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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*) *protonotialis* 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 Haliotoidea Rafinesque, 1815.

Early Jurassic marine gastropods from South America were studied by Bayle and Coquand (1851), Behrendsen (1891, 1922), Möricke (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
acuminata	E.-Deslongchamps, 1843, p. 108	pl. 8, figs. 11-15	*Trochotoma* (*T.*)	*Trochotoma*	France	Bathonian	Suppl. Fig. 1.B
affinis	E.-Deslongchamps, 1843, p. 106	pl. 8, figs. 8-10	*Trochotoma* (*T.*)	*Trochotoma*	Europe	Baj-Bathonian	Fig. 5.5-6
amata	d'Orbigny, 1850b, p. 9	d'Orbigny 1853, pl. 343, figs. 3-8	*T.* (*Placotoma*)	*Ditremaria*	France	Late Jurassic	Suppl. Fig. 5.C
angulata	Münster in Goldfuss, 1844, p. 56	pl. 180, fig. 7	*Trochotoma*?	*Trochus*	Germany	Unter Oolithe	
auris	von Zittel, 1873, p. 347-348	pl. 51, figs. 3-4	*Trochotoma s.l.*	*Trochotoma*	Europe	Late Jurassic	Suppl.
barremica	Cossmann, 1916, p. 29	pl. 2, figs. 30-33	*T.* (*Placotoma*)?	*Trochotoma*	France	Barremian	
bartkoi	Szabó, 1984, p. 70-71	fig. 3	*Urkutitoma*	*Urkutitoma*	Hungary	Sinemurian	
bellampensis	Haber, 1934, p. 329	Gemmellaro 1879, pl. 5, figs. 69-70	*Trochotoma* (*T.*)	*Ditremaria*	Sicily	Early Jurassic	Suppl., see *meneghinii*
bicarinata	d'Orbigny, 1843, p. 276-277	d'Orbigny 1853, pl. 340, figs. 8-11	*Trochotoma* (*T.*)	*Ditremaria*	France	Early Jurassic	Fig. 5.7
blaschkei	Haber, 1934, p. 388-389	Blaschke 1911, pl. 5, figs. 7a-b	*Valfinia*	*Didymodon*	Czeck Rep.	Tithonian	
brocastellensis	Moore, 1867, p. 267	pl. 15, fig. 29	*Trochotoma* (*T.*)	*Trochotoma*	Great Britain	Early Jurassic	Suppl. Fig. 2.C
calix	Phillips, 1829, p. 157	pl. 11, fig. 30	*Trochotoma* (*T.*)	*Solarium*	Great Britain	Aalenian	Fig. 5.1-2
canaliculata	Pictet, 1855, p. 180	Error pro *carinata*	*Trochotoma*	*Trochotoma*	Great Britain	Bathonian	Suppl.
carinata	Lycett, 1850, p. 417	Lycett 1857, pl. 4, fig. 5	*Trochotoma* (*T.*)	*Trochotoma*	Great Britain	Bathonian	Fig. 5.4
carinata	von Zittel, 1873, p. 341	pl. 50, fig. 9	*Valfinia*?	*Ditremaria*	Czeck Rep.	Late Jurassic	
carpatica	Kochanová in Kollárová & Kochanová, 1973, p. 198	pl. 10A, fig. 3	*Trochotoma*?	*Trochotoma*	Slovakia	Norian	
chanoise	Henry, 1875, p. 441	pl. 4, figs. 33-34	?	*Trochotoma*	France	Hettangian	
chordulata	Haber, 1934, p. 373	Morris & Lycett 1851, pl. 10, fig. 10	*T.* (*Placotoma*)	*Ditremaria*	Great Britain	Bathonian	Suppl. Fig. 6.D, see *funiculosa*
clypeus	Terquem, 1855, p. 268	pl. 16, figs. 9-9a	*Trochotoma*?	*Trochotoma*	Europe	Hettangian	Suppl.
conica	Rollier, 1918, p. 57	Cossmann 1885, pl. 13, fig. 14	*Trochotoma* (*T.*)	*Ditremaria*	France	Bathonian	Suppl. Fig. 1.C, see *acuminata*
conuloides	E.-Deslongchamps, 1843, p. 109	pl. 8, figs. 16-19	*Trochotoma* (*T.*)	*Trochotoma*	France	Bathonian	Suppl. Fig. 1.A
cossmanni	Rollier, 1918, p. 59	Cossmann 1900, pl. 16, figs. 3-5	*T.* (*Placotoma*)	*Ditremaria*	France	Bathonian	Suppl. Fig. 6.F
cotteauana	Haber, 1934, p. 335	Cossmann 1885, pl. 8, figs. 13-14	*Trochotoma* (*T.*)	*Ditremaria*	France	Bathonian	Suppl., see *extensa*
crossei	de Folin, 1869 in de Folin & Périer, p. 144	pl. 22, fig. 6	*Sinezona*	*Trochotoma*	Cap Vert	living	
deffneri	Fraas, 1882, p. 144 (nom. nud.)		?	*Ditremaria*	Germany	Kimmeridgian?	
depressa	Gioli, 1889, p. 9-10	pl. 1, fig. 9	*T.* (*Placotoma*)?	*Ditremaria*	Italy	Aalenian	
depressiuscula	Lycett, 1850, p. 417	Hudleston 1896, pl. 41, fig. 10	*T.* (*Placotoma*)	*Trochotoma*	Great Britain	Bathonian	Suppl. Fig. 6.C
desoriana	Cotteau, 1854, p. 36		*Trochotoma* (*T.*)	*Ditremaria*	France	Bathonian	Suppl.
discoidea	Roemer, 1836, p. 150	pl. 11, fig. 12	*Trochotoma*?	*Trochus*	France	Kimmeridgian	Suppl. Fig. 4.E
discoidea	Buvignier, 1852, p. 39	pl. 25, figs. 10-11	*T.* (*Placotoma*)	*Trochotoma*	Europe	Bathonian	Suppl. Fig. 5.D
distefanoi	Scalia, 1903, p. 37	Fucini 1913, pl. 1, figs. 1-2	*Trochotoma*?	*Trochotoma*	Sicily	Early Jurassic	Suppl.
elegans	Gemmellaro, 1889, p. 152	pl. 15, figs. 27-29	?	*Trochotoma*	Sicily	Permian	
elegans	Favre in Joukowsky & Favre, 1913, p. 425	pl. 25, figs. 18-20	*Valfinia*?	*Ditremaria*	France	Portlandian	
elongata	Nalivkin & Akimov, 1917, p. 27-28	pl. 3, fig. 10	*Valfinia*?	*Ditremaria*			
extensa	Morris & Lycett, 1851, p. 83	pl. 10, figs. 19a-b	*Trochotoma* (*T.*)	*Trochotoma*	Europe	Bathonian	Suppl. Fig. 2.A
funata	Lycett, 1850, p. 417	Hudleston 1896, pl. 41, figs. 5a-b	*Trochotoma* (*T.*)	*Trochotoma*	Great Britain	Bathonian	Suppl.
funiculosa	Cossmann, 1885, p. 309	pl. 10, figs. 36-37	*T.* (*Placotoma*)	*Trochotoma*	Europe	Bathonian	Suppl. Fig. 6.D-E
gansuensis	Tong & Erwin, 2001, p. 15	pl. 2, figs. 5-10	*Trochotoma* ?	*T.* (*Discotoma*)	China	Anisian	
gemmellaroi	Haber, 1934, p. 340	Gemmellaro 1879, pl. 6, figs. 18-19	*Trochotoma*?	*Ditremaria*	Sicily, Italy	Sinemurian	
gigantea	von Zittel, 1873, p. 345-346 [463]	pl. 51, figs. 1-2	*Trochotoma* (*T.*)	*Trochotoma*	Czeck Rep.	Late Jurassic	Suppl.
globulus	E.-Deslongchamps, 1843, p. 109	pl. 8, figs. 20-22	*Valfinia*?	*Trochotoma*	France	Bathonian	
gracilis	von Zittel, 1873, p. 343	pl. 50, figs. 11, 13	*Valfinia*	*Ditremaria*	Czeck Rep.	Late Jurassic	
gradata	Gemmellaro, 1879, p. 198	pl. 6, fig. 17	*Trochotoma* (*T.*)	*Ditremaria*	Sicilia	Early Jurassic	Suppl.
gradus	E.-Deslongchamps, 1843, p. 106	pl. 8, figs. 4-7	*Trochotoma* (*T.*)	*Trochotoma*	France	Toarcian	Fig. 5.8-9
granulifera	von Zittel, 1873, p. 342	pl. 50, figs. 10, 12	*Valfinia*?	*Ditremaria*	Czeck Rep.	Late Jurassic	
hamptonensis	Haber, 1934, p. 344-345	Morris & Lycett 1851, pl. 10, figs. 18a, 20	*Trochotoma* (*T.*)	*Ditremaria*	Great Britain	Bathonian	Suppl. Fig. 1.D, see *obtusa*
haueri	Hörnes in von Hauer, 1853, p. 763		*Trochotoma* (*T.*)	*Trochotoma*	Germany	Sin-Pliensbach	Suppl.
hermitei	Gemmellaro, 1879, p. 196	pl. 5, figs. 65-68	*Trochotoma*	*Trochotoma*	Sicily	Early Jurassic	Suppl. Fig. 3.D
hermitei	de Loriol, 1887, p. 208	pl. 23, figs. 6-7	*Valfinia*	*Ditremaria*	France	Oxfordian	

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

Table 1. (Continued)

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

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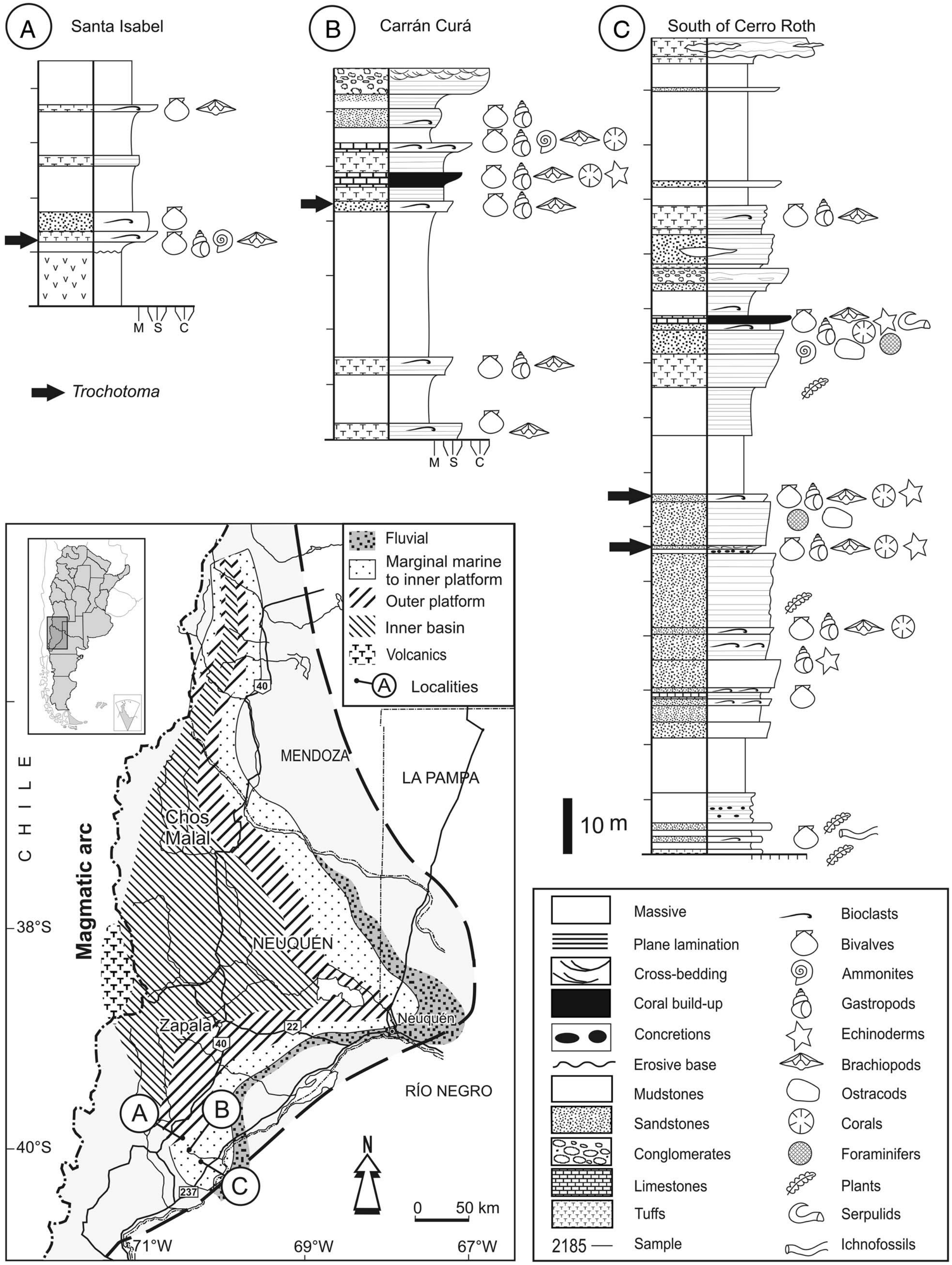

Figure 1. Location map and simplified logged sections at Santa Isabel (**A**), Carrán Curá (**B**) and Cerro Roth (**C**) in southern Neuquén Province, Argentina. Beds with *Trochotoma* indicated with an arrow. Paleogeography after Legarreta and Uliana (2000), sections adapted from Damborenea et al.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

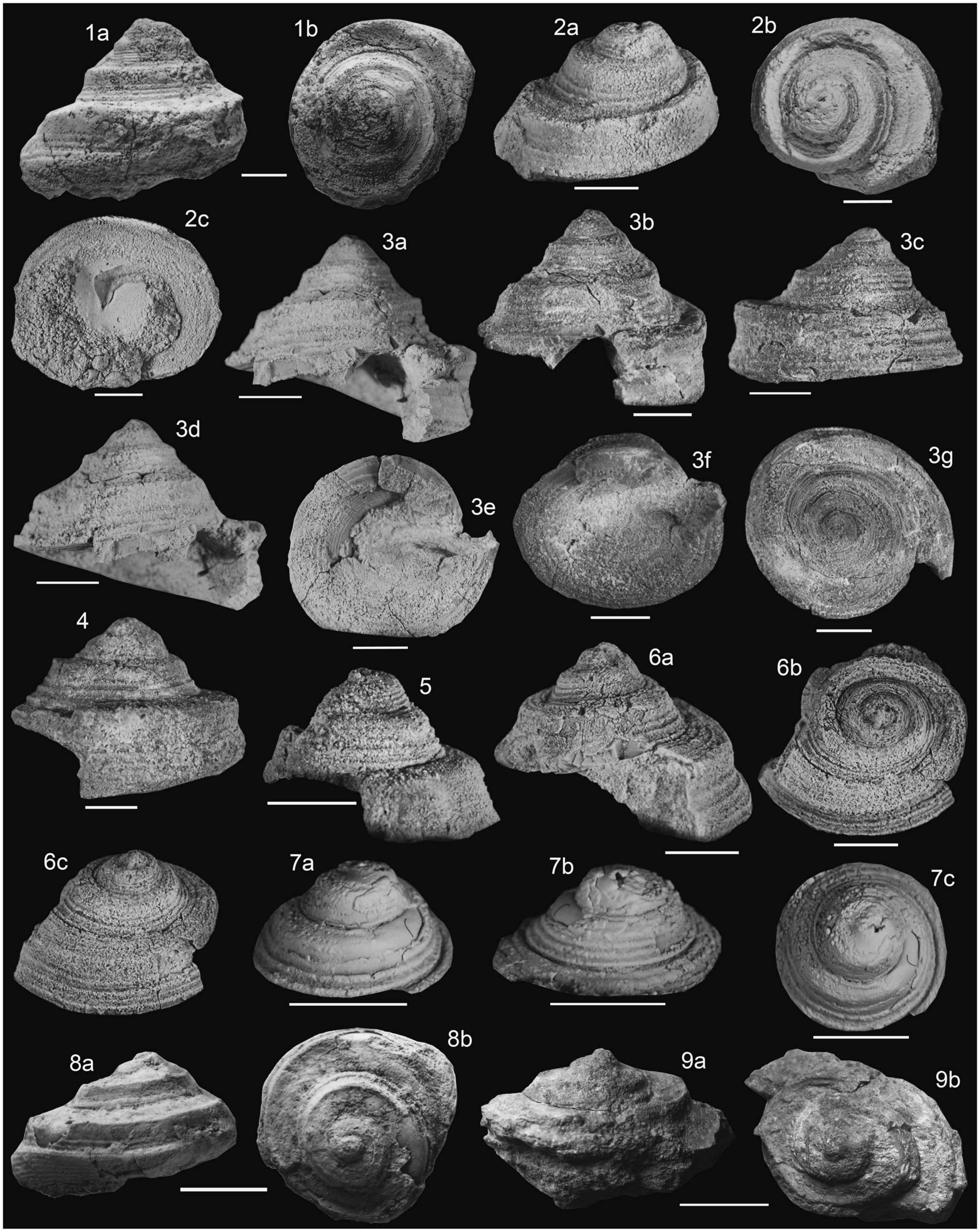

Figure 2. (**1–7**) *Trochotoma* (*Trochotoma*) *protonotialis* n. sp. (**1**) MLP 26172, holotype, (**1a**) lateral view; (**1b**) apical view. (**2**) MLP 12168, paratype. (**2a**) lateral view; (**2b**) apical view; (**2c**) basal view. (**3**) MCF-PIPH 554. (**3a**, **b**, **c**) lateral views; (**3d**) 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.

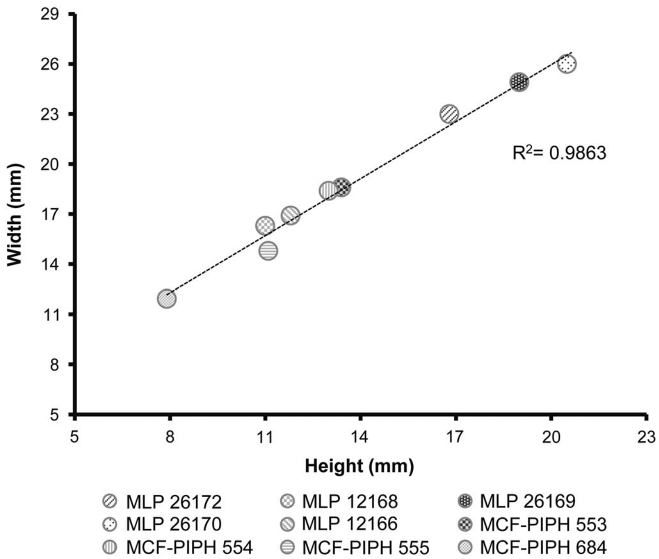

Figure 3. Diagram showing the variations of height/width ratio in *Trochotoma protonotialis* n. sp. Note that R^2 indicates a good correlation between these parameters.

Table 2. Measurements of *Trochotoma* (*T.*) *protonotialis* 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

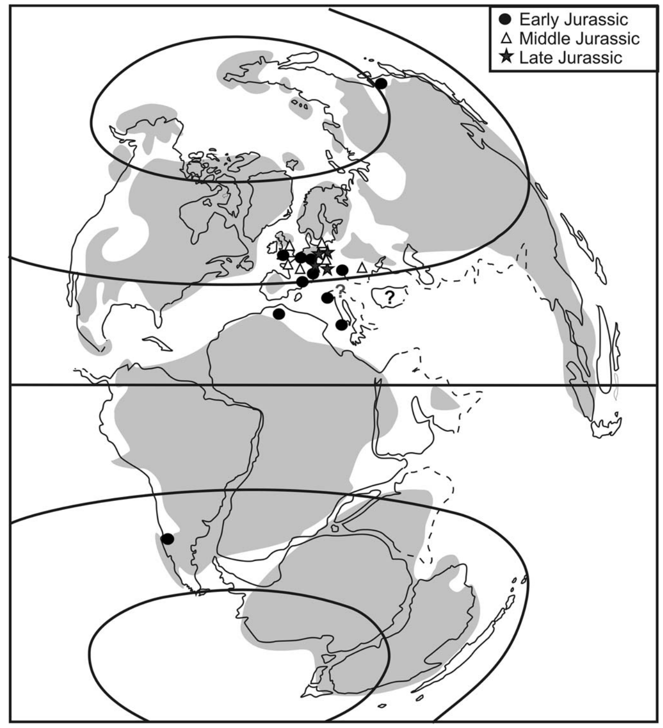

Figure 4. Paleobioegeographical distribution of *Trochotoma* s.l. species. Base map depicting early Jurassic paleogeography compiled from various sources.

inclined. The trema in *Trochotoma* (*T.*) *protonotialis* 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.*) *protonotialis* 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.*) *protonotialis* 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. protonotialis* 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, 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.*) *protonotialis* 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.*) *protonotialis* 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.*) *protonotialis* 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).

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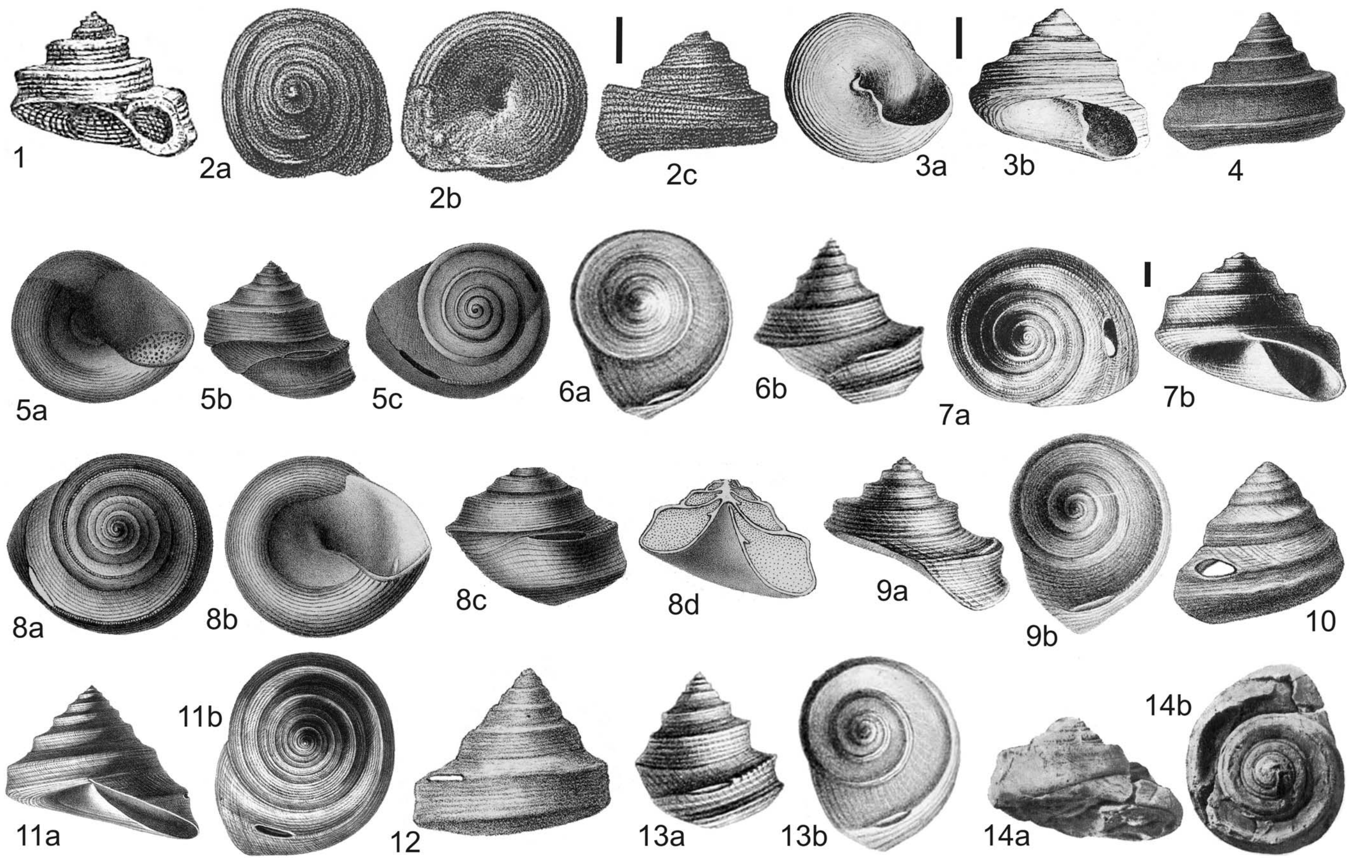

Figure 5. Reproduction of original illustrations of some species comparable to *T. protonotialis* n. sp. (**1, 2**) *Trochotoma* (*T.*) *calix* (Phillips). (**1**) from Phillips 1829, pl. 11, fig. 30; (**2**) from Hudleston 1885, pl. 4, figs. 6, 6a–b. (**3**) *Trochotoma* (*T.*) *magnifica* Cossmann, 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

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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.*) *protonotialis* 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 Scisurellidae than to the anatomy of Pleurotomariidae. He suggested that the extinct families previously included in Pleurotomarioidea might be more appropriately assigned to Scisurelloidea. 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 Scisurellidae. 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 Scisurellidae 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 (Bellerophontidae, 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 paleobioegeographical 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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