

Upper Jurassic (TITHONIAN) belemnites from the Neuquén basin, Argentina

Verónica V Vennari, Beatriz Aguirre-Urreta, Luciana S Marin, Pierre Pellenard, Mathieu Martínez, Maisa Tunik

▶ To cite this version:

Verónica V Vennari, Beatriz Aguirre-Urreta, Luciana S Marin, Pierre Pellenard, Mathieu Martínez, et al.. Upper Jurassic (TITHONIAN) belemnites from the Neuquén basin, Argentina. Journal of South American Earth Sciences, 2023, 124, pp.104200. 10.1016/j.jsames.2023.104200. insu-03999990

HAL Id: insu-03999990 https://insu.hal.science/insu-03999990

Submitted on 22 Feb 2023 $\,$

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Upper Jurassic (TITHONIAN) belemnites from the Neuquén basin, Argentina

Verónica V. Vennari, Beatriz Aguirre-Urreta, Luciana S. Marin, Pierre Pellenard, Mathieu Martínez, Maisa Tunik

PII: S0895-9811(23)00011-1

DOI: https://doi.org/10.1016/j.jsames.2023.104200

Reference: SAMES 104200

To appear in: Journal of South American Earth Sciences

Received Date: 4 July 2022

Revised Date: 27 December 2022

Accepted Date: 15 January 2023

Please cite this article as: Vennari, Veró.V., Aguirre-Urreta, B., Marin, L.S., Pellenard, P., Martínez, M., Tunik, M., Upper Jurassic (TITHONIAN) belemnites from the Neuquén basin, Argentina, *Journal of South American Earth Sciences* (2023), doi: https://doi.org/10.1016/j.jsames.2023.104200.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2023 Published by Elsevier Ltd.



1 UPPER JURASSIC (TITHONIAN) BELEMNITES FROM THE NEUQUÉN

2 **BASIN, ARGENTINA**

- 3
- 4 VERÓNICA V. VENNARI^{*1,3}, BEATRIZ AGUIRRE-URRETA^{2,3}, LUCIANA S. MARIN^{2,3}, PIERRE

5 Pellenard⁴, Mathieu Martínez⁵ and Maisa Tunik⁶

- ⁶ ¹Instituto de Evolución, Ecología Histórica y Ambiente (IDEVEA), Universidad
- 7 Tecnológica Nacional, Facultad Regional San Rafael (UTN-FRSR). Gral. J.J. Urquiza
- 8 314, M5602GCH, San Rafael, Mendoza, Argentina. vvennari@mendoza-conicet.gob.ar
- 9 ² Instituto de Estudios Andinos "Don Pablo Groeber"(IDEAN), Universidad de Buenos
- 10 Aires, Facultad de Ciencias Exactas y Naturales. Intendente Güiraldes 2160 Ciudad
- 11 Universitaria, C1428EGA, CABA, Argentina. aguirre@gl.fcen.uba.ar;
- 12 <u>lmarin@gl.fcen.uba.ar</u>
- ³Consejo Nacional de Investigaciones científicas y Tecnológicas (CONICET)
- ⁴ Biogéosciences, UMR 6282 CNRS/uB/EPHE 6 Bd Gabriel, Université Bourgogne
- 15 Franche-Comté, Dijon, Francia. <u>pierre.pellenard@u-bourgogne.fr</u>
- ⁵ Univ Rennes, CNRS, Géosciences Rennes UMR 6118, F-35000 Rennes, Francia.
- 17 mathieu.martinez@univ-rennes1.fr
- ⁶ Instituto de Investigación en Paleobiología y Geología, CONICET & Universidad de
- 19 Río Negro, Sede Alto Valle, 8332 General Roca, Río Negro, Argentina.
- 20 mtunik@unrn.edu.ar
- 21
- 22 * Corresponding author. e-mail address: vvennari@conicet-mendoza.gob.ar
- 23

24	Abstract. Belemnites were a group of Mesozoic coleoids with a global distribution
25	from the Early Jurassic to the Late Cretaceous. During the Late Jurassic-Early
26	Cretaceous, Gondwana's marine shelves were dominated by Belemnopsis and Hibolithes
27	populations. In contrast to the Austral Basin, where both genera are quite common, their
28	record in the Neuquén Basin (Argentina) is rather scarce and poor, probably due to a
29	combination of locally unfavorable environmental conditions and predation pressure.
30	Here we describe a new belemnite association from the Tithonian of the Vaca Muerta
31	Formation from southern Mendoza and northern Neuquén provinces. Belemnite's
32	findings are assignable to the Tithonian Windhauseniceras internispinosum and
33	Corongoceras alternans Andean ammonoid Biozones. The studied rostra are identified
34	as Belemnopsis cf. B. patagoniensis, Belemnopsis cf. B. launceloti, and Hibolithes
35	argentinus? Affinities of the Neuquén Basin belemnite fauna are referred to the
36	Madagascan-Eastern Africa associations (Ethiopian Subprovince, Tethyan Province),
37	adding evidence to an established Trans-Gondwana seaway enabling the connection
38	between those areas from the Tithonian onwards.
39	

Keywords. Fossil coleoidea. *Belemnopsis. Hibolithes*. Vaca Muerta Formation. TransGondwana seaway.

43 **1.1 Introduction**

44 Belemnites are an extinct group of Mesozoic nektonic cephalopods considered in the most recent contributions as stem-dechabrachian coleoids (Fuchs et al., 2013; Hoffmann 45 46 and Stevens, 2020). Usually reconstructed as externally morphologically close to loginid squids (Naef, 1922; Stevens, 1965), belemnites had a mantle muscle structure 47 48 similar to that of sepiids (Monks et al., 1996). Their mineralized inner shell was generally divided into three parts: proostracum, phragmocone, and rostrum. Of these, 49 the low-Mg calcitic rostrum is the most commonly preserved part due to its resistant 50 structure of radially arranged calcite fibers that, combined with variable amounts of 51 52 organic matter, form concentric rings in cross-section (Stolley, 1911; Jeletzki, 1966; 53 Riegraf, 1980; Hoffmann et al., 2016; Hoffmann and Stevens, 2020). Belemnite taxonomy mostly relies on morphological characters of the rostrum: general 54 55 morphology, both in outline and profile view, shape of the transverse section, form and orientation of the apex, and presence and extension of grooves (apical, ventral, dorsal, 56 and/or lateral). The orientation and form of the apical line and alveolus-related 57 characters (*i.e.*, where the phragmocone lies inside the rostrum) are usually accessorily 58 59 described (Stevens, 1965; Jeletzky, 1966; Doyle and Kelly, 1988; Challinor, 1999). 60 Belemnites are recorded from the Late Triassic (Iba et al., 2014), but it is from the Toarcian onwards that they attain a worldwide distribution (Doyle, 1987). By the 61 Late Jurassic-Early Cretaceous Gondwana shelf-areas were dominated by *Belemnopsis* 62 63 and Hibolithes (Challinor, 1991; Doyle and Pirrie, 1999), both included in the "Belemnopseina," a group characterized by alveolar furrows and whose taxonomic 64 validity has been recently challenged (Stevens, in press). *Hibolithes* was a cosmopolitan 65 66 and ecologically wide-ranged genus whose species are mostly differentiated based on the ventral groove characters (Stevens, 1965; Mutterlose, 1988; Doyle and Kelly, 1988; 67

Challinor, 1991). Belemnopsis is a more variable genus (Stevens, 1965; Combémorel, 68 1988; Howlett, 1989; Challinor, 1991, 2001, 2003; Challinor and Hikuroa, 2007) mostly 69 represented in Gondwana by robust, cylindroconical to slightly depressed rostra with a 70 variably strong ventral groove (Challinor, 1991; Doyle et al., 1996, 1997; Doyle and 71 Pirrie, 1999). In Argentina, both Hibolithes and Belemnopsis had been long recognized 72 from the Upper Jurassic and, mostly, from the Lower Cretaceous of the Austral Basin in 73 south Patagonia (e.g., Dana, 1848; Favre, 1908; Feruglio, 1936, 1949) and have been 74 revised or cited in the literature from there on (e.g., Aguirre-Urreta and Suárez, 1985; 75 Riccardi, 1976, 1977, 1988). In contrast, Neuquén Basin belemnite records of the same 76 77 age are significantly less frequent, and taxonomic-focused contributions are lacking 78 (Stevens, 1965; Doyle et al., 1996; 1997). Therefore, the objective of this work is to fully document new belemnite rostra 79 80 from the Upper Jurassic (Tithonian) of the Neuquén Basin to start filling the gap in the knowledge of this group in west-central Argentina. We also aim to refer the findings to 81

82 the Andean ammonoid-based biostratigraphic framework, and to discuss the

paleobiogeographic, biostratigraphic, and broad paleoecological implications of their
occurrences.

1.2. Previous Neocomian belemnite records in Argentina and nearby regions

86 Upper Jurassic–Lower Cretaceous belemnite records from Argentina are currently

concentrated in the Austral Basin (Fig. 1). *B. patagoniensis* (Favre) was originally

described from the Hauterivian–Barremian of Lago Belgrano area and later restricted to

the Hauterivian (Favre, 1908; Riccardi, 1988). Findings around Lago San Martín, at the

90 top of the Springhill Formation, were alternatively ascribed to the Tithonian (Bonarelli

and Nágera, 1921; Feruglio, 1949), the Hauterivian–Barremian (Riccardi, 1971), or the

92 Berriasian (Riccardi, 1976, 1977). Finally, they were assigned to a Berriasian-

93	Valanginian age (Medina and Riccardi, 2005; Riccardi, 1988). From the same levels,
94	Riccardi (1977) reported B. cf. B. madagascariensis (Besairie) and Hibolites aff. H.
95	jaculum (Phillips). Also from the Lago San Martín area, at the base of the Río Mayer
96	Formation, Medina and Riccardi (2005) reported B. patagoniensis, B. cf. gladiatoris
97	Willey, and Belemnopsis sp. together with the ammonoids Favrella americana (Favre)
98	and F. wilckensi (Favre), thus indicating a Hauterivian age for the association. To the
99	south, in the Lago Argentino area, Estancia La Cristina, Feruglio (1936) introduced a
100	supposedly Valanginian belemnite association composed of B. patagoniensis,
101	Hibolithes argentinus Feruglio, H. aff. H. jaculum, and a specimen openly assigned as
102	Belemnites sp. I, which was reinterpreted as a Belemnopsis sp. by Stevens (1965, p.
103	159) and alternatively as Parahibolites by Challinor (1991, p. 316). The specimen
104	assigned to B. patagoniensis was reassigned to B. gladiatoris Willey due to
105	morphological differences with the type material (Stevens, 1965; Willey, 1973) and
106	subsequently to B. launceloti Howlett (Howlett, 1989). Feruglio (1949, p. 169) also
107	mentioned, but not illustrated, B. patagoniensis from another locality (Cerro de Los
108	Fósiles) within the Lago Argentino area, there associated with Tithonian to Berriasian
109	ammonoid taxa (cf. Leanza, A., 1967). A reassessment of the Indo-Pacific affinity of the
110	whole assemblage (Stevens, 1965) as well as a revision of the ammonoid-related fauna,
111	pointed to an upper Tithonian age for Feruglio's original belemnite collection (Leanza,
112	A., 1967). The same seems valid for related specimens from the Springhill Formation
113	near Lago Argentino, where Hibolithes ranges into the Berriasian and younger beds of
114	the Río Mayer Formation sensu Doyle et al. (1996).
115	Other illustrated records of <i>B. patagoniensis</i> or <i>B.</i> cf. patagoniensis come from

the southernmost end of South America, from Berriasian–Hauterivian beds of the

117 Yaghán Formation, Bahía Nassau, Tierra del Fuego (Dana, 1848; Stevens, 1965;

118 Stolley, 1928) and from the Valanginian?–Hauterivian Beauvoir Formation in the western region of the Isla de los Estados (Harrington, 1943; Caminos and Nullo, 1979). 119 120 Also, Aguirre-Urreta and Suárez (1985) presented new Berriasian–Hauterivian records of *B. madagascariensis* from several sections within the Magallanes Archipelago. 121 122 Recently, Ippolitov et al. (2015) described a single specimen from the Berriasian of Crimea as *Parabelemnopsis* cf. *patagoniensis*, indicating that its presence was probably 123 124 the result of a rare immigration episode to the Northern Hemisphere. Aside from the 125 later record, *Belemnopsis patagoniensis* appears to be a well-distributed species of the Austral Basin during the Lower Cretaceous. 126 127 Other records of Belemnopsis in nearby areas are known from the Valanginian-128 Hauterivian of the Rocas Verdes Basin, Chile, where robust forms were ascribed to the Antarctic species B. cf. B. launceloti Howlett (Stinnesbeck et al., 2014). Additional 129 130 material retrieved from a drill hole at the Falkland/Malvinas Plateau was identified as Belemnopsis spp. and assigned a New Zealand to Himalayan affinity (Jeletzky, 1983). 131 Within the Neuquén Basin (Fig. 1), Upper Jurassic-Lower Cretaceous belemnite 132 records are sparser and poorly known. Oxfordian Belemnopsis with European affinities 133 134 have been mentioned from La Manga Formation in southern Neuquén (Doyle et al., 135 1996; Riccardi et al., 2011) and from the Callovian–Oxfordian of Vega de la Veranada, 136 in northern Neuquén (Alberti et al., 2020). Younger not-illustrated records from Mendoza Province include an indeterminate rostrum fragment from the Tithonian of 137 138 Arroyo Serrucho (Krantz, 1928) and some thin incomplete rostra from the upper Tithonian of the Vaca Muerta Formation in Bardas Blancas (Gerth, 1925; here referred 139 140 as Cañada de Leiva). Additional fragmentary belemnites were reported from a 141 Berriasian interval in the Arroyo La Manga area (Gerth, 1925). Other Tithonian records from Neuquén Province were either identified as *Hibolithes* sp. (e.g., Alberti et al., 142

1/12	2020 from	n Damna Tril)	or not specified (a a	Kietzmann and	Vannari 2013 from
143	2020. from	n Pampa Irii) (or not specified (<i>e.g.</i>	. Kietzmann and	vennari, 2013, from

144 Cerro Domuyo, here revised). Besides, Stevens (1965, p. 158) indicated a possible

145 Kimmeridgian to Tithonian age for *?Hibolithes* sp., *B.* cf. *B. patagoniensis* and

146 ?Dicoelites sp. from Cerro Lotena, and for ?Hibolithes sp. from Arroyo Chacay

147 Melehue, but unfortunately, none of those records were illustrated.

148 FIGURE 1 AROUND HERE

149 **2. Geological setting**

150 The Neuquén Basin (Fig. 1) is a retro-arc basin situated over the western margin of

151 Gondwana, between 32° to 40° South Latitude, extending over central-western

152 Argentina and central Chile (Legarreta and Uliana, 1991; Howell et al., 2005). Its nearly

153 continuous Mesozoic to lower Cenozoic sedimentary infill, intercalated with volcanic

episodes, and the high quality and richness of its fossil record arouse the interest of the

155 international scientific community over the basin.

156 Tithonian successions bearing the belemnite fauna here presented are included in157 the Vaca Muerta Formation (Weaver, 1931), a marine geographically extended unit

158 mainly composed by an alternation of shale/marls with a variety of limestone beds

deposited over a carbonate ramp to basin setting from the lower Tithonian to the lower

160 Valanginian (Kietzmann et al., 2014; Legarreta and Uliana, 1991). Ammonoids are the

161 most common megascopic fossils of the Vaca Muerta Formation, including both

162 endemic and more extended distributed taxa. Their correlation with Tethyan faunas and

163 with calcareous nanofossils and microfossils bioevents provide the current Upper

164 Jurassic–Lower Cretaceous biostratigraphic scheme for the Neuquén Basin (Leanza, H.

165 et al., 2020 and references therein; Lescano et al., 2022).

166 **3. Material and methods**

167 **3.1. Localities**

168 The twenty-one belemnites herein studied come from Tithonian beds of the Vaca

169 Muerta Formation in four localities situated over the northern sector of the Neuquén

170 Basin (Fig. 2). From the northeast to the southwest, they are Cañada de Leiva (fourteen

171 specimens), Las Loicas (one specimen), Las Alcantarillas (one specimen), and Cerro

- 172 Domuyo (five specimens).
- 173 3.1.1. Cañada de Leiva

174 It is a classic locality encompassing the Upper Jurassic–Lower Cretaceous transition in

the Neuquén Basin (35° 48' S, 69° 48' W), 6 km northeast of the Bardas Blancas

settlement (Dessanti, 1973; Gerth, 1925; Gulisano and Gutiérrez-Pleimling, 1994). Here

the Vaca Muerta Formation spans nearly 240 m and is dominated by tempestite-facies

deposited over a middle to proximal outer carbonate ramp setting (Kietzmann and

179 Palma, 2011; Kietzmann et al., 2018). Belemnites from this section come from up to 40

180 cm thick, very consolidated hummocky cross-bedding bioclastic packstone limestones

181 (CLBe) intercalated with laminated marls/siltstone intervals, and a decimetric massive

to laterally concretional wackestone limestone with ammonoids, and located about 24.5

183 m from the base of the logged section in Figure 2. The CLBe sample is a densely

184 packed, poorly sorted, and oriented (Fig. 3) packstone with micrite and organic matter.

185 The grains are 70% echinoderm fragments (Figs. 3.1–3.4), 10% of bone fragments

186 (Figs. 3.1, 3.4), 10% of assorted fragmented bioclasts, probably bivalve shells (Fig. 3.2),

bryozoan fragments and small gastropods (Fig. 3.4), and 10% of siliciclastic material

188 such as volcanic lithic fragments, detrital mono and polycristallyne quartz, feldspar and

abundant pyrite. Among the echinoderm fragments were differentiated: star-shaped

190 crinoid columnals (Fig. 3.1), cross and longitudinal sections of stems, crinoid arm

elements, some with lunate patterns (Figs. 3.1, 3.3), and scarce echinoid spines. Most

192 echinoid fragments are highly reworked, replaced and recrystallized, and some of them

- have microborings (Fig. 3.4). Most of the bone fragments have evidence of microbial
- boring activity as well. The matrix is micritic and some pore spaces are filled with
- authigenic quartz. The belemnite-bearing interval is the same identified by Gerth in
- 196 1911 and 1913 (Gerth, 1925, fig. 10).
- 197 FIGURE 2 and FIGURE 3 AROUND HERE

198 *3.1.2. Las Loicas*

- 199 It is located close to the 145 National Road heading towards the Pehuenche
- 200 International Pass to Chile, approximately 1 km to the west of the homonymous
- settlement (35° 47' S, 70° 09' W). The marine sediments of the Vaca Muerta Formation
- are punctuated by several volcanic layers, some of which have provided precise U/Pb
- absolute ages (Lena et al., 2019; Vennari et al., 2014). Belemnites from this section
- 204 were retrieved from decimetric to metric laminated to massive dark wackestones
- 205 bearing ammonoid and brachiopod impressions, intercalated with dark laminated marls.
- Based on the facies associations interpreted by Kietzmann et al. (2021) in the nearby
- 207 Las Tapaderas section, this interval is assignable to the transition between basinal to
- 208 distal outer ramp settings.
- 209 3.1.3. Las Alcantarillas
- Located about 20 km west of the Las Loicas section, it is well exposed over the right
- 211 margin of the Arroyo Pehuenche that crosses 145 National Road (35° 57' S, 70° 14' W).
- The single belemnite rostrum from this locality comes from a 12 cm thick, dark
- 213 laminated wackestone limestone showing a thin pyritized band, which is intercalated
- within an interval dominated by calcareous-nodule bearing dark laminated marls.
- Likewise, the previous locality, the facies association indicates a distal outer ramp
- setting (Kietzmann et al., 2021).
- 217 *3.1.4. Cerro Domuyo*

This locality is at the foothills of the Cerro Domuyo, at the southern tip of the Cordillera 218 219 del Viento (36° 41' S, 70° 26' W). Here the Vaca Muerta Formation is exposed over the 220 left margin of the Arroyo Covunco, and all belemnites were recorded from centimetric to decimetric grey to dark laminated wackestones, intercalated between large intervals 221 222 of laminated shales and marls. Facies association analyses indicate a basinal to distal 223 outer ramp setting for this interval, occurring just below slumped calcareous sandstone 224 deposits assigned to the Huncal Member of the Vaca Muerta Formation by Kietzmann 225 and Vennari (2013) and reinterpreted by Naipauer et al. (2020).

226 **3.2. Measurements and illustrations**

Belemnite rostra's study and description follow the outlines of Stevens (1965) and

228 Challinor (1999, 2003). Challinor (1999) redefined the flattening index (A) of Stevens

229 (1965) as a percentage ratio:

A = rostrum transverse diameter/rostrum sagittal diameter x 100

231 Rostra linear measurements were acquired using a vernier digital caliper ($\pm 1 \text{ mm}$

accuracy). Angular measurements were obtained with a protractor $(\pm 1^{\circ})$ or by digital

233 means. Pictures of the belemnite rostra covered with sublimated ammonium chloride

were taken with a Canon SX60 semi-reflex camera. Linear illustrations and plates were

prepared with CorelDraw 2020 Graphics Suite and Adobe Photoshop 2020.

236 **3.3. Abbreviations**

237 Institutional abbreviations. BAS KG, British Antarctic Survey Collection, Cambridge,

238 United Kingdom; CPBA, Paleontological Collection of the University of Buenos Aires,

239 Buenos Aires, Argentina; MCNAM-PI, Colección de Paleontología de Invertebrados

240 del Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano," Mendoza,

241 Argentina.

242	Anatomical abbreviations. A, index of flattening; dtM, maximum transverse diameter;
243	dtm, minimum transverse diameter.
244	Stratigraphical abbreviations. BB, Cañada de Leiva section; DO, Cerro Domuyo
245	section; LA, Las Alcantarillas section; LL, Las Loicas section.
246	4. Systematic paleontology
247	Order BELEMNOPSEINA Jeletzky, 1965
248	Family BELEMNOPSEIDAE Naef, 1922, amend Jeletzky, 1946
249	Genus <i>Belemnopsis</i> Bayle, 1878
250	Type species. Belemnopsis apiciconus Blainville, 1827 (pl. 2, figs. 2, 2a). ?Upper
251	Aalenian–Bajocian, England, France, and Southern Germany (cf. Riegraf, 1999).
252	Lectotype subsequently designated by Riegraf (1999, p. 66). A reassessment of the
253	validity of the genus was recently undertaken by Mitchell (2015) and followed here.
254	Belemnopsis sp. cf. Belemnopsis patagoniensis (Favre, 1908)
255	Figures 4.1–4.6; 5.1–5.2
256	cf. 1908 Belemnites patagoniensis n. sp., Favre, p. 640, pl. 37, figs. 6-7
257	Material. Six specimens. One from the Las Alcantarillas section (MCNAM-PI 24881);
258	five fragments witch probably correspond to five individuals from the Cerro Domuyo
259	section (CPBA 22924.1-22924.6).
260	Geographic and stratigraphic occurrence. Las Alcantarillas section, bed LA7, base of
261	Corongoceras alternans Biozone (upper Tithonian) and Cerro Domuyo section, bed DO
262	30 and loosed within the upper portion of Windhauseniceras internispinosum Biozone

Description. Based on the best-preserved specimen MCNAM-PI 24881 (Figs. 4.1–4.3; 264 265 5.1–5.2). Rostrum cylindroconical, elongated and slender, 98 mm long, only preserves 266 the apical portion and part of the stem region. The maximum transverse diameter (dtM= 14 mm) is attained at about 60 mm from the apex. Outline symmetrical, non-hastate 267 268 with margins tapering into an acute dorsally oriented apex. Profile somewhat asymmetrical, dorsally flattened but slightly ventrally inflated around the apical region. 269 270 Cross-section elliptical and depressed throughout (A c. 115 over the stem region), 271 although this character might be accentuated by sedimentary flattening. A narrow, 272 shallow ventral groove with angular margins runs over the mid-region of the stem and 273 extends posteriorly at least up to 18 mm before the apex. The groove is 1 mm deep over the apical region, where it shows a "v" profile in cross-section and appears to deepen 274 275 anteriorly. The apical line is slightly ventral situated, and no lateral lines were observed. Remarks. The Tethyan genus Belemnopsis (Bayle, 1878) groups more than one 276 277 hundred European and Indo-Pacific belemnite species ranging from the Middle Jurassic up to the Lower Cretaceous (Riegraf, 1999). Although we agree with Riegraf (1980), 278 279 Howlett (1989), and Ippolitov et al. (2015) that such a broad taxonomic concept is problematic, there is still no agreement among belemnite workers on the validity of the 280 281 proposed subgeneric categories (e.g., Challinor, 1991; Challinor and Hikuroa, 2007) and 282 the poor preservation state of our material does not enable further insight on the matter, so we follow the classic taxonomic assignation to the genus *Belemnopsis*. 283

The outline and profile general forms, as well as the length and distinctiveness of the ventral groove, are important taxonomic characters (Stevens, 1965) that justify the assignation of the studied material to *Belemnopsis*. The rostrum cross-section appears to be a more variable trait since different authors have described *Belemnopsis* species with either circular to elliptical cross-sections (*e.g.*, Doyle and Kelly, 1988; Howlett, 1989;

289	Challinor and Hikuroa, 2007). More specifically, the elongated rostrum, with an acute
290	apex and a narrow ventral groove with angular margins, enables comparing the
291	Neuquén Basin material with Belemnopsis patagoniensis (Favre, 1908), a well-known
292	Lower Cretaceous species frequently recorded in the Austral Basin from the Berriasian
293	to the Hauterivian (see section 1.2). Upper Tithonian (cf. Leanza, A., 1967) B.
294	patagoniensis described by Feruglio (1936) from Santa Cruz differ from the type
295	material of the species (Stevens, 1965) and has been repeatedly reassigned (see section
296	1.2). Independently of their systematic position, Feruglio's Belemnopsis and Hibolites
297	argentinus show morphological affinities with Indonesian and New Zealand
298	assemblages cf. Stevens (1965) and to elements from Madagascar, cf. Challinor (1991).
299	Nonetheless, Patagonian specimens are typically more robust, almost twice wider and
300	longer than the material described here (e.g., Favre, 1908, pl. 37, figs. 6–7; Riccardi,
301	1977, figs. 6a-c, g-i). A similar slender Berriasian specimen was described from
302	Crimea by Ippolitov et al. (2015), who assigned it to Parabelemnopsis cf. patagoniensis
303	and interpreted its record in the Northern Hemisphere as a singular short invasion
304	episode. The Crimean specimen differs from the Neuquén Basin material in having a
305	much shorter ventral groove. Antarctic Belemnopsis, on the other hand, seem to be
306	closely related to those from New Zealand-Indonesian of the "uhligi Complex"
307	(Stevens, 1965; Challinor, 1991), though more recently Challinor and Hikuroa (2007)
308	indicated some affinities with Madagascan forms.
309	Belemnopsis patagoniensis, B. madagascariensis (Besairie, 1930), and B.

310 *casterasi* Besairie, 1936 are recognized as a cluster of closely related Madagascan-

- 311 South American Late Jurassic–Early Cretaceous large-sized, narrow-grooved
- belemnites (Stevens, 1965; Howlett, 1989). Howlett (1989), Challinor (1991), and
- 313 Ippolitov et al. (2015) have pointed out the strong similitude of some specimens

314	assigned to B. patagoniensis, B. aff. madagascariensis (Riccardi, 1977, 1988) and B.
315	madagascariensis (Aguirre-Urreta and Suarez, 1985). Even more, Combémorel (1988)
316	suggested that B. madagascariensis and B. casterasi might conform to a dimorphic pair.
317	Phylogenetic relationships between them await a detailed revision to assess the extent of
318	ontogenetic and population variability (Challinor, 2003; Challinor and Hikuroa, 2007).
319	FIGURE 4 AND FIGURE 5 AROUND HERE
320	Belemnopsis sp. cf. Belemnopsis launceloti Howlett, 1989
321	Figures 4.7–4.13; 5.3–5.4
322	Material. 14 specimens from the Cañada de Leiva section (MCNAM-PI 24647.1-
323	24647.14).
324	Geographic and stratigraphic occurrence. Cañada de Leiva section, bed BB19, upper
325	Corongoceras alternans Biozone (upper Tithonian), Mendoza Province, Argentina.
326	Description. Based on the most complete specimen, MCNAM-PI 24647.1, unless
327	otherwise stated. MCNAM-PI 24647.1 is most probably a juvenile individual due to the
328	presence of larger and stouter specimens in the assemblage (Figs. 4.10-4.13; 5.3-5.4).
329	Moderately preserved, 119 mm long, slender (nearly 22 times longer than thicker),
330	symmetrical, and markedly hastate rostrum both in outline and profile. The maximum
331	transverse diameter (dtM= 9.84 mm) is attained over the apical region, at about 25 mm
332	from the apex, while the minimum transverse diameter (dtm= 5.4 mm) is placed over
333	the broken anterior portion where no traces of the alveolus is observed. Apex
334	moderately obtuse. Cross-section circular to slightly depressed over the apical and
335	middle-stem region, where the venter is almost flattened, and more compressed to the
336	anterior-stem region where the venter is more excavated. A medium-width, shallow
337	ventral groove with rounded and weakly pronounced edges extends up to two-thirds

338 over the stem. In a probable adult specimen (MCNAM-PI 24647.2; Figs. 4.7–4.9), the 339 groove still has rounded margins, but it is broader (3 mm wide) and runs into the apical 340 region, at least up to 30 mm from the apex. Specimen MCNAM-PI 24647.2 also shows a slightly asymmetrical profile due to inflation of the venter, and the outline appears to 341 342 be cylindroconical (dtM= 12.2 mm) with a circular cross-section (A= 100). No dorsal or 343 lateral grooves are observed in any of the specimens. The rest of the rostra recorded in the same bed, 15.4 mm long on average (dtM= 1.4), are too poorly preserved to provide 344 345 any further insights into ontogenetic traits.

346 **Remarks.** The studied specimens were retrieved from the same interval where Gerth 347 (1925) collected some material which was then revised by Stolley and identified as 348 Hibolithes sp. (cf. Gerth, 1925, p. 42, footnote). However, some rostra traits, like the 349 slender and long stem region and the shallow, medium to broad ventral groove, make 350 them akin to Belemnopsis launceloti Howlett (1989, p. 40, pl. 6, figs. 1-2, 6-7; pl. 8, 351 figs. 5–6) from the Alexander Island. Still, the Antarctic material is less hastate, has a 352 maximum transverse diameter over the middle stem region, and the ventral groove 353 narrows anteriorly (pictures of the type material of *B. launceloti* are available at the BAS website: 354

355 <u>https://legacy.bas.ac.uk/bas_research/data/access/fossildatabase/filter.php?taxonKeywor</u>

356 <u>d=BELEMNITIDA</u>). Some of the mentioned differences might have an ontogenetic

357 explanation. Stevens (1965, p. 40) indicated that *Belemnopsis* suffered changes in its

degree of hastation in the early growth stages of the rostrum. Challinor (2001, p. 234)

also pointed out that *Belemnopsis aucklandica* presents the point of maximum

transverse diameter nearer the apex in juvenile specimens but higher up in adults, a trait

that affects the degree of hastation of the rostrum. He also noted that in more hastated

individuals, the ventral groove tends to weaken at about the mid-rostrum and extend

363	apically as a wide shallow depression. Unfortunately, the poor preservation state of the
364	material hinders further insight into its ontogeny, so its systematic assignation is left
365	open.
366	Howlett (1989) included in the B. launceloti synonymy list two specimens
367	described by Feruglio (1936, pl. 10, figs. 3-4) from the Austral Basin, formerly
368	reassigned to <i>B. gladiatoris</i> by Willey (1973), both of which are more robust than the
369	Neuquén Basin material. Howlett (1989), also renamed as B. launceloti a specimen
370	from Madagascar figured as <i>B. africanus</i> Tate, 1867 by Besairie (1936, p. 23, figs. 6–7).
371	Genus Hibolithes Montfort, 1808
372	Type species. Hibolithes hastatus Montfort, 1808 (text-fig. 47), by monotypy.
373	Bajocian-Aptian of some Boreal and most Tethyan regions (Doyle and Kelly, 1988;
374	Howlett, 1989).
375	Hibolithes argentinus? (Feruglio, 1936)
376	Figure 4.14–4.16
377	Material. One fragmentary specimen from the Las Loicas section (CPBA 23224).
378	Geographic and stratigraphic occurrence. Las Loicas section, bed LL062–063, upper
379	Windhauseniceras internispinosum Biozone (upper lower Tithonian), Mendoza
380	Province, Argentina.
381	Description. Rostrum fragment of 27.68 mm of maximum length, probably hastate both
382	in outline and profile. The maximum transverse diameter (dtM= 12.2 mm) is recorded
383	over the broken anterior, and the cross-section is almost circular (A= 103). No ventral
384	or lateral grooves are observed. The apical line seems ortholineate.

385 **Remarks.** The circular form of the rostrum cross-section and the absence of a ventral groove in the preserved portion leads us to consider this fragment as part of the lower 386 stem region of an Hibolithes representative. The most frequent Hibolithes species in 387 Argentina is *H. argentinus* (Feruglio, 1936), which is characterized by a slender hastate 388 rostrum with circular to slightly depressed transverse sections and a shallow ventral 389 groove that extends no further than the upper stem region. Howlett (1989, p. 52) 390 designated one of the specimens figured by Feruglio (1936, pl. 10, fig. 17) as lectotype 391 392 and added new material from Alexander Island. The fragment here described agrees well both with the lower stem regions of the lectotype and the with the specimen BAS 393 394 KG 2909.18 figured by Howlett (1989, pl. 6, figs. 4, 10), but as no other features are 395 preserved, the assignation to *H. argentinus* is stated with doubts.

396 **5. Discussion**

397 5.1. Paleobiogeographic considerations

398 Several authors differentiated an Indo-Pacific Province within the Tethyan Realm from 399 the Kimmeridgian onwards over the basis of belemnite geographic distribution, 400 particularly of *Belemnopsis* and *Hibolithes* regional assemblages (e.g., Combémorel, 401 1988; Doyle and Howlett, 1989; Mutterlose, 1986, 1992, Stevens, 1965, 1973). Alternatively, Challinor (1991; Challinor in Grant-Mackie et al., 2000) proposed a 402 403 different subdivision of the Tethyan Realm into two provinces, 1) Tethyan Province, 404 including a Mediterranean, Ethiopian and Tethyan Subprovinces (the last partly 405 equivalent to the Indo-Pacific Province), and 2) South Pacific Province, extending along 406 the Pacific coasts of Gondwana, from southern South America (including the Neuquén 407 Basin) through West Antarctica to New Zealand, and probably including New 408 Caledonia. The South Pacific Province was not completely isolated from the Tethyan 409 Province and at least from the latest Jurassic, some belemnite migrations took place

410 from the Ethiopian Subprovince into Antarctica and South America (Challinor, 1991; 411 Mutterlose, 1992). From the Oxfordian to the Valanginian, a long-ranging lineage of 412 narrowly-grooved Belemnopsis developed in Madagascar and Eastern Africa, forming the B. madagascariensis-B. casterasi group (Besairie, 1930; Stevens, 1965; 413 414 Combémorel, 1988). Some components of that cluster, as well as Hibolithes, might 415 have reached the South Pacific coast from the Tithonian onwards through the Trans-416 Gondwana or Indo-Madagascan seaway (e.g., Cecca, 1999; Mutterlose, 1986; Fig. 6). Even more, during the Berriasian, that marine connection is supposed to have held a 417 "relict" population of *Belemnopsis* of the *madagascariensis-casterasi* group, since 418 Belemnopsis is unknown or poorly represented from European and most Indo-Pacific 419 420 regions at that time (Doyle and Howlett, 1989; Stevens, 1965). That remnant population is thought to be related to the *Belemnopsis patagoniensis* assemblages of the Austral 421 422 Basin (Riccardi, 1977, 1988) and now from the upper Tithonian in the Neuquén Basin. 423 The same is valid for B. launceloti, recorded in Madagascar, Alexander Island, and in the Austral Basin. Belemnopsis records here described add new elements connecting the 424 Neuquén Basin assemblages with those of Madagascar and Eastern Africa, passing 425 426 through Antarctica during the Upper Jurassic. These basins are known to share several 427 ammonoid genera among other marine invertebrate and vertebrate taxa (Mutterlose, 428 1986; Riccardi, 1991; Vennari and Aguirre-Urreta, 2019 and references therein; Campos et al., 2021). 429

430 FIGURE 6 AROUND HERE

431 **5.2.** Biostratigraphic considerations

Belemnites' biostratigraphic potential has long been acknowledged for Jurassic and

433 Cretaceous successions, though belemnite-based correlations are more widely used for

the Cretaceous of the Northern Hemisphere, as summarized by Christensen (1990) and

435	Mutterlose (1990). Doyle and Bennet (1995) complemented those contributions by
436	reviewing Jurassic belemnite occurrences of the Southern Hemisphere, and then Doyle
437	et al. (1996, 1997) focused on the Antarctic and the Argentinean Jurassic records. The
438	former includes the Kimmeridgian–Tithonian Belemnopsis fauna described from the
439	Antarctic Peninsula and Alexander Island (Crame and Howlett, 1988; Howlett, 1989;
440	Mutterlose, 1986; Riley et al., 1997). Upwards, the Tithonian/Berriasian transition is
441	encompassed by the Hibolithes fauna (or Biozone according to Howlett, 1989), which
442	includes several species of Hibolithes, with H. argentinus, and Belemnopsis species of
443	Indo-Pacific affinities as rare components. Tithonian Antarctic belemnite associations
444	also include Duvalia/Produvalia (Mutterlose, 1986; Crame and Howlett, 1988), a
445	strongly compressed genus with a dorsal median groove that is supposed to have
446	immigrated into the Indo-Pacific region from the Tethys during the Tithonian (Stevens,
447	1965) or as early as the Callovian (Challinor and Hikuroa, 2007).
448	Concerning Argentinean Jurassic successions, Doyle et al. (1996) recognized two
449	successive belemnite faunas for the Upper Jurassic-Lower Cretaceous namely early
450	Belemnopsis (Oxfordian) and Hibolithes (Tithonian-Berriasian), which was named after
451	H. argentinus. In that contribution, the Lower Cretaceous occurrences of B.
452	patagoniensis were treated separately. Meanwhile, B. launceloti is an upper Tithonian-
453	Hauterivian species that defines an assemblage biozone in Antarctica (Howlett, 1989)
454	and has been recorded from the lower Valanginian of Madagascar (Besairie, 1936;
455	Combémorel, 1988), the upper Tithonian of the Austral Basin in the Lago Argentino
456	area (cf. Leanza, A., 1967), and with reservations from the Valanginian-Hauterivian of
457	southern Chile (Stinnesbeck et al., 2014). So, Belemnopsis records described in this
458	contribution indicate that this genus should also be considered in the Neuquén Basin as

a component of the well-established Upper Jurassic–Lower Cretaceous *Hibolithes* fauna
of Gondwana (Doyle et al., 1996; Challinor, 1991).

461 Whenever possible, the correlation of the Neuquén Basin belemnite records in

462 each locality with the current ammonoid Andean zonation (Aguirre-Urreta et al., 2019;

Leanza et al., 2020; Lescano et al., 2022) is summarized in Figure 7. *Hibolithes* sp. from

the Arroyo La Manga area was found by Gerth (1925) in beds assigned to the

465 Argentiniceras noduliferum Biozone, just above an interval bearing Lytohoplites

466 *burckhardti* (Mayer-Eymar) and *Spiticeras acutum* Gerth among other ammonoids of

467 the Substeueroceras koeneni Biozone. Hibolithes sp. reported from Pampa Tril were

468 retrieved from the Virgatosphinctes and esensis/Pseudolissoceras zitteli,

469 Windhauseniceras internispinosum, and Corongoceras alternans Biozones, according

470 to Alberti et al. (2020). *Belemnopsis* cf. *B. patagoniensis* from Cerro Domuyo were

471 found in two positions within the *W. internispinosum* Biozone, near its base (bearing *W.*

472 *internispinosum* and *Corongoceras lotenoense* Spath) and loosed near its top. From the

473 upper portion of the *W. internispinosum* Biozone as well, in Las Loicas, were recorded

474 three successive beds with fragmentary *Hibolithes argentinus*? rostra associated with

475 Catutosphinctes rafaeli Leanza, H. and Zeiss. In Las Alcantarillas, Belemnopsis cf. B.

476 patagoniensis was retrieved from a bed with Himalayites concurrens Leanza, A. and

477 *Micracanthoceras*? sp. at the base of the *Corongoceras alternans* Biozone. From the

478 same locality was recorded a poorly preserved *Hibolithes* sp. from the *A. noduliferum*

479 Biozone, just below a bed with Andiceras fallax (Steuer) and Substeueroceras

480 disputabile Leanza, A. Finally, at Cañada de Leiva, Belemnopsis cf. B. launceloti was

481 recorded from the top of the *C. alternans* Biozone, from an interval sandwiched

482 between "Berriasella" bardensis Krantz (= Blanfordiceras bardense in Parent et al.,

483 2011), "Thurmanniceras discoidalis" (Gerth) (= Parodontoceras calistoides in Parent et

- 484 al. 2011) and *Substeueroceras striolatissimum* (Steuer) occurrences, being the later an
- index species of the *S. koeneni* Biozone across the basin (*e.g.*, Groeber et al., 1952;

486 Vennari and Aguirre-Urreta, 2019).

487 FIGURE 7 AROUND HERE

488 **5.3.** Paleoecological, paleogeographical and paleoenvironmental considerations.

In stark contrast with the fossil record of the Upper Jurassic and, particularly, the Lower
Cretaceous successions of the Austral Basin, belemnite occurrences in time-equivalent
units of the Neuquén Basin are quite infrequent or even surprisingly absent from the
Valanginian onwards, both in shallow and deep facies (Aguirre-Urreta et al., 2008).
Here we discuss paleogeographical, paleoenvironmental, and paleoecological factors
concerning belemnite occurrences in the Neuquén Basin.

Episodes of transgressive or high sea level could have facilitated the access of 495 496 active swimming belemnites (or aid in the dispersing of their early ontogenetic stages) to the Neuquén Basin. Belemnite records from Cerro Domuyo, Las Alcantarillas, and 497 Las Loicas were found in middle outer ramp to basinal deposits of a transgressive 498 system tract of the second-order Second Composite Depositional sequence, involving 499 500 the lower portion of the W. internispinosum Biozone to the lower portion of the S. 501 koeneni Biozone (Kietzmann et al., 2014, 2021). Meanwhile, belemnites from Cañada 502 de Leiva come from a storm-dominated middle ramp setting, corresponding to a 503 highstand system tract (Kietzmann et al., 2014, 2018). However, other factors than a 504 high local sea level alone would have influenced belemnite distribution. Although some authors have modeled the existence of counter-oceanic currents at 505 506 the latitude of the Neuquén Basin (Parrish, 1992), up to the authors' best knowledge,

- there were no physical geographic barriers between the Austral and the Neuquén Basin
- that prevented a free interchange of nektonic fauna as both were retro-arc basins open to

509	the Paleo-Pacific. Indeed, both basins share several ammonoid genera (Riccardi, 1991),
510	although comparatively poorly preserved and less abundant in the case of the former
511	(Riccardi, 2008). Nevertheless, two alternative paleogeographic models for the western-
512	margin configuration of the Neuquén Basin were proposed, either enabling a direct
513	connection with the Paleopacific Ocean through a discontinuous arc of volcanic islands
514	(e.g., Howell et al., 2005) or a more restricted seaway in the north-western sector: the
515	Curepto Strait (Vicente et al., 2005). Nevertheless, the high diversity and Tethyan
516	affinities of several Neuquén Basin ammonoids and herpetofauna militate against the
517	possibility of a confined basin (Gasparini and Fernández, 2005; Riccardi, 2015).
518	Besides, Alberti et al. (2020) recently demonstrated, over Sr/Ca ratios and their
519	comparison with the global curve, the existence of water exchange with the open ocean
520	in several localities of the Neuquén Province.
521	Regarding average seawater temperature and salinity, Alberti et al. (2020) found
522	some strong influence of rainfall and/or a continental freshwater influx in their
523	northernmost sampled sites, and interpreted a water temperature of 20–25 $^{\circ}\mathrm{C}$ from $\delta^{18}\mathrm{O}$
524	data from oyster and brachiopod shells. That temperature range agrees well with
525	previous estimations by Gómez Dacal (2018) and Gómez Dacal et al. (2019) of a
526	medium water temperature of 23 °C from oysters of the Neuquén Basin, and 24 °C from
527	belemnites (Belemnopsis sp.) of the Austral Basin. Temperatures obtained in both cases
528	are in agreement with the supposed range of 10–30 $^{\circ}$ C that belemnites inhabited by
529	comparison with modern cephalopod preferences (Hoffmann and Stevens, 2020),
530	though we do not know to which extent minor temperature changes affected belemnite
531	distribution since it is considered the main parameter controlling their migration routes
532	at species and genus levels (e.g., Mutterlose, 1988; Mutterlose et al., 2022; Stevens,
533	1973). Other paleoecologic requirements listed by Hoffmann and Stevens (2020), such

as well-oxygenated waters, with a normal salinity of 27–37 psu and a depth range of no 534 535 more than 200 m would characterize the Vaca Muerta Formation Upper Jurassic 536 carbonate ramp (e.g., Kietzmann et al., 2014). Even if, locally, some of the parameters would deviate from the optimum (*e.g.*, by the influx of freshwater), belemnites could 537 have just actively swum away from such conflicting areas. 538 In most recent revisions of the group, belemnites are considered medium-sized 539 540 predators of Mesozoic food webs, most likely feeding upon small vertebrates, mollusks, 541 and crustaceans (Hoffman and Stevens, 2020 and references therein). All these food 542 sources were present at the Neuquén Basin, and possibly some v-shaped scars over 543 ammonoid shells were caused by non-lethal belemnite attacks (Vennari, 2011). In time, belemnites were occasionally preved upon by marine reptiles such as ichthyosaurs and 544 metriorhynchids (Fernández et al., 2019), which might have gotten into the basin mostly 545 546 for reproductive purposes (Gasparini and Fernández, 2005). However, most probably, belemnite hatchlings were consumed by pachycormids, a stem-teleost clade of 547 suspensivorous-feeding fishes that were quite successful from the Early Jurassic to the 548 Late Cretaceous (Friedman et al., 2010). Pachycormids, which are well-known from the 549 550 Neuquén Basin (Gouiric-Cavalli, 2017; Gouiric-Cavalli and Arratia, 2022), to date have 551 not been recorded in the Austral Basin, though they have cited from Chile (Arratia, 552 2015). Although pachycormid gill rakers spacing was suitable to filter out both 553 hatchlings and juvenile ammonites (Tajika et al., 2018), the different reproductive 554 strategies of both cephalopod groups may have turned the odds in favor of ammonite survival. On the one hand, ammonites, either semelparous or iteroparous, are assumed 555 556 to have been extreme r-strategists, with high fecundity rates and the possibility, for 557 medium-sized macroconchs, to lay more than 10,000 eggs (De Baets et al., 2015; Mironenko and Rogov, 2015; Tajika et al., 2018; Greif et al., 2022). Even more, 558

559 ovoviviparity has been proven for some ammonites (Mironenko and Rogov, 2015), thus 560 incrementing the chances of post-hatching survival. Nevertheless, direct evidence of this predation relation should be proven through bromalite analyses (*i.e.*, oral or anal 561 depositions or intestinal content) as conducted in other basins (Zatón and Salamon, 562 563 2008; Bigurrarena et al., 2019; Lukeneder et al., 2020). Belemnites, on the other hand, are assumed to have been r-strategists (e.g., Doguzhaeva et al. 2013) and to have 564 565 depicted high fecundity rates as well, but of several magnitude order lower than that of 566 ammonites due to a smaller size difference between adults and embryos (Tajika et al., 2018). In consequence, ammonite surviving into adulthood was more likely than for 567 568 belemnites. 569 To sum up, marine connections, seawater physical parameters, or food sources 570 availability seem not to have constrained, on their own, the presence of belemnites in 571 the Neuquén Basin in favor of ammonites. However, they were likely affected by the predation pressure exerted by filter-feeding organisms on hatchlings, combined with 572 unsuitable paleoecological conditions over shallow marine settings relatively close to 573

the coast where belemnites were assumed to inhabit (Naef, 1922; Doguzhaeva et al.,

575 2013, Mutterlose, 2022).

576 6. Concluding remarks

We presented in this contribution new records of Upper Jurassic belemnites from the Vaca Muerta Formation, Neuquén Basin, west-central Argentina. The studied rostra were assigned to *Belemnopsis* cf. *B. patagoniensis*, *Belemnopsis* cf. *B. launceloti*, and *Hibolithes argentinus*?. These are the first thoroughly described belemnites from the Neuquén Basin. By their association with ammonoid faunas, the new belemnite records can be referred to the Tithonian *Windhauseniceras internispinosum* to *Corongoceras alternans* Biozones. The biostratigraphic framework suggests that *Belemnopsis* should

be contemplated as a component of the widely-known Hibolithes fauna recorded across 584 585 the Late Jurassic-Early Cretaceous of Gondwana. Affinities of the described fauna seem 586 close to Madasgascan-Eastern African belemnite associations of the Ethiopian Subprovince, thus reinforcing the hypothesis of a Trans-Gondwana seaway as an open 587 588 marine connection at least since the Tithonian. The baffling scarcity of belemnites from the Late Jurassic in the Neuquén Basin and 589 590 their absence from the Early Cretaceous upwards is in utter contrast with their abundant 591 record in the Austral Basin. Though still unresolved, it is suggested that a combination 592 of factors, such as local variations in seawater salinity/temperature in shallow 593 environments and, particularly, the predation pressure of filter-feeding fishes on 594 belemnite hatchlings, may have affected the presence of the group in the basin. Also, the possible existence of counter-currents at the latitude of the Neuquén Basin may have 595 596 limited the extension to lower latitudes of the Belemnopsis/Hibolithes Gondwanan

597 faunas.

598 Acknowledgments

The authors are grateful to all field assistants, to Leonardo Pazo (Fundación Azara) for 599 600 preparing the specimens, and to the editors and reviewers that greatly improved this 601 contribution. This work was partially financed by the ANPCyT PICT 1016-2016 and PICT 2020-02067 (V.V.V); Sepkoski Grant 2019 (V.V.V.); PIP CONICET 602 11220170101117CO (B.A.U.) and 11220200102844CO (V.V.V.); CNRS Grants 603 SYSTER-TELLUS "ACJC" in 2019 and "GC-JC" in 2021; and MITI AAP Temps 604 "AstroCarb" (M.M. and P.P.). This is contribution R-445 of the Instituto de Estudios 605 Andinos "Don Pablo Groeber". 606

607 **References**

608	Aguirre-Urreta, B., Naipauer, M., Lescano, M., López-Martínez, R., Pujana, I., Vennari,
609	V., Concheyro, A., De Lena, L.F., Ramos, V. 2019. The Tithonian chrono-
610	biostratigraphy of the Neuquén Basin and related Andean areas: a review and
611	update. Journal of South American Earth Sciences, 92, 350-367.
612	https://doi.org/10.1016/j.jsames.2019.03.019
613	Aguirre-Urreta, M.B., Casadío, S., Cichowolski, M., Lazo, D.G., Rodriguez, D.L.,
614	2008. Afinidades paleobiogeográficas de los invertebrados cretácicos de la
615	Cuenca Neuquina. Ameghiniana, 45, 593–613.
616	Aguirre-Urreta, M.B., Suárez, M., 1985. Belemnites de una secuencia turbidítica
617	volcanoclástica de la Formación Yaghán, Titoniano–Cretácico Inferior del
618	extremo sur de Chile. 4º Congreso Geológico Chileno, Antofagasta, Actas 1, 1–
619	16.
620	Alberti, M., Parent, H., Garrido, A.C., Andersen, N., Garbe-Schönberg, D., Danise, S.,
621	2020. Stable isotopes (δ 13C, δ 18O) and element ratios (Mg/Ca, Sr/Ca) of Jurassic
622	belemnites, bivalves and brachiopods from the Neuquén Basin (Argentina):
623	challenges and opportunities for palaeoenvironmental reconstructions. Journal of
624	the Geological Society, 178, JGS2020-163. https://doi.org/10.1144/jgs2020-163
625	Arratia, G. 2015. Los peces osteíctios fósiles de Chile y su importancia en los contextos
626	paleobiogeográfico y evolutivo. Publicación Ocasional del Museo de Historia
627	Natural, Chile, 63, 35–83.
628	Bayle, E., 1878. Atlas. Première partie. Fossiles principaux des terrains. –Explication de
629	la Carte géologique de la France, Paris, 4, part 1, 158 plates.
630	Besairie, H., 1930. Recherches geologiques a Madagascar. Bulletin de la Société d'
631	Histoire naturelle de Toulouse, 60, 345–642.

632	Besairie, H., 1936. Recherches geologiques a Madagascar. Premiere suite. La geologie
633	du Nord-Ouest. Memoires de L'Académie Malgache, 21, 145–148.
634	Bigurrarena Ojeda, M.A., Gouiric-Cavalli, S., Pérez, L.M., Burlaille, L.A., Moly, J.J.,
635	Reguero, M., Santillana, S. 2019. Las bromalitas de la Formación Ameghino
636	(Jurásico Tardío) de la Península Antártica. Publicación Electrónica de la
637	Asociación Paleontológica Argentina. Suplemento Resúmenes, R17.
638	Blainville, H.D., 1827. Memoire sur les belemnites, considerees zoologiquement et
639	geologiquement. F. G. Levrault, Paris, 136 pp.
640	Bonarelli, G., Nágera, J.J., 1961. Observaciones geológicas en las inmediaciones del
641	Lago San Martín. Boletín de la Dirección Nacional de Minería y Geología, B27,
642	1–39.
643	Caminos, R., Nullo, F., 1979. Descripción geológica de la Hoja 67e, Isla de los Estados.
644	Servicio Geológico Nacional, Boletín, 175, 5–52.
645	Campos, L., Fernández, M.S., Herrera, Y., Talevi, M., Concheyro, A., Gouiric-Cavalli,
646	S., O'Gorman, J.P., Santillana, S.N., Acosta-Burlaille, L., Moly, J.J., Reguero,
647	M.A., 2020. Bridging the southern gap: First definitive evidence of Late Jurassic
648	ichthyosaurs from Antarctica and their dispersions routes. Journal of South
649	American Earth Sciences, 109, 103259.
650	https://doi.org/10.1016/j.jsames.2021.103259
651	Cecca, F., 1999. Palaeobiogeography of Tethyan ammonites during the Tithonian (latest
652	Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology, 147, 1–37.
653	https://doi.org/10.1016/S0031-0182(98)00149-7

- 654 Challinor, A.B., 1991. Belemnite successions and faunal provinces in the southwest
- Pacific, and the belemnites of Gondwana. BMR Journal of Australian Geologyand Geophysics, 12, 301–325.
- 657 Challinor, A.B., 1999. Belemnite biostratigraphy of the New Zealand Late Jurassic
- 658 Mangaoran (Early Puaroan) Substage and the Puaroan Stage revisited, New
- Example 2 Control of Geology and Geophysics, 42, 369–393.

660 <u>https://doi.org/10.1080/00288306.1999.9514852</u>

- 661 Challinor, A.B., 2001. Stratigraphy of Tithonian (Ohauan-Puaroan) marine beds near
- 662 Port Waikato, New Zealand, and a redescription of *Belemnopsis aucklandica*
- (Hochstetter). New Zealand Journal of Geology and Geophysics, 44, 219–242.
- 664 <u>https://doi.org/10.1080/00288306.2001.9514936</u>
- 665 Challinor, A.B., 2003. Synonymy and stratigraphic ranges of *Belemnopsis* in the
- 666 Heterian and Ohauan Stages (Callovian-Tithonian), southwest Auckland, New
- 2667 Zealand, New Zealand Journal of Geology and Geophysics, 46, 79–94.
- 668 https://doi.org/10.1080/00288306.2003.9514997
- 669 Challinor, A.B., Hikuroa, D.C.H., 2007. New Middle and Upper Jurassic Belemnite
- 670 Assemblages from West Antarctica (Latady Group, Ellsworth Land): Taxonomy
- and Paleobiogeography. Palaeontologia Electronica, 10, 1–29. <u>http://palaeo-</u>
- 672 <u>electronica.org/paleo/2007_1/assemblage/index.html</u>
- 673 Christensen, W.K., 1990. Upper Cretaceous belemnite biostratigraphy of Europe.
- 674 Cretaceous Research, 11, 371–386. <u>https://doi.org/10.1016/S0195-</u>
- 675 6671(05)80048-5
- 676 Combémorel, R., 1988. Les bélemnites de Madagascar. Documents de la Laboratoire de
 677 Géologie de la Faculté des Sciences de Lyon, 104, 1–239.

- 678 Crame, J.A, Howlett, P.J., 1988. Late Jurassic and Early Cretaceous biostratigraphy of
 679 the Fossil Bluff Formation, Alexander Island. British Antarctic Survey Bulletin,
 680 78, 1–35.
- Dana, J.D., 1848. Geology. In U.S. Exploring Expedition 1839–1842, under Ch.

682 Wilkes. Chapters 15–16. New York Public Library, New York.

- 683 De Baets, K., Landman, N.H., Tanabe, K. 2015. Ammonoid embryonic development.
- In: Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R.H. (eds), Ammonold
 paleoblology: from anatomy to paleoecology. 113–205 Dordrecht: Springer.
- 686 Dessanti, R.N., 1973. Descripción geológica de la Hoja 29b, Bardas Blancas, provincia
- 687 de Mendoza. Servicio Nacional de Minería y Geología, Boletín, 139, 1–70.
- 688 Doguzhaeva, L.A., Weis, R., Delsate, D., Mariotti , N. 2013. Embryonic shell structure
- of Early–Middle Jurassic belemnites, and its significance for belemnite expansion
 and diversification in the Jurassic. Lethaia, 47, 49–65.
- 691 Doyle, P., 1987. Lower Jurassic–Lower Cretaceous belemnite biogeography and the
- origin of the Mesozoic Boreal Realm. Palaeogeography, Palaeoclimatology,
 Palaeoecology, 61, 237–254.
- Doyle, P., Bennet, M.R., 1995. Belemnites in biostratigraphy. Palaeontology, 38, 815–
 829.
- Doyle, P., Howlett, P., 1989. Antarctic belemnites biogeography and the breack-up of
- 697 Gondwana. In: J.A. Crame (ed.), Origins and Evolution of the Antarctic Biota,
- 698 Geological Society Special Publication, 47, pp. 167–182.
- 699 <u>https://doi.org/10.1144/GSL.SP.1989.047.01.13</u>
- Doyle, P., Kelly, S.R.A., 1988. The Jurassic and Cretaceous belemnites of Kong Karls
 land, Svalbard. Norsk Polarinstitut Skrifter, 189, 1–77.

	urn		Ð	re.	-n	rn	~ 1
U	սու	lai					U

702	Dovle P K	elly SRA	Pirrie D	Riccardi A C	1997 Jurassic	belemnite	distribution
70Z	Doyle, F., K	спу, э.к.а.,	r mile, D .	, Riccalul, A.C.,	1997. Julassic	Delemme	uistitution

- 703 patterns: implications of new data from Antarctica and Argentina. Alcheringa: An
- Australasian Journal of Paleontology, 21, 219–228.
- 705 <u>http://dx.doi.org/10.1080/03115519708619175</u>
- Doyle, P., Kelly, S.R.A., Pirrie, D., Riccardi, A.C., Olivero, E.B., 1996. Jurassic
- belemnite biostratigraphy of the Southern Hemisphere: a comparative study from
- 708Antarctica and Argentina. Revista de la Asociación Geológica Argentina, 51,
- 709 331–338.
- 710 Doyle, P., Pirrie, D., 1999. Belemnite distribution patterns. In F. Olóriz, F.J.,
- 711 Rodríguez-Tovar (eds), Advancing Research on Living and Fossil Cephalopods
- pp. 419–436. Kluwer Academic-Plenum Publishers, New York.
- Favre, F., 1908. Die Ammoniten der unteres Kreide Patagonien. Neues Jahrbuch für
 Mineralogie, Geologie und Paläontologie, 25, 601–647.
- Fernández, M., Herrera, Y., Vennari, V., Campos, L., de la Fuente, M., Talevi, M.,
- Aguirre-Urreta, M.B. 2019. Marine reptiles from the Jurassic/Cretaceous
- 717 transition at the High Andes, Mendoza, Argentina. Journal of South American
- Earth Sciences, 92, 658–673. <u>https://doi.org/10.1016/j.jsames.2019.03.013</u>
- Feruglio, E., 1936. Paleontographica Patagónica. Memoria del Instituto Geológico de
 Padova, 11, 1–384.
- Feruglio, E., 1949. Geología de la Patagonia. Vol. 1, pp. 1–323. Dirección General de
- 722 Y.P.F., Buenos Aires.
- Friedman, M., Shimada, K., Martin, L.D., Everhart, M.J., Liston, J., Maltese, A.,
- Triebold, M. 2010. 100-million year dynasty of giant planktivorous bony fishes in
- the Mesozoic seas. Science 327: 990-993.

αuri	Dr	n		\sim	
oun			IU	U.	

726	Fuchs, D., Iba, Y., Ifrim, C., Nishimura, T., Kennedy, W.J., Keupp, H., Stinnesbeck,
727	W., Tanabe, K., 2013. Longibelus gen. nov., a new Cretaceous coleoid genus
728	linking Belemnoidea and early Decabrachia. Palaeontology, 56, 1081–1106.
729	https://doi.org/10.1111/pala.12036
730	Gasparini, Z., Fernández, M.S., 2005. Jurassic marine reptiles of the Neuquén Basin:
731	records, faunas and their palaeobiogeographic significance. In: G.D. Veiga, L.A.
732	Spalletti, J.A. Howell, E. Schwarz (eds.), The Neuquén Basin: A case study in
733	sequence stratigraphy and basin dynamics, Geological Society, London, Special
734	Publication 252, 279–294. https://doi.org/10.1144/GSL.SP.2005.252.01.14
735	Gerth, H., 1925. Contribuciones a la estratigrafía y la paleontología de los Andes
736	Argentinos II. La Fauna Neocomiana de la Cordillera Argentina en la parte
737	meridional de la provincia de Mendoza: Academia Nacional de Ciencias,
738	Córdoba, Actas, 9, 57–132.
739	Gómez Dacal, A.R., 2018. Petrología, geoquímica y diagénesis de sedimentitas y fósiles
740	carbonáticos del Jurásico Superior-Cretácico Inferior de las cuencas Neuquina y
741	Austral, Argentina. PhD Thesis (unpublished). Universidad de La Plata, La Plata,
742	Argentina.
743	Gómez Dacal, A.R., Richiano, S.M., Gómez Peral, L.E., Spalletti, L.A., Sial, A.N.,
744	Poiré, D.G., 2019. Evidence of Warm Seas in High Latitudes of Southern South
745	America During the Early Cretaceous. Cretaceous Research, 95, 8–20.
746	https://doi.org/10.1016/j.cretres.2018.10.021.
747	Gouiric-Cavalli, S., 2017. Large and mainly unnoticed: the first lower Tithonian record
748	of a suspension-feeding pachycormid from Southern Gondwana. Ameghiniana,
749	54, 283-289. https://doi.org/10.5710/AMGH.16.11.2016.3029

		D		nr		
	lat		11	рι	U	

750	Gouiric-Cavalli, S., Arratia G., 2022. A new Pachycormiformes (Actinopterygii) from
751	the Upper Jurassic of Gondwana sheds light on the evolutionary history of the
752	group, Journal of Systematic Palaeontology, DOI:
753	10.1080/14772019.2022.2049382
754	Grant-Mackie, J.A., Aita, Y., Balme, B.E., Campbell, H.J., Challinor, A.B., MacFarlan,
755	D.A.B., Molnar, R.E., Stevens, G.R., Thulborn, R.A., 2000. Jurassic
756	palaeobiogeography of Australasia. Memoir of the Association of Australasian
757	Palaeontologists, 23, 311–353.
758	Greif, M., Nebelsick, J.H., and Klug, C. 2022. Extreme abundance of ammonoids in
759	mass accumulations from the Late Devonian of the Moroccan Anti-Atlas. Acta
760	Palaeontologica Polonica 67: 667–684. https://doi.org/10.4202/app.00935.2021
761	Groeber, P., Stipanicic, P.N., Mingramm, A., 1952. Jurásico. In: Geografía de la
762	República Argentina, tomo 2. Sociedad Argentina de Estudios Geográficos,
763	Buenos Aires, pp. 143–347.
764	Gulisano, C.A., Gutiérrez-Pleimling, A.R., 1994. The Jurassic of the Neuquén Basin.
765	Field Guide, Mendoza Province. Asociación Geológica Argentina, Serie E, 3,
766	Secretaría de Minería de la Nación, Publicación, 159, 1-103.
767	Harrington, H.H., 1943. Observaciones geológicas en la Isla de los Estados. Anales del
768	Museo Argentino de Ciencias Naturales, 49, Geología 29, 29–52.
769	Hoffmann, R., Richter, D.K., Neuser, R.D., Jöns, N., Linzmeier, B.J., Lemanis, R.E.,
770	Fusseis, F., Xiao, X., Immenhauser, A., 2016. Evidence for a composite organic-
771	inorganic fabric of belemnite rostra: implications for palaeoceanography and
772	palaeoecology. Sedimentary Geology, 341, 203-215.
773	https://doi.org/10.1016/j.sedgeo.2016.06.001

- Hoffmann, R., Stevens, K., 2020. The palaeobiology of belemnites –foundation for the
- interpretation of rostrum geochemistry. Biological Reviews, 95, 94–123.

776 <u>https://doi.org/10.1111/brv.12557</u>

- Howell, J.A., Schwarz, E., Spalletti, L.A., Veiga, G.D., 2005. The Neuquén Basin: an
- 778 overview. In: G.D. Veiga, L.A. Spalletti, J.A. Howell, E. Schwarz (eds.), The
- 779 Neuquén Basin: A case study in sequence stratigraphy and basin dynamics,
- 780 Geological Society, London, Special Publication, 252, 1–14.
- 781 <u>https://doi.org/10.1144/GSL.SP.2005.252.01.01</u>
- 782 Howlett, P.J., 1989, Late Jurassic–Early Cretaceous cephalopods of eastern Alexander
- 783 Island, Antarctica. Special Papers in Palaentology, 41, 5–72.
- Iba, Y., Sano, S.I., Mutterlose, J., 2014. The early evolutionary history of belemnites:
- new data from Japan. PLosOne, 9, e95632.
- 786 <u>https://doi.org/10.1371/journal.pone.0095632</u>
- 787 Ippolitov, A.P., Desai, B., Arkadiev, V.V., 2015. First find of Parabelemnopsis, the
- alien belemnite from the Southern Hemisphere, in the Upper Berriasian of Central
- 789 Crimea. The International Scientific Conference on the Jurassic/Cretaceous
- Boundary, Proceedings volume, Samara, 52–59.
- 791 Jeletzky, J.A., 1965. Taxonomy and phylogeny of fossil Coleoidea (= Dibranchiata).

Geological Survey of Canada, paper 65-2, 72–76.

- 793 Jeletzky, J.A., 1946. Zur Kenntnis der oberkretazischen Belemniten. Geologiska
- Föreningens i Stockholm Förhandlingar, 68, 87–105.
- 795 Jeletzky, J.A., 1966. Comparative morphology, phylogeny, and classification of fossil
- *coleoidea*. The University of Kansas Paleontological Contributions, Mollusca
- 797 Article 7, pp. 1–162. University of Kansas Paleontological Institute, Lawrence.

- 798 Jeletzky, J.A., 1983. Macroinvertebrate paleontology, biochronology, and
- 799 paleoenvironments of Lower Cretaceous and Upper Jurassic rocks, Deep Sea
- Drilling Project Hole 511, Eastern Falkland Plateau. DSDP report 35, 951–975.
- 801 <u>https://doi.org/10.2973/dsdp.proc.71.135.1983</u>
- 802 Kietzmann, D.A., Vennari, V.V., 2013. Sedimentología y estratigrafía de la Formación
- 803 Vaca Muerta (Tithoniano-Berriasiano) en el área del cerro Domuyo, norte de
- Neuquén, Argentina. Andean Geology, 40, 41–65.

805 <u>http://dx.doi.org/10.5027/andgeoV40n1-a02</u>

- Kietzmann, D.A., Iglesia Llanos, M.P., Palacio, J.P., Sturlesi, M.A., 2021. Facies
- analysis and stratigraphy across the Jurassic-Cretaceous boundary in a new
- 808 basinal Tithonian–Berriasian section of the Vaca Muerta Formation, Las
- 809 Tapaderas, Southern Mendoza Andes, Argentina. Journal of South American
- Earth Sciences, 109, 103267. https://doi.org/10.1016/j.jsames.2021.103267
- 811 Kietzmann, D.A., Iglesia-Llanos, M.P., Martínez, M.K., 2018. Astronomical calibration
- of the Tithonian–Berriasian in the Neuquén Basin, Argentina: A contribution from
- the Southern Hemisphere to the Geologic Time Scale. In: M. Montenari (ed.),
- 814 Stratigraphy & Timescales 3, Elsevier, 328–355.
- 815 <u>https://doi.org/10.1016/bs.sats.2018.07.003</u>
- 816 Kietzmann, D.A., Palma, R.M., 2011. Las tempestitas peloidales de la Formación Vaca
- 817 Muerta (Tithoniano-Valanginiano) en el sector surmendocino de la Cuenca
- 818 Neuquina, Argentina. Latin American Journal of Sedimentology and Basin
- Analysis, 18, 121–149.
- 820 Kietzmann, D.A., Palma, R.M., Riccardi, A.C., Martín-Chivelet, J., López-Gómez, J.,
- 821 2014. Sedimentology and sequence stratigraphy of a Tithonian–Valanginian
- 822 carbonate ramp (Vaca Muerta Formation): a misunderstood exceptional source

823	rock in the southern Mendoza area of the Neuquén basin, Argentina. Sedimentary
824	Geology, 302, 64-86. http://dx.doi.org/10.1016/j.sedgeo.2014.01.002
825	Krantz, F., 1928. La Fauna del Tithono superior y medio en la parte meridional de la
826	provincia de Mendoza. Academia Nacional de Ciencias, Córdoba, Actas, 10, 9–
827	57.
828	Leanza, A.F., 1967. Anotaciones sobre los fósiles Jurásico-Cretácicos de Patagonia
829	Austral (Colección Feruglio) conservados en la Universidad de Bologna. Acta
830	Geológica Lilloana, 9, 121–186.
831	Leanza, H.A., Vennari, V.V., Aguirre-Urreta, B., Concheyro, A., Lescano, M., Ivanova,
832	D., Kietzmann, D.A., López-Martínez, R., Martz, P.A., Paolillo, M.A., Guler, V.,
833	Pujana, I., Paz, M., 2020. Relevant marine paleobiological markers of the Vaca
834	Muerta Formation. AAPG Memoir, 121, 61–98. DOI:
835	10.1306/13682224M1203830
836	Legarreta, L., Uliana, M.A., 1991. Jurassic-Cretaceous marine oscillations and
837	geometry of back-arc basin fill, central Argentine Andes. International
838	Association of Sedimentologists, Special Publication, 12, 429–450.
839	https://doi.org/10.1002/9781444303896.ch23.
840	Lena, L., López-Martínez, R., Lescano, M., Aguirre-Urreta, B., Concheyro, A., Vennari,
841	V., Naipauer, M., Samankassou, E., Pimentel, M., Ramos, V.A., Schaltegger, U.,
842	2019. High-precision U-Pb ages in the early Tithonian to early Berriasian and
843	implications for the numerical age of the Jurassic-Cretaceous boundary. Solid
844	Earth, 10, 1-14. https://doi.org/10.5194/se-10-1-2019
845	Lescano, M., Vennari, V., López-Martínez, R., Concheyro, A., Aguirre-Urreta, B.,
846	Pellenard, P., Martínez, M. 2022. New Tithonian biostratigraphic data from the

847	Neuquén Basin, Argentine Andes: a contribution from the Southern Hemisphere.
848	11° International Congress on the Jurassic System. Budapest, p. 68.
849	Lukeneder, A., Surmik, D., Gorzelak, P., Niedźwiedzki, P., Brachaniec, T., Salamon,
850	M. 2020. Bromalites from the Upper Triassic Polzberg section (Austria); insights
851	into trophic interactions and food chains of the Polzberg palaeobiota. Nature
852	Scientific Reports 10, 20545. https://doi.org/10.1038/s41598-020-77017-x
853	Medina, F.A., Riccardi, A.C., 2005. Desmoceratidae, Silesitidae and Kossmaticeratidae
854	(Ammonitida) from the Upper Aptian–Albian of Patagonia (Argentina). Revue de
855	Paléobiologie, Genève, 24, 251–286.
856	Mironenko, A.A., Rogov, M.A. 2015. First direct evidence of ammonoid ovoviviparity.
857	Lethaia, 49: 245–260. https://doi.org/10.1111/let.12143.
858	Mitchell, F.S., 2015. A reassessment of the validity and affinities of <i>Belemnites sulcatus</i>
859	Miller, 1826, Belemnopsis Edwards in Gray, 1849, and Belemnopsis Bayle, 1878.
860	Carnet de Géologie, 15, 31–39. https://doi.org/10.4267/2042/56399
861	Monks, N., Hardwick, J.D., Gale, A.S., 1996. The function of the belemnite guard.
862	Paläontologische Zeitschrift, 70, 425–431.
863	Montfort, D. De, 1808. Conchyliologie systematique et classification methodique des
864	Coquilles. Coquilles univalves, cloisonnees. Tome I. Chez F. Schoell, Paris, 410
865	pp.
866	Mutterlose, J., 1986. Upper Jurassic Belemnites from the Orville Coast, Western
867	Antarctica, and their palaeobiogeographical significance. British Antarctic Survey
868	Bulletin, 70, 1–22.

- 869 Mutterlose, J., 1988. Migration and evolution patterns in Upper Jurassic and Lower
- 870 Cretaceous belemnites. In Wiedmann, J., Kullmann, J. (eds) Cephalopods: Present
- and past. Schweizerbart, Stuttgart, pp. 525–537.
- 872 Mutterlose, J., 1990. A belemnite scale for the Lower Cretaceous. Cretaceous Research,
- 873 11, 1–15. <u>https://doi.org/10.1016/S0195-6671(05)80039-4</u>
- 874 Mutterlose, J., 1992. Early Cretaceous belemnites from the East Indian Ocean and their
- paleobiogeographic implications. Proceedings of the Ocean Drilling Program,
- 876 Scientific Results, 123, 443–450.
- 877 https://doi.org/<u>10.2973/odp.proc.sr.123.123.1992</u>
- 878 Mutterlose, J., Picollier, M.-C., Dzyuba, O. 2022. The first belemnite of boreal ancestry
- from the Early Cretaceous (Valanginian) of the western Tethys: implications for
 belemnite ecology. Papers in Paleontology, e1455.
- 881 Naef, A., 1922. Die fossilen Tintenfische. Gustav Fischer, Jena, 322 pp.
- 882 Naipauer, M., Comerio, M., Lescano, M., Vennari, V., Aguirre-Urreta, M.B., Pimentel,
- 883 M., Ramos, V.A., 2020. The Huncal Member of the Vaca Muerta Formation,
- 884 Neuquén Basin of Argentina: insight into biostratigraphy, structure, U-Pb detrital
- zircon, ages and provenance. Journal of South American Earth Sciences, 100,
- 886 102567. <u>https://doi.org/10.1016/j.jsames.2020.102567</u>
- 887 Olivero, E.B., 1987. Cefalópodos y bivalvos titonianos y hauterivianos de la Formación
- Lago La Plata, Chubut. Ameghiniana 24, 181–202.
- 889 Parent, H., Garrido, A.C., Scherzinger, A., Schweigert, G., Fözy, I., 2015. The
- 890 Tithonian–Lower Valanginian stratigraphy and ammonite fauna of the Vaca
- 891 Muerta Formation in Pampa Tril, Neuquén Basin, Argentina. Boletín del Instituto
- de Fisiografía y Geología, 86, 1–96.

- 893 Parent, H., Scherzinger, A., Schweigert, G., 2011. The Tithonian–Berriasian ammonite
- fauna and stratigraphy of Arroyo Cieneguita, Neuquén- Mendoza Basin,
- Argentina. Boletín del Instituto de Fisiografía y Geología, 79–81, 21–94.
- 896 Parent, H., Schweigert, G., Scherzinger, A., Garrido, A.C., 2017. Additional Tithonian
- and Berriasian ammonites of the Vaca Muerta Formation in Pampa Tril, Neuquén
- Basin, Argentina. Volumina Jurassica, 15, 139–154.
- 899 <u>https://doi.org/10.5604/01.3001.0010.6576</u>
- 900 Parrish, J.T., 1992. Jurassic climate and oceanography of the Pacific region. In: G.E.G.
- 901 Westermann (ed.), The Jurassic of the Circum-Pacific, Cambridge University
- 902 Press, Cambridge, pp. 365–379.
- 903 Riccardi, A.C., 1971. Estratigrafía en el Oriente de la Bahía de La Lancha, Lago San
 904 Martín, Santa Cruz, Argentina. Revista del Museo de la Plata, Sección Geología,
 905 7, 245–318.
- 906 Riccardi, A.C., 1976. Paleontología y edad de la Formación Springhill. 1º Congreso

907 Geológico Chileno, Santiago de Chile, Actas 1, 41–56.

- 908 Riccardi, A.C., 1977. Berriasian invertebrate faunas from the Springhill Formation in
 909 southern Patagonia. Neues Jarhbuch für Geologie und Paläontologie, 155, 216–
 910 152.
- 911 Riccardi, A.C., 1988. The Cretaceous System of southern South America. Geological
 912 Society of America Memoir, 168, 1–161.
- 913 Riccardi, A.C., 1991. Jurassic and Cretaceous marine connections between the
- 914 Southeast Pacific and Tethys. Palaeogeography, Palaeoclimatology,
- 915 Palaeoecology, 87, 155–189. https://doi.org/<u>10.1016/0031-0182(91)90134-D</u>

- 916 Riccardi, A.C., 2008.El Jurásico de la Argentina y sus amonites. Revista de la
- 917 Asociación Geológica Argentina, 63, 625–643.
- 918 Riccardi, A.C., 2015. Remarks on the Tithonian–Berriasian ammonite biostratigraphy

of west-central Argentina. Volumina Jurassica, 13, 23–52.

- 920 Riccardi, A.C., Damborenea, S.E., Manceñido, M.O., Leanza, H.A., 2011.
- 921 Megainvertebrados jurásicos y su importancia geobiológica. In: H.A. Leanza, C.
- 922 Arregui, O. Carbone, J.C. Danieli, J.M. Vallés (eds.), Geología y Recursos
- 923 Naturales de la Provincia del Neuquén, Asociación Geológica Argentina, Buenos
- 924 Aires, p. 441–464.
- Riegraf, W., 1980. Revision der Belemniten der Schwäbischen Jura. Part 7. Palaeontographica Abteilung A, 169, 128–206.
- 927 Riegraf, W., 1999. Taxonomic status of the belemnite genus *Belemnopsis* Bayle 1878.
 928 Paläontologische Zeitschrift, 73, 59–76.
- 929 Riley, T.R, Crame, J.A., Thomson, M.R.A., Cantrill, D.J., 1997. Late Jurassic
- 930 (Kimmeridgian-Tithonian) macrofossil assemblage from Jason Peninsula, Graham
- 931 Land: evidence for a significant northward extension of the Latady Formation.
- 932 Antarctic Science, 9, 434–442.
- 933 Smith, A.G., Smith, D.G., and Funnell, B.M., 1994. Atlas of Mesozoic and Cenozoic

934 Coastlines. Cambridge, Cambridge University Press, 99 p.

- 935 Stevens, G.R., 1965. The Jurassic and Cretaceous belemnites of New Zealand, and a
- review of the Jurassic and Cretaceous belemnites of the Indo-Pacific region.
- 937 Geological Survey of New Zealand, Palaeontological Bulletin, 36, 1–233.

- 938 Stevens, G.R., 1973. Jurassic belemnites. In: A. Hallam (ed.), Atlas of
- Palaebiogeography, Elsevier, New York, pp. 259–274.
- 940 Stevens, K., in press. Belemnite phylogeny and decline during the mid-Cretaceous.

941 BioRxiv. <u>https://doi.org/10.1101/2021.10.11.463885</u>

- 942 Stinnesbeck, W., Frey, E., Rivas, L., Pardo Pérez, J., Leppe Cartes, M., Salazar Soto,
- 943 C., Zambrano Lobos, P., 2014. A Lower Cretaceous ichthyosaur graveyard in
- deep marine slope channel deposits at Torres del Paine National Park, southern

945 Chile. Geology Society of America Bulletin, 126, 1317–1339.

- 946 https://doi.org/10.1130/B30964.1
- 947 Stolley, E., 1911. Beiträge zur Kenntnis der Cephalopoden der Norddeutschen Unteren
- 948 Kreide 1: Die Belemnitiden der Norddeutschen Unteren Kreide. Geologische und
 949 paläontologische Abhandlungen: Neue Folge, 10: 201–272.
- 950 Stolley, E., 1928. Helicerus Dana als Erhaltungszundstand von Belemnopsis. Neues
- Järbuch für Mineralogie, Geologie und Paläontologie, Beilage Band B, 60, 315–
 324.
- Tajika, A., Nützel, A., Klug, C., 2018. The old and the new plankton: ecological
- 954 replacement of associations of mollusc plankton and giant filter feeders after the
 955 Cretaceous? PeerJ 6: e4219. https://doi.org/10.7717/peerj.4219
- Tate, R., 1867. On some secondary fossils from South Africa. Quarterly Journal of the
 Geological Society of London, 23, 139–175.
- 958 Vennari, V., 2011. Estudio preliminar del registro de heridas letales y subletales en
 959 amonoideos del Jurásico Tardío (Tithoniano) de Mendoza. 18º Congreso
- 960 Geológico Argentino, Neuquén, Actas, 1494-1495.

961	Vennari, V	V.V., Aguirre-	Urreta, M.B.,	2019.	Intraspecific	variability,	biostratigraph	y and
-----	------------	----------------	---------------	-------	---------------	--------------	----------------	-------

- 962 paleobiological significance of the Southern Gondwana ammonoid genus
- 963 *Lytohoplites* Spath. Journal of Paleontology, 93, 702–726.
- 964 <u>https://doi.org/10.1017/jpa.2019.1</u>.
- 965 Vennari, V.V., Lescano, M.A., Naipauer, M., Aguirre-Urreta, M.B., Concheyro, A.,
- 966 Shaltegger, U., Armstrong, R., Pimentel, M., Ramos, V.A., 2014. New constraints
- 967 in the Jurassic/Cretaceous boundary in the High Andes using high precision U-Pb
- 968 data. Gondwana Research, 26, 374–385. <u>https://doi.org/10.1016/j.gr.2013.07.005</u>
- 969 Vicente, J.C., 2005. Dynamic paleogeography of the Jurassic Andean Basin: patterns of
- 970 transgression and localization of main straits through the magmatic arc. Revista de
- 971 la Asociación Geológica Argentina, 60, 221–250.
- 972 Weaver, C., 1931. Paleontology of the Jurassic and Cretaceous of West Central

973 Argentina. Memoirs of the University of Washington, 1, 1–496.

- 974 Willey, I.E., 1973. Belemnites from South-Eastern Alexander Island. II, The occurrence
- of the Family Belemnopseidae in the Upper Jurassic and Lower Cretaceous.
- Bulletin of the British Antarctic Survey, 36, 33–59.
- 277 Zatón, M., Salamon, M. 2008. Durophagus predation on middle Jurassic Molluscs, as
- evidenced from shell fragmentation. Palaeontology 51, 1, 63–70.
- 979 https://doi.org/10.1111/j.1475-4983.2007.00736.x
- 980 Figure captions
- 981 Figure 1. 1.1. Upper Jurassic–Lower Cretaceous outcrops in the Neuquén and Austral
- 982 Basin, Argentina, with referred (in bold) and studied (circled) belemnite bearing
- 983 localities: **BN**, Bahía Nassau; **CL**, Cañada de Leiva; **CM**, Chacay Melehue; **DO**, Cerro
- 984 Domuyo; IE, Isla de los Estados; LA, Las Alcantarillas; LAR, Lago Argentino; LB,

985 Lago Belgrano; LL, Las Loicas; LO, Cerro Lotena; LSM, Lago San Martín; 1.2–1.4.

986 Detailed maps of the studied belemnite-bearing localities, **1.2.** Cañada de Leiva; **1.3.**

987 Las Loicas and Las Alcantarillas; **1.4.** Cerro Domuyo.

Figure 2. Log sections of the belemnite-bearing localities indicating the stratigraphic
position of belemnite records and selected ammonoid taxa.

990 Figure 3. Hummocky cross-bedding bioclastic packstone (CLBe) thin section, views of

the densely packed poorly sorted and oriented packstone with micrite and organic

matter. 1, In the center, star-shaped crinoid columnals (O) in between other highly

993 fragmented echinoderm fragments with micrite cement, and bone fragment (B) with

silica replacement. 2, Note orientated fragmented bioclasts, probably bivalve shells

995 (white arrows), bone fragment (B) and echinoderm stems. 3, Different sections of stems

996 (S) in a micritic matrix (M). 4, Bone fragments (B), small gastropods and, (G) pyrite

with abundant stems fragments (S). Scales bars= 2 mm(1, 2), 1 mm(3); 0.5 mm (4).

998 Figure 4. Belemnites from the Vaca Muerta Formation, Neuquén Basin. 1–6,

999 Belemnopsis cf. B. patagoniensis (Favre, 1908). 1–3, MCNAM-PI 24881, 1, ventral

view, 2, right lateral view, 3, cross-section; 4–6, CPBA 22924.6, 4, ventral view, 5, left

1001 lateral view, 6, cross-section. 7–13, *Belemnopsis* cf. B. launceloti Howlett, 1989. 7–9,

1002 MCNAM-PI 24647.2, 7, right lateral view, 8, ventral view, 9, cross-section; 10–13,

1003 MCNAM-PI 24647.1, 10, ventral view, 11, left lateral view, 12, upper stem cross-

section, 13, lower stem cross-section. 14–16, *Hibolithes argentinus*? CPBA 23224, 14,

1005 outline view, 15, lateral view, 16, cross-section. All specimens were covered with

1006 ammonium chloride. Scale bars= 10 mm.

1007 Figure 5. Belemnopsis rostra sketch diagrams. 1–2, Belemnopsis cf. B. patagoniensis

1008 (Favre, 1908), MCNAM-PI 24881, 1, outline; 2, right profile; 3–4, *Belemnopsis* cf. B.

1009 *launceloti* Howlett, 1989, MCNAM-PI 24647.1, **3**, left profile, **4**, outline.

1010	Figure 6. Paleobiogeographic distribution of <i>Belemnopsis</i> and <i>Hibolithes</i> during the
1011	upper Tithonian–lower Berriasian. Data from Favre (1908), Besairie (1930, 1936),
1012	Feruglio (1936-1937, 1949), Harrington (1943), Stevens (1965, and references therein),
1013	Willey (1973), Riccardi (1977), Jeletzki (1983), Combémorel (1988), Crame and
1014	Howlett (1988), Howlett (1989), Doyle and Howlett (1989, and references therein),
1015	Aguirre-Urreta and Suárez (1985, and references therein), Mutterlose (1986, and
1016	references therein), Olivero (1987), Challinor (1991, and references therein), Challinor
1017	and Hikuroa (2007), Crame et al. (2000), and Stinnesbeck et al. (2014). Map based on
1018	Smith et al. (1994). 1, Neuquén Basin; 2, Lago San Martín, Austral Basin; 3, Lago
1019	Argentino, Austral Basin; 4, Torres del Paine, Chile; 5, Tierra del Fuego Archipelago);
1020	6, Alexander Island, Antarctic Peninsula; 7, Malvinas/Falkland Plateau; 8, Orville Coast
1021	and Ellsworth Land, Western Antarctica; 9, Eastern Wedell Sea; 10, Madagascar; 11,
1022	Kutchh; 12, Northwestern Pakistan; 13, Spiti Shales; 14, Australia; 15, New Guinea; 16,
1023	Moluccas and Sula Islands; 17, Misool, Indonesia; 18, New Zealand.
1024	Figure 7. Summary of occurrences of the Tithonian–Berriasian Neuquén Basin
1025	belemnite records according to the current Andean ammonoid-based biostratigraphic
1026	scheme (modified from Aguirre-Urreta et al., 2019; Leanza et al., 2020, Lescano et al.,
1027	in press). White stars, Hibolithes sp. records (Gerth, 1925; Alberti et al., 2020); grey
1028	stars, Hibolithes argentinus and H. argentinus? records (this work); black stars,
1029	Belemnopsis cf. B. patagoniensis records (this work). DO, Cerro Domuyo; CL, Cañada
1030	de Leiva; LA, Las Alcantarillas; LL, Las Loicas; LM, Arroyo La Manga; PT, Pampa

1031 Tril.















Highlights

- New Tithonian belemnite data from the Neuquén Basin, western Argentina.
- 21 Belemnites are assigned to the genera *Belemnopsis* and *Hibolithes*.
- The belemnite association is close to Madagascan-Eastern African faunas.
- Generic composition and affinity of the belemnite fauna add new evidence • supporting an open Trans-Gondwana seaway from the Tithonian onwards.

, from the

Authors statement

Verónica V. Vennari: Conceptualization, methodology, data acquisition, investigation, writing, supervision, and funding acquisition. Beatriz Aguirre-Urreta: investigation, data acquisition, writing, and funding acquisition. Luciana S. Marin: data acquisition, methodology and writing. Pierre Pellenard: data acquisition, writing, and funding acquisition. Maisa Tunik: data acquisition and writing.

Journal Press

Declaration of interests

 \boxtimes The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

□The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: