

First record of a nonpaleotropical intejocerid cephalopod from Darriwilian (Middle Ordovician) strata of central Spain

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Abstract.—The order Intejocerida is an enigmatic, short-lived cephalopod taxon known previously only from Early– Middle Ordovician beds of Siberia and the United States. Here we report a new genus, *Cabaneroceras*, and a new species, *C. aznari*, from Middle Ordovician strata of central Spain. This finding widens the paleogeographic range of the order toward high-paleolatitudinal areas of peri-Gondwana. A curved conch, characteristic for the new genus, was previously unknown from members of the Intejocerida.

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Introduction

Intejocerids are a unique group of cephalopods, previously known only from Siberia (Balashov, 1960, 1962, 1968) and North America (Flower, 1964, 1968; VanCamp Gil, 1988). The most conspicuous characters of intejocerids are their long septal necks and their large siphuncles, which are filled with heavy lamellar deposits and which form a coral-like radial pattern in cross section. Like other cephalopods with long septal necks and heavy endosiphuncular deposits, intejocerids were relatively large for their time, with conch diameters reaching more than 100 mm. The isolated, several-decimeters-long steinkerns of the specimens described herein occur exclusively and in relatively high abundance at a single locality in the northern Ciudad Real province where they are found as the weathered residue of the soft mudstone of the Navas de Estena Formation. The steinkerns are often superficially eroded, and parts of the phragmocone, such as septa and outer shell, are not preserved. This obstructed the correct identification of these remains as cephalopods; they were originally interpreted as remains of hexactinellid dictyospongids (Gutiérrez-Marco et al., 2013, p. 596, fig. 4c; 2015a, p. 130, fig. 20A). Here we identify and describe these fossils for the first time in detail.

Geological setting

The examined material comes from three nearby localities in the central part of the Mounts of Toledo area, central Spain. Two of them situated within the Cabañeros National Park ('Los Medianiles' and 'Navaldelchorro'; see Gutiérrez-Marco et al., 2013, 2015a), and the third is immediately adjacent to same ('Cuesta de Valderuelo' section, see Reyes-Abril et al., 2010; Gutiérrez-Marco and Sá, 2017) (Fig. 1). This area belongs to the southern part of the Central Iberian Zone of the Iberian Massif, where large outcrops of Paleozoic fossiliferous rocks have been known since the middle half of the nineteenth century, including early reports and illustrations of Middle Ordovician cephalopods from both the Portuguese (Sharpe, 1849) and Spanish parts (Verneuil and Barrande, 1855).

All studied specimens come from a relatively narrow (5–45 m) stratigraphic interval of fossiliferous mudstones located at the lower third of the Navas de Estena Formation. The formation is a thick (up to 800 m) Darriwilian succession of massive dark mudstones and siltstones, partly with noduliferous horizons. The Navas de Estena Formation stratigraphically overlies the Lower Ordovician sandstone group comprising the Armorican Quartzite (Floian age) and the transitional Marjaliza beds (Floian–Dapingian ages).

From north to south, the fossiliferous localities in the Navas de Estena Formation are as follows:

Locality 'Navaldelchorro' is ~10,000 m to the south of Los Navalucillos (province of Toledo), east of Posturero's house on the left bank of La Calanchera stream $(39^{\circ}34'28''N, 4^{\circ}39'13.7''W)$. From this locality (Fig. 1.2a) came a single limonitic siphuncle (MGM-8196O), from mudstone beds ~100 m above the base of the Navas de Estena Formation.

Locality 'Cuesta de Valderuelo' is located ~5,600 m southeast from Navas de Estena, province of Ciudad Real ($39^{\circ}27'33''N$, $4^{\circ}28'31''W$). This locality corresponds to the bed NE-IIIA of the section (Reyes-Abril et al., 2010), from which some brachiopods (Reyes-Abril et al., 2010) and ichnofossils (Gutiérrez-Marco and Sá, 2017) were described and illustrated. The locality (Fig. 1.2b) is ~120–135 m above the base of the Navas de Estena Formation, in the southwestern flank of the Navas de Estena syncline. A single siphuncle preserved in shale was found at Cuesta de Valderuelo (MGM-8197O).

Locality 'Los Medianiles' is \sim 8,700 m east-northeast of Horcajo de los Montes, province of Ciudad Real, in the northern bank of La Chorrera stream south of Sierra de Valdefuertes (39°21'42.2"N, 4°33'41"W). From this locality (Fig. 1.2c), we have recovered about 90 fragments of isolated steinkerns of



Figure 1. Details of fossil localities and stratigraphy of the occurrences of *Cabaneroceras aznari* n. gen. n. sp., Middle Ordovician, central Spain. (1) General location of the studied area in the Iberian Peninsula (arrow). Gray area corresponds to the Neoproterozoic basement and Paleozoic rocks affected by the Variscan Orogeny (Iberian Massif). (2) Geological sketch map of a part of the central Mounts of Toledo region showing the position of the localities yielding *Cabaneroceras aznari* n. gen n. sp. (type locality in c). (3) Stratigraphic log of a part of the Navas de Estena Formation with the range of the new taxon.

intejocerid siphuncles. Only a few specimens of this collection occurred strictly in situ, \sim 80–85 m above the base of the Navas de Estena Formation. Most specimens have been collected on a labor field that gently dips south from the narrow outcropping area in the northern flank of La Chorrera syncline.

All three localities contain an assemblage of trilobites, brachiopods, mollusks, ostracods, and echinoderms, detailed by Gutiérrez-Marco et al. (2013, 2015a) for assemblages from Cabañeros National Park (see also Reyes-Abril et al., 2010; Gutiérrez-Marco and Sá, 2017) for the Cuesta de Valderuelo section. The occurrence of the graptolite *Didymograptus artus* Elles and Wood, 1901 plus some trilobites and brachiopods of regional biochronological significance, indicate an early Oretanian age to the assemblage according to the Bohemo-Iberian regional scale (Gutiérrez-Marco et al., 2015b, 2017), equivalent to an early mid-Darriwilian age at the global chronostratigraphy (Bergström et al., 2009).

Materials

The available material consists of isolated steinkerns of siphuncles, some with impressions of septal necks as molds within the sediment. The steinkerns consist of massive limonite and limonitic mudstone. No original calcareous material is preserved. Preserved parts of septa and septal necks are silicified. Differences in texture of the limonite allow tracing of the original characters of the siphuncle. The cross sections of the specimens are often slightly diagenetically deformed, which is indicated by the similarly deformed endosiphuncular lamellae. Imprints of bryozoan epizoans occur on the silicified shelly surface of the septal necks and on the surface of the steinkern itself (Figs. 2.8, 3.2) (specimen MGM-8181O).

Repository and institutional abbreviation.—The material described herein is deposited at the Museo Geominero of Madrid (MGM), which belongs to the Instituto Geológico y Minero de España / IGME (Spanish Geological Survey).

Systematic paleontology

Order Intejocerida Balashov, 1960 Family Padunoceratidae Balashov, 1960 Genus *Cabaneroceras* new genus

Type species.—Cabaneroceras aznari new species, by monotypy.



Figure 2. Siphuncular fragments of *Cabaneroceras aznari* n. gen. n. sp., from Navas de Estena Formation, Middle Ordovician, central Spain: (1) holotype, MGM-8183O, adapical view; (2) specimen MGM-8182O, adapical view; (3) specimen MGM-8184O, adapical view; (4) specimen MGM-8184O, dorsal view; (5) holotype, ventral view; (6) holotype, lateral view; (7) MGM-8186O, lateral view; (8) specimen MGM-8181O, ventral view, note horizontal traces of bryozoan overgrowth (see details in Fig. 3.2); (9) specimen MGM-8198O, lateral view; (10) specimen MGM-8187O, lateral view. (1-8) Upper scale bar = 10 mm; (9, 10) lower scale bar = 10 mm. All specimens were whitened with MgO before photography.

Diagnosis.—As for the type species by monotypy.

Occurrence.—Mounts of Toledo, Navas de Estena Formation, central Spain.

Etymology.—The name refers to the Cabañeros National Park in Spain. All currently known specimens of this genus are

from this territory or its immediate surroundings (Valderuelo section).

Remarks.—The placement of the new genus within the Padunoceratidae is justified by the occurrence of branching, irregularly shaped lamellar endosiphuncular deposits and the holochoanitic septal necks. *Cabaneroceras* n. gen. differs



Figure 3. Details of siphuncular fragments of *Cabaneroceras aznari* n. gen. n. sp. from Navas de Estena Formation, Middle Ordovician, central Spain. (1) Longitudinal cross section of steinkern of siphuncular fragment of *Cabaneroceras aznari*, specimen MGM-81990. Dark area is massive limonite and probably originally was calcareous endosiphuncular deposit. (2) Detail of traces of bryozoan epizoans on specimen MGM-81810 (marked with arrow). Specimen was whitened with MgO before photography. Scale bars = 10 mm.

from other intejocerids in having a curved conch, a relatively large angle of expansion, and relatively shallow concave siphuncular segments. The endosiphuncular lamellae of *Cabaneroceras* n. gen. are relatively widely spaced, similar to *Evencoceras*, from which they differ in forming an irregularly spaced ventral endosiphotube.

Cabaneroceras aznari new species Figures 2–4

Holotype.—MGM-8183O (Figs. 2.1, 2.5, 2.6, 4.4), Navas de Estena Formation, ~100 m above the base. Lower mid-Darriwilian, *Didymograptus artus* graptolite Zone, 'Los Medianiles' site in the northern flank of La Chorrera syncline, northeast of Horcajo de los Montes, province of Ciudad Real, central Spain.

Diagnosis.—Slightly curved brevicones with marginal siphuncle. Siphuncle at concave margin of conch curvature with slightly compressed or circular cross section with angle of expansion of $\sim 8^{\circ}-12^{\circ}$. Ventral margin of siphuncle slightly flattened. Siphuncle diameter about three to four times the septal distance. Siphuncular segments slightly concave. Septal necks holochoanitic. Endosiphuncular deposits longitudinally subdivided into ~ 25 irregularly spaced radially arranged lamellae separated by narrow, folded blades as interspaces. Lamellae laterally downcurved toward the ventral side forming an endosiphuncular tube with an irregularly compressed semicircular shape in cross section at ventral side of siphuncle.

Occurrence.—As for genus, by monotypy.

Description.—The holotype is a fragment of a siphuncle, slightly diagenetically laterally compressed with а dorsoventral diameter of 46-73 mm, a width of 38-60 mm, and a length of 135 mm, expanding with an angle of 11.5° dorsoventrally. The siphuncle is slightly curved, with the ventral side less curved than the dorsal side. Traces of the septa and septal necks are visible on the steinkern only on the dorsal side of the holotype, indicating a slightly concave shape of the siphuncular segments and an at least holochoanitic length of the septal necks that ranges over the entire height of chamber. The former position of the septa is visible around the surface of the holotype as rounded ridges. These ridges are oblique toward the growth axis, with an angle that is $\sim 20^{\circ}$ from the angle perpendicular to the growth axis and slopes toward the dorsal (antisiphuncular) side of the conch. In places where the steinkern exposes the inner surface



Figure 4. Camera lucida drawings of cross-section view of siphuncle steinkerns of *Cabaneroceras aznari* n. gen. n. sp. from Navas de Estena Formation, Middle Ordovician, central Spain. The radial structures are interpreted here either as interspaces between folded siphuncles or as endosiphoblades (sensu Flower, 1964). All figured specimens are arranged in a position with assumed ventral side down. Note the different orientations and grades of diagenetic compression, which reflect the original position in the sediment. (1) Specimen MGM-81880. (2) Specimen MGM-81890. (3) Specimen MGM-81820. (4) Holotype, specimen MGM-81830. (5) Specimen MGM-81800.

of siphuncular deposits (which is the outer surface of the siphuncle), ~25 lamellae are visible as broad bands divided by thin (<1 mm) longitudinal grooves. In cross section, these lamellae are visible, reaching into a depth of up to 20 mm of the siphuncle, where they are radially arranged and irregularly folded, leaving a central space or tube filled with massive limonite. The central tube is eccentrically positioned within the siphuncle with a ventral contact to the siphuncular wall and irregularly compressed, with semicircular cross section.

Specimen MGM-8184O (Fig. 2.4) is a part of a steinkern of a siphuncle with a maximum diameter of 71 mm; it has a slightly compressed cross section with particularly well-preserved holochoanitic septal necks; at its ventral side, it is in contact with the outer shell, which in its best-preserved parts is smooth. Details of potential ornamentation are not visible, probably due to preservation.

Etymology.—The name was given in honor of Alejandro Aznar, the owner of the private property of the type locality, supporter of the 11th International Symposium on the Ordovician System, Spain, 2011, and producer of the fine Rioja wine 'Marqués de Riscal.'

Materials.—Seventeen paratype specimens (MGM-81800–MGM-81890, MGM-81910–MGM-81950, MGM-81980, and MGM-81990) were available for closer examination. Fourteen additional, less valuable or more incomplete specimens, were deposited in the same collection (MGM-81960–MGM-81970, MGM-82000–MGM-82060, and MGM-82250–MGM-82300).

Remarks.—The material of *Cabaneroceras aznari* n. gen. n. sp. consists exclusively of fragments of siphuncles. Many of the specimens are also diagenetically slightly deformed. This fragmentary preservation constrains the diagnosis of this new species to the preserved internal characters. However, the erection of a new species and genus is justified because the known internal features are unique (see discussion of *Cabaneroceras* n. gen.) and unknown in this combination from any other padunoceratid cephalopod.

Discussion

Little can be said about the taphonomy and depositional history of the material. The now limonitic mineralogy of the steinkerns probably represents a primary deposition and burying under anoxic conditions with pyrite (FeS) as replacement of organic rich spaces, and later oxidation and dissolution of the calcareous deposits. Alternatively, massive pyrite may have preferentially replaced the shelly material rich in organics (e.g., nacre), while carbonate-poor inorganics may have been replaced by crystalline pyrite (personal communication, D. Evans, 2019). The local presence of bryozoan epizoans, which covered parts of already broken septa and outer surfaces of the septal necks, is evidence of a relatively complex depositional history with potential secondary reworking.

The massive limonitic parts of the siphuncles are interpreted by us as originally organic rich shelly material. By contrast, the less massive, more porous limonitic spaces are interpreted as representing areas originally filled with porous calcareous endosiphuncular deposits. This results in a reconstruction of a pattern with a number of radially arranged lamellae and elongated endoconic cells or compartments that where divided by folded interspaces or endosiphoblades (sensu Flower, 1964; see Fig. 4), a reconstruction that is consistent with siphuncular features of better-preserved material of intejocerids, specifically with *Evencoceras Balashov*, 1960 (Balashov, 1960, pl. 28, fig 1; VanCamp Gil, 1988, fig. 14.6). The siphuncles described herein differ from those of all other known intejocerids in having a wider angle of expansion and in being slightly curved, which justifies the erection of a new genus and probably would be adequate to suggest a new family if more complete material were available.

Conclusions

Our interpretation and systematic classification of the cephalopod siphuncles collected from the Navas de Estena Formation has two main consequences: (1) the known paleogeographic range of the Intejocerida now widens from being restricted to low-paleolatitude Siberia and Laurentia toward high-latitude peri-Gondwana; (2) the known morphological diversity of the Intejocerida widens significantly from originally being restricted to slender orthoconic forms to now also including slightly curved brevicones. Notably, distinct groups of curved brevicones are known also from other predominantly hemiholochoantic higher cephalopod taxa, such as the Piloceratidae of the Bisonocerida (cf. Evans and King, 2012) and Cyrtendoceratidae of the Endocerida (Teichert, 1964).

The intejocerids reported herein also add to the known diversity of Ordovician cephalopods from the Iberian Peninsula. Currently, this incudes members of the Ascoceridae, Ellesmerocerida, Endocerida, Orthocerida, Lituitida, and Tarphycerida (for previous compilation see Babin and Gutiérrez-Marco, 1992; Sá and Gutiérrez-Marco, 2009). With the exception of two tarphycerid species, most of the previously published taxa are based on poorly preserved material occurring as incomplete molds and casts in siliceous mudstones and sandstones. The absence of critical internal structures in many of these specimens does not allow for a taxonomic identification at genus or species level, and many taxa are in need of a revision. We hope that the recent reappraisals of early Paleozoic peri-Gondwanan cephalopod faunas from elsewhere (e.g., Kröger and Lefebvre, 2012; Evans et al., 2013, 2015; Bogolepova et al., 2014; Niko and Sone, 2014, 2015; Aubrechtová, 2015; Cichowolski et al., 2015, 2018; Ghavidel-Syooki et al., 2015; Rolet and Plusquellec, 2016; Aubrechtová and Turek, 2018; Manda and Turek, 2018; Ebbestad et al., 2019; Fang et al., 2019) will stimulate future research on the Iberian cephalopods.

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References

- Aubrechtová, M., 2015, A revision of the Ordovician cephalopod *Bactrites* sandbergeri Barrande: Systematic position and palaeobiogeography of *Bactroceras*: Geobios, v. 48, p. 193–211.
- Aubrechtová, M., and Turek, V., 2018, Lituitid cephalopods from the Middle Ordovician of Bohemia and their paleobiogeographic affinities: Bulletin of Geosciences, v. 93, p. 401–417.
- Babin, C., and Gutiérrez-Marco, J.C., 1992, Intéret paléobiogeographique de la présence du genre *Trocholites* (Cephalopoda, Nautiloidea) dans le Dobrotivá (Llandeilo) inférieur d'Espagne: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 1992, p. 519–541.
- Balashov, E.G., 1960, Novye ordovikskie nautiloidei SSSR [New Ordovician nautiloids of the USSR]: Novye Vidy Drevnikh Rastennyi i Besposvonochnykh SSSR, v. 2, p. 123–137. [in Russian]
- Balashov, E.G., 1962, Nautiloidei ordovika sibirskoi platformy [Nautiloids of the Ordovician of the Siberian Platform]: Izdatel'stvo Leningradskogo Universiteta, 205 p. [in Russian]
- Balashov, E.G., 1968, Endoceratoidei ordovika SSSR [Ordovician Endoceratoidea of the USSR]: Izdatel'stvo Leningradskogo Universiteta, 170 p. [in Russian].
- Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C., and Dronov, A.V., 2009, The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and $\delta^{13}C$ chemostratigraphy: Lethaia, v. 42, p. 97–107.
- Bogolepova, O.K., Kröger, B., Falahatgar, M., and Javidan, M., 2014, Middle Ordovician cephalopods from the Abarsaj area, northern Iran: GFF, v. 136, p. 34–37.
- Cichowolski, M., Waisfeld, B.G., Vaccari, N.E., and Marengo, L., 2015, The nautiloid family Eothinoceratidae from the Floian of the Central Andean Basin (NW Argentina and South Bolivia): Geological Journal, v. 50, p. 764–782.
- Cichowolski, M., Uriz, N.J., Alfaro, M.B., and Galeano Inchausti, J.C., 2018, Ascocerid cephalopods from the Hirnantian? – Llandovery stages of the southern Paraná Basin (Paraguay, South America, first record from high paleolatitudes): Journal of Paleontology, v. 93, no. 1, p. 1–11.
- Ebbestad, J.O.R., Polechová, M., Kröger, B., and Gutiérrez-Marco, J.C., 2019, Late Ordovician molluscs of eastern Anti-Atlas, Morocco, *in* Hunter, A.W., Álvaro, J.J., Lefebvre, B., van Roy, P., and Zamora, S., eds., The Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco: The Geological Society, London, Special Publication, v. 485, doi:10.1144/SP485.9.
- Elles, G.L., and Wood, E.M., 1901, A monograph of British graptolites, pt. 1. Dichograptidae: Monographs of the Palaeontographical Society, v. 55, p. 1–54.
- Evans, D.H., and King, A.H., 2012, Resolving polyphyly within the Endocerida: The Bisonocerida nov., a new order of early Palaeozoic nautiloids: Geobios, v. 45, p. 19–28.
- Evans, D.H., Ghobadi Pour, M., and Popov, L.E., 2013, Review of Early to Mid Ordovician orthoconic cephalopods from Iran: Bulletin of Geosciences, v. 88, p. 21–44.
- Evans, D.H., Ghobadi Pour, M., Popov, L.E., and Jahangir, H., 2015, An early Silurian (Aeronian) cephalopod fauna from Kopet-Dagh, north-eastern Iran: Including the earliest records of non-Orthocerid cephalopods from the Silurian of Northern Gondwana: Bulletin of Geosciences, v. 90, p. 479–507.
- Fang, X., Burrett, C., Li, W., Zhang, Y., Zhang, Y., Chen, T., and Wu, X., 2019, Dynamic variation of Middle to Late Ordovician cephalopod provincialism

in the northeastern peri-Gondwana region and its implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 521, p. 127–137.

- Flower, R.H., 1964, Nautiloid shell morphology: New Mexico Bureau of Mines and Mineral Resources Memoir, v. 13, p. 1–79.
- Flower, R.H., 1968, Part I. The first great expansion of the actinoceroids. Part II. Some additional Whiterock cephalopods: New Mexico Bureau of Mines and Mineral Resources Memoir, v. 19, p. 1–120.
- Ghavidel-Syooki, M., Evans, D.H., Ghobadi Pour, M., Popov, L.E., Álvaro, J.J., Rakhmonov, U., Klishevich, I.A., and Ehsani, M.H., 2015, Late Ordovician cephalopods, tentaculitides, machaeridians and echinoderms from Kuh-e Faraghan, High Zagros, Iran: Alcheringa, v. 39, p. 530–549.
- Gutiérrez-Marco, J.C., and Sá, A.A., 2017, Primer registro del icnogénero *Phycodes* en el Ordovícico Medio de los Montes de Toledo (Zona Centroibérica, España): Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica, v. 110, p. 43–48.
- Gutiérrez-Marco, J.C., Rábano, I., Sá, A.A., García-Bellido, D.C., and Sarmiento, G.N., 2013, Patrimonio paleontológico del Ordovícico Medio del Parque Nacional de Cabañeros (Castilla-La Mancha), *in* Vegas, J., Salazar, A., Díaz-Martínez, E., and Marchán, C., eds., Patrimonio geológico, un recurso para el desarrollo: Cuadernos del Museo Geominero, v. 15, p. 591–599.
- Gutiérrez-Marco, J.C., Rábano, I., Sá, A.A., Baeza Chico, E., Sarmiento, G.N., Herranz Araújo, P., and San José Lancha, M.A. de., 2015a, Geodiversidad e itinerarios geológicos en el Parque Nacional de Cabañeros [Geodiversity and geological routes in the Cabañeros National Park], *in* Amengual, P., and Asensio, B., eds., Proyectos de investigación en parques nacionales: 2010–2013: Organismo Autónomo Parques Nacionales, Serie investigación en la red, v. 7, p. 105–142.
- Gutiérrez-Marco, J.C., et al., 2015b, Iberian Ordovician and its international correlation: Stratigraphy, v. 12, no. 3–4, p. 257–263.
- Gutiérrez-Marco, J.C., Sá, A.A., García-Bellido, D.C., and Rábano, I., 2017, The Bohemo-Iberian regional chronostratigraphic scale for the Ordovician System and palaeontological correlations within South Gondwana: Lethaia, v. 50, p. 258–295.
- Kröger, B., and Lefebvre, B., 2012, Palaeogeography and palaeoecology of early Floian (Early Ordovician) cephalopods from the Upper Fezouata Formation, Anti-Atlas, Morocco: Fossil Record, v. 15, p. 61–75.
- Manda, S., and Turek, V., 2018, Silurian tarphycerid *Discoceras* (Cephalopoda, Nautiloidea) systematics, embryonic development and paleoecology: Journal of Paleontology, v. 92, p. 412–431.
- Niko, S., and Sone, M., 2014, Actinocerid cephalopods from the Ordovician of Myanmar, and their paleobiogeographic implications for northern Gondwana: Paleontological Research, v. 18, p. 94–104.
- Niko, S., and Sone, M., 2015, Gondwanan nautiloid cephalopods from the Ordovician of Myanmar: Paleontological Research, v. 19, p. 288–294.
- Reyes-Abril, J., Villas, E., and Gutiérrez-Marco, J.C., 2010, Orthid brachiopods from the Middle Ordovician of the Central Iberian Zone (Spain): Acta Palaeontologica Polonica, v. 55, p. 285–308.
- Rolet, J., and Plusquellec, Y., 2016, Découverte d'un nautiloïde cyrtocône dans les grès ordoviciens de Bréhec (Massif Armoricain): Bulletin de la Société Géologique et Minéralogique de Bretagne [D], v. 14, p. 3–14.
- Sá, A.A., and Gutiérrez-Marco, J.C., 2009, Cefalópodos del Ordovícico Medio de la Formación Valongo, norte de Portugal: Geogaceta, v. 47, p. 9–12.
- Sharpe, D., 1849, On the geology of the neighbourhood of Oporto, including the Silurian coal and slates of Valongo: Quarterly Journal of the Geological Society, v. 5, p. 142–153.
- Teichert, C., 1964, Endoceratoidea, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part K, Mollusca 3: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and the University of Kansas Press, p. K160–K189.
- VanCamp Gil, A., 1988, Whiterock (lower Middle Ordovician) cephalopod fauna from the Ibex area, Millard County, western Utah: New Mexico Bureau of Mines and Mineral Resources Memoir, v. 44, p. 27–41.
- Verneuil, E. de, and Barrande, J., 1855, Descriptions des fossiles trouvés dans les terrains silurien et dévonien d'Almaden, d'une partie de la Sierra Morena et des montagnes de Tolède: Bulletin de la Société Géologique de France [2^e série], v. 12, p. 964–1025.

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