Lamellorthoceratid cephalopods in the cold waters of southwestern Gondwana: Evidences from the Lower Devonian of Argentina

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Cichowolski, M. and Rustán, J.J. 2020. Lamellorthoceratid cephalopods in the cold waters of southwestern Gondwana: Evidences from the Lower Devonian of Argentina. *Acta Palaeontologica Polonica* 65 (2): 305–312.

Based on three specimens assigned to *Arthrophyllum* sp., the family Lamellorthoceratidae is reported from the Lower Devonian Talacasto Formation in the Precordillera Basin, central western Argentina. These Devonian cephalopods have been known only from low to mid palaeolatitudes and its presence in the cold water settings of southwestern Gondwana is notable. A nektonic mode of life, not strictly demersal but eventually pelagic, with a horizontal orientation of the conch is proposed for adults lamellorthoceratids, whereas a planktonic habit is suggested for juvenile individuals. These features would had allow their arrival to this southern basin, explaining their unusual presence in the Malvinokaffric Realm, and reinforcing the need of re-evaluate the distribution pattern of several groups of cephalopods.

Key words: Cephalopoda, Lamellorthoceratidae, *Arthrophyllum*, Palaeozoic, Talacasto Formation, Malvinokaffric Realm, Precordillera Basin, Argentina.

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Received 1 November 2019, accepted 3 January 2020, available online 2 April 2020.

Introduction

The family Lamellorthoceratidae Teichert, 1961 is a small group of Early to Middle Devonian non-ammonoid cephalopods possessing orthoconic shells characterized by abundant cameral deposits composed of more or less closely spaced sets of radial lamellae. They have been exclusively known, along with other cephalopod taxa, from the warm-waters of low to middle paleolatitudinal regions, including Morocco (e.g., Termier and Termier 1950; Kröger 2008; Pohle and Klug 2018), Algeria (Le Maitre 1952), France (e.g., Teichert 1961; Babin 1966), Germany (e.g., Beyrich 1850; Bandel and Stanley 1989), Russia (Zhuravleva 1961; Zhuravleva and Doguzhaeva 2004), North America, Turkey (e.g., Stanley and Teichert 1976; Bandel and Stanley 1989), and Japan (Niko 1991). Other groups with restricted known palaeolatitudinal distribution are the actinoceratids, discosorids, and ascoceratids (e.g., Kröger 2013). For the last group, new findings from the Paraná Basin (Brazil) have recently shown that their distribution pattern should be revised (Cichowolski et al. 2018).

By contrast, the cold water settings of the Early to Middle Devonian austral circumpolar region known as the Malvinokaffric Realm (Richter and Richter 1942) was claimed to have an extremely poor cephalopod record (Boucot and Racheboeuf 1993). This major Devonian paleobiogeographic unit corresponds to southwestern Gondwanan marine basins and is recognized in the modern regions of South Africa, Ghana, Antarctica, and southern South America. It is certainly characterized by a high level of supra-generic endemic taxa (namely trilobites) and a scarcity (or absence) of some typical Palaeozoic groups such as stromatoporoids, graptolites, conodonts, and goniatites (Boucot and Racheboeuf 1993).

Here, we report the first record of lamellorthoceratids from the Devonian of Argentina. This discovery is significant in this scenario, especially with regard to the alleged scarcity of Malvinokaffric cephalopods was recently discussed in relation to the first records of bactritoids from the Devonian of South America (Cichowolski and Rustán 2017), a group with evolutionary significance and a wider distribu-

https://doi.org/10.4202/app.00699.2019

tion than previously recognised. Based on the preservation of the specimens and previous studies, the distribution and mode of life of lamellorthoceratids are discussed.

Institutional abbreviations.—CEGH-UNC, Cátedra de Estratigrafía y Geología Histórica-Universidad Nacional de Córdoba, Córdoba, Argentina; CICTERRA, Centro de Investigaciones en Ciencias de la Tierra, CONICET-Universidad Nacional de Córdoba, Córdoba, Argentina; CIPAL, Centro de Investigaciones Paleobiológicas, Córdoba, Argentina.

Material and methods

The material described herein is housed at the Centro de Investigaciones en Ciencias de la Tierra (CICTERRA) with the prefix CEGH-UNC. We studied three specimens from two collecting sites in the San Juan Province (Fig. 1): Quebrada de los Algarrobos at GPS coordinates 31°11’21.4” S, 68°49’18.5” W (CEGH-UNC 27426), and Loma de los Piojos at GPS waypoint 30°17’2.6” S, 68°46’34.86” W (CEGH-UNC 27427-28). CEGH-UNC 27426 is an incomplete phragmocone preserved within a nodule. It was longitudinally cut and polished to see internal details of the siphuncle and cameral deposits. CEGH-UNC 27427 is a small part of the phragmocone preserved without shell wall, so that the internal lamellae can be seen in three dimensions filling the whole chamber space, and forming an internal mould. CEGH-UNC 27428 consists of three separate fragments: one is an external mould with a small part of the internal mould of one chamber (mainly consisting in cameral deposits), and the others consist of internal moulds of phragmocone chambers, composed of somewhat altered cameral lamellar deposits.

Specimens were prepared using pneumatic air scribes and needles under a binocular microscope. They were photographed dry and also submersed in water or alcohol (in particular the cut and polished specimen). We used a Canon Power Shot S50 digital camera mounted on a Leica MZ75 binocular. All measurements were taken using digital calipers with a resolution of 0.1 mm. The measurements were taken according to Evans (2005).

Geological setting

In the context of the Andean region of southern South America, the area from which these specimens were recorded corresponds to the Argentine Precordillera Basin in west-central Argentina. The studied specimens come from the Lower Devonian Talacasto Formation (Padula et al. 1967), widely exposed in San Juan Province (Fig. 1), but with isolated outcrops in the northern La Rioja Province (Rustán et al. 2011). The succession is composed of intensely bioturbated greenish-gray mudstone with intercalated beds of fine-grained sandstone. It typically consists of dark argillaceous horizons basally (black to greenish mudstone and shale), passing upwards into sand-rich horizons (Fig. 1). This unit corresponds to a muddy shelf depositional system developed during a high stand system tract (Astini 1991). In San Juan Province, this unit increases in thickness from the south, where it is 300 m thick (in the Talacasto section), to more than 1000 m in the north (near Río Jáchal, Fig. 1). It overlies the mainly late Silurian shelf deposits of the Los Espejos Formation, and underlies the turbiditic deposits of the Early to, probably, Middle Devonian Punta Negra Formation (Bracaccini 1950; Bustos and Astini 1997). The Talacasto Formation has yielded the bulk of Devonian fossils described from Argentina. As in other closely related Early to Middle Devonian Malvinokaffric basins, conodonts and graptolites are absent and goniatites are extremely rare. Thus, an early Lochkovian to Emsian age has been proposed for this unit based on brachiopod and palynological data (Benedetto et al. 1992; Herrera 1993, 1995a, b; Lé Herissé et al. 1996; Herrera and Bustos 2001; García-Muro et al. 2014, 2018). Further precision in relation to the stratigraphy and age of the cephalopod-bearing horizons were provided by Cichowolski and Rustán (2017).

CEGH-UNC 27426 came from the horizon corresponding to that described by Carrera et al. (2013: fig. 2) where branched corals in life position are present. It is in the green muddy lower interval of the unit, about 70 m above the boundary with the underlying Los Espejos Formation. García Muro et al. (2014) proposed a most probable Pragian age for this stratigraphic position. CEGH-UNC 27427 and CEGH-UNC 27428 came from the Loma de los Piojos section, approximately 7 km to the southwest of the city of Jáchal (Fig. 1). They were collected from a horizon nearly 5 m above the Keidel’s bed (see Cichowolski and Rustán 2017). These specimens originate from a slightly more indurate and darker portion of a massive greenish-brown dark muddy bed (Fig. 1). Although this was previously considered to be Emsian in age, it is probably Pragian in age, according to recent palynological evidences reported by García Muro et al. (2018).

Systematic palaeontology

Class Cephalopoda Cuvier, 1797

Subclass Orthoceratia Teichert, 1967

Order Astroviida Zhuravleva and Doguzhaeva, 2004

Suborder Pallioceratina Marek, 1998

Remarks.—The assignment of the family Lamellorthoceratidae to a higher rank group lacks a general consensus. Initially treated as Michelinoceratida (= Orthoceratida) by Teichert (1961), Kröger (2008), followed by Klug et al. (2008a) and Pohle and Klug (2018), considered lamellorthoceratids as Lituitida based on the presence of epichoanitic deposits. Marek (1998), and thereafter Zhuravleva and Doguzhaeva (2004), included this family in the order Pallioceratida Marek, 1998, arguing that the presence of a cameral mantle was responsible for the formation of the lamellar deposits, as

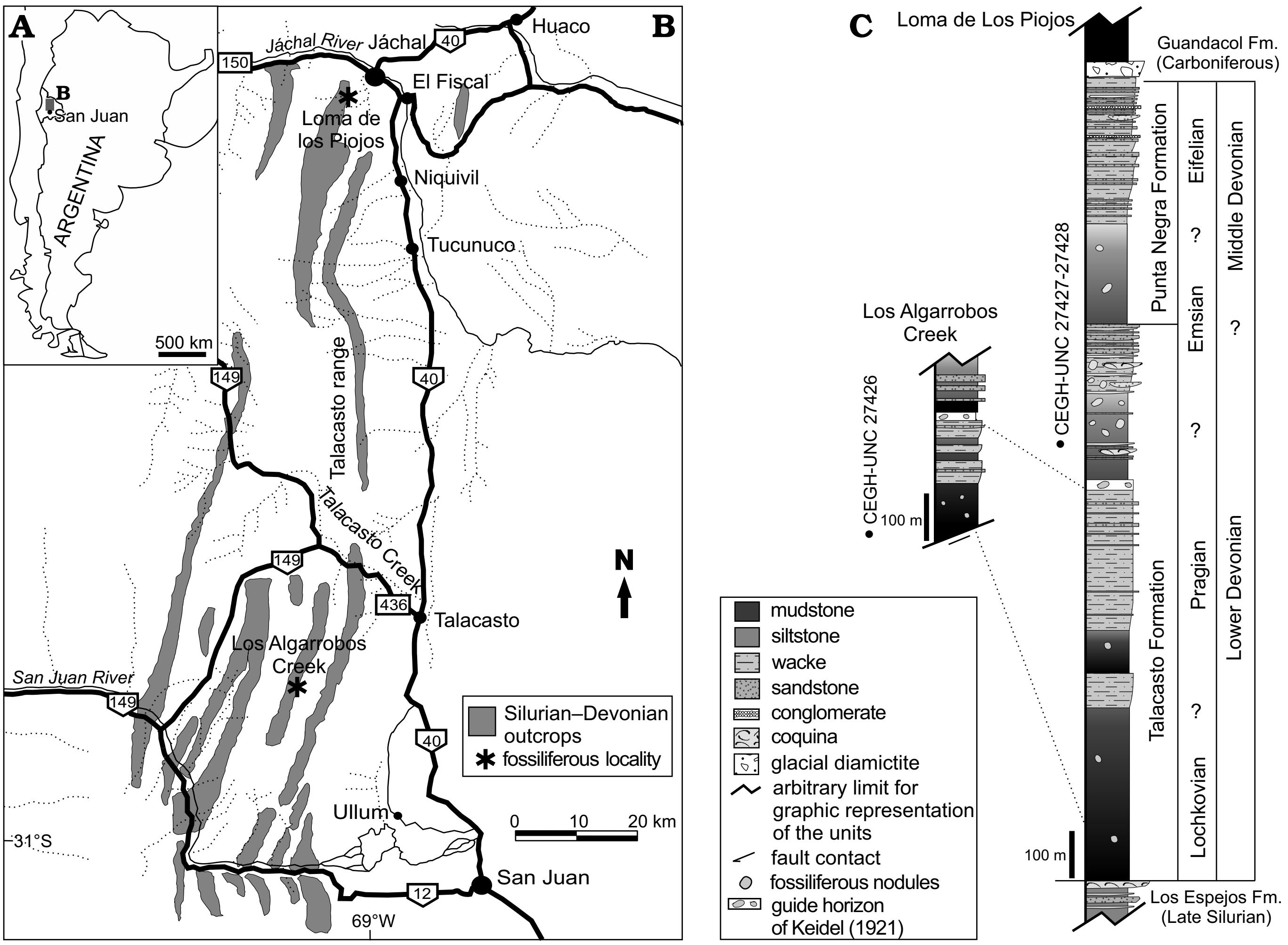

Fig. 1. Location map of the studied fossil localities and middle Palaeozoic outcrops (**A**, **B**) and stratigraphic sections with fossil occurrences indicated (**C**).

well as the puncture connecting rings. Kröger (2008) considered the erection of a taxon based on a so-called physiological hypothesis to be invalid. In addition, he argued that longitudinal lamellae were present across disparate groups of cephalopods, and could not therefore be regarded as a unique character marking out the pallioceratids. As our material does not add new evidence to solve this dispute, we decided to follow the taxonomic scheme currently proposed by King and Evans (2019) for the future revised part K of the Treatise.

Family Lamellorthoceratidae Teichert, 1961

Remarks.—The controversy surrounding this family concerns not only the higher taxonomic rank including it, but also the generic level. While some researchers considered the Lamellorthoceratidae as more or less monogeneric (e.g., Babin 1966; Bandel and Stanley 1989; Niko 1991; Kröger 2008), others proposed several genera to be included in it (e.g., Sweet 1964; Stanley and Teichert 1976; Zhuravleva and Doguzhaeva 2004). The Lamellorthoceratidae was first established in order to unite the genera *Arthrophyllum* Beyrich, 1850, and *Lamellorthoceras* Termier and Termier, 1950. Additional genera were described subsequently: *Gorgonoceras* Zhuravleva, 1961, from the Middle Devonian of the Central Urals, *Coralloceras* Balashov and Zhuravleva, 1962, from the Lower and Middle Devonian of Algeria, *Esopoceras* Stanley and Teichert, 1976, from the Lower Devonian of USA, *Plicatoceras* Niko, 1991, from the Lower Devonian of Japan, *Nucleoceras* Kolebaba, 1999, from the Ludlow of the Czech Republic, and *Syndikoceras* Zhuravleva and Doguzhaeva, 2004, from the Lower Devonian of the Russian Arctic and the Middle Devonian of North Africa. The validity of these genera has been disputed (e.g., Sweet 1964; Babin 1966; Bandel and Stanley 1989; Niko 1991; Zhuravleva and Doguzhaeva 2004). While Zhuravleva and Doguzhaeva (2004) proposed five lamellorthoceratid genera (*Arthrophyllum*, *Lamellorthoceras*, *Esopoceras*, *Coralloceras*, and *Syndikoceras*), based on the ultrastructure of shell wall and internal parts, apical angle, septal necks, ornamentation, etc., others considered these traits as having a low taxonomic value, being rather variable intraspecifically, and through ontogeny (e.g., Bandel and Stanley 1989). With the exception of newly proposed taxa, Zhuravleva and Doguzhaeva (2004) did not provide diagnosis of each genus. It is therefore difficult make comparisons between these genera in terms of Zhuravleva's and Doguzhaeva's (2004) work.

Genus *Arthrophyllum* Beyrich, 1850

Type species: *Orthoceratites crassus* Rœmer, 1844; Wissenbach Slate, Eifelian of Schalke, Harz Mountains, Germany.

Arthrophyllum sp.

Fig. 2.

Material.—Three specimens: CEGH-UNC 27426, an incomplete phragmocone preserved within a nodule, from the Quebrada de los Algarrobos locality, Pragian; CEGH-UNC 27427 and CEGH-UNC 27428, moulds of incomplete phragmocones from the Loma de los Piojos locality, Pragian or Emsian.

Description.—CEGH-UNC 27426 is an incomplete phragmocone with seven complete chambers preserved (Fig. 2A). In order to orient the specimens we assume the side with cameral deposits is the ventral side. This specimen is 40 mm long, with a dorsoventral apical diameter of 11.4 mm and a lateral apical diameter of 9.3 mm, indicating a slightly compressed cross section (compression ratio 0.8). Adorally, the dorsoventral diameter is 13.2 mm and the lateral diameter is 11.7 mm (compression ratio 0.88). In the dorsoventral plane, therefore, the expansion rate is 0.045, and the apical angle is 2.6°. The lateral expansion rate is 0.06 and the apical angle in that plane is 3.4°. The length of the chambers varies between 5 and 6 mm (cameral depth of ~0.4). The septal depth is ~0.28. The shell surface does not show ornamentation, neither does the external mould, although the most external layer is probably not preserved (Fig. 2A_6). The siphuncle diameter is 2 mm in a section of 11.4 mm (ratio 0.17). Its position is nearly central (Fig. 2A_1, A_2). In the longitudinal polished section, the septal necks appear to be orthochoanitic (Fig. 2A_3), with a length of ~1.6 mm within a chamber length of 5.4 mm (ratio 0.3). On one side of the section, the connecting rings are preserved, whereas on the other side they are not present (Fig. 2A_1–A_3). On the side where the connecting rings are preserved, the camerae are filled with very sinuous lamellar deposits along the length of the specimen. In the adapical camerae, the deposits are denser, while in the adoral camerae, the deposits are more open, with spaces being visible between the lamellas (Fig. 2A_1). However, on the opposite side of the conch, lamellar deposits are seen to be developed at the adapical end, where the partial removal of the septum facilitates their visibility within the lumen of the camera (Fig. 2A_7). In the other chambers, cameral deposits are present but much less developed, thinly covering the septa as epi- and hyposeptal deposits, as well as occasionally covering the septal necks as epichoanitic deposits (Fig. 2A_3). The counterpart of the longitudinal section is a sagital section does not include the siphuncle. The ventral side of the chambers consists of insipient lamellar deposits that develop from the shell margin into the chamber lumen towards the siphuncle.

CEGH-UNC 27427 is a small phragmocone fragment, consisting of one chamber and part of a second chamber, slightly compacted due to taphonomic processes, and without the shell wall (Fig. 2B). The chamber filling consists of radial lamellae, which are recrystallized. They are straighter near the center and more sinuous towards the margins (Fig. 2B_2, B_3). The siphuncle is not distinguishable in posterior view, and we cannot identify dorsal and ventral sides. The fragment is 9.3 mm long, 7.4 mm wide and 5.4 mm high adapically. Adorally the fragment is covered and impossible to be measured. The length of the only complete chamber is 5.7 mm.

CEGH-UNC 27428 is broken into three parts of a fragmentary phragmocone (Fig. 2C). One part is an external mould of some chambers, on which the sutures are visible (Fig. 2C_6). The external mould is included in a rock fragment, and contains a partial internal mould of a chamber in its apicalmost part, represented by the infill of the interlamellar spaces and of the siphuncle (Fig. 2C_5, C_6). The external-most part of the chamber space is empty, maybe due to lamellar dissolution (Fig. 2C_5). The external mould is 13.2 mm long and the apical part has a diameter of 4.7 mm. The sutures are straight and separated by ~3.5 mm. The infill in the apical part is 2.8 mm wide and shows the lamellar deposits lining the cameral surfaces of the siphuncle as well as the infill of the siphuncle itself. The siphuncle diameter is 0.8 mm (ratio with the conch diameter of 0.17) and is located more or less centrally.

The other two parts consist of an isolated chamber and one fragment of some (probably three) chambers that remain intact and are preserved without the external wall, the lamellar deposits are visible filling the entire space, with the siphuncle preserved in the middle (Fig. 2C_1–C_3). The larger portion consists of three chambers that represent the most adorally preserved part of the phragmocone. This fragment is 15 mm long and has been compacted in some parts (especially adorally). Therefore the diameters are not precise, and we cannot distinguish between the ventral and dorsal side (in any of the three fragments). The cross section appears to be almost circular. The apical diameter is ca. 5 mm, with a siphuncle diameter of 0.76 mm (0.15). The length of the chambers varies between 4 and 4.5 mm. The shape of the lamellar deposits is straight in the middle part of the chamber (adjacent to the siphuncle) and become more sinuous towards the shell wall, a trait that can be observed externally in this specimen. Although it is not possible to measure the apical angle accurately due to the compaction of the specimen, it is very low. The last part of this specimen to be described is an isolated chamber (that fits between the external mould and the previously described part). This is also preserved with the cameral deposits filling the entire space and without the shell wall. That infill is broken through the siphuncle, forming a “half-chamber”. Its length is ~5 mm, with similar measurement for the width and the siphuncle diameter being 1.2 mm (the relation with the cameral width being 0.2).

Remarks.—We consider that CEGH-UNC 27427 and CEGH-UNC 27428 probably represent the most adapical region of the conch, since lamellae entirely fill each chamber. By contrast, the most adoral chambers are usually partially devoid of cameral deposits (Bandel and Stanley 1989). CEGH-UNC 27426 corresponds to a more adoral region of the phragmocone,

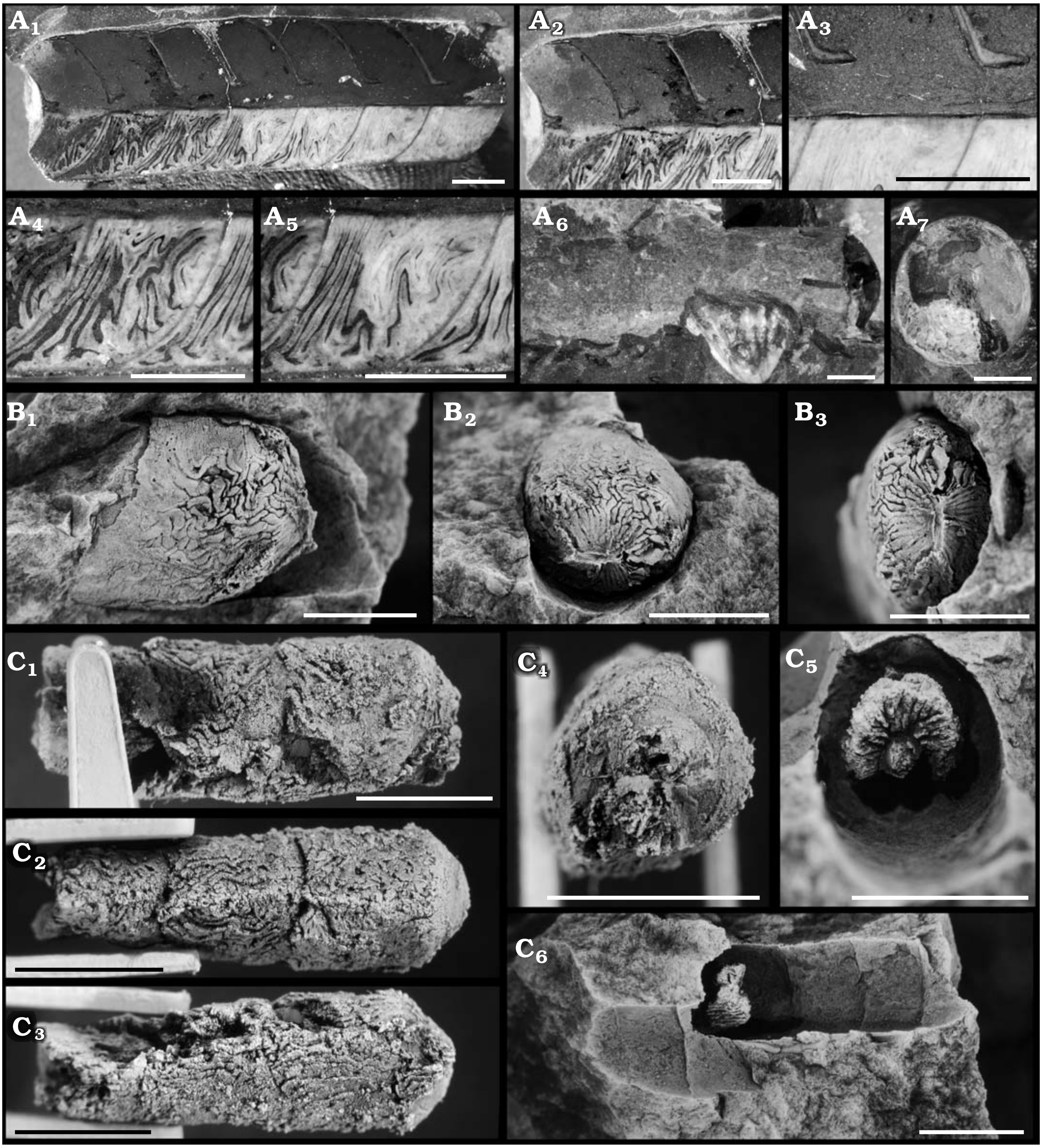

Fig. 2. Lamellorthoceratid cephalopod *Arthrophyllum* sp. from the Lower Devonian Talacasto Formation in the Precordillera Basin, Argentina. **A**. CEGH-UNC 27426, general view of the longitudinal section of the specimen (A_1), details showing a closer view of the lamellae and siphuncle structure (A_2–A_5), external view (A_6), specimen before cutting in posterior view (A_7). Note the lamellar deposits where the septum is removed. **B**. CEGH-UNC 27427, specimen in lateral view (B_1), posterior views with different orientations (B_2, B_3). **C**. CEGH-UNC 27428, lateral views of the internal mould with different orientations (C_1–C_3), internal mould in posterior view (C_4), external mould in anterior view, showing the lamellar deposits inside the apicalmost chamber (C_5), external mould in lateral view with the same lamellar deposits in the posterior part (C_6). Scale bars 5 mm.

since lamellae occupy the whole of the apical-most chambers but only the ventral part in the remaining chambers.

It is beyond the scope of this work to discuss the taxonomic composition of the family, or to evaluate the validity of previously described genera. Although we only have three incomplete specimens, two of which are deficiently preserved, we have assigned them to *Arthrophyllum* because the observed characters conform the concept of this genus according to e.g., Kröger (2008). We prefer to leave the material in open nomenclature because of the incompleteness and scarcity of these conchs. As mentioned in previous studies, the species assigned to *Arthrophyllum* show a high degree of internal variability in different respects, especially in the apical angle, shape of the cross section, chamber lengths, siphuncle position and shape of the lamellae. High variability was also documented for several traits through ontogeny (e.g., Babin 1966; Bandel and Stanley 1989).

Our specimens differ from *Arthrophyllum vermiculare* reported by Kröger (2008) and Pohle and Klug (2018) from the Pragian and Emsian of Morocco in having a lower apical angle and maybe longer phragmocone chambers. The growth pattern of lamellae is, however, similar, with a different development between dorsum and venter. It is also evident from one of their figures (Pohle and Klug 2018: fig. 10T) that the lamellae are present in adapical chambers but absent in adoral ones. *A. gracile* was considered to be a synonym of *A. vermiculare* by Kröger (2008), who suggested that it represented a different growth stage. He did not, however, comment on the species *A. crassus* (the type species), the type material of which is apparently lost (Zhuravleva and Doguzhaeva 2004).

Concluding remarks

In addition to the debate relating to the systematic position of the lamellorthoceratids, the interpretation of the anatomy and mode of life of these organisms are also controversial. Kröger (2008), based on what he regarded as a "morphological signal", included *Arthrophyllum* within a group denominated as "euorthocones", along with the Actinoceratida, Pseudorthoceratida, and Geisonoceratidae. The main characters that unite these taxa are "a comparatively high angle of expansion, wide siphuncle that may be expanded within the chambers and massive cameral and endosiphuncular deposits" (Kröger 2008: 19). Kröger (2008) proposed that these cephalopods could have been active vertical migrants, interpreting the large siphuncular surface and increased internal cameral surfaces as evidence of active buoyancy regulation. However, he also considered these traits as having a high metabolic cost, requiring active foraging, mainly from the benthic zone. Hence, Kröger (2008) hypothesized a probable demersal mode of life, similar to that of *Nautilus,* in contrast with the slender "angustocones" interpreted as planktonic dwellers at distal sites where food may have been scarce. The siphuncle of *Arthrophyllum* is not particularly wide (ratio siphuncle diameter to cameral diameter less than 0.2); the connecting rings are not inflated within the chambers, and the conchs are not all that big. Hence, *Arthrophyllum* is not a typical euorthocone, but neither does it fit clearly within the "angustocones" of Kröger (2008).

Further, lamellorthoceratids characteristically exhibit camerae filled by calcareous deposits arranged as convoluted lamellae of enigmatic origin and morpho-functional meaning. There are a variety of views regarding the origin and formation of the lamellar deposits (e.g., Seuss et al. 2012) and the role the siphuncle played in that process. Zhuravleva and Doguzhaeva (2004) explored the anatomy of the conchs in great detail, but did not consider the palaeoecology of the group. Bandel and Stanley (1989) proposed a sophisticated mechanism for the formation of cameral deposits in lamellorthoceratids. Different mechanisms for cameral deposits formation were proposed in general for orthocones (Mutvei 1956, 2002, 2018; Vermeij 2014), and in particular for the Astroviida (Teichert 1964; Marek 1998; Kolebaba 1999, 2002; Zhuravleva and Doguzhaeva 2004) where the cameral deposits were considered to have been deposited by extra-pallial fluid from cameral mantle that entered the camerae via the broken connecting rings that characterise these taxa. They suggested that the lamellae formed through the gradual encrustation of calcite layers over organic membranes secreted by the visceral mass of the body in the process of chamber formation. According to them, the cameral deposits are present only in those specimens that have more than 20–25 chambers, suggesting a high degree of fragmentation of our specimens. In turn, these authors considered the possibility that the conchs of lamellorthoceratids were internal with the cameral deposits acting as an "internal rostrum" equivalent to that of belemnoids, which (in case of being homologous) would situate the group closer to the coleoids within the phylogeny of cephalopods (Jenny et al. 2019; Hoffmann and Stevens 2019). Chamber deposits tend to occupy half of the shell, so they would define a dorso-ventral polarity. Bandel and Stanley (1989) suggested that the individual lamellorthoceratids probably lived in a manner similar to living *Sepia*, spending much time resting on the bottom where it fed. They concluded that, if these animals were ectocochleate, they could not swim backward in a stabilized way without fins that could guide the slender conch (Bandel and Stanley 1989: 408).

However, such a putative "internal rostrum" might not be homologous at all to the rostrum of belemnoids and would then just indicate that these organisms would have adopted "coleoid-like" strategies. We consider that, without additional support (as for example the microstructure of the shell), available evidences are inconclusive to consider lamellorthoceratids as phylogenetically closer to the coleoids than other Orthoceratia (sensu King and Evans 2019).

Furthermore, the interpretation of *Arthrophyllum* as endocochleate by Bandel and Stanley (1989) is based on the presence of putative long muscle attachment scars on the surface of the internal moulds. These muscle attachment scars, however, are questionable and strongly resemble drag bands as discussed by Klug et al. (2008b), thus casting doubt on the idea of *Arthrophyllum* being endocochleate. Unfortunately, our material is preserved in such a way that we cannot test the presence of such marks.

In this context, it is worth mentioning putative evidence of flexible deformation sensu Mutvei et al. (2012) in the shell wall of CEGH-UNC 27426, over the third chamber from the anterior part (see Fig. 2A_1, A_2,). Although this deformation might be explained by a very local diagenetic artifact in the opinion of one of us (JJR), it also may suggest the shell would be somewhat flexible due to high organic content, according to Harry Mutvei (personal communication 2019), which could imply the shell was internal.

Either endocochleate or ectocochleate, the cameral deposits as described suggest a horizontal orientation of the long body axis of *Arthrophyllum*, which would indicate a nektonic mode of life (Westermann 1999). Bandel and Stanley (1989: 400) documented shells of *Arthrophyllum* from the Early Devonian of the Hunsrück Slate, Germany, with the apical parts introduced visibly deeper in the sediment than their apertural portion, as is also known with some belemnoids (e.g., Schweigert 1999; Fürsich et al. 2007; Stevens et al. 2014; Jenny et al. 2019), as well as with some orthoceratids (Evans 1994: fig. 9.1–3). They concluded that they must have been buoyant to some degree before their drop to the sea floor. This suggests that *Arthrophyllum* was rather not strictly demersal and at least temporally inhabited the water column.

In any case, the conch of the hatchling as described by Bandel and Stanley (1989) is about 5 mm long, has a spherical initial chamber and perhaps one or two additional chambers. Accordingly, it could probably attain neutral buoyancy and lived as plankton (Peterman et al. 2019). In turn, this would explain the wide geographic distribution of the family, avoiding the restrictions of a chambered shell to certain depths.

Hence, an eurytopic (demersal and pelagic) inferred mode of life of adult *Arthrophyllum*, following an initial planktonic stage after hatching, would satisfactorily explain the observed widespread geographic distribution, that now includes the cold waters of the southwestern Gondwanan basins. In particular, the Devonian faunas from Argentina were described as typically Malvinokaffric (endemic to Southwestern Gondwana), although palaeobiogeographic information from different groups offers contrasting insights (e.g., Carrera et al. 2019). The lamellorthoceratids were unexpected in this scenario, because they were previously known only from warm waters regions (see Introduction herein). In addition, they were extremely scarce in faunal associations from this region and time, since our few specimens represent the current total of records of the group known, in spite of the fact that their thick cameral deposits probably enhanced their chances of preservation. Such a poor fossil record along with the absence of specific studies could have biased their previously known distribution pattern toward better studied regions of low palaeolatitudes. In this regard, an analogous case might be the bactritid cephalopods, recently reported from the same units in Argentina, which, although more abundant, also were unknown from high Gondwanan palaeolatitudes (Cichowolski and Rustán 2017). With the increasing knowledge of the austral cephalopod faunas, the distribution pattern of several other groups may need to be reevaluated.

Acknowledgements

MC is grateful to Harry Mutvei (Naturhistoriska Riksmuseet, Stockholm, Sweden) for his help with the interpretation of the specimens and bibliographic support. We thank Ralph T. Becker (University of Münster, Germany) for his advice about the presence of *Arthrophyllum*. Christian Klug (University of Zürich, Switzerland) and David H. Evans (Natural England, York, United Kingdom) are warmly acknowledged by their positive criticism on a previous version on this manuscript that highly improved its content. The present study was financed by the PUE granted to CICTERRA, PICT 2017-3095 and Universidad Nacional de La Rioja, PIC 2017-6993 granted to JJR. This is the contribution R-310 of the Instituto de Estudios Andinos “Don Pablo Groeber” (IDEAN).

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