species is even superficially similar to some extant Scissurellidae, with the most obvious difference being size. *Sinezona singeri* Geiger (2006, p. 19, figs. 14–16), from the western Indian Ocean, is much smaller than *T. (T.) protonotalis* n. sp., and it has an adult teleoconch with 23–26 fine axial ribs, a convex outer face, and a convex base with a strong constriction below the selenizone. *Sukashitrochus morleti* (Crosse, 1880), from New Caledonia to central Pacific, has more developed prosocline axial ribs on the shell surface, a stronger adapical keel on the outer face, and a more convex base (Geiger, 2006, p. 23, fig. 17). Figure 5 shows illustrations of some species comparable to *T. (T.) protonotalis* n. sp.

Subgenus *Placotoma* (= *Discotoma* Haber, 1934 non Mulsant, 1850) new subgenus

Type species.—*Ditremaria amata* d'Orbigny, 1850b, p. 9, from the Callovian of France, by original designation (Haber 1934, p. 366).

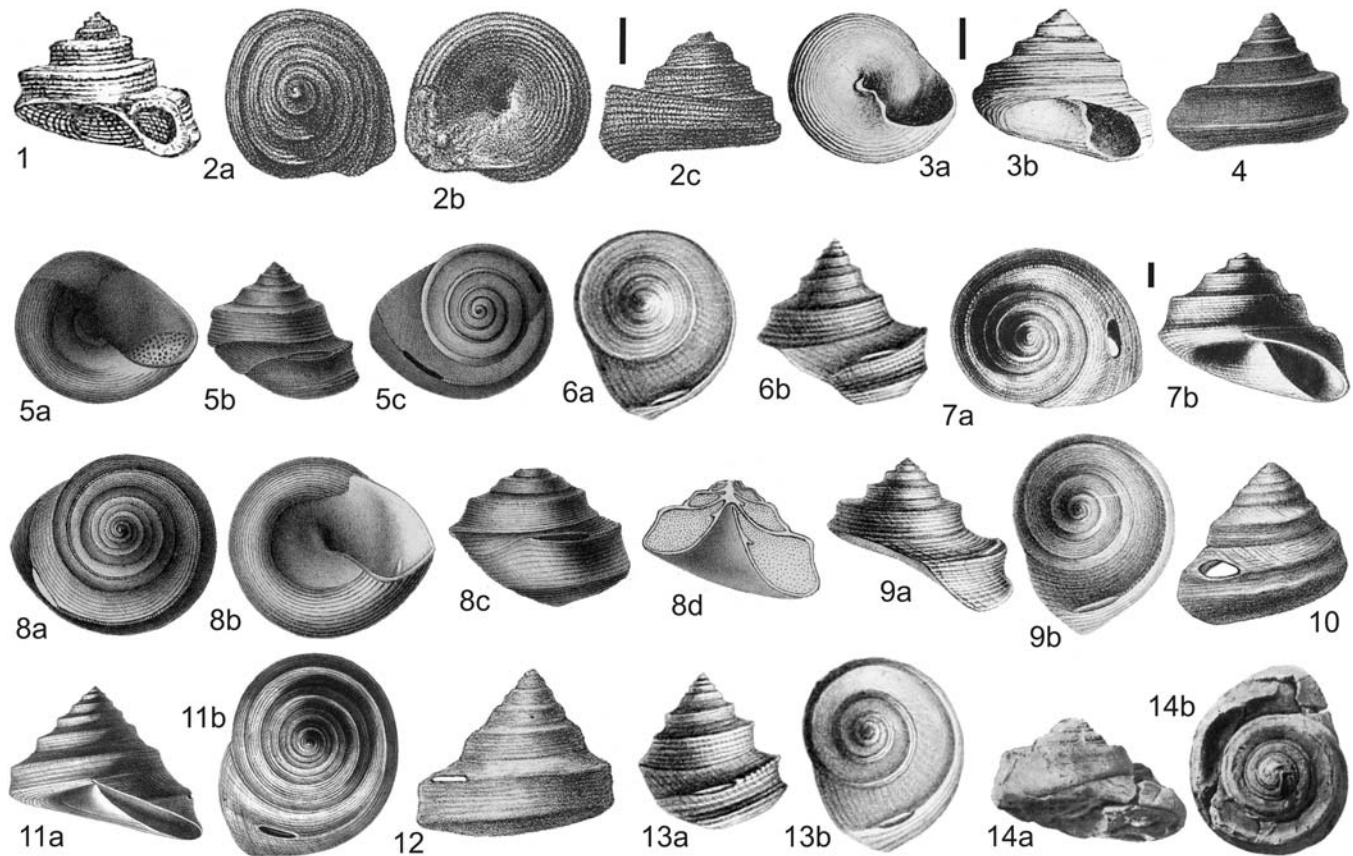


Figure 5. Reproduction of original illustrations of some species comparable to *T. protonotalis* n. sp. (1, 2) *Trochotoma (T.) calix* (Phillips). (1) from Phillips 1829, pl. 11, fig. 30; (2) from Hudleston 1885, pl. 4, figs. 6, 6a–b. (3) *Trochotoma (T.) magnifica* Cossmann, from Cossmann 1885, pl. 8, figs. 15, 16. (4) *Trochotoma (T.) carinata* Lycett, from Lycett 1857, pl. 4, fig. 5. (5, 6) *Trochotoma (T.) affinis* Eudes-Deslongchamps. (5) from Eudes-Deslongchamps 1843, pl. 8, fig. 8–10; (6) from Eudes-Deslongchamps 1868, pl. 8, fig. 6a, b. (7) *Trochotoma (T.) bicarinata* (d'Orbigny), from d'Orbigny 1853, pl. 340, fig. 9, 10. (8, 9) *Trochotoma (T.) gradus* Eudes-Deslongchamps; (8) from Eudes-Deslongchamps 1843, pl. 8, fig. 4–7; (9) from Eudes-Deslongchamps 1868, pl. 4, figs. 2a, b. (10) *Trochotoma (T.) obtusa* Morris and Lycett, from Morris and Lycett 1851, pl. 10, fig. 15b. (11) *Trochotoma (T.) rathieriana* (d'Orbigny), from d'Orbigny 1853, pl. 342, figs. 7, 8. (12) *Trochotoma (T.) tabulata* Morris and Lycett, from Morris and Lycett 1851, pl. 10, fig. 17a. (13) *Trochotoma (T.) schlumbergeri* Eudes-Deslongchamps, from Eudes-Deslongchamps 1868, pl. 8, fig. 5a, b. (14) *Trochotoma (T.) orientalis* (Kiparisova), from Kiparisova 1952, pl. 6, figs. 1a, c. Scale bars = 5 mm.

Diagnosis.—Same as the diagnosis provided for the pre-occupied name “*Discotoma*” in Haber (1934, p. 368).

Etymology.—Derived from the Greek *plakos* = plate, and *tome* = a cutting, referring to the strongly depressed shell with trema.

Remarks.—Haber (1934, p. 368) proposed *Discotoma* as a subgenus of *Ditremaria*. Depressed trochotomid shells have been widely referred to this taxon, which may be retained at subgeneric level. However, the name *Discotoma* was already in use for a coleopteran genus (Mulsant, 1850, p. 215), a fact overlooked by previous authors, and thus it cannot be used for this gastropod taxon. We propose here the name *Placotoma* to replace the pre-occupied name *Discotoma* Haber non Mulsant.

Trochotoma (Placotoma) neuquensis new species
Figure 2.8, 2.9

Type material.—Holotype: one almost complete shell (MLP 26171) from uppermost Lower Pliensbachian beds at Cerro Roth, Piedra Pintada, Neuquén Province. Paratype: a slightly deformed shell (MLP 26173) from the same locality and level.

Diagnosis.—Shell trochiform, gradate, depressed; teleoconch with four convex whorls; suture slightly impressed; whorls strongly angular at midwhorl; last whorls delimited by an irregular peripheral swollen belt; trema elongate, elliptical on midwhorl angulation; peristome prosocline, discontinuous; base flat to slightly convex, with eight regularly spaced spiral cords.

Type locality and horizon.—Cerro Roth, Neuquén Province, Argentina; lower Pliensbachian (*Austromorphites behrendseni* Zone), Piedra Pintada Formation.

Description.—Trochiform, gradate and depressed shell, with mean height of 11.50 mm and mean width of 23.47 mm. Protoconch not preserved. Fragmentary teleoconch comprising four convex whorls. Suture slightly impressed in narrow spiral furrow. Upper portion of whorls forming flat, almost horizontal ramp. Ramp smooth, rendering shell outline strongly gradate. Outer face slightly concave to flat, ornamented with three spiral cords. Periphery of last whorl subangular, with irregular, keel-like swollen belt. Elongate elliptical trema present on adapical angulation very near aperture. Angulation bearing selenizone terminating at trema. Base convex, ornamented with

eight regularly spaced spiral cords. Peristome strongly prosocline, discontinuous. Dimensions: MLP 26171 (holotype), height: 11.0, width: 23.6; MLP 26173 (paratype), height: 12.03, width: 23.34.

Etymology.—Refers to the occurrence in Neuquén Province, Argentina.

Remarks.—The most similar species to the one described here is *Trochotoma (Placotoma) cossmanni* (Rollier, 1918, p. 59; figured by Cossmann, 1900, pl. 16, figs. 3–5 as *Trochotoma imbricata*; Bigot, 1935, pl. 39, fig. 4 as *Trochotoma petrariae*; Fischer, 1953, pl. 1, figs. 1–2; 1964, pl. 2, figs. 10–11), from the Bathonian of France, but this apparently lacks spiral threads on the base. *T. cossmanni* is one of the few species illustrated with good photographs (Cossmann, 1900; Fischer, 1964). Fischer (1969, p. 125) considered *Trochotoma petrariae* Bigot to be a junior synonym of *T. cossmanni*.

Trochotoma funiculosa Cossmann (1885, pl. 10, figs. 36–37; Fischer, 1969, pl. 14, figs. 22a–c), also from the Bathonian of Europe, has a wider and slightly convex upper portion of the whorls, with more prominent spiral threads, and a nearly vertical outer face of the whorls. The specimens described and figured by Morris and Lycett (1851, pl. 10, figs. 10a–c) as *Trochotoma discoidea* Roemer, 1836, which have been referred either to *T. cossmanni* (Rollier, 1918) or to *T. funiculosa* Cossmann (1885), have no trema or exhalant outlet on the shell; however, these specimens were included by those authors in *Trochotoma* because their general shell morphology agree with that of species referred to this genus.

The type species of *Placotoma*, *Trochotoma amata* d'Orbigny (1850b, p. 9; 1853, p. 389, pl. 343, figs. 3–8; de Loriol, 1890, pl. 18, figs. 3–4; Knight et al., 1960, figs. 135.2a–b) from the late Jurassic of France, can also be compared to *T. (P.) neuquensis* n. sp. The European species, however, is more depressed than the Argentinean one, and has a more prominent marked spiral ornament and prosocline threads on the ramp. *Trochotoma? discoidea* Buvignier (1852, pl. 25, figs. 10–11), from the Bathonian of Europe, has fewer whorls (three) and a more depressed, lower shell than the Argentinean species. The shell of the European species is also more discoidal and widely umbilicate, and the spiral cords are crossed by very fine, oblique striae.

Trochotoma (Discotoma) gansuensis Tong and Erwin (2001, p. 15, pl. 2, figs. 5–10), from the Triassic of China, differs from *Trochotoma (P.) neuquensis* n. sp. in having more convex whorls, with the last teleoconch whorl more expanded than the spire whorls, ornament consisting of spiral threads and collabral lines, and a row of elongate opisthocline nodes on the ramp. Such characters are missing in *T. (P.) neuquensis* n. sp. Most probably the species described by Tong and Erwin (2001) does not belong to *Trochotoma*, considering that it has very convex whorls and lacks the elliptical trema. *Trochotoma? gansuensis* seems to be more similar to other pleurotomarid forms, such as the representatives of Ptychomphalidae Wenz, 1938.

Finally, *Trochotoma (P.) neuquensis* n. sp. differs from *T. (T.) protonotalis* n. sp. in having a more depressed shell, a

more convex base with better-developed spiral cords and in lacking prosocline collabral growth lines.

Systematic affinities

Trochotomids are currently included in the Pleurotomarioidea, but in the past they were alternatively referred to Eotomarioidea Wenz, 1938 and Haliotoidea Rafinesque, 1815 (Hudleston, 1881; Tong and Erwin, 2001). The family Pleurotomariidae Swainson is the only family of Pleurotomarioidea to survive beyond the Jurassic into the Recent fauna. Pleurotomarioideans were abundant and diverse components of shallow-water marine faunas throughout the Paleozoic and Mesozoic, while most living Pleurotomariidae are restricted to depths ranging from 100–1000 m (Harasewych, 2002).

According to Harasewych (2002), the majority of contemporary classifications follows Knight et al. (1960), and defines Pleurotomarioidea as containing 20 extinct families (one of which is the family Trochotomidae), and considers the Pleurotomariidae, Scissurellidae, and Haliotidae as the living members of the superfamily. The inclusion of Haliotidae and Scissurellidae within the Pleurotomarioidea was based on the presence of a slit or series of tremata, and vestiges of bilateral symmetry in the mantle cavity. These families appear in the fossil record during the late Mesozoic. Haszprunar (1989) pointed out that the anatomy of the Paleozoic and Mesozoic families usually included into Pleurotomarioidea might have been more similar to that of living Scissurellidae than to the anatomy of Pleurotomariidae. He suggested that the extinct families previously included in Pleurotomarioidea might be more appropriately assigned to Scissurelloidea. The family Trochotomidae, as defined by Knight et al. (1960), is an extinct member of Pleurotomarioidea. However, trochotomid species share some anatomical and functional features, such as the trema or foramen for the exhalant water current, characteristic of some extant Scissurellidae. On the other hand, species of Haliotidae have a row of siphonal holes a short distance away from the edge of the shell. Living members of the Haliotidae are grazers on marine algae and live on exposed shores at low-tide level. In contrast, extant members of Scissurellidae and Pleurotomariidae are more commonly found from intertidal to abyssal depths, even though fossil members of Pleurotomariidae were diverse and abundant in shallow marine environments until the Late Cretaceous.

Probably, the development of a trema or row of tremata for an excretory function that is present in different gastropod clades (Bellerophonitidae, Haliotidae, Fissurelloidea, Trochotomidae) evolved independently during the Paleozoic and Mesozoic and, as suggested by Szabó (1984), it was the result of an adaptation to strongly agitated waters.

Paleoecology

Szabó (1984) regarded the development of a trema, rather than an open selenizone, as an adaptation to strongly agitated waters because an uninterrupted peristome is more resistant to mechanical damage; thus trochotomids were common in reefs whereas other pleurotomarioids were rare or absent in that environment.

The deep slit of most pleurotomarioids is also expected to affect negatively the resistance of the gastropod shell to breakage by predation (Lindström and Peel, 2010). The proportion of specimens with repaired shell injuries is high in both fossil (Lindström and Peel, 2010) and living (Harasewych, 2002) slit-bearing pleurotomarioids. A continuous peristome is more resistant to predator attacks, especially crustacean peeling, which is a very common shell injury in slit-bearing living pleurotomariids in comparison to sympatric trochids with a continuous aperture (see examples and discussion in Harasewych, 2002, figs. 13–15).

The distribution of most Jurassic trochotomid species shows a high environmental dependency, being associated with coral reefs in the shallow Tethys (Dubar, 1948; Bertling and Insalaco, 1998). The Argentinean trochotomid specimens are found in tuffs and sandstones, and are associated with epifaunal bivalves, ammonites, brachiopods, echinoderms, and coral patch reefs at one of the localities (Cerro Roth, Piedra Pintada). They are also restricted to litho- and biofacies that include coral biostromes or small bioherms (Damborenea et al., 1975).

Paleobiogeography

Cretaceous and Cenozoic gastropods have proven to be very useful from a paleobiogeographical point of view, but the Jurassic gastropod fauna is still very unevenly known, especially in the Southern Hemisphere. Thus, any new addition to the faunas of poorly known regions, such as South America, provides new and interesting material for paleobiogeographical analyses.

The extinct genus *Trochotoma* is well represented in the Tethyan region. It has been found commonly in the Mesozoic of Europe, ranging from the early to late Jurassic, and has also been recovered from the early Jurassic of Russia and northern Africa (Table 1). The oldest (although doubtful; see above) occurrence of *Trochotoma* is dated from the Middle Triassic of China (Tong and Erwin, 2001). In the present research, we provide the southernmost record of this particular vetigastropod group from the early Jurassic (Pliensbachian) of Neuquén basin, Argentina (Fig. 4).

Monari et al. (2011) discussed the distribution in time and space of two species from Europe, *Trochotoma vetusta* Terquem, 1855 and *T. clypeus* Terquem, 1855. Monari et al. (2011) pointed out that the evolutionary history of *Trochotoma* was characterized by a Sinemurian major adaptive radiation that involved the European epicontinental shelf and the marginal and intra-Tethyan carbonate platforms. They argued that the occurrence of a number of *Trochotoma* species in Hettangian sediments demonstrates that the diversification of these pleurotomarioidean taxa began very early in the Jurassic.

The occurrence of *Trochotoma* in the Pliensbachian deposits of Neuquén Basin certainly testifies to paleobiogeographical connections with the Western Tethys at that time, and possibly provides evidence of the faunal radiation that occurred during the early Jurassic.

The new species reported here are endemic to the Argentinean Jurassic and represent the southernmost occurrence of the genus *Trochotoma* (Fig. 4) and also of the family Trochotomidae. Particularly, the subgenus *Trochotoma* (*Placotoma*) was known

previously from the Triassic of China (?) and the Jurassic of Europe. The presence of *Trochotoma* (*Placotoma*) *neuquensis* n. sp. in the Pliensbachian marine deposits of Argentina extends the paleobiogeographical distribution of the subgenus into the Mesozoic of South America, showing a new early Jurassic record of this group in the Southern Hemisphere.

Ferrari (2011, 2014) suggested that the Jurassic distribution patterns of some Patagonian marine gastropods might be clarified taking into consideration the dispersal routes of the shallow marine bivalve faunas during the early Jurassic. This supports the idea of a shallow marine connection between the western Tethys and the eastern Pacific as early as Pliensbachian times, related to the Hispanic Corridor (see Damborenea and Manceñido, 1979; Damborenea et al., 2012a, and references therein). The Hispanic Corridor seems to be the most plausible hypothesis to explain the trochotomid faunal exchange between the western Tethys and the Neuquén Basin through the eastern Pacific during the Pliensbachian.

The Argentinean material is associated with coral patch reefs of shallow, open-marine environments within the photic zone, and in this it agrees with the known habitats for other trochotomid species from the western Tethys. Thus, these new data support the statements by Conti and Monari (1991) and Gatto and Monari (2010), who pointed out that the diffusion of suitable environmental conditions played a major control on Tethyan gastropod dispersal and spatial distribution.

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Supplementary Material

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References

- Ammon, L.V., 1892, Die Gastropodenfauna des Hochfellsn-Kalkes und über Gastropoden-Reste aus Ablagerungen von Adnet, Monte Nota und den Raibler Schichten: Geognostische Jahreshefte, v. 5, p. 161–221.
- Arregui, C., Carbone, O., and Martínez, R., 2011, El Grupo Cuyo (Jurásico Temprano-Medio) en la Cuenca Neuquina, in Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C., and Vallés, J.M., eds., Geología y Recursos Naturales de la Provincia del Neuquén: Buenos Aires, Relatorio del 18° Congreso Geológico Argentino, p. 77–89.
- Bayle, E., and Coquand, H., 1851, Mémoire sur les fossiles recueillis dans le Chili par M. Ignace Domeyko et sur les terrains auxquels ils appartiennent: Mémoires de la Société Géologique de France, ser. 2, v. 4, p. 1–47.

- Behrendsen, O., 1891, Zur Geologie des Ostabhanges der Argentinischen Cordillere, Teil I: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 43, p. 369–420.
- Behrendsen, O., 1922, Contribución a la geología de la pendiente oriental de la Cordillera Argentina: Actas de la Academia Nacional de Ciencias (Córdoba), v. 7, p. 161–227.
- Bertling, M., and Insalaco, E., 1998, Late Jurassic coral/microbial reefs from the northern Paris Basin –facies, paleoecology and paleobiogeography: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 139, p. 139–175, doi:10.1016/j.palaeo.2005.03.009.
- Bigot, A., 1935, Les récifs Bathoniens de Normandie: Bulletin de la Société Géologique de France, ser. 5, v. 4, p. 697–736.
- Blaschke, F., 1911, Zur Tithonfauna von Stramberg in Mähren: Annalen der K.K. Naturhistorischen Hofmuseum, v. 25, p. 143–222.
- Bouchet, P., and Rocroi, J.P., 2005, Classification and nomenclature of gastropod families: Malacologia, v. 47, p. 1–397.
- Burckhardt, C., 1897, Zur Systematik und Phylogenie der Pleurotomariiden: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 1897, v. 1, p. 198–210.
- Burckhardt, C., 1900, Profils géologiques transversaux de la Cordillère Argentino-Chilienne, Stratigraphie et tectonique: Anales del Museo de La Plata, Sección Geología y Mineralogía, v. 2, p. 1–136.
- Burckhardt, C., 1902, Le Lias de la Piedra Pintada (Neuquén), III, Sur les fossiles marines du Lias de la Piedra Pintada, avec quelques considérations sur l'âge et l'importance du gisement: Revista del Museo de La Plata, v. 10, p. 243–249.
- Buvignier, N.A., 1852, Description d'une partie des fossiles inédits ou peu connus recueillis dans les terrains du Département de la Meuse, in Statistique Géologique, Minéralogique, Minéralurgique et Paléontologique du Département de la Meuse: Paris, Baillière, p. 1–52.
- Conti, M.A., and Monari, S., 1991, Bivalve and gastropod fauna from the Liassic Ammonitico Rosso facies in the Bilecik Area (western Pontides, Turkey), in Farinacci, A., Ager, D.V., and Nicosia, U., eds., Geology and paleontology of western Pontides, Turkey, Jurassic–Early Cretaceous stratigraphy, tectonics and paleogeographical evolution: Geologica Romana, v. 27, p. 245–301.
- Cossmann, M., 1885, Contribution à l'étude de la faune de l'étage Bathonien en France (Gastropodes): Mémoires de la Société Géologique de France, 3ème ser., v. 3, p. 1–374.
- Cossmann, M., 1900 [1899], Note sur les gastropodes du gisement Bathonien de Saint-Gaultier (Indre): Bulletin de la Société Géologique de France, 3 ser., v. 27, p. 543–585.
- Cossmann, M., 1902, Rectifications de nomenclature: Revue Critique de Paléozoologie, v. 6, p. 96–98.
- Cossmann, M., 1916, Complément à l'étude paléontologique des gisements de Brouzet-les-Alais (Gard): Mémoires de la Société Géologique de France, Paléontologie v. 21, no. 4, p. 1–56.
- Cotteau, G.H., 1853–1857, Études sur les Mollusques fossiles du département de l'Yonne, Premier Fascicule: Paris, J.B. Baillière et Fils, 441 p.
- Cox, L.R., 1958, Three Mesozoic gastropod generic homonyms renamed: Proceedings of the Malacological Society of London, v. 33, p. 71–72.
- Cox, L.R., 1960, Family Trochotomidae Cox n. fam., in Moore, C., and Pitrat, W., eds., Treatise on Invertebrate Paleontology, Part I, Mollusca 1: Lawrence, Geological Society of America and University of Kansas Press, p. 1220–1221.
- Crosse, H., 1880, Description de mollusques inédits, provenant de la Nouvelle-Calédonie et de la Nouvelle-Bretagne: Journal de Conchyliologie, v. 28, p. 142–149.
- Damborenea, S.E., 1987, Early Jurassic Bivalvia of Argentina, Part I, stratigraphical introduction and superfamilies Nuculanacea, Arcacea, Mytilacea and Pinnacea: Palaeontographica, Abteilung A, Band A199, Lieferung 1–3, p. 23–111.
- Damborenea, S.E., and Ferrari, S.M., 2008, El género *Lithotrochus* Conrad (Gastropoda, Vetigastropoda) en el Jurásico temprano de Argentina: Ameghiniana, v. 45, p. 197–209.
- Damborenea, S.E., and Manceñido, M.O., 1979, On the palaeogeographical distribution of the pectinid genus *Weyla* (Bivalvia, Lower Jurassic): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 27, p. 85–102, doi:10.1016/0031-0182(79)90095-6.
- Damborenea, S.E., Manceñido, M.O., and Riccardi, A.C., 1975, Biofacies y estratigrafía del Liásico de Piedra Pintada, Neuquén, Argentina: Actas 1º Congreso Argentino de Paleontología y Bioestratigrafía (Tucumán), v. 2, p. 173–228.
- Damborenea, S.E., Echevarría, J., and Ros, S., 2012a, Southern Hemisphere Palaeobiogeography of Triassic–Jurassic Marine Bivalves, Springer Briefs in Earth System Sciences: Dordrecht, Springer, 141 p.
- Damborenea, S.E., Ferrari, S.M., Manceñido, M.O., and Griffin, M., 2012b, La familia Trochotomidae (Vetigastropoda: Pleurotomarioidea) en el Jurásico temprano de Cuenca Neuquina, Argentina: Ameghiniana Suplemento Resúmenes, v. 49, R141.
- Deshayes, G.P., 1865, Note sur le genre *Trochotoma* et description d'une espèce nouvelle des sables de Bordeaux: Journal de Conchyliologie, v. 13, p. 230–239.
- Dubar, G., 1948, Études paléontologiques sur le Lias du Maroc. La fauna Domérienne du Djebel Bou-Dahar, près de Béni-Tajjite, Étude suivie de celle de quelques Mollusques d'autres gisements Marocains, Notes et Mémoires: Maroc, Service Géologique, v. 68, p. 1–250.
- Étallon, A., 1862, Études paléontologiques sur le Haut-Jura. Monographie du Corallien: Mémoires de la Société d'Émulation du Département du Doubs, 3ème ser., v. 6, p. 53–244.
- Étallon, A., 1864, Études paléontologiques sur le Jura Graylois: Mémoires de la Société d'Émulation du Département du Doubs, 3ème ser., v. 8, p. 221–506.
- Eudes-Deslongchamps, E., 1864, Études sur les étages Jurassiques inférieurs de la Normandie: Thèses Présentées à la Faculté des Sciences de Paris, 296 p.
- Eudes-Deslongchamps, E., 1868, Note sur les genres *Trochotoma* et *Ditremaria*. Bulletin de la Société Linnéenne de Normandie, 2º sér., v. 1, p. 215–221 (for 1866).
- Eudes-Deslongchamps, J.-A., 1843, Mémoire sur les *Trochotoma*, nouveau genre de coquilles fossiles voisins des Pleurotomaires et appartenant, comme eux, aux terrains secondaires: Mémoires de la Société linnéenne de Normandie, v. 7, p. 99–110.
- Ferrari, S.M., 2009, Cosmopolitan early Jurassic marine gastropods from west-central Patagonia, Argentina: Acta Palaeontologica Polonica, v. 54, p. 449–461, doi: 10.4202/app.2008.0070.
- Ferrari, S.M., 2011, Early Jurassic Ataphridae (Mollusca: Gastropoda) from Chubut, Argentina: paleogeographic and paleoecologic implications: Ameghiniana, v. 48, p. 64–78.
- Ferrari, S.M., 2012, The genera *Cryptaulax* and *Procerithium* (Procerithiidae, Caenogastropoda) in the early Jurassic of Patagonia, Argentina: Alcheringa, v. 36, p. 323–336.
- Ferrari, S.M., 2013, New early Jurassic gastropods from west-central Patagonia, Argentina: Acta Palaeontologica Polonica, v. 58, p. 579–593, doi: 10.4202/app.2011.0090.
- Ferrari, S.M., 2014, Patellogastropoda and Vetigastropoda (Mollusca, Gastropoda) from the marine Jurassic of Patagonia, Argentina: Historical Biology, v. 26, p. 563–581. doi: 10.1080/08912963.2013.804518.
- Ferrari, S.M., Kaim, A., and Damborenea, S.E., 2014, The genera *Calliotropis* Seguenza and *Ambercyclus* n. gen. (Vetigastropoda, Eucyclidae) from the early Jurassic of Argentina. Journal of Paleontology, v. 88, p. 1174–1188. doi: 10.1666/13–147.
- Feruglio, E., 1934, Fossili Liassici della Valle del Rio Genua (Patagonia): Giornale di Geologia, Annali del R. Museo Geologico di Bologna, v. 9, p. 1–64.
- Finlay, H.J., 1926, A further commentary on New Zealand molluscan systematics: Transactions and Proceedings of the New Zealand Institute, v. 57, p. 320–485.
- Fischer, J.C., 1953, Note sur les Gastéropodes d'un nouveau gîte coquillier du Bathonien des Ardennes: Journal de Conchyliologie, v. 93, p. 3–25.
- Fischer, J.C., 1964, Contribution à l'étude de la faune Bathonienne dans la Vallée de la Creuse (Indre), brachiopodes et mollusques: Annales de Paléontologie (Invertébrés), v. 50, p. 21–101.
- Fischer, J.C., 1969, Géologie, paléontologie et paléoécologie du Bathonien au Sud-Ouest du Massif Ardennais: Mémoires du Muséum National d'Histoire Naturelle n.s. Ser. C., Sciences de la Terre, v. 20, p. 1–321.
- Fischer, J.C., and Weber, C., 1997, Révision critique de la Paléontologie Française d'Alcide d'Orbigny, Volume II, Gastropodes Jurassiques: Paris, Masson éd.: Muséum National d'Histoire Naturelle, 300 + 272 p.
- de Folin, L., and Périer, L., 1867–1871, Les Fonds de la Mer. Étude Internationale sur les Particularités Nouvelles des Régions Sous-marines: Paris, Savy, v. 1, 316 p.
- Fraas, O.F., 1882, Geognostische Beschreibung von Württemberg, Baden und Hohenzollern: Stuttgart, E. Schweizerbartsche Verlagshandlung, 217 p.
- Gatto, R., and Monari, S., 2010, Pliensbachian gastropods from Venetian Southern Alps (Italy) and their palaeogeographical significance: Palaeontology, v. 53, p. 771–802, doi: 10.1111/j.1475-4983.2010.00961.x.
- Geiger, D., 2006, Eight new species of Scissurellidae and Anatomidae (Mollusca: Gastropoda: Vetigastropoda) from around the world, with discussion of two new senior synonyms: Zootaxa, v. 1128, p. 1–33.
- Geiger, D., 2012, Monograph of the Little Slit Shells. Volume 1. Introduction, Scissurellidae: Santa Barbara, Santa Barbara Museum of Natural History Monographs 7, Studies in Biodiversity 5., 728 p.
- Gemmellaro, G.G., 1879, Sui fossili del Calcare cristallino delle Montagne del Casale e di Bellampo, nella provincia di Palermo: Giornale di Scienze Naturali ed Economiche di Palermo, v. 14, p. 157–212.
- Gemmellaro, G.G., 1889, La Fauna dei Calcarei con Fusulina della Valle del Fiume Sosio nella Provincia di Palermo, Fasc 2, Nautiloidea e Gastropoda: Giornale di Scienze Naturali ed Economiche, v. 20, p. 97–182.

- Gioli, G., 1889, Fossili della Oolite Inferiore di San Vigilio e di Monte Grappa: Atti della Società Toscana di Scienze Naturali, v. 10, p. 1–19.
- Goldfuss, A., 1841–1844, Petrefacta Germaniae, Abbildungen und Beschreibungen der Petrefakten Deutschlands und der angränzenden Länder: Düsseldorf, Arnz & Comp. 692 p.
- Gray, J. E., 1847, A list of genera of Recent Mollusca, their synonyma and types: Proceedings of the Zoological Society of London, v. 15, p. 129–182.
- Gründel, J., 2001, Gastropoden aus dem Jura der südamerikanischen Anden: Paläontologie, Stratigraphie, Fazies 9, Freiburger Forschungshefte, C 492, p. 43–84.
- Gulisano, C.A., and Gutiérrez-Pleimling, A., 1995, Field guide. The Jurassic of the Neuquén Basin. a) Neuquén Province: Asociación Geológica Argentina, serie E, v. 2, p. 1–111.
- Gulisano, C.A., and Pando, G.A., 1981, Estratigrafía y facies de los depósitos jurásicos entre Piedra del Águila y Sañicó, Departamento Collón Curá, Provincia de Neuquén: 8° Congreso Geológico Argentino, Actas, v. 3, p. 553–577.
- Habe, T., and Kosuge, S., 1964, List of the Indo-Pacific Mollusca concerning to the Japanese Fauna, 1 Superfamily Pleuromarioidea: Tokyo, National Science Museum, 8 p.
- Haber, G., 1934, Gastropoda, Amphineura et Scaphopoda Jurassica, II, Pars 65, in Quenstedt, W., ed., Fossilium Catalogus, I, Animalia: Berlin, W. Junk, p. 305–400.
- Harasewych, M.G., 2002, Pleuromarioidean gastropods: Advances in Marine Biology, v. 42, p. 237–294.
- Haszprunar, G., 1989, New slit limpets (Scissurellacea and Fissurellacea) from hydrothermal vents, Part 2, Anatomy and relationships: Los Angeles County Museum, Contributions to Science, v. 408, p. 1–17.
- von Hauer, F.R., 1853, Ueber die Gliederung der Trias-, Lias- und Juragebilde in den nordöstlichen Alpen. K. k.: Geologische Reichsanstalt, v. 4, p. 715–784.
- Henry, J., 1875, l'Infralias dans la Franche-Comté: Mémoires de la Société d'Émulation du Département du Doubs, 4 ème. ser., v. 10, p. 285–476.
- Hermite, H., 1877, Note sur le genre *Trochotoma*: Bulletin de la Société Géologique de France, 3ème serie, v. 5, p. 687–698.
- Hudleston, W.H., 1881, Contributions to the Palaeontology of the Yorkshire Oolites, Part VII: Geological Magazine, v. 2, p. 119–131.
- Hudleston, W.H., 1885, Contributions to the Palaeontology of the Yorkshire Oolites: Geological Magazine, v. 3, p. 151–159.
- Hudleston, W.H., 1887–1896, British Jurassic Gasteropoda, Part 1, A Monograph of the Inferior Oolite, Gasteropoda: Monograph Palaeontographical Society of London, 514 p.
- Jaworski, E., 1925, Contribución a la paleontología del Jurásico Sudamericano: Publicación de la Dirección General de Minería, Geología e Hidrología, Sección Geológica, v. 4, p. 1–160.
- Jaworski, E., 1926a, La fauna del Lias y Dogger de la Cordillera Argentina en la parte meridional de la Provincia de Mendoza: Actas de la Academia Nacional de Ciencias (Córdoba), v. 9, p. 137–316.
- Jaworski, E., 1926b, Beiträge zur Paläontologie und Stratigraphie des Lias, Doggers, Tithons und der Unterkreide in der Kordillieren im Süden der Provinz Mendoza (Argentinien), Teil I, Lias und Dogger: Geologische Rundschau, v. 17a, p. 373–427.
- Joukowsky, E., and Favre, J., 1913, Monographie géologique et paléontologique du Salève (Haute Savoie, France): Mémoire de la Société de Physique et d'Histoire Naturelle de Genève, v. 37, p. 295–523.
- Kiparisova, L.D., 1952, New Lower Jurassic fauna from the Amur River Region: Trudy VSEGEI. Moscow Gosgeoltekhizdat, p. 1–40.
- Knight, J.B., Cox, L.R., Keen, A.M., Smith, A.G., Batten, R.L., Yochelson, E. L., Ludbrook, N.H., Robertson, R. Yonge, C.M., and Moore, R.C., 1960, Treatise on Invertebrate Paleontology, Part I, Mollusca 1: Lawrence, Geological Society of America and University of Kansas Press, 351 p.
- Koch, F.C.L., 1848, *Pleurotomaria solarium*, eine neue Schnecke aus den Belemniten-schichten des Lias bei Kahlefeld unfern Nordheim: Palaeontographica, v. 1, p. 174–175.
- Kollárová-Andrusovová, V., and Kochanová, M., 1973, Molluskenfauna des Bleskový Prameň bei Drnava (Nor. Westkarpaten): Bratislava, Verlag der Slowakischen Akademie der Wissenschaften, 214 p.
- Legarreta, L., and Gulisano, C.A., 1989, Análisis estratigráfico-secuencial de la Cuenca Neuquina (Triásico superior-Terciario inferior), in Chebli, G.A., and Spalletti, L.A., eds., Cuencas Sedimentarias Argentinas: Serie Correlación Geológica, v. 6, p. 221–243.
- Legarreta, L., and Uliana, M.A., 1996, The Jurassic succession in west-central Argentina: stratal patterns, sequences, and paleogeographic evolution: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 120, p. 303–330, doi:10.1016/0031-0182(95)00042-9.
- Legarreta, L., and Uliana, M.A., 2000, El Jurásico y Cretácico de la Cordillera Principal y la Cuenca Neuquina. 1, Facies sedimentarias: Instituto de Geología y Recursos Minerales (Argentina): Anales, v. 29, p. 399–432.
- Lindström, A., and Peel, J.S., 2010, Shell repair and shell form in Jurassic pleuromarioid gastropods from England: Bulletin of Geosciences, v. 85, p. 541–550, doi: 10.3140/bull.geosci.1205.
- de Loriol, P., 1887, Études sur les mollusques des couches Coralligènes de Valfin (Jura), seconde partie: Mémoires de la Société Paléontologique Suisse, v. 14, p. 121–224.
- de Loriol, P., 1890, Études sur les mollusques des couches Coralligènes inférieures du Jura Bernois, deuxième partie: Mémoires de la Société Paléontologique Suisse, v. 17, p. 82–174.
- de Loriol, P., 1893, Description des mollusques et brachiopodes des couches séquanienues de Tonerre (Yonne): Mémoires de la Société Paléontologique Suisse, v. 20, p. 1–174.
- Lozouet, P., Lesport, J.-F., and Renard, R. 2001, Révision des Gastropoda (Mollusca) du stratotype de L'Aquitainien (Miocène inf.), site de Saucats "Larrey", Gironde, France: Cossmanniana, v. 8, p. 1–18.
- Lycett, J., 1850, Tabular view of fossil shells from the middle divisions of the Inferior Oolite in Gloucestershire: The Annals and Magazine of Natural History (second series), v. 6, p. 401–425.
- Lycett, J., 1857, The Cotteswold Hills. Hand-book Introductory to their Geology and Palaeontology: London, Piper, Stephenson & Spence, 170 p.
- Lycett, J., 1863, Supplementary Monograph on the Mollusca from the Stonesfield Slates, Great Oolite, Forest Marble and Combrass: Monograph Palaeontographical Society, 129 p.
- Maire, V., 1927, Études géologiques et paléontologiques sur l'arrondissement de Gray. Les Gastropodes du Jurassique supérieur Graylois (fin): Bulletin de la Société Grayloise d'Émulation, v. 19, p. 85–173 (for 1925).
- Monari, S., Valentini, M., and Conti, M.A., 2011, Earliest Jurassic patellogastropod, vetigastropod, and neritimorph gastropods from Luxembourg with considerations on the Triassic-Jurassic faunal turnover: Acta Palaeontologica Polonica, v. 56, p. 349–384, doi: 10.4202/app.2010.0098.
- Moore, C., 1867, On abnormal conditions of secondary deposits when connected with the Somersetshire and South Wales coal-basins; and on the age of the Sutton and Southerndown series: Quarterly Journal of the Geological Society of London, v. 23, p. 449–568.
- Möricker, W., 1894, Versteinerungen des Lias und Unteroolith von Chile: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie B.B., v. 9, p. 1–100.
- Morris, E.G.S., and Lycett, J., 1851, A monograph of the Mollusca from the Great Oolite, chiefly from Minchinhampton and the Coast of Yorkshire, Part I, Univalves: Monograph of the Palaeontographical Society of London, 130 p.
- Mulsant, É., 1850, Species de Coléoptères trimères sécuripalpes: Annales des Sciences Physiques et Naturelles et d'Industrie (Lyon), v. 2, p. 1–1104.
- Nalivkin, W., and Akimov, M., 1917, La faune du Jura de Donetz, III, Gastropoda: Mémoires du Comité Géologique. N. S., v. 136, p. 1–48.
- d'Orbigny, A., 1841–1842, Mollusques, Tome Premier, in de la Sagra, R., ed., Histoire Physique, Politique et Naturelle de l'Île de Cuba: Paris, Arthus Bertrand, 265 p.
- d'Orbigny, A., 1842–1843, Paléontologie Française. Terrains Crétacés, Gastéropodes: Paris, l'auteur & Arthus Bertrand, v. 2, 456 p.
- d'Orbigny, A., 1850a, Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnées: Paris, Victor Masson, v. 1, 394 p.
- d'Orbigny, A., 1850b, Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnées: Paris, Victor Masson, v. 2, 428 p.
- d'Orbigny, A., 1853, Paléontologie Française. Terrains Jurassiques II, Gastéropodes: Paris, Masson, 622 p.
- Pan, H.-Z., 1977, Mesozoic and Cenozoic fossil gastropoda from Yunnan, in Nanjing Institute of Geology and Palaeontology, Academia Sinica, Mesozoic Fossils from Yunnan: Beijing, Science Press, pt. 2, p. 83–153.
- Pan, H.-Z., 1982, Triassic marine fossil gastropods from SW China: Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica, v. 4, p. 153–188.
- Phillips, J., 1829, Illustrations of the Geology of Yorkshire; or, a Description of the Strata and Organic Remains of the Yorkshire Coast: Accompanied by a Geological Map, Sections, and Plates of the Fossil Plants and Animals: York, Thomas Wilson and Sons, 192 p.
- Pictet, F.J., 1855, Traité de Paléontologie ou Histoire Naturelle des Animaux Fossiles Considérés dans Leurs Rapports Zoologiques et Géologiques, seconde édition, Tome 3 ème: Paris, J.B. Baillière, 654 p.
- Quenstedt, F.A., 1858, Der Jura: Tübingen, Laupp'schen Buchhandlung, 842 p.
- Quenstedt, F.A., 1881–1884, Petrefaktenkunde Deutschlands, 1, 7, Die Gasteropoden: Leipzig, Fuess Verlag (R. Reissland), 867 p.
- Rafinesque, G.S., 1815, Analyse de la nature ou tableau de l'univers et des corps organizes: Palerme, 223 p.
- Remeš, M., 1909, Nachträge zur Fauna von Stramberg. VIII. Über die Gastropoden der Stramberger Schichten: Beiträge zur Paläontologie und Geologie Oesterreich-Ungarns und des Orients, v. 22, p. 177–189.
- Riccardi, A.C., 2008a, The marine Jurassic of Argentina: a biostratigraphic framework: Episodes, v. 31, p. 326–335.
- Riccardi, A.C., 2008b, El Jurásico de Argentina y sus amonites: Revista de la Asociación Geológica Argentina, v. 63, p. 625–643.
- Riccardi, A.C., Damborenea, S.E., Manceñido, M.O., and Leanza, H.A., 2011, Megainvertebrados del Jurásico y su importancia geobiológica, in Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C., and Vallés, J.M., eds.,

- Geología y Recursos Naturales de la Provincia del Neuquén: Buenos Aires, Relatorio del 18° Congreso Geológico Argentino, p. 441–464.
- Roemer, F.A., 1836–1839, Die Versteinerungen des Norddeutschen Oolithen-Gebirges. Mit ein Nachtrag: Hanover, Hahnschen Hofbuchhandlung, 218 p.
- Rollier, L., 1918, Fossiles nouveaux ou peu connus des terrains secondaires (Mésozoïque) du Jura et des contrées environnantes, Septième fascicule (Tome second, Ire partie): Mémoires de la Société Paléontologique Suisse, v. 43, p. 1–71.
- Roth, S., 1899, Reconocimiento de la región andina de la República Argentina. Apuntes sobre la geología y la paleontología de los territorios del Rio Negro y Neuquén (diciembre de 1895 a junio de 1896): Revista del Museo de La Plata, v. 9, p. 141–196.
- Scalia, S., 1903, Sopra alcune nuove specie di fossili del calcare bianco cristallino della montagna del Casale, in Provincia di Palermo (Nota preliminare): Bollettino delle sedute della Accademia Gioenia di Scienze Naturali in Catania, v. 76, p. 33–37.
- Schlosser, M., 1882, Die Fauna des Kelheimer Diceras-Kalkes. Erste Abtheilung, p. Vertebrata, Crustacea, Cephalopoda und Gastropoda: Palaeontographica, v. 28, p. 41–110.
- Stipančić, P.N., Rodrigo, F., Baulies, O.L., and Martínez, C.G., 1968, Las formaciones presenonianas en el denominado Macizo Nordpatagónico y regiones adyacentes: Revista de la Asociación Geológica Argentina, v. 22, p. 67–98.
- Stoliczka, F., 1861, Über die Gastropoden und Acephalen der Hierlatz-Schichten: Sitzungberichte der Mathematisch-naturwissenschaftlichen Classe der k. Akademie der Wissenschaften Wien, v. 43, p. 157–204.
- Stoliczka, F., 1867–1868, The Gastropoda of the Cretaceous Rocks of southern India: Memoirs of the Geological Survey of India, Palaeontologia Indica, v. 5, p. 1–497.
- Stoppani, A., 1857, Studii Geologici e Paleontologici sulla Lombardia: Milano, Presso C. Turati, 461 p.
- Stoppani, A., 1861, Monographie des fossiles de l'Azzarola appartenant a la zone supérieure des Couches à *Avicula contorta* en Lombardie, in Stoppani, A., ed., Paléontologie Lombarde ou Description des Fossiles de Lombardie, avec le Concours de Plusieurs Savants, 3° ser.: Milan, Impr. Joseph Bernardoni, p. 33–116.
- Swainson, W., 1840, A Treatise on Malacology or Shells and Shell-fish: London, Longman, 499 p.
- Szabó, J., 1984, Two new archaeogastropod genera from the Tethyan Liassic: Annales Historico-Naturales Musei Nationalis Hungarici, v. 76, p. 65–71.
- Szabó, J., 2009, Gastropoda of the early Jurassic Hierlatz Limestone Formation; part 1: a revision of type collections from Austrian and Hungarian localities: Fragmenta Palaeontologica Hungarica, v. 26, p. 1–108.
- Terquem, O., 1855, Paléontologie de l'étage inférieur de la formation Liasique de la province de Luxembourg, Grand-Duché (Hollande), et de Hettange, du département de la Moselle: Mémoire de la Société Géologique de France, ser. 2, v. 3, p. 219–343.
- Terquem, O., and Piette, E., 1865, Le Lias inférieur de l'est de la France comprenant la Meurthe, la Moselle, le Grand-Duché du Luxembourg, la Belgique et la Meuse: Mémoires de la Société Géologique de France, 2ème Série, v. 8, p. 1–175.
- Thurmann, J., and Étallon, A., 1861–1864, Lethea Bruntrutana: ou, Études paléontologiques et stratigraphiques sur le Jura bernois et en particulier les environs de Porrentruy: Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft für die gesammten Naturwissenschaften, v. 18, p. 1–145 [1861]; v. 19, p. 147–353 [1862]; v. 20, p. 355–500 [1864].
- Tong, J., and Erwin, D.H., 2001, Triassic gastropods of the southern Qinling Mountains, China: Smithsonian Contributions to Paleobiology, v. 92, p. 1–47.
- Uliana, M.A., and Biddle, K.T., 1988, Mesozoic-Cenozoic paleogeographic and geodynamic evolution of southern South America: American Association of Petroleum Geologists, Memoir, v. 46, p. 599–614.
- Vicente, J.C., 2005, Dynamic paleogeography of the Jurassic Andean Basin: patterns of transgression and localisation of main straits through the magmatic arc: Revista de la Asociación Geológica Argentina, v. 60, p. 221–250.
- Wahnish, E., 1942, Observaciones geológicas en el Oeste del Chubut. Estratigrafía y fauna del Liásico en los alrededores del Rio Genua: Boletín, Servicio Geológico Nacional, v. 51, p. 1–73.
- Wang, H., 1978, Gastropoda, in Palaeontological Atlas of Southwest China, Guizhou, Volume 2, Carboniferous-Quaternary: Beijing, Geology Publishing House, p. 394–412.
- Weaver, C., 1931, Paleontology of the Jurassic and Cretaceous of west central Argentina: Memoir, University of Washington, v. 1, p. 1–469.
- Wenz, W., 1938–1944, Teil 1: Allgemeiner Teil und Prosobranchia, in Schindewolf, O.H., ed., Handbuch der Paläozoologie, Band 6, Gastropoda: Berlin, Borntraeger, 1639 p.
- Woodward, S.P., 1851, A Manual of the Mollusca (Including the Brachiopoda and Tunicata); or a Rudimentary Treatise of Recent and Fossil Shells, Part I, London, John Weale, 158 p.
- Yu, W., Pan, H.Z., and Wang, H.J., 1974, Triassic gastropods, in Nanjing Institute of Geology and Paleontology, Academia Sinica, The Stratigraphical and Paleontological Handbook of Southwestern China: Beijing, Science Press, p. 320–326.
- von Zieten, C.H., 1830–1833, Die Versteinerungen Württembergs: Stuttgart, Verlag & Lithographie der Expedition des Werkes unsere Zeit, 102 p.
- von Zittel, K.A., 1873, Die Gastropoden der Stramberger Schichten: Palaeontographica Supplement II, v. 3, p. 193–373.