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1 **UPPER JURASSIC (TITHONIAN) BELEMNITES FROM THE NEUQUÉN**  
2 **BASIN, ARGENTINA**

3

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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 *Windhausenicerias 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

40 **Keywords.** Fossil coleoidea. *Belemnopsis*. *Hibolithes*. Vaca Muerta Formation. Trans-  
41 Gondwana seaway.

42

## 43 1.1 Introduction

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

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

79 Therefore, the objective of this work is to fully document new belemnite rostra  
80 from the Upper Jurassic (Tithonian) of the Neuquén Basin to start filling the gap in the  
81 knowledge of this group in west-central Argentina. We also aim to refer the findings to  
82 the Andean ammonoid-based biostratigraphic framework, and to discuss the  
83 paleobiogeographic, biostratigraphic, and broad paleoecological implications of their  
84 occurrences.

## 85 **1.2. Previous Neocomian belemnite records in Argentina and nearby regions**

86 Upper Jurassic–Lower Cretaceous belemnite records from Argentina are currently  
87 concentrated in the Austral Basin (Fig. 1). *B. patagoniensis* (Favre) was originally  
88 described from the Hauterivian–Barremian of Lago Belgrano area and later restricted to  
89 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  
91 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 *Hibolites 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. launzeloti* 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 *Hibolites* ranges into the Berriasian and younger beds of  
114 the Río Mayer Formation *sensu* Doyle et al. (1996).

115 Other illustrated records of *B. patagoniensis* or *B. cf. patagoniensis* come from  
116 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  
119 western region of the Isla de los Estados (Harrington, 1943; Caminos and Nullo, 1979).  
120 Also, Aguirre-Urreta and Suárez (1985) presented new Berriasian–Hauterivian records  
121 of *B. madagascariensis* from several sections within the Magallanes Archipelago.  
122 Recently, Ippolitov et al. (2015) described a single specimen from the Berriasian of  
123 Crimea as *Parabelemnopsis* cf. *patagoniensis*, indicating that its presence was probably  
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  
126 Austral Basin during the Lower Cretaceous.

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  
129 Antarctic species *B.* cf. *B. launceloti* Howlett (Stinnesbeck et al., 2014). Additional  
130 material retrieved from a drill hole at the Falkland/Malvinas Plateau was identified as  
131 *Belemnopsis* spp. and assigned a New Zealand to Himalayan affinity (Jeletzky, 1983).

132 Within the Neuquén Basin (Fig. 1), Upper Jurassic–Lower Cretaceous belemnite  
133 records are sparser and poorly known. Oxfordian *Belemnopsis* with European affinities  
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  
137 Mendoza Province include an indeterminate rostrum fragment from the Tithonian of  
138 Arroyo Serrucho (Krantz, 1928) and some thin incomplete rostra from the upper  
139 Tithonian of the Vaca Muerta Formation in Bardas Blancas (Gerth, 1925; here referred  
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  
142 from Neuquén Province were either identified as *Hibolithes* sp. (e.g., Alberti et al.,



143 2020, from Pampa Tril) or not specified (*e.g.*, Kietzmann and Vennari, 2013, from  
144 Cerro Domuyo, here revised). Besides, Stevens (1965, p. 158) indicated a possible  
145 Kimmeridgian to Tithonian age for ?*Hibolites* sp., *B. cf. B. patagoniensis* and  
146 ?*Dicoelites* sp. from Cerro Lotena, and for ?*Hibolites* 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  
154 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 in  
157 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  
159 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  
175 the Neuquén Basin (35° 48' S, 69° 48' W), 6 km northeast of the Bardas Blancas  
176 settlement (Dessanti, 1973; Gerth, 1925; Gulisano and Gutiérrez-Pleimling, 1994). Here  
177 the Vaca Muerta Formation spans nearly 240 m and is dominated by tempestite-facies  
178 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  
182 to laterally concretionary 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),  
187 bryozoan fragments and small gastropods (Fig. 3.4), and 10% of siliciclastic material  
188 such as volcanic lithic fragments, detrital mono and polycrystalline quartz, feldspar and  
189 abundant pyrite. Among the echinoderm fragments were differentiated: star-shaped  
190 crinoid columnals (Fig. 3.1), cross and longitudinal sections of stems, crinoid arm  
191 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

193 have microborings (Fig. 3.4). Most of the bone fragments have evidence of microbial  
194 boring activity as well. The matrix is micritic and some pore spaces are filled with  
195 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  
201 settlement (35° 47' S, 70° 09' W). The marine sediments of the Vaca Muerta Formation  
202 are punctuated by several volcanic layers, some of which have provided precise U/Pb  
203 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.  
206 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**

210 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).  
212 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  
214 within an interval dominated by calcareous-nodule bearing dark laminated marls.  
215 Likewise, the previous locality, the facies association indicates a distal outer ramp  
216 setting (Kietzmann et al., 2021).

### 217 **3.1.4. Cerro Domuyo**

218 This locality is at the foothills of the Cerro Domuyo, at the southern tip of the Cordillera  
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  
221 to decimetric grey to dark laminated wackestones, intercalated between large intervals  
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**

227 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:

$$230 \quad A = \text{rostrum transverse diameter} / \text{rostrum sagittal diameter} \times 100$$

231 Rostra linear measurements were acquired using a vernier digital caliper ( $\pm 1$  mm  
232 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  
234 were taken with a Canon SX60 semi-reflex camera. Linear illustrations and plates were  
235 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 *Belemnopsis* 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 which 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 located within the upper portion of *Windhauseniceras internispinosum* Biozone  
 263 (upper lower Tithonian), Mendoza Province, Argentina.

264 **Description.** Based on the best-preserved specimen MCNAM-PI 24881 (Figs. 4.1–4.3;  
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=  
267 14 mm) is attained at about 60 mm from the apex. Outline symmetrical, non-hastate  
268 with margins tapering into an acute dorsally oriented apex. Profile somewhat  
269 asymmetrical, dorsally flattened but slightly ventrally inflated around the apical region.  
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  
274 the apical region, where it shows a "v" profile in cross-section and appears to deepen  
275 anteriorly. The apical line is slightly ventral situated, and no lateral lines were observed.

276 **Remarks.** The Tethyan genus *Belemnopsis* (Bayle, 1878) groups more than one  
277 hundred European and Indo-Pacific belemnite species ranging from the Middle Jurassic  
278 up to the Lower Cretaceous (Riegraf, 1999). Although we agree with Riegraf (1980),  
279 Howlett (1989), and Ippolitov et al. (2015) that such a broad taxonomic concept is  
280 problematic, there is still no agreement among belemnite workers on the validity of the  
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,  
283 so we follow the classic taxonomic assignation to the genus *Belemnopsis*.

284 The outline and profile general forms, as well as the length and distinctiveness of  
285 the ventral groove, are important taxonomic characters (Stevens, 1965) that justify the  
286 assignation of the studied material to *Belemnopsis*. The rostrum cross-section appears to  
287 be a more variable trait since different authors have described *Belemnopsis* species with  
288 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  
312 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, Combémoré (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  
341 a slightly asymmetrical profile due to inflation of the venter, and the outline appears to  
342 be cyliandroconical (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  
344 the same bed, 15.4 mm long on average (dtM= 1.4), are too poorly preserved to provide  
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  
354 BAS website:  
355 [https://legacy.bas.ac.uk/bas\\_research/data/access/fossildatabase/filter.php?taxonKeywor](https://legacy.bas.ac.uk/bas_research/data/access/fossildatabase/filter.php?taxonKeyword=BELEMNITIDA)  
356 [d=BELEMNITIDA](https://legacy.bas.ac.uk/bas_research/data/access/fossildatabase/filter.php?taxonKeyword=BELEMNITIDA)). Some of the mentioned differences might have an ontogenetic  
357 explanation. Stevens (1965, p. 40) indicated that *Belemnopsis* suffered changes in its  
358 degree of hastation in the early growth stages of the rostrum. Challinor (2001, p. 234)  
359 also pointed out that *Belemnopsis aucklandica* presents the point of maximum  
360 transverse diameter nearer the apex in juvenile specimens but higher up in adults, a trait  
361 that affects the degree of hastation of the rostrum. He also noted that in more hastated  
362 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 *B. gladiatoris* 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 *B. africanus* 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 *Windhausenicerias 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  
386 groove in the preserved portion leads us to consider this fragment as part of the lower  
387 stem region of an *Hibolithes* representative. The most frequent *Hibolithes* species in  
388 Argentina is *H. argentinus* (Feruglio, 1936), which is characterized by a slender hastate  
389 rostrum with circular to slightly depressed transverse sections and a shallow ventral  
390 groove that extends no further than the upper stem region. Howlett (1989, p. 52)  
391 designated one of the specimens figured by Feruglio (1936, pl. 10, fig. 17) as lectotype  
392 and added new material from Alexander Island. The fragment here described agrees  
393 well both with the lower stem regions of the lectotype and the with the specimen BAS  
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.*, Combémorél,  
401 1988; Doyle and Howlett, 1989; Mutterlose, 1986, 1992, Stevens, 1965, 1973).  
402 Alternatively, Challinor (1991; Challinor in Grant-Mackie et al., 2000) proposed a  
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  
413 the *B. madagascariensis*-*B. casterasi* group (Besairie, 1930; Stevens, 1965;  
414 Combémoré, 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).  
417 Even more, during the Berriasian, that marine connection is supposed to have held a  
418 "relict" population of *Belemnopsis* of the *madagascariensis-casterasi* group, since  
419 *Belemnopsis* is unknown or poorly represented from European and most Indo-Pacific  
420 regions at that time (Doyle and Howlett, 1989; Stevens, 1965). That remnant population  
421 is thought to be related to the *Belemnopsis patagoniensis* assemblages of the Austral  
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  
424 the Austral Basin. *Belemnopsis* records here described add new elements connecting the  
425 Neuquén Basin assemblages with those of Madagascar and Eastern Africa, passing  
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;  
429 Campos et al., 2021).

430 FIGURE 6 AROUND HERE

## 431 **5.2. Biostratigraphic considerations**

432 Belemnites' biostratigraphic potential has long been acknowledged for Jurassic and  
433 Cretaceous successions, though belemnite-based correlations are more widely used for  
434 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. launzeloti* 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 Combémoré, 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

459 a component of the well-established Upper Jurassic–Lower Cretaceous *Hibolithes* fauna  
460 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;  
463 Leanza et al., 2020; Lescano et al., 2022) is summarized in Figure 7. *Hibolithes* sp. from  
464 the Arroyo La Manga area was found by Gerth (1925) in beds assigned to the  
465 *Argentiniceras noduliferum* Biozone, just above an interval bearing *Lytrochoplites*  
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 andesensis/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. launzeloti* 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  
485 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.**

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

495       Episodes of transgressive or high sea level could have facilitated the access of  
496 active swimming belemnites (or aid in the dispersing of their early ontogenetic stages)  
497 to the Neuquén Basin. Belemnite records from Cerro Domuyo, Las Alcantarillas, and  
498 Las Loicas were found in middle outer ramp to basinal deposits of a transgressive  
499 system tract of the second-order Second Composite Depositional sequence, involving  
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.

505       Although some authors have modeled the existence of counter-oceanic currents at  
506 the latitude of the Neuquén Basin (Parrish, 1992), up to the authors' best knowledge,  
507 there were no physical geographic barriers between the Austral and the Neuquén Basin  
508 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 °C from  $\delta^{18}\text{O}$   
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 °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



534 as well-oxygenated waters, with a normal salinity of 27–37 psu and a depth range of no  
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  
537 would deviate from the optimum (*e.g.*, by the influx of freshwater), belemnites could  
538 have just actively swum away from such conflicting areas.

539 In most recent revisions of the group, belemnites are considered medium-sized  
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,  
544 belemnites were occasionally preyed upon by marine reptiles such as ichthyosaurs and  
545 metriorhynchids (Fernández et al., 2019), which might have gotten into the basin mostly  
546 for reproductive purposes (Gasparini and Fernández, 2005). However, most probably,  
547 belemnite hatchlings were consumed by pachycormids, a stem-teleost clade of  
548 suspensivorous-feeding fishes that were quite successful from the Early Jurassic to the  
549 Late Cretaceous (Friedman et al., 2010). Pachycormids, which are well-known from the  
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  
555 survival. On the one hand, ammonites, either semelparous or iteroparous, are assumed  
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;  
558 Mironenko and Rogov, 2015; Tajika et al., 2018; Greif et al., 2022). Even more,

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  
561 predation relation should be proven through bromalite analyses (*i.e.*, oral or anal  
562 depositions or intestinal content) as conducted in other basins (Zatón and Salamon,  
563 2008; Bigurrarena et al., 2019; Lukeneder et al., 2020). Belemnites, on the other hand,  
564 are assumed to have been r-strategists (e.g., Doguzhaeva et al. 2013) and to have  
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.,  
567 2018). In consequence, ammonite surviving into adulthood was more likely than for  
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  
572 predation pressure exerted by filter-feeding organisms on hatchlings, combined with  
573 unsuitable paleoecological conditions over shallow marine settings relatively close to  
574 the coast where belemnites were assumed to inhabit (Naef, 1922; Doguzhaeva et al.,  
575 2013, Mutterlose, 2022).

## 576 **6. Concluding remarks**

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

584 be contemplated as a component of the widely-known *Hibolithes* fauna recorded across  
585 the Late Jurassic–Early Cretaceous of Gondwana. Affinities of the described fauna seem  
586 close to Madagascan–Eastern African belemnite associations of the Ethiopian  
587 Subprovince, thus reinforcing the hypothesis of a Trans-Gondwana seaway as an open  
588 marine connection at least since the Tithonian.

589 The baffling scarcity of belemnites from the Late Jurassic in the Neuquén Basin and  
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,  
595 the possible existence of counter-currents at the latitude of the Neuquén Basin may have  
596 limited the extension to lower latitudes of the *Belemnopsis/Hibolithes* Gondwanan  
597 faunas.

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## 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.

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

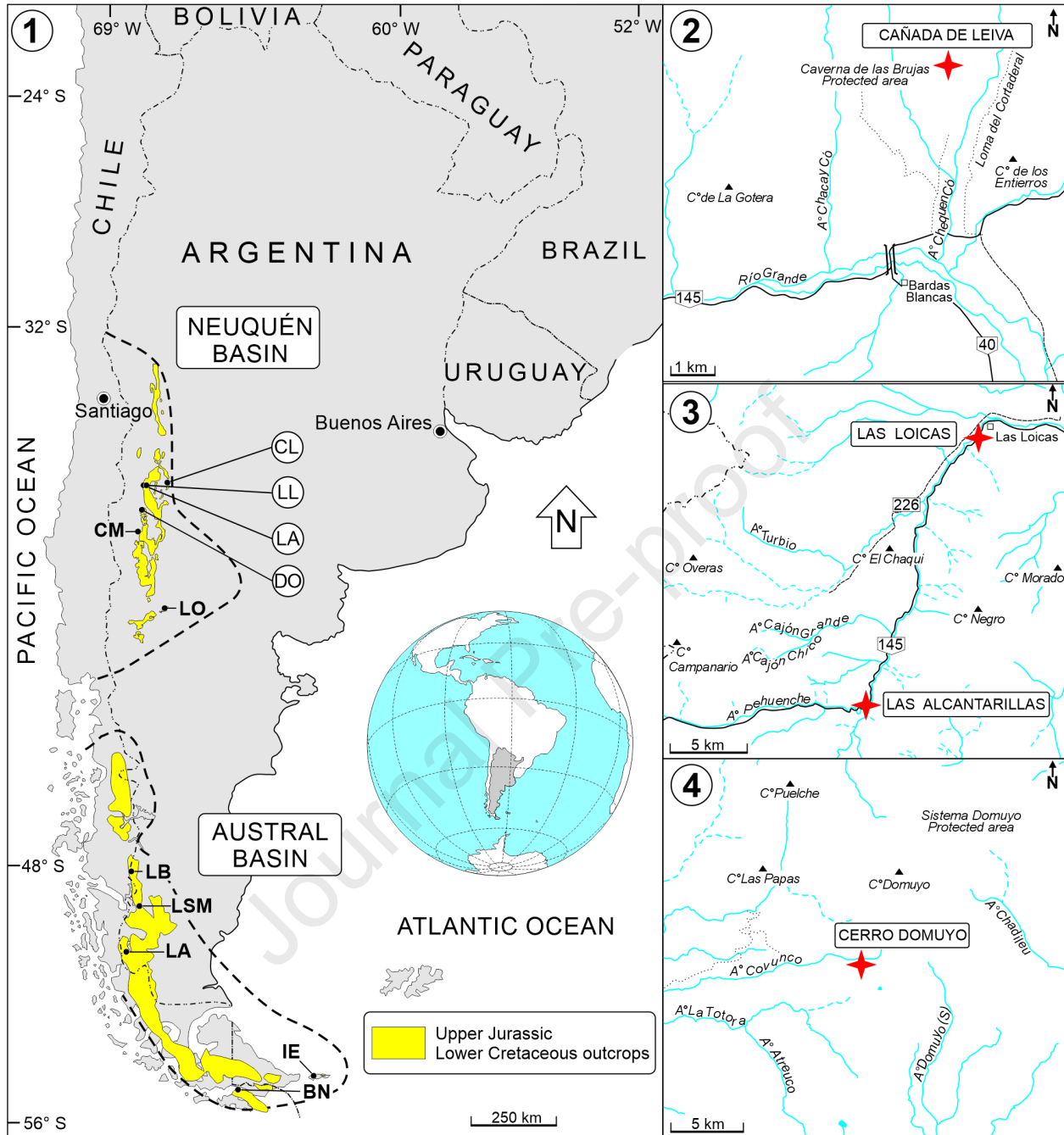
990 **Figure 3.** Hummocky cross-bedding bioclastic packstone (**CLBe**) thin section, views of  
 991 the densely packed poorly sorted and oriented packstone with micrite and organic  
 992 matter. **1**, In the center, star-shaped crinoid columnals (**O**) in between other highly  
 993 fragmented echinoderm fragments with micrite cement, and bone fragment (**B**) with  
 994 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  
 997 with abundant stems fragments (**S**). Scales bars= 2 mm (**1, 2**), 1 mm (**3**); 0.5 mm (**4**).

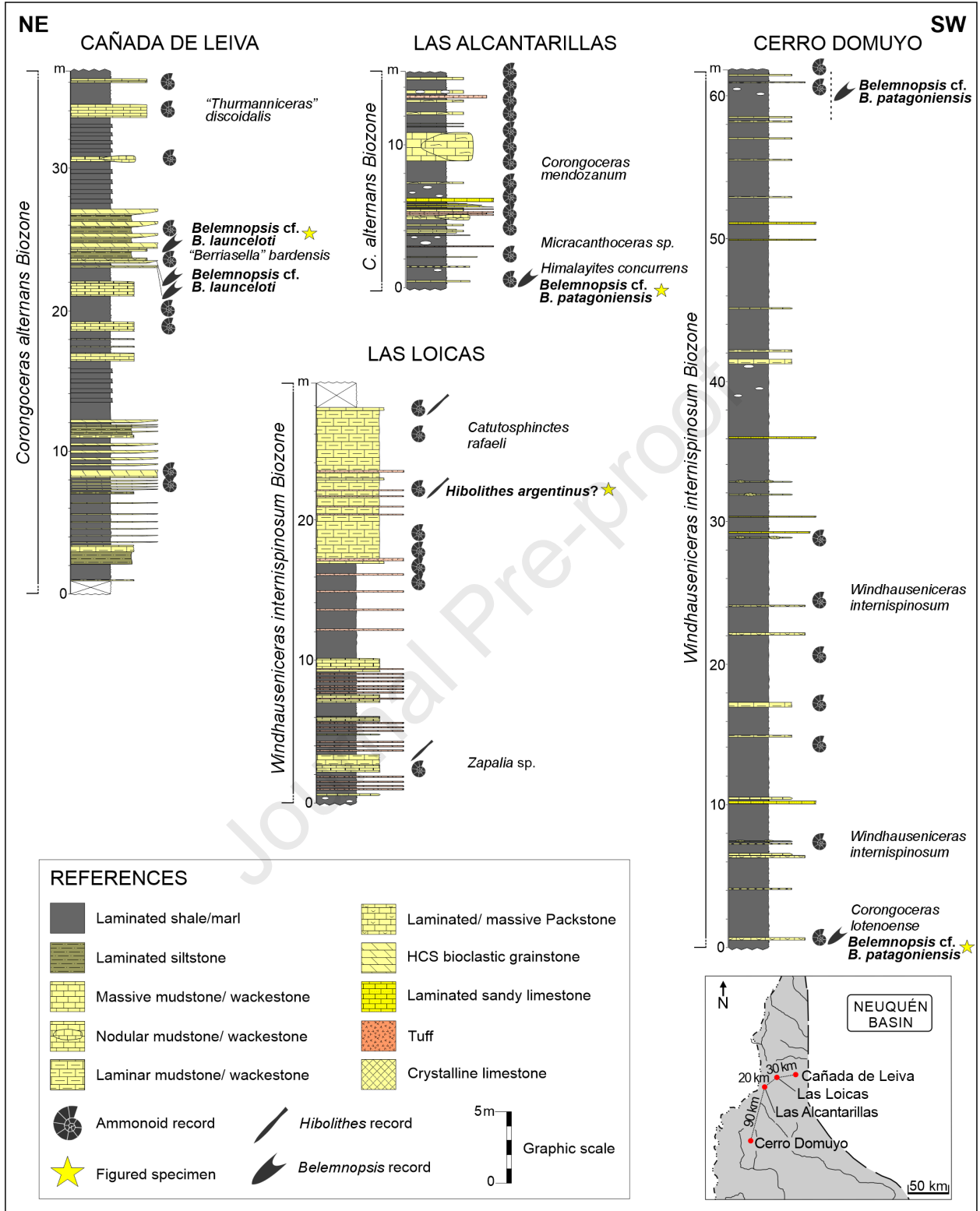
998 **Figure 4.** Belemnites from the Vaca Muerta Formation, Neuquén Basin. **1–6**,  
 999 *Belemnopsis* cf. *B. patagoniensis* (Favre, 1908). **1–3**, MCNAM-PI 24881, **1**, ventral  
 1000 view, **2**, right lateral view, **3**, cross-section; **4–6**, CPBA 22924.6, **4**, ventral view, **5**, left  
 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-  
 1004 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.

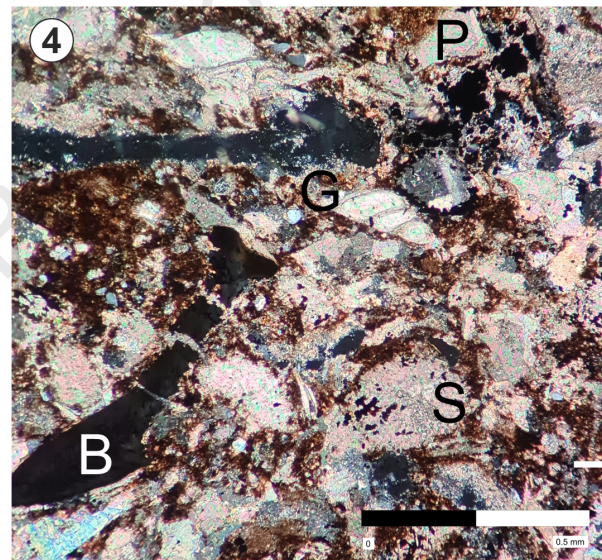
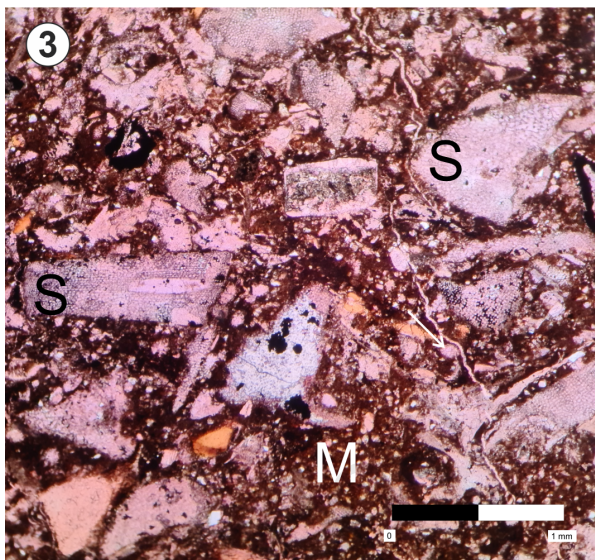
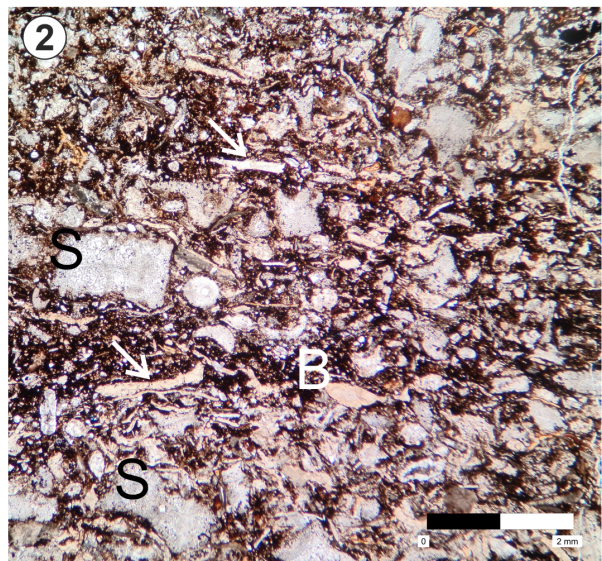
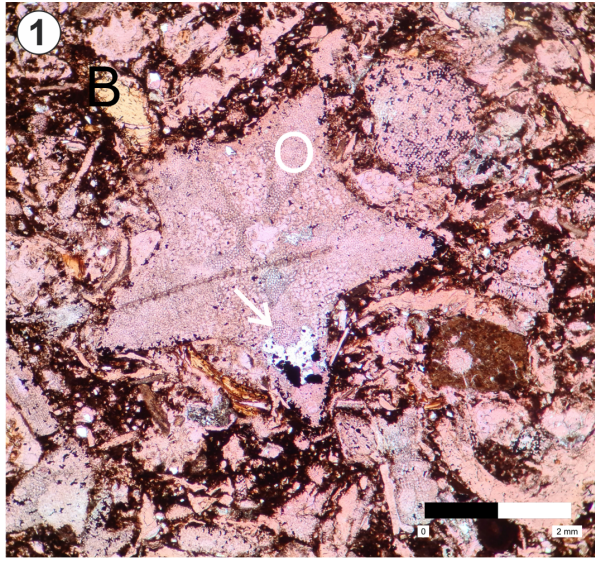
1007 **Figure 5.** *Belemnopsis* rostra sketch diagrams. **1–2**, *Belemnopsis* cf. *B. patagoniensis*  
 1008 (Favre, 1908), MCNAM-PI 24881, **1**, outline; **2**, right profile; **3–4**, *Belemnopsis* cf. *B.*  
 1009 *launceloti* Howlett, 1989, MCNAM-PI 24647.1, **3**, left profile, **4**, outline.

1010 **Figure 6.** Paleobiogeographic distribution of *Belemnopsis* and *Hibolithes* 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), Combémorrel (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.

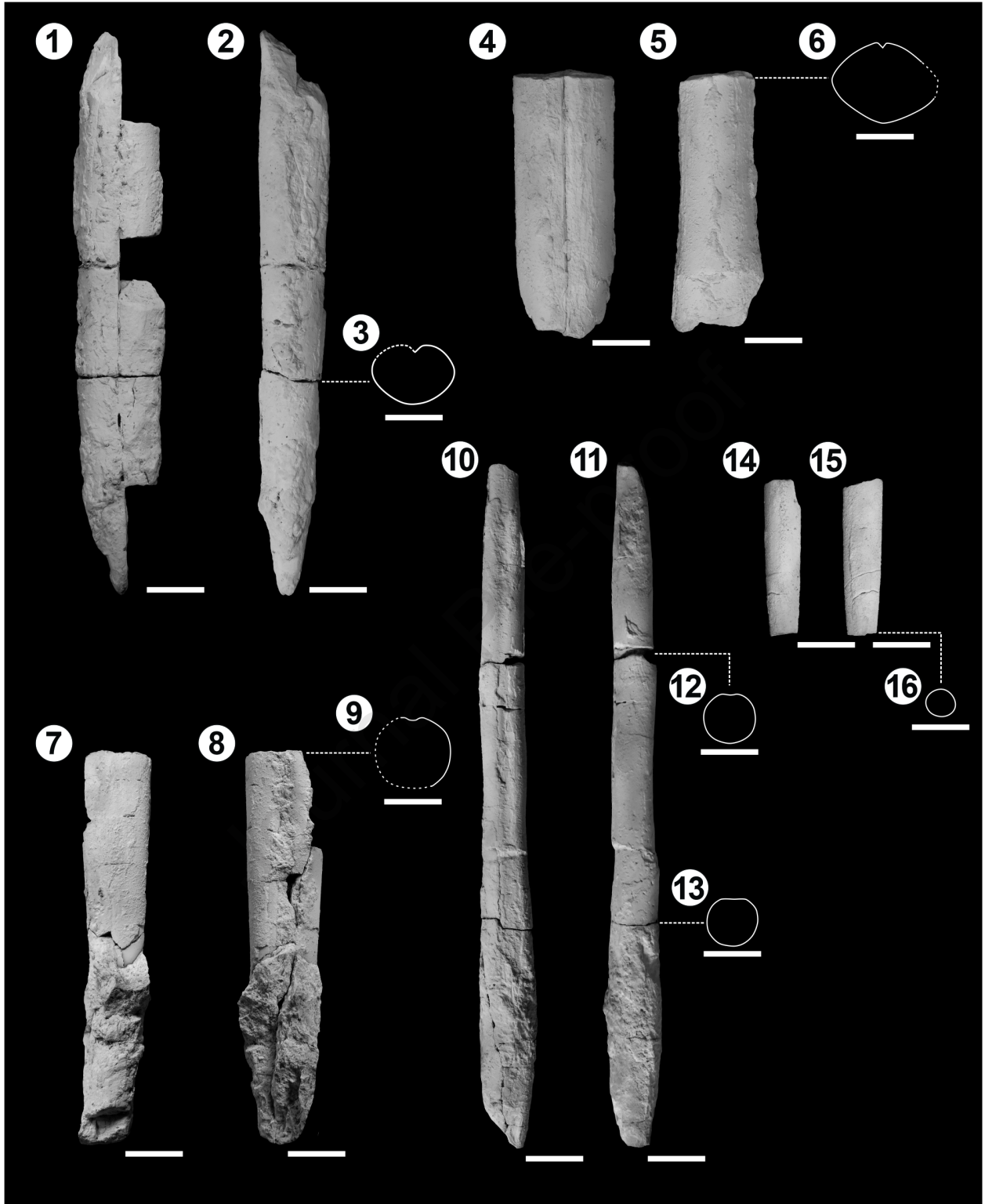
1024 **Figure 7.** Summary of occurrences of the Tithonian–Berriasian Neuquén Basin  
 1025 belemnite records according to the current Andean ammonoid-based biostratigraphic  
 1026 scheme (modified from Aguirre-Urreta *et al.*, 2019; Leanza *et al.*, 2020, Lescano *et al.*,  
 1027 *in press*). **White 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.

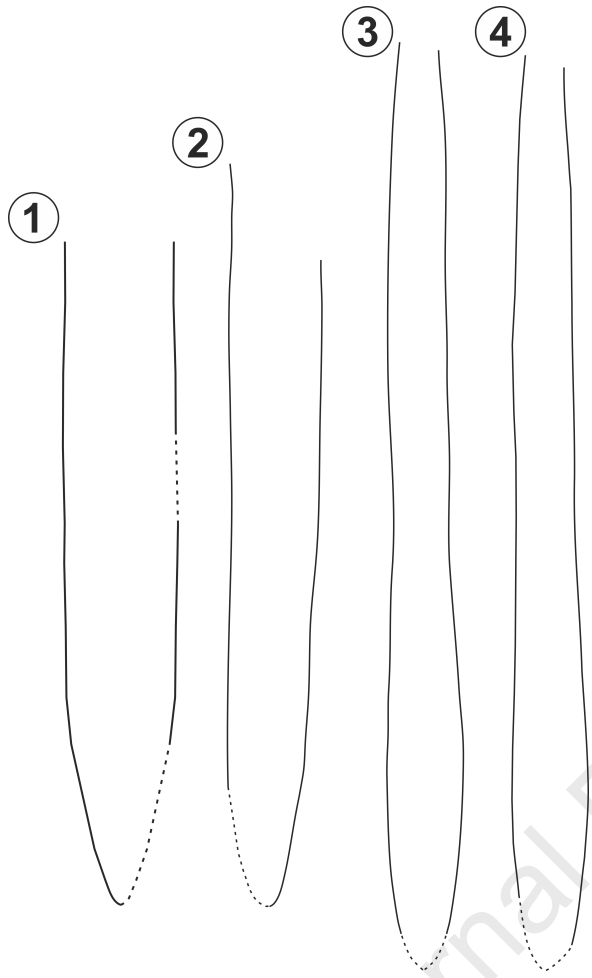


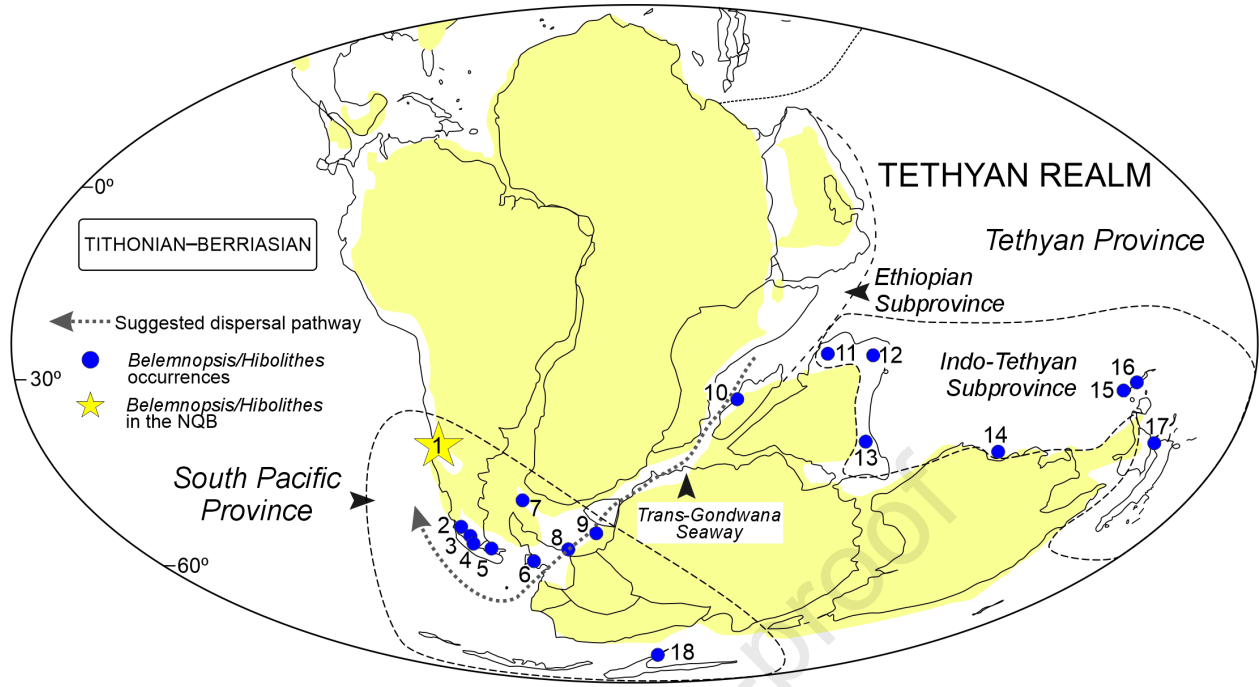












| AGE        |       | BIOZONE                          | OCCURRENCES                        |    |    |    |    |    |
|------------|-------|----------------------------------|------------------------------------|----|----|----|----|----|
|            |       |                                  | LM                                 | CL | LL | LA | DO | PT |
| Berriasian | Late  | ?                                |                                    |    |    |    |    |    |
|            | Mid.  | <i>Argentinerias noduliferum</i> | ☆                                  |    |    | ☆  |    |    |
|            | Early | ?                                |                                    |    |    |    |    |    |
| Tithonian  | Late  | <i>Substeueroceras koeneni</i>   |                                    | ★  |    |    |    |    |
|            |       | <i>Corongoceras alternans</i>    |                                    |    |    |    |    | ☆  |
|            | Early | ?                                | <i>W. internispinosum</i>          |    |    | ★  |    |    |
|            |       | ?                                | <i>A. proximus</i>                 |    |    |    | ★  |    |
|            |       |                                  | <i>Pseudolissoceras zitteli</i>    |    |    |    |    | ☆  |
|            |       |                                  | <i>Virgatosphinctes andesensis</i> |    |    |    |    |    |
|            |       | ?                                | ?                                  |    |    |    |    |    |

**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.

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. **Mathieu Martinez:** data acquisition, writing, and funding acquisition. **Maisa Tunik:** data acquisition and writing.

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**Declaration of interests**

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:

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