



Upper Jurassic (Tithonian) belemnites from the Neuquén Basin, Argentina

Verónica V. Vennari^{a,c,*}, Beatriz Aguirre-Urreta^{b,c}, Luciana S. Marin^{b,c}, Pierre Pellenard^d,
Mathieu Martinez^e, Maisa Tunik^{c,f}

^a Instituto de Evolución, Ecología Histórica y Ambiente (IDEVEA), Universidad Tecnológica Nacional, Facultad Regional San Rafael (UTN-FRSR). Gral. J.J. Urquiza 314, M5602GCH, San Rafael, Mendoza, Argentina

^b Instituto de Estudios Andinos "Don Pablo Groeber" (IDEAN), Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales. Intendente Güiraldes 2160 Ciudad Universitaria, C1428EGA, CABA, Argentina

^c Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Argentina

^d Laboratoire Biogéosciences, Université Bourgogne Franche-Comté. UMR 6282 CNRS/uB/EPHE 6 Bd Gabriel, Dijon, France

^e Géosciences Rennes, Université Rennes 1, UMR 6118 CNRS, 35000, Rennes, France

^f Instituto de Investigación en Paleobiología y Geología, Universidad de Río Negro, Sede Alto Valle, 8332, General Roca, Río Negro, Argentina

ARTICLE INFO

Keywords:

Fossil coleoidea

Belemnopsis

Hibolithes

Vaca Muerta Formation

Trans-Gondwana seaway

ABSTRACT

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

1. Introduction

Belemnites are an extinct group of Mesozoic nektonic cephalopods considered in the most recent contributions as stem-decachabrachian coleoids (Fuchs et al., 2013; Hoffmann and Stevens, 2020). Usually reconstructed as externally morphologically close to loginid squids (Naef, 1922; Stevens, 1965), belemnites had a mantle muscle structure 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, the low-Mg calcitic rostrum is the most commonly preserved part due to its resistant structure of radially arranged calcite fibers that, combined with variable amounts of organic matter, form concentric rings in cross-section (Stolley, 1911; Jeletzky, 1966; Riegraf, 1980; Hoffmann et al., 2016; Hoffmann and Stevens, 2020). Belemnite taxonomy mostly relies on morphological characters of the rostrum:

general 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, and/or lateral). The orientation and form of the apical line and alveolus-related characters (i. e., where the phragmocone lies inside the rostrum) are usually accessorially described (Stevens, 1965; Jeletzky, 1966; Doyle and Kelly, 1988; Challinor, 1999).

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 Late Jurassic–Early Cretaceous Gondwana shelf-areas were dominated by *Belemnopsis* and *Hibolithes* (Challinor, 1991; Doyle and Pirrie, 1999), both included in the “Belemnopseina,” a group characterized by alveolar furrows and whose taxonomic validity has been recently challenged (Stevens in press). *Hibolithes* was a cosmopolitan and ecologically wide-ranged genus whose species are

* Corresponding author. Instituto de Evolución, Ecología Histórica y Ambiente (IDEVEA), Universidad Tecnológica Nacional, Facultad Regional San Rafael (UTN-FRSR). Gral. J.J. Urquiza 314, M5602GCH, San Rafael, Mendoza, Argentina.

E-mail addresses: vvennari@conicet-mendoza.gob.ar (V.V. Vennari), aguirre@gl.fcen.uba.ar (B. Aguirre-Urreta), lmartin@gl.fcen.uba.ar (L.S. Marin), pierre.pellenard@u-bourgogne.fr (P. Pellenard), mathieu.martinez@univ-rennes1.fr (M. Martinez), mtunik@unrn.edu.ar (M. Tunik).

<https://doi.org/10.1016/j.jsames.2023.104200>

Received 4 July 2022; Received in revised form 27 December 2022; Accepted 15 January 2023

Available online 16 February 2023

0895-9811/© 2023 Elsevier Ltd. All rights reserved.

mostly differentiated based on the ventral groove characters (Stevens, 1965; Mutterlose, 1988; Doyle and Kelly, 1988; Challinor, 1991). *Belemnopsis* is a more variable genus (Stevens, 1965; Combémere, 1988; Howlett, 1989; Challinor, 1991, 2001, 2003; Challinor and Hikuroa, 2007) mostly represented in Gondwana by robust, cylindroconical to slightly depressed rostra with a variably strong ventral groove (Challinor, 1991; Doyle et al., 1996, 1997; Doyle and Pirrie, 1999). In

Argentina, both *Hibolithes* and *Belemnopsis* had been long recognized from the Upper Jurassic and, mostly, from the Lower Cretaceous of the Austral Basin in south Patagonia (e.g., Dana, 1848; Favre, 1908; Feruglio, 1936, 1949) and have been revised or cited in the literature from there on (e.g., Aguirre-Urreta and Suárez, 1985; Riccardi, 1976, 1977, 1988). In contrast, Neuquén Basin belemnite records of the same age are significantly less frequent, and taxonomic-focused contributions are

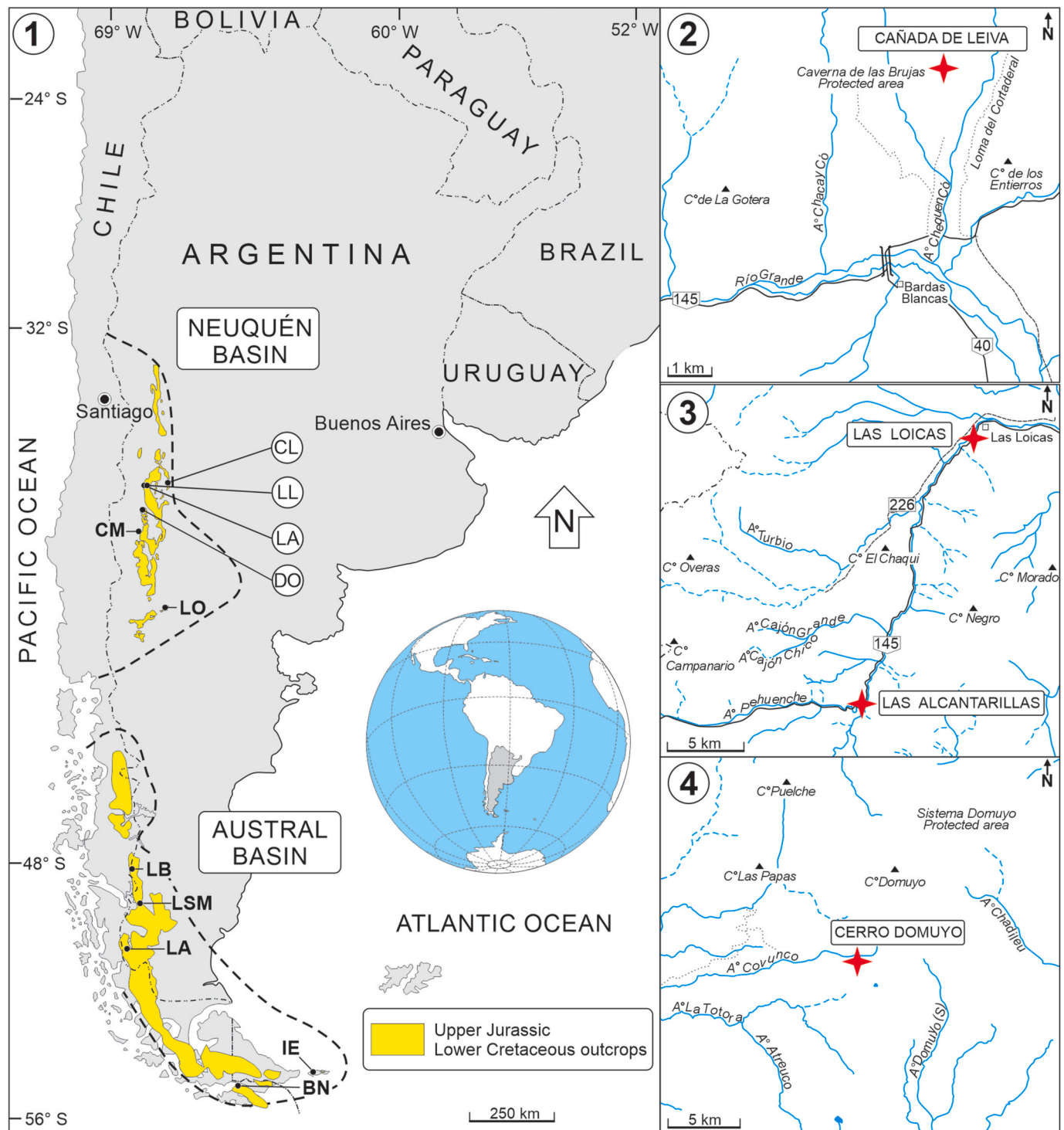


Fig. 1. 1.1. Upper Jurassic–Lower Cretaceous outcrops in the Neuquén and Austral basins, Argentina, with referred (in bold) and studied (circled) belemnite bearing localities: BN, Bahía Nassau; CL, Cañada de Leiva; CM, Chacay Melehue; DO, Cerro Domuyo; IE, Isla de los Estados; LA, Las Alcantarillas; LB, Lago Belgrano; LSM, Lago San Martín; LO, Cerro Lotena; 1.2–1.4. Detailed maps of the studied belemnite-bearing localities, 1.2. Cañada de Leiva; 1.3. Las Loicas and Las Alcantarillas; 1.4. Cerro Domuyo.

lacking (Stevens, 1965; Doyle et al., 1996, 1997).

Therefore, the objective of this work is to fully document new belemnite rostra 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 the Andean ammonoid-based biostratigraphic framework, and to discuss the paleobiogeographic, biostratigraphic, and broad paleoecological implications of their occurrences.

1.1. Previous Neocomian belemnite records in Argentina and nearby regions

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 the Lago Belgrano area and later restricted to the Hauterivian (Favre, 1908; Riccardi, 1988). Findings around Lago San Martín, at the top of the Springhill Formation, were alternatively ascribed to the Tithonian (Bonarelli and Nágera, 1921; Feruglio, 1949), the Hauterivian–Barremian (Riccardi, 1971), or the Berriasian (Riccardi, 1976, 1977). Finally, they were assigned to a Berriasian–Valanginian age (Medina and Riccardi, 2005; Riccardi, 1988). From the same levels, Riccardi (1977) reported *B. cf. B. madagascariensis* (Besairie) and *Hibolites* aff. *H. jaculum* (Phillips). Also from the Lago San Martín area, at the base of the Río Mayer Formation, Medina and Riccardi (2005) reported *B. patagoniensis*, *B. cf. gladiatoris* Willey, and *Belemnopsis* sp. together with the ammonoids *Favrella americana* (Favre) and *F. wilckensi* (Favre), thus indicating a Hauterivian age for the association. To the south, in the Lago Argentino area, Estancia La Cristina, Feruglio (1936) introduced a supposedly Valanginian belemnite association composed of *B. patagoniensis*, *Hibolites argentinus* Feruglio, *H. aff. H. jaculum*, and a specimen openly assigned as *Belemnites* sp. I, which was reinterpreted as a *Belemnopsis* sp. by Stevens (1965, p. 159) and alternatively as *Parahibolites* by Challinor (1991, p. 316). The specimen assigned to *B. patagoniensis* was reassigned to *B. gladiatoris* Willey due to morphological differences with the type material (Stevens, 1965; Willey, 1973) and subsequently to *B. launeloti* Howlett (1989). Feruglio (1949, p. 169) also mentioned, but not illustrated, *B. patagoniensis* from another locality (Cerro de Los Fósiles) within the Lago Argentino area, there associated with Tithonian to Berriasian ammonoid taxa (cf. Leanza, A., 1967). A reassessment of the Indo-Pacific affinity of the whole assemblage (Stevens, 1965) as well as a revision of the ammonoid-related fauna, pointed to an upper Tithonian age for Feruglio's original belemnite collection (Leanza, A., 1967). The same seems valid for related specimens from the Springhill Formation near Lago Argentino, where *Hibolites* ranges into the Berriasian and younger beds of the Río Mayer Formation *sensu* Doyle et al. (1996).

Other illustrated records of *B. patagoniensis* or *B. cf. patagoniensis* come from the southernmost end of South America, from Berriasian–Hauterivian beds of the Yagán Formation, Bahía Nassau, Tierra del Fuego (Dana, 1848; Stevens, 1965; 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). Also, Aguirre-Urreta and Suárez (1985) presented new Berriasian–Hauterivian records of *B. madagascariensis* from several sections within the Magallanes Archipelago. Recently, Ippolitov et al. (2015) described a single specimen from the Berriasian of Crimea as *Parabelemnopsis* cf. *patagoniensis*, indicating that its presence was probably the result of a rare immigration episode to the Northern Hemisphere. Aside from the later record, *Belemnopsis patagoniensis* appears to be a well-distributed species of the Austral Basin during the Lower Cretaceous.

Other records of *Belemnopsis* in nearby areas are known from the Valanginian–Hauterivian of the Rocas Verdes Basin, Chile, where robust forms were ascribed to the Antarctic species *B. cf. B. launeloti* Howlett (Stinnesbeck et al., 2014). Additional 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).

Within the Neuquén Basin (Fig. 1), Upper Jurassic–Lower Cretaceous belemnite records are sparser and poorly known. Oxfordian *Belemnopsis* with European affinities have been mentioned from La Manga Formation in southern Neuquén (Doyle et al., 1996; Riccardi et al., 2011) and from the Callovian–Oxfordian of Vega de la Veranada, in northern Neuquén (Alberti et al., 2020). Younger not-illustrated records from Mendoza Province include an indeterminate rostrum fragment from the Tithonian of 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 as Cañada de Leiva). Additional fragmentary belemnites were reported from a Berriasian interval in the Arroyo La Manga area (Gerth, 1925). Other Tithonian records from Neuquén Province were either identified as *Hibolites* sp. (e.g., Alberti et al., 2020, from Pampa Tril) or not specified (e.g., Kietzmann and Vennari, 2013, from Cerro Domuyo, here revised). Besides, Stevens (1965, p. 158) indicated a possible Kimmeridgian to Tithonian age for ? *Hibolites* sp., *B. cf. B. patagoniensis* and ? *Dicoelites* sp. from Cerro Lotena, and for ? *Hibolites* sp. from Arroyo Chacay Melehue, but unfortunately, none of those records were illustrated.

2. Geological setting

The Neuquén Basin (Fig. 1) is a retro-arc basin situated over the western margin of Gondwana, between 32° and 40° South Latitude, extending over central-western Argentina and central Chile (Legarreta and Uliana, 1991; Howell et al., 2005). Its nearly 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 international scientific community over the basin.

Tithonian successions bearing the belemnite fauna here presented are included in the Vaca Muerta Formation (Weaver, 1931), a marine geographically extended unit 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 Valanginian (Kietzmann et al., 2014; Legarreta and Uliana, 1991). Ammonoids are the most common megascopic fossils of the Vaca Muerta Formation, including both endemic and more extended distributed taxa. Their correlation with Tethyan faunas and with calcareous nanofossils and microfossils bioevents provide the current Upper Jurassic–Lower Cretaceous biostratigraphic scheme for the Neuquén Basin (Leanza, H. et al., 2020 and references therein; Lescano et al., 2022).

3. Material and methods

3.1. Localities

The twenty-one belemnites herein studied come from Tithonian beds of the Vaca Muerta Formation in four localities situated over the northern sector of the Neuquén Basin (Fig. 2). From the northeast to the southwest, they are Cañada de Leiva (fourteen specimens), Las Loicas (one specimen), Las Alcantarillas (one specimen), and Cerro Domuyo (five specimens).

3.1.1. Cañada de Leiva

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 Palma, 2011; Kietzmann et al., 2018). Belemnites from this section come from up to 40 cm thick, very consolidated hummocky cross-bedding bioclastic packstone limestone (CLBe) intercalated with laminated marls/siltstone intervals, and a decimetric massive to

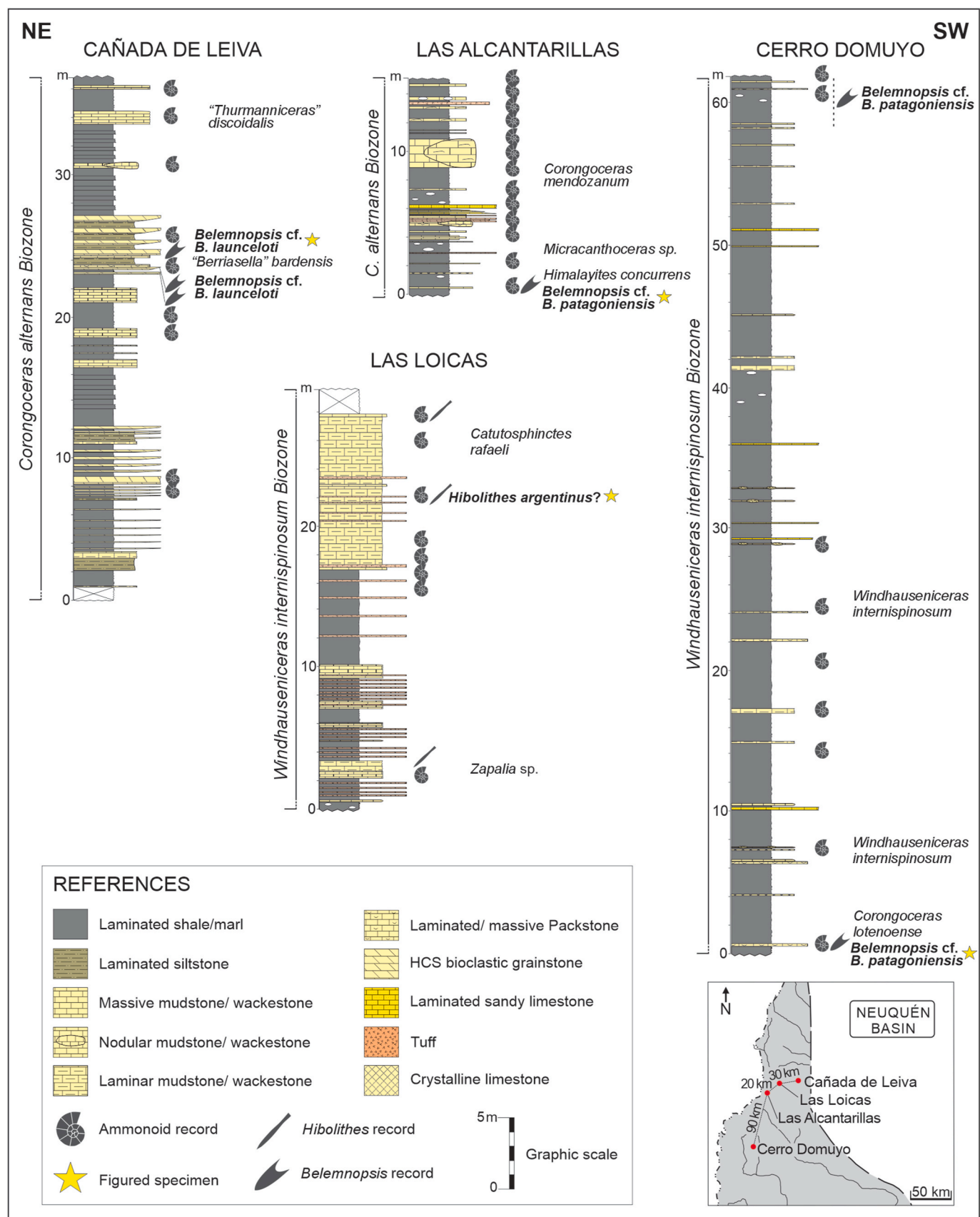


Fig. 2. Log sections of the belemnite-bearing localities indicating the stratigraphic position of belemnite records and selected ammonoid taxa.

laterally concretionary wackestone limestone with ammonoids, located about 24.5 m from the base of the logged section in Fig. 2. The CLBe sample is a densely packed, poorly sorted, and oriented (Fig. 3) packstone with micrite and organic matter. The grains are 70% echinoderm fragments (Figs. 3.1 and 3.4), 10% of bone fragments (Figs. 3.1 and 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 such as volcanic lithic fragments, detrital mono and polycrystalline quartz, feldspar and abundant pyrite. Among the echinoderm fragments were differentiated: star-shaped crinoid columnals (Fig. 3.1), cross and longitudinal sections of stems, crinoid arm elements, some with lunate patterns (Fig. 3.1 and 3.3), and scarce echinoid spines. Most 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 1911 and 1913 (Gerth, 1925).

3.1.2. Las Loicas

It is located close to the 145 National Road heading towards the Pehuenche 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 were retrieved from decimetric to metric laminated to massive dark wackestones bearing ammonoid and brachiopod impressions, intercalated with dark laminated marls. Based on the facies associations interpreted by Kietzmann et al. (2021) in the nearby Las Tapaderas section, this interval is assignable to the transition between basinal to distal outer ramp settings.

3.1.3. Las Alcantarillas

Located about 20 km west of the Las Loicas section, it is well exposed over the right margin of the Arroyo Pehuenche that crosses the 145 National Road (35° 57' S, 70° 14' W). The single belemnite rostrum from this locality comes from a 12 cm thick, dark 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).

3.1.4. Cerro Domuyo

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

3.2. Measurements and illustrations

Belemnite rostra's study and description follow the outlines of Stevens (1965) and Challinor (1999, 2003). Challinor (1999) redefined the flattening index (A) of Stevens (1965) as a percentage ratio:

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

Rostra linear measurements were acquired using a vernier digital caliper (± 1 mm accuracy). Angular measurements were obtained with a protractor ($\pm 1^\circ$) or by digital 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.

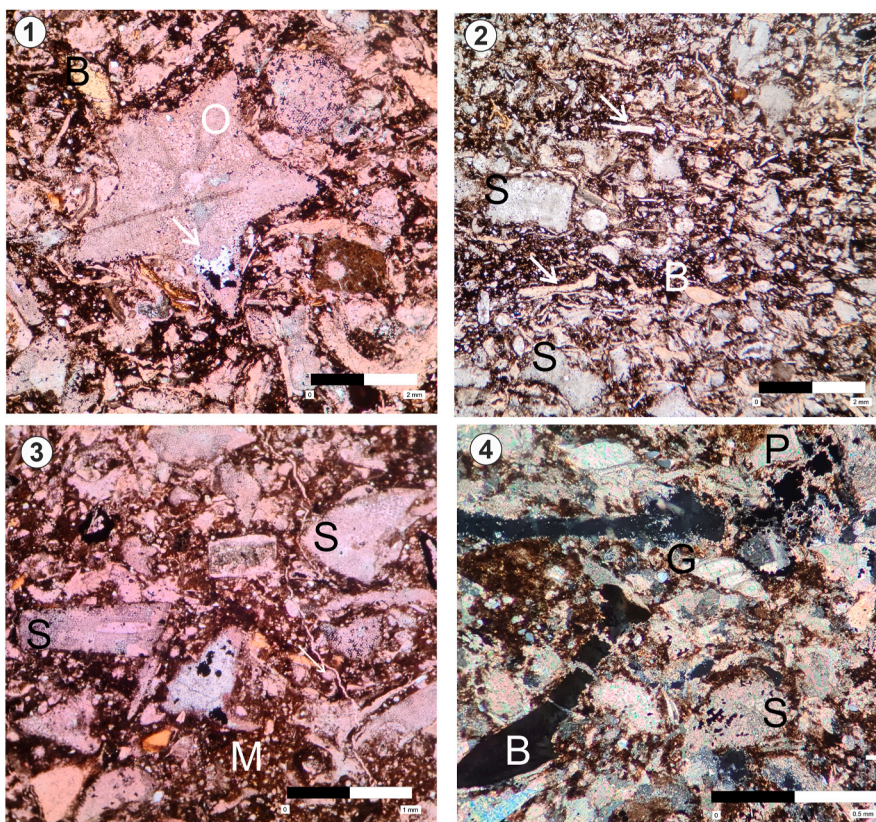


Fig. 3. Hummocky cross-bedding bioclastic packstone (CLBe) thin section, views of the densely packed poorly sorted and oriented packstone with micrite and organic matter. 1, In the center, star-shaped crinoid columnals (O) in between other highly fragmented echinoderm fragments with micrite cement, and bone fragment (B) with silica replacement. 2, Note orientated fragmented bioclasts, probably bivalve shells (white arrows), bone fragment (B) and echinoderm stems (S). 3, Different sections of stems (S) in a micritic matrix (M). 4, Bone fragments (B), small gastropods and, (G) pyrite with abundant stems fragments (S). Scale bars = 2 mm (1, 2), 1 mm (3); 0.5 mm (4).

3.3. Abbreviations

Institutional abbreviations. BAS KG, British Antarctic Survey Collection, Cambridge, United Kingdom; CPBA, Paleontological Collection of the University of Buenos Aires, Buenos Aires, Argentina; MCNAM-PI, Colección de Paleontología de Invertebrados del Museo de Ciencias Naturales y Antropológicas “Juan Cornelio Moyano,” Mendoza, Argentina.

Anatomical abbreviations. A, index of flattening; dtM, maximum transverse diameter; dtm, minimum transverse diameter.

Stratigraphical abbreviations. BB, Cañada de Leiva section; DO, Cerro Domuyo section; LA, Las Alcantarillas section; LL, Las Loicas section.

4. Systematic paleontology

Order BELEMNOPSEINA Jeletzky (1965).

Family BELEMNOPSEIDAE Naef (1922), amend Jeletzky (1946).

Genus *Belemnopsis* Bayle, 1878

Type species.

Belemnopsis apiciconus Blainville (1827) (pl. 2, Fig. 2 and 2a). ?Upper

Aalenian–Bajocian, England, France, and Southern Germany (cf. Riegraf, 1999). Lectotype subsequently designated by Riegraf (1999, p. 66). A reassessment of the validity of the genus was recently undertaken by Mitchell (2015) and followed here.

Belemnopsis sp. cf. *Belemnopsis patagoniensis* (Favre, 1908).

Based on the best-preserved specimen MCNAM-PI 24881 (Figs. 4.1–4.6; 5.1–5.2).

cf. 1908 *Belemnites patagoniensis* n. sp., Favre, p. 640, pl. 37, Figs. 6 and 7

Material. Six specimens. One from the Las Alcantarillas section (MCNAM-PI 24881); five fragments which probably correspond to five individuals from the Cerro Domuyo section (CPBA 22924.1–22924.6).

Geographic and stratigraphic occurrence. Las Alcantarillas section, bed LA7, base of *Corongoceras alternans* Biozone (upper Tithonian) and Cerro Domuyo section, bed DO 30 and loosed within the upper portion of *Windhausenicerias internispinosum* Biozone (upper lower Tithonian), Mendoza Province, Argentina.

Description. Rostrum cylindroconical, elongated and slender, 98 mm long, only preserves 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 with margins tapering into an acute dorsally oriented apex. Profile somewhat

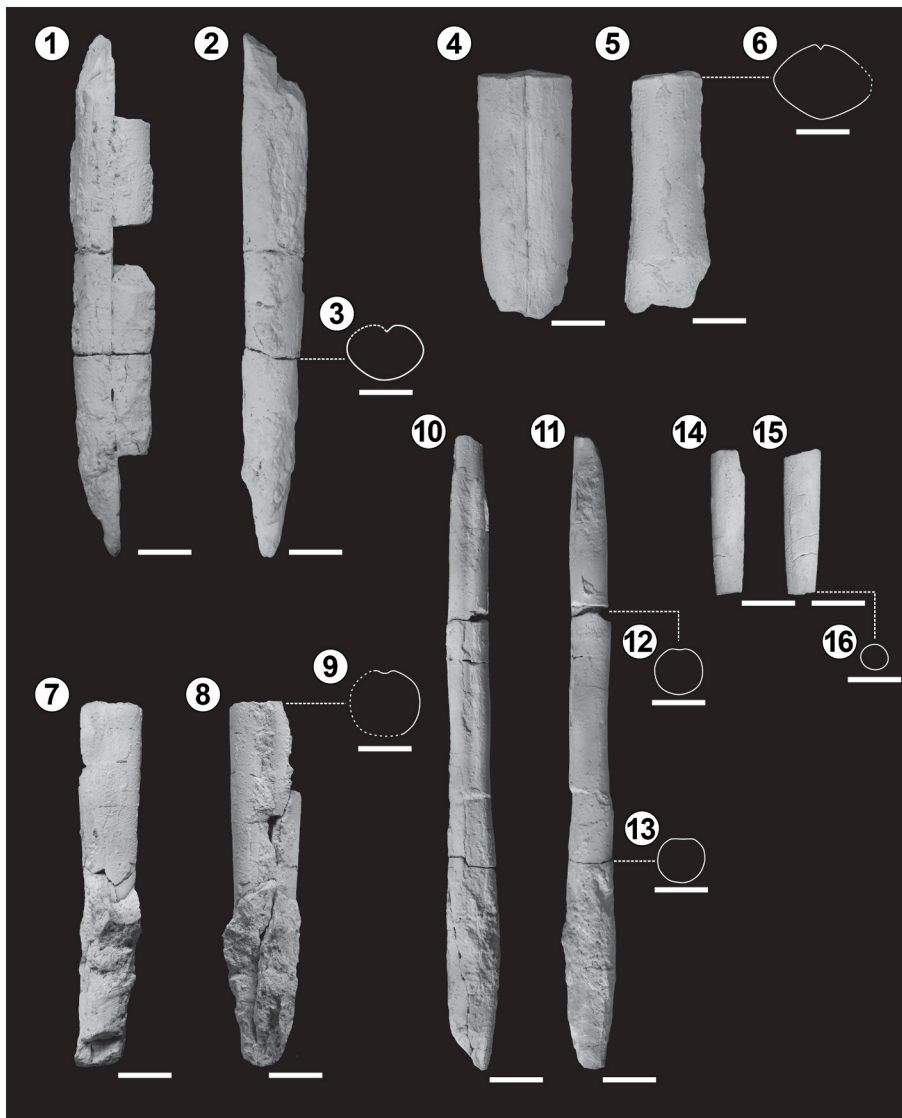


Fig. 4. Belemnites from the Vaca Muerta Formation, Neuquén Basin. 1–6, *Belemnopsis* cf. *B. patagoniensis* (Favre, 1908). 1–3, MCNAM-PI 24881, 1, ventral view, 2, right lateral view, 3, cross-section; 4–6, CPBA 22924.6, 4, ventral view, 5, left lateral view, 6, cross-section. 7–9, *Belemnopsis* cf. *B. launceloti* Howlett (1989). 7–9, MCNAM-PI 24647.2, 7, right lateral view, 8, ventral view, 9, cross-section; 10–13, 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, outline view, 15, lateral view, 16, cross-section. All specimens were covered with ammonium chloride. Scale bars = 10 mm.

asymmetrical, dorsally flattened but slightly ventrally inflated around the apical region. Cross-section elliptical and depressed throughout (A c. 115 over the stem region), although this character might be accentuated by sedimentary flattening. A narrow, shallow ventral groove with angular margins runs over the mid-region of the stem and 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 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 hundred European and Indo-Pacific belemnite species ranging from the Middle Jurassic up to the Lower Cretaceous (Rieggraf, 1999). Although we agree with Rieggraf (1980), 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 proposed subgeneric categories (e.g., Challinor, 1991; Challinor and Hikuroa, 2007) and 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*.

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; Challinor and Hikuroa, 2007). More specifically, the elongated rostrum, with an acute apex and a narrow ventral groove with angular margins, enables comparing the Neuquén Basin material with *Belemnopsis patagoniensis* (Favre, 1908), a well-known Lower Cretaceous species frequently recorded in the Austral Basin from the Berriasian to the Hauterivian (see section 1.2). Upper Tithonian (cf. Leanza, A., 1967) *B. patagoniensis* described by Feruglio (1936) from Santa Cruz differs from the type material of the species (Stevens, 1965) and has been repeatedly reassigned (see section 1.2). Independently of their systematic position, Feruglio's *Belemnopsis* and *Hibolithes argentinus* show morphological affinities with Indonesian and New Zealand assemblages cf. Stevens (1965) and to elements from Madagascar, cf. Challinor (1991).

Nonetheless, Patagonian specimens are typically more robust, almost twice wider and longer than the material described here (e.g., Favre, 1908, pl. 37, Figs. 6 and 7; Riccardi, 1977, Fig. 6a–c, g–i). A similar slender Berriasian specimen was described from Crimea by Ippolitov et al. (2015), who assigned it to *Parabelemnopsis* cf. *patagoniensis* and interpreted its record in the Northern Hemisphere as a singular short invasion episode. The Crimean specimen differs from the Neuquén Basin material in having a much shorter ventral groove. Antarctic *Belemnopsis*, on the other hand, seem to be closely related to those from New Zealand-Indonesian of the “uhligi Complex” (Stevens, 1965; Challinor, 1991), though more recently Challinor and Hikuroa (2007) indicated some affinities with Madagascan forms.

Belemnopsis patagoniensis, *B. madagascariensis* (Besairie, 1930), and *B. casterasi* Besairie (1936) are recognized as a cluster of closely related Madagascan-South American Late Jurassic–Early Cretaceous large-sized, narrow-grooved belemnites (Stevens, 1965; Howlett, 1989). Howlett (1989), Challinor (1991), and Ippolitov et al. (2015) have pointed out the strong similitude of some specimens assigned to *B. patagoniensis*, *B. aff. madagascariensis* (Riccardi, 1977, 1988) and *B. madagascariensis* (Aguirre-Urreta and Suárez, 1985). Even more, Combémoré (1988) suggested that *B. madagascariensis* and *B. casterasi* might conform to a dimorphic pair. Phylogenetic relationships between them await a detailed revision to assess the extent of ontogenetic and population variability (Challinor, 2003; Challinor and Hikuroa, 2007).

Belemnopsis sp. cf. *Belemnopsis launceloti* Howlett (1989).

Figs. 4.7–4.13; 5.3–5.4

Material. 14 specimens from the Cañada de Leiva section (MCNAM-PI 24647.1–24647.14).

Geographic and stratigraphic occurrence. Cañada de Leiva section, bed BB19, upper *Corongoceras alternans* Biozone (upper Tithonian), Mendoza Province, Argentina.

Description. Based on the most complete specimen, MCNAM-PI 24647.1, unless otherwise stated. MCNAM-PI 24647.1 is most probably a juvenile individual due to the presence of larger and stouter specimens in the assemblage (Fig. 4.10–4.13; 5.3–5.4). Moderately preserved, 119 mm long, slender (nearly 22 times longer than thicker), symmetrical, and markedly hastate rostrum both in outline and profile. The maximum transverse diameter (dtM = 9.84 mm) is attained over the apical region, at about 25 mm from the apex, while the minimum transverse diameter (dtm = 5.4 mm) is placed over the broken anterior portion where no traces of the alveolus is observed. Apex moderately obtuse. Cross-section circular to slightly depressed over the apical and middle-stem region, where the venter is almost flattened, and more compressed to the anterior-stem region where the venter is more excavated. A medium-width, shallow ventral groove with rounded and weakly pronounced edges extends up to two-thirds over the stem. In a probable adult specimen (MCNAM-PI 24647.2; Fig. 4.7–4.9), the groove still has rounded margins, but it is broader (3 mm wide) and runs into the apical 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 be cylindroconical (dtM = 12.2 mm) with a circular cross-section (A = 100). No dorsal or 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 any further insights into ontogenetic traits.

Remarks. The studied specimens were retrieved from the same interval where Gerth (1925) collected some material which was then revised by Stolley and identified as *Hibolithes* sp. (cf. Gerth, 1925, p. 42, footnote). However, some rostra traits, like the slender and long stem region and the shallow, medium to broad ventral groove, make them akin to *Belemnopsis launceloti* Howlett (1989, p. 40, pl. 6, Figs. 1–2, 6–7; pl. 8, Figs. 5 and 6) from the Alexander Island. Still, the Antarctic material is less hastate, has a maximum transverse diameter over the middle stem region, and the ventral groove narrows anteriorly (pictures of the type material of *B. launceloti* are available at the BAS website: https://legacy.bas.ac.uk/bas_research/data/access/fossildatabase/filer.php?taxonKeyword=BELEMNITIDA). Some of the mentioned differences might have an ontogenetic 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 apically as a wide shallow depression. Unfortunately, the poor preservation state of the material hinders further insight into its ontogeny, so its systematic assignation is left open.

Howlett (1989) included in the *B. launceloti* synonymy list two specimens described by Feruglio (1936, pl. 10, Figs. 3 and 4) from the Austral Basin, formerly reassigned to *B. gladiatoris* by Willey (1973), both of which are more robust than the Neuquén Basin material. Howlett (1989), also renamed as *B. launceloti* a specimen from Madagascar figured as *B. africanus* Tate (1867) by Besairie (1936, p. 23, Figs. 6 and 7).

Genus *Hibolithes* Montfort, 1808

Type species. *Hibolithes hastatus* Montfort (1808) (text-fig. 47), by monotypy. Bajocian–Aptian of some Boreal and most Tethyan regions (Doyle and Kelly, 1988; Howlett, 1989).

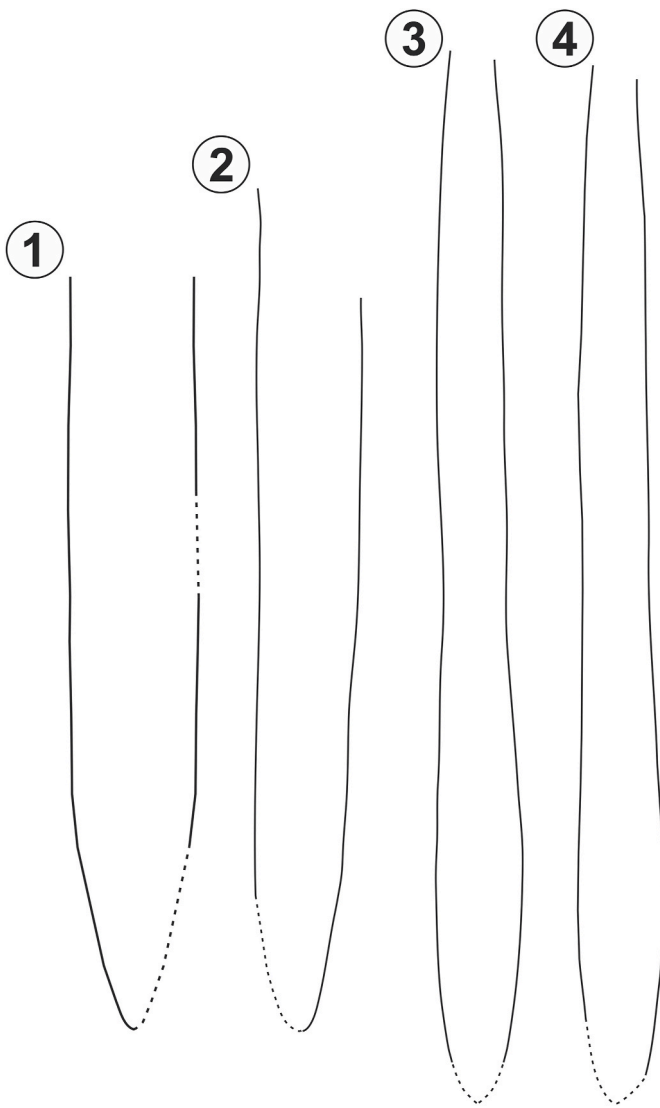


Fig. 5. *Belemnopsis* rostra sketch diagrams. 1–2, *Belemnopsis* cf. *B. patagoniensis* (Favre, 1908), MCNAM-PI 24881, 1, outline; 2, right profile; 3–4, *Belemnopsis* cf. *B. launceloti* Howlett (1989), MCNAM-PI 24647.1, 3, left profile, 4, outline.

Hibolites argentinus? (Feruglio, 1936)

Figs. 4.14–4.16

Material. One fragmentary specimen from the Las Loicas section (CPBA 23224).

Geographic and stratigraphic occurrence. Las Loicas section, bed LL062–063, upper *Windhausenicerias internispinosum* Biozone (upper lower Tithonian), Mendoza Province, Argentina.

Description. Rostrum fragment of 27.68 mm of maximum length, probably hastate both in outline and profile. The maximum transverse diameter (dtM = 12.2 mm) is recorded over the broken anterior, and the cross-section is almost circular ($A = 103$). No ventral or lateral grooves are observed. The apical line seems ortholineate.

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 stem region of an *Hibolites* representative. The most frequent *Hibolites* species in Argentina is *H. argentinus* (Feruglio, 1936), which is characterized by a slender hastate rostrum with circular to slightly depressed transverse sections and a shallow ventral groove that extends no further than the upper stem region. Howlett (1989, p. 52) designated one of the specimens figured by

Feruglio (1936, pl. 10) as lectotype 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 KG 2909.18 figured by Howlett (1989, pl. 6, Figs. 4 and 10), but as no other features are preserved, the assignment to *H. argentinus* is stated with doubts.

5. Discussion

5.1. Paleobiogeographic considerations

Several authors differentiated an Indo-Pacific Province within the Tethyan Realm from the Kimmeridgian onwards over the basis of belemnite geographic distribution, particularly of *Belemnopsis* and *Hibolites* regional assemblages (e.g., Combémoré, 1988; Doyle and Howlett, 1989; Mutterlose, 1986, 1992, Stevens, 1965, 1973). Alternatively, Challinor (1991; Challinor in Grant-Mackie et al., 2000) proposed a different subdivision of the Tethyan Realm into two provinces, 1) Tethyan Province, including a Mediterranean, Ethiopian and Tethyan Subprovinces (the last partly equivalent to the Indo-Pacific Province), and 2) South Pacific Province, extending along the Pacific coasts of Gondwana, from southern South America (including the Neuquén Basin) through West Antarctica to New Zealand, and probably including New Caledonia. The South Pacific Province was not completely isolated from the Tethyan Province and at least from the latest Jurassic, some belemnite migrations took place from the Ethiopian Subprovince into Antarctica and South America (Challinor, 1991; Mutterlose, 1992). From the Oxfordian to the Valanginian, a long-ranging lineage of narrowly-grooved *Belemnopsis* developed in Madagascar and Eastern Africa, forming the *B. madagascariensis*-*B. casterasi* group (Besairie, 1930; Stevens, 1965; Combémoré, 1988). Some components of that cluster, as well as *Hibolites*, might have reached the South Pacific coast from the Tithonian onwards through the Trans-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 “relict” population of *Belemnopsis* of the *madagascariensis*-*casterasi* group, since *Belemnopsis* is unknown or poorly represented from European and most Indo-Pacific 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 Basin (Riccardi, 1977, 1988) and now from the upper Tithonian in the Neuquén Basin. 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 Neuquén Basin assemblages with those of Madagascar and Eastern Africa, passing through Antarctica during the Upper Jurassic. These basins are known to share several ammonoid genera among other marine invertebrate and vertebrate taxa (Mutterlose, 1986; Riccardi, 1991; Vennari and Aguirre-Urreta, 2019 and references therein; Campos et al., 2021).

5.2. Biostratigraphic considerations

Belemnites’ biostratigraphic potential has long been acknowledged for Jurassic and Cretaceous successions, though belemnite-based correlations are more widely used for the Cretaceous of the Northern Hemisphere, as summarized by Christensen (1990) and Mutterlose (1990). Doyle and Bennet (1995) complemented those contributions by reviewing Jurassic belemnite occurrences of the Southern Hemisphere, and then Doyle et al. (1996, 1997) focused on the Antarctic and the Argentinean Jurassic records. The former includes the Kimmeridgian–Tithonian *Belemnopsis* fauna described from the Antarctic Peninsula and the Alexander Island (Crame and Howlett, 1988; Howlett, 1989; Mutterlose, 1986; Riley et al., 1997). Upwards, the Tithonian/Berriasian transition is encompassed by the *Hibolites* fauna (or Biozone according to Howlett, 1989), which includes several species of *Hibolites*, with *H. argentinus*, and *Belemnopsis* species of Indo-Pacific

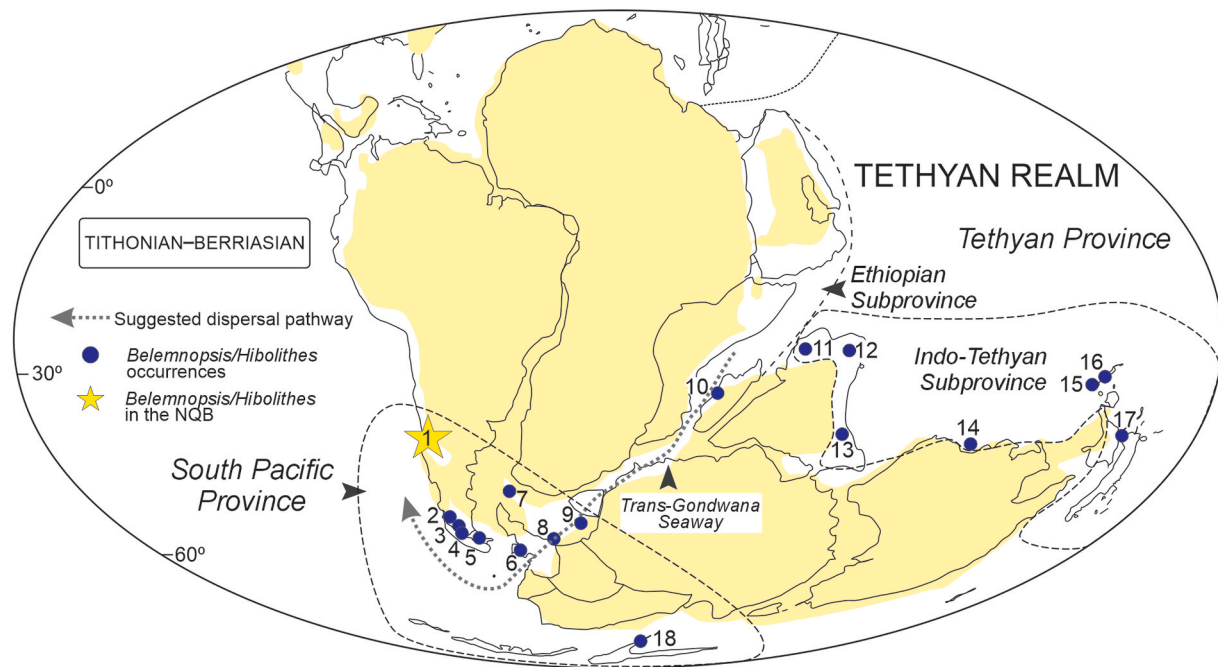


Fig. 6. Paleobiogeographic distribution of *Belemnopsis* and *Hibolites* during the upper Tithonian–lower Berriasian. Data from Favre (1908), Besairie (1930, 1936), Feruglio (1936–1937, 1949), Harrington (1943); Stevens (1965, and references therein), Willey (1973), Riccardi (1977), Jeletzky (1983), Combémoré (1988); Crame and Howlett (1988); Howlett (1989); Doyle and Howlett (1989, and references therein), Aguirre-Urreta and Suárez (1985, and references therein), Mutterlose (1986, and references therein), Olivero (1987), Challinor (1991, and references therein), Challinor and Hikuroa (2007), Crame and Howlett (1988), and Stinnesbeck et al. (2014). Map based on Smith et al. (1994). 1, Neuquén Basin; 2, Lago San Martín, Austral Basin; 3, Lago Argentino, Austral Basin; 4, Torres del Paine, Chile; 5, Tierra del Fuego Archipelago; 6, Alexander Island, Antarctic Peninsula; 7, Malvinas/Falkland Plateau; 8, Orville Coast and Ellsworth Land, Western Antarctica; 9, Eastern Wedell Sea; 10, Madagascar; 11, Kutchh; 12, Northwestern Pakistan; 13, Spiti Shales; 14, Australia; 15, New Guinea; 16, Moluccas and Sula Islands; 17, Misool, Indonesia; 18, New Zealand.

affinities as rare components. Tithonian Antarctic belemnite associations also include *Duvalia/Produvalia* (Mutterlose, 1986; Crame and Howlett, 1988), a strongly compressed genus with a dorsal median groove that is supposed to have immigrated into the Indo-Pacific region from the Tethys during the Tithonian (Stevens, 1965) or as early as the Callovian (Challinor and Hikuroa, 2007).

Concerning Argentinean Jurassic successions, Doyle et al. (1996) recognized two successive belemnite faunas for the Upper Jurassic–Lower Cretaceous namely early *Belemnopsis* (Oxfordian) and *Hibolites* (Tithonian–Berriasian), the later named after *H. argentinus*. In that contribution, the Lower Cretaceous occurrences of *B. patagoniensis* were treated separately. Meanwhile, *B. launzeloti* is an upper Tithonian–Hauterivian species that defines an assemblage biozone in Antarctica (Howlett, 1989) and has been recorded from the lower Valanginian of Madagascar (Besairie, 1936; Combémoré, 1988), the upper Tithonian of the Austral Basin in the Lago Argentino area (cf. Leanza, A., 1967), and with reservations from the Valanginian–Hauterivian of southern Chile (Stinnesbeck et al., 2014). So, *Belemnopsis* records described in this contribution indicate that this genus should also be considered in the Neuquén Basin as a component of the well-established Upper Jurassic–Lower Cretaceous *Hibolites* fauna of Gondwana (Doyle et al., 1996; Challinor, 1991).

Whenever possible, the correlation of the Neuquén Basin belemnite records in each locality with the current ammonoid Andean zonation (Aguirre-Urreta et al., 2019; Leanza et al., 2020; Lescano et al., 2022) is summarized in Fig. 7. *Hibolites* sp. from the Arroyo La Manga area were found by Gerth (1925) in beds assigned to the *Argentinites noduliferum* Biozone, just above an interval bearing *Lytroplites burckhardtii* (Mayer-Eymar) and *Spiticerus acutum* Gerth among other ammonoids of the *Substeuerceras koeneni* Biozone. *Hibolites* sp. reported from Pampa Tril were retrieved from the *Virgatospinctes andensis/Pseudolissoceras zitteli*, *Windhauseniaceras internispinosum*, and *Corongoceras alternans*

Biozones, according to Alberti et al. (2020). *Belemnopsis* cf. *B. patagoniensis* from Cerro Domuyo were found in two positions within the *W. internispinosum* Biozone, near its base (bearing *W. internispinosum* and *Corongoceras lotenense* Spath) and loosed near its top. From the upper portion of the *W. internispinosum* Biozone as well, in Las Loicas, were recorded three successive beds with fragmentary *Hibolites argentinus*? rostra associated with *Catutospinctes rafaeli* Leanza, H. and Zeiss. In Las Alcantarillas, *Belemnopsis* cf. *B. patagoniensis* was retrieved from a bed with *Himalayites concurrens* Leanza, A. and *Micracanthoceras*? sp. at the base of the *Corongoceras alternans* Biozone. From the same locality was recorded a poorly preserved *Hibolites* sp. from the *A. noduliferum* Biozone, just below a bed with *Andiceras fallax* (Steuer) and *Substeuerceras disputabile* Leanza, A. Finally, at Cañada de Leiva, *Belemnopsis* cf. *B. launzeloti* was recorded from the top of the *C. alternans* Biozone, from an interval sandwiched between “*Berriasella*” *bardensis* Krantz (= *Blanfordiceras bardense* in Parent et al., 2011), “*Thurmanniceras discoidalis*” (Gerth) (= *Parodontoceras calistoides* in Parent et al., 2011) and *Substeuerceras striolatifissimum* (Steuer) occurrences, being the later an index species of the *S. koeneni* Biozone across the basin (e.g., Groeber et al., 1952; Vennari and Aguirre-Urreta, 2019).

5.3. Paleoeological, 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.

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

Fig. 7. Summary of occurrences of the Tithonian–Berriasian Neuquén Basin belemnite records according to the current Andean ammonoid-based biostratigraphic scheme (modified from Aguirre-Urreta et al., 2019; Leanza et al., 2020; Lescano et al., 2022). **White stars**, *Hibolites* sp. records (Gerth, 1925; Alberti et al., 2020); **grey stars**, *Hibolites argentinus* and *H. argentinus*? records (this work); **black stars**, *Belemnopsis* cf. *B. patagoniensis* records (this work). **DO**, Cerro Domuyo; **CL**, Cañada de Leiva; **LA**, Las Alcantarillas; **LL**, Las Loicas; **LM**, Arroyo La Manga; **PT**, Pampa Tril.

Episodes of transgressive or high sea level could have facilitated the access of 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 Las Loicas were found in middle outer ramp to basinal deposits of a transgressive system tract of a second-order Second Composite Depositional sequence, involving the lower portion of the *W. internispinosum* Biozone to the lower portion of the *S. koeneni* Biozone (Kietzmann et al., 2014, 2021). Meanwhile, belemnites from Cañada de Leiva come from a storm-dominated middle ramp setting, corresponding to a highstand system tract (Kietzmann et al., 2014, 2018). However, other factors than a high local sea level alone would have influenced belemnite distribution.

Although some authors have modeled the existence of counter-oceanic currents at 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 basins that prevented a free interchange of nektonic fauna as both were retro-arc basins open to the Paleo-Pacific. Indeed, both basins share several ammonoid genera (Riccardi, 1991), although comparatively poorly preserved and less abundant in the case of the former (Riccardi, 2008). Nevertheless, two alternative paleogeographic models for the western-margin configuration of the Neuquén Basin were proposed, either enabling a direct connection with the Paleopacific Ocean through a discontinuous arc of volcanic islands (e.g., Howell et al., 2005) or a more restricted seaway in the north-western sector: the Curepto Strait (Vicente, 2005). Nevertheless, the high diversity and Tethyan affinities of several Neuquén Basin ammonoids and herpetofauna militate against the possibility of a confined basin (Gasparini and Fernández, 2005; Riccardi, 2015). Besides, Alberti et al. (2020) recently demonstrated, over Sr/Ca ratios and

their comparison with the global curve, the existence of water exchange with the open ocean in several localities of the Neuquén Province.

Regarding average seawater temperature and salinity, Alberti et al. (2020) found some strong influence of rainfall and/or a continental freshwater influx in their northernmost sampled sites, and interpreted a water temperature of 20–25 °C from $\delta^{18}\text{O}$ data from oyster and brachiopod shells. That temperature range agrees well with previous estimations by Gómez Dacal (2018) and Gómez Dacal et al. (2019) of a medium water temperature of 23 °C from oysters of the Neuquén Basin, and 24 °C from belemnites (*Belemnopsis* sp.) of the Austral Basin. Temperatures obtained in both cases are in agreement with the supposed range of 10–30 °C that belemnites inhabited by comparison with modern cephalopod preferences (Hoffmann and Stevens, 2020), though we do not know to which extent minor temperature changes affected belemnite distribution since it is considered the main parameter controlling their migration routes at species and genus levels (e.g., Mutterlose, 1988; Mutterlose et al., 2022; Stevens, 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 more than 200 m would characterize the Vaca Muerta Formation Upper Jurassic 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 have just actively swum away from such conflicting areas.

In most recent revisions of the group, belemnites are considered medium-sized predators of Mesozoic food webs, most likely feeding upon small vertebrates, mollusks, and crustaceans (Hoffmann and Stevens, 2020 and references therein). All these food sources were present at the Neuquén Basin, and possibly some v-shaped scars over ammonoid shells were caused by non-lethal belemnite attacks (Vennari, 2011). In time, belemnites were occasionally preyed upon by marine reptiles such as ichthyosaurs and metriorhynchids (Fernández et al., 2019), which might have gotten into the basin mostly for reproductive purposes (Gasparini and Fernández, 2005). However, most probably, belemnite hatchlings were consumed by pachycormids, a stem-teleost clade of suspensivorous-feeding fishes that were quite successful from the Early Jurassic to the Late Cretaceous (Friedman et al., 2010). Pachycormids, which are well-known from the Neuquén Basin (Gouiric-Cavalli, 2017; Gouiric-Cavalli and Arratia, 2022), to date have not been recorded in the Austral Basin, though they have cited from Chile (Arratia, 2015). Although pachycormid gill rakers spacing was suitable to filter out both hatchlings and juvenile ammonites (Tajika et al., 2018), the different reproductive 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 to have been extreme r-strategists, with high fecundity rates and the possibility, for 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, ovoviviparity has been proven for some ammonites (Mironenko and Rogov, 2015), thus 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 depositions or intestinal content) as conducted in other basins (Zatón and Salamon, 2008; Bigurarena Ojeda 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 depicted high fecundity rates as well, but of several magnitude order lower than that of 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 belemnites.

To sum up, marine connections, seawater physical parameters, or food sources availability seem not to have constrained, on their own, the presence of belemnites in 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 unsuitable paleoecological conditions over shallow marine settings relatively close

to the coast where belemnites were assumed to inhabit (Naef, 1922; Doguzhaeva et al., 2013; Mutterlose et al., 2022).

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. launzeloti*, and *Hibolites 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 *Windhausenicerias inter-nispinosum* to *Corongoceras alternans* Biozones. The biostratigraphic framework suggests that *Belemnopsis* should be contemplated as a component of the widely-known *Hibolites* fauna recorded across the Late Jurassic–Early Cretaceous of Gondwana. Affinities of the described fauna seem close to Madagascan–Eastern African belemnite associations of the Ethiopian Subprovince, thus reinforcing the hypothesis of a Trans-Gondwana seaway as an open marine connection at least since the Tithonian.

The baffling scarcity of belemnites from the Late Jurassic in the Neuquén Basin and their absence from the Early Cretaceous upwards is in utter contrast with their abundant record in the Austral Basin. Though still unresolved, it is suggested that a combination of factors, such as local variations in seawater salinity/temperature in shallow environments and, particularly, the predation pressure of filter-feeding fishes on 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 limited the extension to lower latitudes of the *Belemnopsis*/*Hibolites* Gondwanan faunas.

CRediT authorship contribution statement

Verónica V. Vennari: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Beatriz Aguirre-Urreta:** Investigation, Data curation, Writing – original draft, Funding acquisition. **Luciana S. Marin:** Data curation, Methodology, Writing – original draft. **Pierre Pellenard:** Data curation, Writing – original draft, Funding acquisition. **Mathieu Martinez:** Data curation, Writing – original draft, Funding acquisition. **Maisa Tunik:** Data curation, Writing – original draft.

Declaration of competing interest

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.

Data availability

Data will be made available on request.

Acknowledgments

The authors are grateful to all field assistants, to Leonardo Pazo (Fundación Azara) for preparing the specimens, and to the editors and reviewers that greatly improved this 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 1122017010117CO (B.A.U.) and 11220200102844CO (V.V.V.); CNRS Grants SYSTER-TELLUS “ACJC” in 2019 and “GC-JC” in 2021; and MITI AAP Temps “AstroCarb” (M.M. and P.P.). This is contribution R-445 of the Instituto de Estudios Andinos “Don Pablo Groeber”.

References

- Aguirre-Urreta, B., Naipauer, M., Lescano, M., López-Martínez, R., Pujana, I., Vennari, V., Concheyro, A., De Lena, L.F., Ramos, V., 2019. The Tithonian chrono-biostratigraphy of the Neuquén Basin and related Andean areas: a review and update. *J. S. Am. Earth Sci.* 92, 350–367. <https://doi.org/10.1016/j.jsames.2019.03.019>.
- Aguirre-Urreta, M.B., Casadio, S., Cichowski, M., Lazo, D.G., Rodríguez, D.L., 2008. Afinidades paleobiogeográficas de los invertebrados cretácicos de la Cuenca Neuquina. *Ameghiniana* 45, 593–613.
- Aguirre-Urreta, M.B., Suárez, M., 1985. Belemnites de una secuencia turbidítica volcánoclastica de la Formación Yagán, Titiánico–Cretácico Inferior del extremo sur de Chile. 4^o Congreso Geológico Chileno, Antofagasta, Actas 1, 1–16.
- Alberti, M., Parent, H., Garrido, A.C., Andersen, N., Garbe-Schönberg, D., Danise, S., 2020. Stable isotopes ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) and element ratios (Mg/Ca, Sr/Ca) of Jurassic belemnites, bivalves and brachiopods from the Neuquén Basin (Argentina): challenges and opportunities for palaeoenvironmental reconstructions. *J. Geol. Soc.* 178, JGS2020–J2163. <https://doi.org/10.1144/jgs2020-163>.
- Arratia, G., 2015. Los peces osteictios fósiles de Chile y su importancia en los contextos paleobiogeográfico y evolutivo. *Publicación Ocasional del Museo de Historia Natural. Chile* 63, 35–83.
- Bayle, E., 1878. Atlas. Première partie. Fossiles principaux des terrains. –Explication de la Carte géologique de la France, Paris 4 part 1, 158 plates.
- Besairie, H., 1930. Recherches géologiques a Madagascar. *Bulletin de la Société d' Histoire naturelle de Toulouse* 60, 345–642.
- Besairie, H., 1936. Recherches géologiques a Madagascar. Première suite. La géologie du Nord-Ouest. *Mem. Acad. Malgache* 21, 145–148.
- Bigurarena Ojeda, M.A., Gouiric-Cavalli, S., Pérez, L.M., Burlaille, L.A., Moly, J.J., Reguero, M., Santillana, S., 2019. Las bromalites de la Formación Ameghino (Jurásico Tardío) de la Península Antártica. *Publicación Electrónica de la Asociación Paleontológica Argentina. Suplemento Resúmenes*, p. R17.
- Blainville, H.D., 1827. Mémoire sur les bélemnites, considérées zoologiquement et géologiquement. F. G. Levrault, Paris, p. 136.
- Bonarelli, G., Nágera, J.J., 1921. Observaciones geológicas en las inmediaciones del Lago San Martín. *Boletín de la Dirección Nacional de Minería y Geología B27*, 1–39.
- Caminos, R., Nullo, F., 1979. Descripción geológica de la Hoja 67e, Isla de los Estados. *Servicio Geológico Nacional, Boletín* 175, 5–52.
- Campos, L., Fernández, M.S., Herrera, Y., Talevi, M., Concheyro, A., Gouiric-Cavalli, S., O'Gorman, J.P., Santillana, S.N., Acosta-Burlaille, L., Moly, J.J., Reguero, M.A., 2021. Bridging the southern gap: first definitive evidence of Late Jurassic ichthyosaurs from Antarctica and their dispersal routes. *J. S. Am. Earth Sci.* 109, 103259 <https://doi.org/10.1016/j.jsames.2021.103259>.
- Cecca, F., 1999. Palaeobiogeography of Tethyan ammonites during the Tithonian (latest Jurassic). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 147, 1–37. [https://doi.org/10.1016/S0031-0182\(98\)00149-7](https://doi.org/10.1016/S0031-0182(98)00149-7).
- Challinor, A.B., 1991. Belemnite successions and faunal provinces in the southwest Pacific, and the belemnites of Gondwana. *BMR (Bur. Miner. Resour.) J. Aust. Geol. Geophys.* 12, 301–325.
- Challinor, A.B., 1999. Belemnite biostratigraphy of the New Zealand Late Jurassic Manganoran (early Puroan) substage and the Puroan stage revisited. *N. Z. J. Geol. Geophys.* 42, 369–393. <https://doi.org/10.1080/00288306.1999.9514852>.
- Challinor, A.B., 2001. Stratigraphy of Tithonian (Ohaian-Puroan) marine beds near Port Waikato, New Zealand, and a redescription of *Belemnopsis aucklandica* (Hochstetter). *N. Z. J. Geol. Geophys.* 44, 219–242. <https://doi.org/10.1080/00288306.2001.9514936>.
- Challinor, A.B., 2003. Synonymy and stratigraphic ranges of *Belemnopsis* in the Heterian and Ohaian stages (Callovian-Tithonian), southwest Auckland, New Zealand. *N. Z. J. Geol. Geophys.* 46, 79–94. <https://doi.org/10.1080/00288306.2003.9514997>.
- Challinor, A.B., Hikuroa, D.C.H., 2007. New Middle and Upper Jurassic belemnite assemblages from West Antarctica (Latady Group, Ellsworth Land): taxonomy and paleobiogeography. *Palaeontol. Electron.* 10, 1–29. <http://palaeo-electronica.org/paleo/2007/1/assemblage/index.html>.
- Christensen, W.K., 1990. Upper Cretaceous belemnite biostratigraphy of Europe. *Cretac. Res.* 11, 371–386. [https://doi.org/10.1016/S0195-6671\(05\)80048-5](https://doi.org/10.1016/S0195-6671(05)80048-5).
- Combémourel, R., 1988. Les bélemnites de Madagascar, vol. 104. *Documents de la Laboratoire de Géologie de la Faculté des Sciences de Lyon*, pp. 1–239.
- Crame, J.A., Howlett, P.J., 1988. Late Jurassic and Early Cretaceous biostratigraphy of the Fossil Bluff Formation, Alexander Island. *Br. Antarct. Surv. Bull.* 78, 1–35.
- Dana, J.D., 1848. *Geology*. In: *U.S. Exploring Expedition 1839–1842*. New York Public Library, New York under Ch. Wilkes. Chapters 15–16.
- 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.), *Ammonoid Paleobiology: from Anatomy to Paleocology*. 113–205. Springer, Dordrecht.
- Dessanti, R.N., 1973. Descripción geológica de la Hoja 29b, Bardas Blancas, provincia de Mendoza. *Servicio Nacional de Minería y Geología, Boletín* 139, 1–70.
- 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.
- Doyle, P., 1987. Lower Jurassic–Lower Cretaceous belemnite biogeography and the origin of the Mesozoic Boreal Realm. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 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 break-up of Gondwana. In: Crame, J.A. (Ed.), *Origins and Evolution of the Antarctic Biota*, vol. 47. Geological Society Special Publication, pp. 167–182. <https://doi.org/10.1144/GSL.SP.1989.047.01.13>.

- Doyle, P., Kelly, S.R.A., 1988. The Jurassic and Cretaceous belemnites of Kong Karls Land, Svalbard. *Nor. Polarinst. Skr.* 189, 1–77.
- Doyle, P., Kelly, S.R.A., Pirrie, D., Riccardi, A.C., 1997. Jurassic belemnite distribution patterns: implications of new data from Antarctica and Argentina. *Alcheringa* 21, 219–228. <https://doi.org/10.1080/03115519708619175>.
- 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 Antarctica and Argentina. *Rev. Asoc. Geol. Argent.* 51, 331–338.
- Doyle, P., Pirrie, D., 1999. Belemnite distribution patterns. In: Olóriz, F., Rodríguez-Tovar, F.J. (Eds.), *Advancing Research on Living and Fossil Cephalopods*. Kluwer Academic-Plenum Publishers, New York, pp. 419–436.
- Favre, F., 1908. Die Ammoniten der unteren 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 transition at the High Andes, Mendoza, Argentina. *J. S. Am. Earth Sci.* 92, 658–673. <https://doi.org/10.1016/j.jsames.2019.03.013>.
- Feruglio, E., 1936. *Paleontographica Patagónica*, vol. 11. Memoria del Instituto Geológico de Padova, pp. 1–384.
- Feruglio, E., 1949. *Geología de la Patagonia*, vol. 1. Dirección General de Y.P.F., Buenos Aires, pp. 1–323.
- 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.
- Fuchs, D., Iba, Y., Ifrim, C., Nishimura, T., Kennedy, W.J., Keupp, H., Stinnesbeck, W., Tanabe, K., 2013. *Longibelus* gen. nov., a new Cretaceous coleoid genus linking Belemnoidea and early Decabrachia. *Palaeontology* 56, 1081–1106. <https://doi.org/10.1111/pala.12036>.
- Gasparini, Z., Fernández, M.S., 2005. Jurassic marine reptiles of the Neuquén Basin: records, faunas and their palaeobiogeographic significance. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E. (Eds.), *The Neuquén Basin: A Case Study in Sequence Stratigraphy and Basin Dynamics*, vol. 252. Geological Society, London, Special Publication, pp. 279–294. <https://doi.org/10.1144/GSL.SP.2005.252.01.14>.
- Gerth, H., 1925. Contribuciones a la estratigrafía y la paleontología de los Andes Argentinos II. La Fauna Neocomiana de la Cordillera Argentina en la parte meridional de la provincia de Mendoza: Academia Nacional de Ciencias, Córdoba. Acta 9, 57–132.
- Gómez Dacal, A.R., 2018. Petrología, geoquímica y diagénesis de sedimentos y fósiles carbonáticos del Jurásico Superior–Cretácico Inferior de las cuencas Neuquina y Austral, Argentina. Universidad de La Plata, La Plata, Argentina. PhD Thesis (unpublished).
- Gómez Dacal, A.R., Richiano, S.M., Gómez Peral, L.E., Spalletti, L.A., Sial, A.N., Poiré, D. G., 2019. Evidence of warm seas in high latitudes of southern South America during the Early Cretaceous. *Cretac. Res.* 95, 8–20. <https://doi.org/10.1016/j.cretres.2018.10.021>.
- Gouric-Cavalli, S., 2017. Large and mainly unnoticed: the first lower Tithonian record of a suspension-feeding pachycormid from Southern Gondwana. *Ameghiniana* 54, 283–289. <https://doi.org/10.5710/AMGH.16.11.2016.3029>.
- Gouric-Cavalli, S., Arratia, G., 2022. A new Pachycormiformes (Actinopterygii) from the Upper Jurassic of Gondwana sheds light on the evolutionary history of the group. *J. Syst. Palaeontol.* <https://doi.org/10.1080/14772019.2022.2049382>.
- Grant-Mackie, J.A., Aita, Y., Balme, B.E., Campbell, H.J., Challinor, A.B., MacFarlan, D. A.B., Molnar, R.E., Stevens, G.R., Thulborn, R.A., 2000. Jurassic Palaeobiogeography of Australasia, vol. 23. *Memoir of the Association of Australasian Palaeontologists*, pp. 311–353.
- Greif, M., Nebelsick, J.H., Klug, C., 2022. Extreme abundance of ammonoids in mass accumulations from the Late Devonian of the Moroccan Anti-Atlas. *Acta Palaeontol. Pol.* 67, 667–684. <https://doi.org/10.4202/app.00935.2021>.
- Groeber, P., Stipanovic, P.N., Mingramm, A., 1952. Jurásico. In: *Geografía de la República Argentina*, tomo 2. Sociedad Argentina de Estudios Geográficos, Buenos Aires, pp. 143–347.
- Gulisan, C.A., Gutiérrez-Pleimling, A.R., 1994. The Jurassic of the Neuquén Basin. *Field Guide, Mendoza Province. Asociación Geológica Argentina, Serie E*, 3 159, 1–103. Secretaría de Minería de la Nación, Publicación.
- Harrington, H.H., 1943. In: *Observaciones geológicas en la Isla de los Estados*. Geología 29. *Anales del Museo Argentino de Ciencias Naturales* 41, 29–52.
- Hoffmann, R., Richter, D.K., Neuser, R.D., Jöns, N., Linzmeier, B.J., Lemanis, R.E., Füsseis, F., Xiao, X., Immenhauser, A., 2016. Evidence for a composite organic-inorganic fabric of belemnite rostra: implications for palaeoceanography and palaeoecology. *Sediment. Geol.* 341, 203–215. <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. *Biol. Rev.* 95, 94–123. <https://doi.org/10.1111/brev.12557>.
- Howell, J.A., Schwarz, E., Spalletti, L.A., Veiga, G.D., 2005. The Neuquén Basin: an overview. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwarz, E. (Eds.), *The Neuquén Basin: A Case Study in Sequence Stratigraphy and Basin Dynamics*, vol. 252. Geological Society, London, Special Publication, pp. 1–14. <https://doi.org/10.1144/GSL.SP.2005.252.01.01>.
- Howlett, P.J., 1989. Late Jurassic–Early Cretaceous cephalopods of Eastern Alexander Island, Antarctica. *Special Papers in Palaeontology* 41, 5–72.
- Iba, Y., Sano, S.I., Mutterlose, J., 2014. The early evolutionary history of belemnites: new data from Japan. *PLoS One* 9, e95632. <https://doi.org/10.1371/journal.pone.0095632>.
- 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 Crimea. The international scientific conference on the Jurassic/Cretaceous boundary. *Proceedings volume*, Samara 52–59.
- Jeletzky, J.A., 1965. Taxonomy and Phylogeny of Fossil Coleoidea (= Dibranchiata). *Geological Survey of Canada paper* 65-2, 72–76.
- Jeletzky, J.A., 1946. Zur Kenntnis der oberkretazischen Belemniten. *GFF (Geol. Foren. Stockh. Forh.)* 68, 87–105.
- Jeletzky, J.A., 1966. Comparative Morphology, Phylogeny, and Classification of Fossil Coleoidea. The University of Kansas Paleontological Contributions. University of Kansas Paleontological Institute, Lawrence, pp. 1–162. *Mollusca Article* 7.
- Jeletzky, J.A., 1983. Macroinvertebrate paleontology, biochronology, and paleoenvironments of Lower Cretaceous and Upper Jurassic rocks, deep sea drilling Project hole 511, Eastern Falkland Plateau. DSDP report 35, 951–975. <https://doi.org/10.2973/dsdp.proc.71.135.1983>.
- Kietzmann, D.A., Vennari, V.V., 2013. Sedimentología y estratigrafía de la Formación Vaca Muerta (Tithoniano-Berriasiano) en el área del cerro Domuyo, norte de Neuquén, Argentina. *Andean Geol.* 40, 41–65. <https://doi.org/10.5027/andgeoV40n1-a02>.
- 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 basinal Tithonian–Berriasian section of the Vaca Muerta Formation, Las Tapaderas, southern Mendoza Andes, Argentina. *J. S. Am. Earth Sci.* 109, 103267. <https://doi.org/10.1016/j.jsames.2021.103267>.
- 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: Montenari, M. (Ed.), *Stratigraphy & Timescales*, vol. 3. Elsevier, pp. 328–355. <https://doi.org/10.1016/bs.sats.2018.07.003>.
- Kietzmann, D.A., Palma, R.M., 2011. Las tempestitas peloidales de la Formación Vaca Muerta (Tithoniano-Valanginiano) en el sector surmendocino de la Cuenca Neuquina, Argentina. *Lat. Am. J. Sedimentol. Basin Anal.* 18, 121–149.
- Kietzmann, D.A., Palma, R.M., Riccardi, A.C., Martín-Chivelet, J., López-Gómez, J., 2014. Sedimentology and sequence stratigraphy of a Tithonian–Valanginian carbonate ramp (Vaca Muerta Formation): a misunderstood exceptional source rock in the southern Mendoza area of the Neuquén basin, Argentina. *Sediment. Geol.* 302, 64–86. <https://doi.org/10.1016/j.sedgeo.2014.01.002>.
- Krantz, F., 1928. La Fauna del Tithono superior y medio en la parte meridional de la provincia de Mendoza. *Academia Nacional de Ciencias, Córdoba, Actas* 10, 9–57.
- Leanza, A.F., 1967. Anotaciones sobre los fósiles Jurásico-Cretácicos de Patagonia Austral (Colección Feruglio) conservados en la Universidad de Bologna. *Acta Geol. Lilloana* 9, 121–186.
- Leanza, H.A., Vennari, V.V., Aguirre-Urreta, B., Concheyro, A., Lescano, M., Ivanova, D., Kietzmann, D.A., López-Martínez, R., Martz, P.A., Paolillo, M.A., Guler, V., Pujana, I., Paz, M., 2020. Relevant marine paleobiological markers of the Vaca Muerta Formation. *APG Memoir* 121, 61–98. <https://doi.org/10.1306/13682224M1203830>.
- Legarreta, L., Uliana, M.A., 1991. Jurassic–Cretaceous Marine Oscillations and Geometry of Back-Arc Basin Fill, Central Argentine Andes, vol. 12. *International Association of Sedimentologists, Special Publication*, pp. 429–450. <https://doi.org/10.1002/9781444303896.ch23>.
- Lena, L., López-Martínez, R., Lescano, M., Aguirre-Urreta, B., Concheyro, A., Vennari, V., Naipauer, M., Samankassov, E., Pimentel, M., Ramos, V.A., Schaltegger, U., 2019. High-precision U-Pb ages in the early Tithonian to early Berriasian and implications for the numerical age of the Jurassic–Cretaceous boundary. *Solid Earth* 10, 1–14. <https://doi.org/10.5194/se-10-1-2019>.
- Lescano, M., Vennari, V., López-Martínez, R., Concheyro, A., Aguirre-Urreta, B., Pellenard, P., Martínez, M., 2022. New Tithonian Biostratigraphic Data from the Neuquén Basin, Argentine Andes: A Contribution from the Southern Hemisphere. *11th International Congress on the Jurassic System*, Budapest, p. 68.
- Lukeneder, A., Surmik, D., Gorzelak, P., Niedźwiedzki, P., Brachanec, T., Salamon, M., 2020. Bromalites from the Upper Triassic Polzberg section (Austria): insights into trophic interactions and food chains of the Polzberg palaeobiota. *Nature Scientific Reports* 10, 20545. <https://doi.org/10.1038/s41598-020-77017-x>.
- Medina, F.A., Riccardi, A.C., 2005. Desmoceratidae, Silesitidae and Kossmaticeratidae (Ammonitida) from the upper Aptian–Albian of Patagonia (Argentina). *Revue de Paléobiologie, Genève* 24, 251–286.
- Mironenko, A.A., Rogov, M.A., 2015. First direct evidence of ammonoid ovoviviparity. *Lethaia* 49, 245–260. <https://doi.org/10.1111/let.12143>.
- Mitchell, F.S., 2015. A reassessment of the validity and affinities of *Belemnites sulcatus* Miller, 1826, *Belemnopsis* Edwards in Gray, 1849, and *Belemnopsis* Bayle, 1878. *Carnets Géol.* 15, 31–39. <https://doi.org/10.4267/2042/56399>.
- Monks, N., Hardwick, J.D., Gale, A.S., 1996. The function of the belemnite guard. *Palaeontol. Z.* 70, 425–431.
- Montfort, D. De, 1808. *Conchyliologie systématique et classification méthodique des Coquilles. Coquilles univalves, cloisonnées*. Tome I. Chez F. Schoell, Paris, p. 410.
- Mutterlose, J., 1986. Upper Jurassic belemnites from the Orville coast, Western Antarctica, and their palaeobiogeographical significance. *Br. Antarct. Surv. Bull.* 70, 1–22.
- Mutterlose, J., 1988. Migration and evolution patterns in Upper Jurassic and Lower Cretaceous belemnites. In: Wiedmann, J., Kullmann, J. (Eds.), *Cephalopods: Present and Past*. Schweizerbart, Stuttgart, pp. 525–537.
- Mutterlose, J., 1990. A belemnite scale for the Lower Cretaceous. *Cretac. Res.* 11, 1–15. [https://doi.org/10.1016/S0195-6671\(05\)80039-4](https://doi.org/10.1016/S0195-6671(05)80039-4).
- Mutterlose, J., 1992. Early Cretaceous belemnites from the East Indian Ocean and their palaeobiogeographic implications. *Proc. Ocean Drill. Progr. Sci. Results* 123, 443–450. <https://doi.org/10.2973/odp.proc.sr.123.123.1992>.

- 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. *Pap. Paleontol.* e1455.
- Naef, A., 1922. Die Fossilen Tintenfische. Gustav Fischer, Jena, p. 322.
- Naipauer, M., Comerio, M., Lescano, M., Vennari, V., Aguirre-Urreta, M.B., Pimentel, M., Ramos, V.A., 2020. The Huncal Member of the Vaca Muerta Formation, Neuquén Basin of Argentina: insight into biostratigraphy, structure, U-Pb detrital zircon, ages and provenance. *J. S. Am. Earth Sci.* 100, 102567 <https://doi.org/10.1016/j.jsames.2020.102567>.
- Olivero, E.B., 1987. Cefalópodos y bivalvos titonianos y hauterivianos de la Formación Lago La Plata, Chubut. *Ameghiniana* 24, 181–202.
- Parent, H., Scherzinger, A., Schweigert, G., 2011. In: The Tithonian–Berriasian Ammonite Fauna and Stratigraphy of Arroyo Cieneguita, Neuquén–Mendoza Basin. *Boletín del Instituto de Fisiografía y Geología* 79, 21–94.
- Parrish, J.T., 1992. Jurassic climate and oceanography of the Pacific region. In: Westermann, G.E.G. (Ed.), *The Jurassic of the Circum-Pacific*. Cambridge University Press, Cambridge, pp. 365–379.
- Riccardi, A.C., 1971. Estratigrafía en el Oriente de la Bahía de La Lancha, Lago San Martín, Santa Cruz, Argentina. *Revista del Museo de la Plata. Sección Geología* 7, 245–318.
- Riccardi, A.C., 1976. Paleontología y edad de la Formación Springhill. 1° Congreso Geológico Chileno, Santiago de Chile, Actas 1, 41–56.
- Riccardi, A.C., 1977. Berriasian invertebrate faunas from the Springhill Formation in southern Patagonia. *Neues Jahrbuch für Geologie und Paläontologie* 155, 216, 152.
- Riccardi, A.C., 1988. In: *The Cretaceous System of Southern South America*. Geological Society of America Memoir 168, 1–161.
- Riccardi, A.C., 1991. Jurassic and Cretaceous marine connections between the southeast Pacific and Tethys. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 87, 155–189. [https://doi.org/10.1016/0031-0182\(91\)90134-D](https://doi.org/10.1016/0031-0182(91)90134-D).
- Riccardi, A.C., 2008. El Jurásico de la Argentina y sus amonites. *Rev. Asoc. Geol. Argent.* 63, 625–643.
- Riccardi, A.C., 2015. Remarks on the Tithonian–Berriasian ammonite biostratigraphy of west-central Argentina. *Volumina Jurassica* 13, 23–52.
- Riccardi, A.C., Damborenea, S.E., Mancenido, M.O., Leanza, H.A., 2011. Megainvertebrados jurásicos y su importancia geobiológica. In: Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C., Vallés, J.M. (Eds.), *Geología y Recursos Naturales de la Provincia del Neuquén*. Asociación Geológica Argentina, Buenos Aires, pp. 441–464.
- Riegraf, W., 1980. Revision der Belemniten der Schwäbischen jura. Part 7. *Palaeontograph. Abteilung* 169, 128–206.
- Riegraf, W., 1999. Taxonomic status of the belemnite genus *Belemnopsis* Bayle 1878. *Paläontol. Z.* 73, 59–76.
- Riley, T.R., Crame, J.A., Thomson, M.R.A., Cantrill, D.J., 1997. Late Jurassic (Kimmeridgian–Tithonian) macrofossil assemblage from Jason Peninsula, Graham Land: evidence for a significant northward extension of the Latady Formation. *Antarct. Sci.* 9, 434–442.
- Smith, A.G., Smith, D.G., Funnell, B.M., 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge University Press, Cambridge, p. 99.
- 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. *Geological Survey of New Zealand, Palaeontological Bulletin* 36, 1–233.
- Stevens, G.R., 1973. Jurassic belemnites. In: Hallam, A. (Ed.), *Atlas of Palaeobiogeography*. Elsevier, New York, pp. 259–274.
- Stevens, K., in press. Belemnite phylogeny and decline during the mid-Cretaceous. *BioRxiv*. <https://doi.org/10.1101/2021.10.11.463885>.
- Stinnesbeck, W., Frey, E., Rivas, L., Pardo Pérez, J., Leppe Cartes, M., Salazar Soto, C., Zambrano Lobos, P., 2014. A Lower Cretaceous ichthyosaur graveyard in deep marine slope channel deposits at Torres del Paine National Park, southern Chile. *Geology Society of America Bulletin* 126, 1317–1339. <https://doi.org/10.1130/B30964.1>.
- Stolley, E., 1911. Beiträge zur Kenntnis der Cephalopoden der Norddeutschen Unteren Kreide I: die Belemniten der Norddeutschen Unteren Kreide. *Geologische und paläontologische Abhandlungen: Neue Folge* 10, 201–272.
- Stolley, E., 1928. *Heliceras* Dana als erhaltungszustand von Belemnopsis. *Neues Jahrbuch 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 replacement of associations of mollusc plankton and giant filter feeders after the Cretaceous? *PeerJ* 6, e4219. <https://doi.org/10.7717/peerj.4219>.
- Tate, R., 1867. On some secondary fossils from South Africa. *Q. J. Geol. Soc. Lond.* 23, 139–175.
- Vennari, V., 2011. Estudio preliminar del registro de heridas letales y subletales en amonoides del Jurásico Tardío (Tithoniano) de Mendoza. 18° Congreso Geológico Argentino, Neuquén, Actas, pp. 1494–1495.
- Vennari, V.V., Aguirre-Urreta, M.B., 2019. Intraspecific variability, biostratigraphy and paleobiological significance of the Southern Gondwana ammonoid genus *Lythopliotes* Spath. *J. Paleontol.* 93, 702–726. <https://doi.org/10.1017/jpa.2019.1>.
- Vennari, V.V., Lescano, M.A., Naipauer, M., Aguirre-Urreta, M.B., Concheyro, A., Shaltegger, U., Armstrong, R., Pimentel, M., Ramos, V.A., 2014. New constraints in the Jurassic/Cretaceous boundary in the High Andes using high precision U-Pb data. *Gondwana Res.* 26, 374–385. <https://doi.org/10.1016/j.gr.2013.07.005>.
- Vicente, J.C., 2005. Dynamic paleogeography of the Jurassic Andean Basin: patterns of transgression and localization of main straits through the magmatic arc. *Rev. Asoc. Geol. Argent.* 60, 221–250.
- Weaver, C., 1931. *Paleontology of the Jurassic and Cretaceous of West Central Argentina*, 1. *Memoirs of the University of Washington*, pp. 1–496.
- Willey, I.E., 1973. Belemnites from South-Eastern Alexander Island. II, the occurrence of the Family Belemnopsidae in the Upper Jurassic and Lower Cretaceous. *Bulletin of the British Antarctic Survey* 36, 33–59.
- Zatón, M., Salamon, M., 2008. Durophagus predation on middle Jurassic Molluscs, as evidenced from shell fragmentation. *Palaeontology* 51 (1), 63–70. <https://doi.org/10.1111/j.1475-4983.2007.00736.x>.