

## The oldest record of Eothinoceratidae (Ellesmerocerida, Nautiloidea): Middle Tremadocian of the Cordillera Oriental, NW Argentina

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Middle Tremadocian cephalopods from the Sierra de Mojotoro, Cordillera Oriental, NW Argentina, are assigned to *Saloceras* cf. *sericeum* (Salter) based on the siphuncle morphology and general shape of the conch. *Saloceras sericeum* (Salter) is known from the Upper Tremadocian and Floian of England and Wales, a region that formed part of eastern Avalonia during the Early Ordovician, located at a high southern latitude to the north of the Gondwanan margin. This is the oldest record of this genus and of the family Eothinoceratidae, and extends the geographical range of *Saloceras*, being the first positive record of its presence in Argentina and the Central Andean Basin. These remains are amongst the oldest cephalopods described from NW Argentina. They represent the third mid Tremadocian record of nautiloids at relatively high palaeolatitudes and away from the low latitude carbonate platform palaeoenvironments where the bulk of the earliest cephalopods resided. Copyright © 2010 John Wiley & Sons, Ltd.

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### 1. INTRODUCTION

Early Ordovician nautiloid cephalopods are of particular relevance for the understanding of the evolutionary pattern of the group. Following their origin during the Late Cambrian, which was succeeded by the end Cambrian extinction event (Teichert, 1988), Tremadocian assemblages are of particular interest as they represent the beginning of what became the great Ordovician radiation of cephalopods.

Ordovician cephalopods from the Central Andean Basin are mainly known from the work of Cecioni (1953, 1965), Cecioni and Flower (1985) and Evans (2007), who reported many species from northwestern Argentina, Bolivia and Perú, respectively. Only from NW Argentina were any Tremadocian species described (Cecioni, 1965), although some of these are now considered to be younger (Cichowolski, 2009). In addition, those species previously reported from NW Argentina and Bolivia require taxonomic revision. With the information provided by newly collected material, this revision is under way and this paper is a

contribution towards this work. Furthermore, the described specimens are amongst the oldest cephalopods recorded from NW Argentina.

The Family Eothinoceratidae Ulrich *et al.*, 1944, is considered to belong to the Order Ellesmerocerida Flower (*in* Flower and Kummel, 1950), Suborder Cyrtocerina Flower, 1964. It has a rather wide distribution, from low to high palaeolatitudes, being known from Gondwana and Perigondwana (Bolivia, Perú, Australia, eastern Avalonia and Armorica), as well as North China, Siberia, Thailand and Laurentia (Chen and Teichert, 1987; Evans, 2005). From Argentina, only the genus *Desioceras* Cecioni, 1953, first assigned to Protocycloceratidae (Cecioni, 1953) and later to Bathmoceratidae (Cecioni and Flower, 1985), was considered as an eothinoceratid based on the original photographs of the type material (Chen and Teichert, 1987). Its age is uncertain, as it was found in an erratic boulder at Río San Lorenzo. Chen and Teichert (1987) and Evans (2005) have suggested a probable Darriwilian age for the specimen. The only other Cyrtoceriniid described from NW Argentina is *Bathmoceras* cf. *australe* Teichert (Cecioni and Flower, 1985), from the locality of Dique La Ciénaga, Jujuy, the age of which was regarded as uncertain. This specimen is considered further below.

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Evans (2005) (p. 10) wrote: 'the family (Eothinoceratidae) first appears during the latter portion of the Tremadoc Series (Lancefieldian 2) and appears to have spread rapidly across climate zones and oceanic divides. This might suggest that the origination of the family took place earlier in the Tremadoc Series, or that the family itself is paraphyletic. Such alternatives are unlikely to be resolved without the discovery of additional material'. The importance of the present report is our documentation of the oldest records of this family, extending its stratigraphical range into the Middle Tremadocian. The Eothinoceratidae are represented by several specimens collected from the Floresta Formation (Sierra de Mojotoro, Cordillera Oriental, NW Argentina), which show a close taxonomic affinity with Avalonian forms described by Evans (2005).

*Institutional abbreviations.* CIPAL: Centro de Investigaciones Paleobiológicas (Córdoba, Argentina). CEGH-UNC: Cátedra de Estratigrafía y Geología Histórica de la Universidad Nacional de Córdoba (Córdoba, Argentina). JUY: Instituto de Geología y Minería, Universidad Nacional de Jujuy (San Salvador de Jujuy, Argentina).

## 2. MATERIALS AND METHODS

A total of 36 (CEGH-UNC 24038-24070 and 24071a-c) cephalopods were studied, all of which are housed at the CIPAL, Universidad Nacional de Córdoba, Argentina. These were collected by N. E. V., Teresa M. Sánchez and Juan L. Benedetto (CIPAL, UNC) from the locality of La Cornisa, Floresta Formation (Sierra de Mojotoro, Cordillera Oriental, NW Argentina). The specimens are preserved in light green siltstones, with an accompanying macrofauna composed mainly of trilobites. Only one specimen (CEGH-UNC 24040) was found in a micaceous sandstone, at a slightly lower level in the succession. The conchs are badly preserved, being strongly compacted. Often, the conch is compacted in its lateral plane with the marginal siphuncle visible to one side. In some specimens, the compaction is in the dorsoventral plane and here the siphuncle is observed close to the mid-line of the flattened conch (if the ventral surface is exposed). Many of the specimens are represented by external moulds, whilst others consist of internal moulds. The bulk of specimens represent parts of the phragmocones (CEGH-UNC 24038, 24044, 24071a-c, 24069, 24043, 24041, 24064, 24062, 24046, 24061, 24059, 24051, 24065, 24050, 24070, 24060, 24066, 24055, 24063, 24049, 24054, 24058 and 24048), but parts of living chambers are also preserved (CEGH-UNC 24042, 24067, 24057, 24056, 24052, 24047 and 24068). These are commonly broken. Some phragmocones have been found still attached to living chambers (CEGH-UNC 24045,

24039, 24053 and 24040), but no complete specimens have been found and no apical portions are known. Because of the high degree of compaction of these specimens, as well as their mouldic preservation, no internal characters could be examined. The characters measured from the specimens have been set out in the explanation to Table 1. All measurements were taken using digital callipers with a resolution of 0.1 mm. Due to the compaction of the conchs, their diameters and that of the siphuncles could not be measured directly. Instead, the width of the fragments was used as a proxy. In some cases both adoral and adapical width could be measured (or/ap, respectively), but when only one measurement was possible, by convention it is placed in the oral WF cell of the table.

## 3. GEOLOGICAL SETTING

The Sierra de Mojotoro is approximately 80 km long and forms the southern part of the Cordillera Oriental. It contains an uninterrupted section through Tremadocian, Floian and Dapingian strata that are well exposed along the old National Road 9 from Salta to Jujuy cities (Figure 1). Fossiliferous strata are located in Jujuy Province, on the eastern flank of the Sierra de Mojotoro, where the early Ordovician succession includes, in ascending order, the La Pedrera, San José, Caldera, Floresta and Áspero formations (Moya, 1998). The cephalopods described herein were found in the lower to middle part of the Floresta Formation (Figure 2), exposed on the road-cut at 1651.5 km of Road 9 (24°29'21.90"S, 65°17'45.07"W). In the section studied (Figure 1) the Floresta Formation is more than 150 m thick and consists mainly of light-green siltstones interbedded with subordinate fine-grained sandstone beds (Figure 2). From this locality were collected the bivalves described by Sánchez and Vaccari (2003) that were assigned to a new family of Anomalodesmata, and the new species of brachiopod *Lipanorthis santalaurae* described by Benedetto and Carrasco (2002).

This formation overlies sandstones with *Kainella meridionalis* Kobayashi of the Caldera Formation and its top is not exposed (Figure 2). Although Moya (1998) proposed that the deposits of the Floresta Formation correspond to an offshore environment (distal external shelf), the scattered nature of the outcrops makes the detailed facies analysis that would be necessary to arrive to this conclusion very difficult. All the specimens except one (CEGH-UNC 24040, from a slightly lower level with *Bienvillia* sp.) come from levels with *Parabolinella* sp. nov. (see Figure 2), the most abundant species occurring in the biozone of *Bienvillia tetragonalis*–*Conophrys minutula* in the Rupasca Member of the Santa Rosita Formation of the Alfarcito region, where the zone was

Table 1. Measurements of *Saloceras* cf. *sericeum* (Salter in Ramsay, 1866), from the Middle Tremadocian Floresta Formation, Sierra de Mojotoro

Specimen number	24038	24038	24039	24040	24041	24041	24042	24043	24044	24045	24046	24050	24051	24053	24054	24055	24056	24058	24058	24058
	(E m)	(I m)			(E m)	(I m)				(I m)										
LF (in mm)	51.12	47.7	76.72	37.44	70.48	65.72	20.8	54.36	45.65	44.18	30.19	39	29	33.94	18.12	49	28.60	45.24	29.46	29.46
WF <sub>or</sub> (in mm)	16.81	16.86	20.70	15	19	21.56	17.3	19.34	17.62	21.88	19	17.74	18.51	22.38	—	17.26	—	—	—	16.23
WF <sub>ap</sub> (in mm)	15.43	—	19.88	—	17	17	15.78	17.72	—	18.12	16.42	16.33	—	—	—	—	—	—	—	15.32
LM (in mm)	51.12	—	62.71	—	54.60	65.72	20.8	54.36	—	44.18	23.54	39	—	—	—	—	—	—	—	29.46
WS (%)	46	46	36	40	—	47–54	—	29	40	—	—	—	—	45	—	30	—	—	—	—
LCham (in mm)	2–2.4	2–2.4	2.3–2.5	—	2–2.7	2	—	1.85–2	1.9–2.3	1.7–2.2	1.8–2.3	2.5	2–2.3	—	—	—	—	—	—	2
Cham/LPhrag	27	26	18	—	30	32	—	33	25	6	14	—	17	—	10	—	4	22	15	—
LLiCham	—	—	38.45	—	—	—	20.8	—	—	28	—	—	—	12.6	—	—	20.90	—	—	—
LPhrag	51.75	48	36.07	—	70.48	65.72	—	—	45.65	16	30.19	—	29	2134	18.12	—	7.70	45.24	29.46	29.46
Specimen number	24060	24061	24064	24065	24066	24067	24068	24069	24070	24071a										
LF (in mm)	23.69	27.42	33.25	45.36	44.63	17.2	24.27	83.78	38.8	33										
WF <sub>or</sub> (in mm)	—	14.96	15.39	17.36	19.90	21.35	20.5	16.04	18.30	16.78										
WF <sub>ap</sub> (in mm)	—	10.69	11.79	12.31	18.30	—	—	—	16.7	—										
LM (in mm)	—	27.42	33.25	45.36	44.63	—	—	54.55	38.8	—										
WS (%)	—	—	—	—	40	—	—	—	—	—										
LCham (in mm)	—	2–2.5	2.3	2.5	—	—	—	—	—	—				1.67–1.82	—	—	1.8–2	—	—	50
Cham/LPhrag	12	12	17	—	—	—	—	—	—	—				—	—	—	—	—	—	1.6
LLiCham	—	—	—	—	—	—	—	—	—	—				—	—	—	—	—	—	—
LPhrag	23.69	27.42	33.25	—	—	17.2	24.27	—	—	—				—	—	—	—	—	—	33

Specimen number is always under the prefix CEGH-UINC. LF: maximum length of the fragment (including phragmocone and living chamber). WFor: preserved width of the fragment at adoral end. WFap: preserved width of the fragment at adapical end. LM: length over which measured (when this does not coincide with LF). WS: preserved width of the siphuncle in relation to the preserved width of the conch at the same point of growth (as a percentage). LCham: length of the chambers, measured as the distance between two adjacent suture lines. Usually a range of measures is considered (a maximum and a minimum value). Cham/LPhrag: number of chambers in the preserved length of the fragment (if part of the fragment corresponds to the body chamber, only the length of the phragmocone fragment is considered). LLiCham: length of the preserved fragment of body chamber of the specimen, when present. LPhrag: length of the preserved fragment of phragmocone. E m: external mould. I m: internal mould. Note: considering the special preservation of the specimens, it is considered that almost all measurements are approximate.

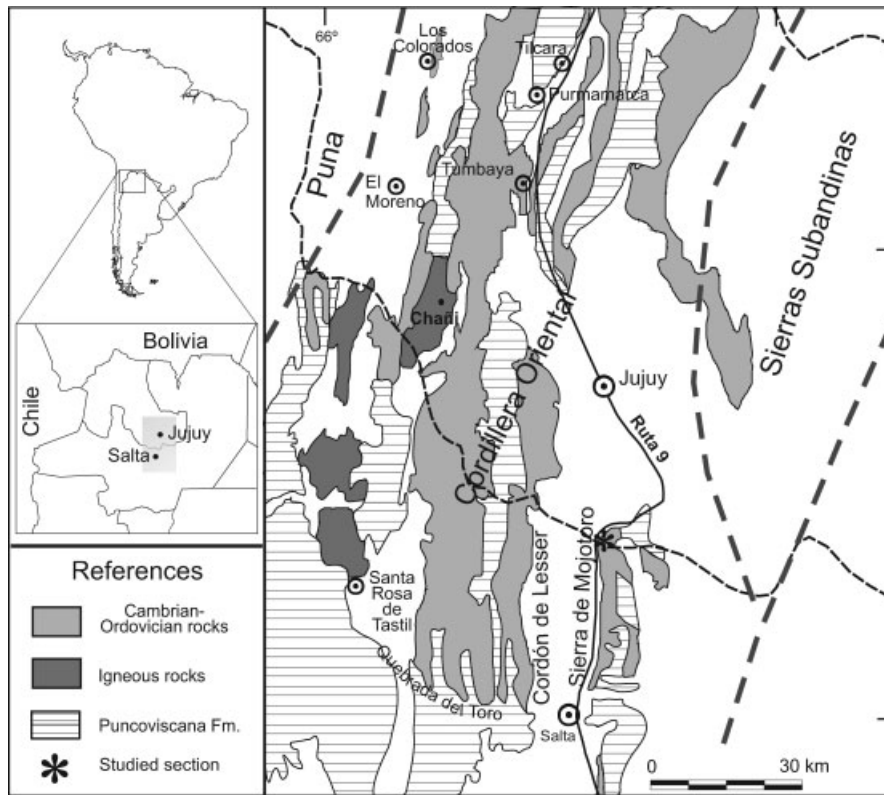


Figure 1. Location map indicating the place where nautiloids were collected.

defined by Harrington (*in* Harrington and Leanza, 1957). This zone was correlated with the *Paltodus deltifera* Conodont Zone, *Paltodus deltifera pristinus* Subzone (Zeballos *et al.*, 2005) and then assigned to the Middle Tremadocian (considering the tripartite division of the Tremadocian; Bergström *et al.*, 2009). At the locality of Cuesta de la Pedrera (Sierra de Mojotoro), the age of the Floresta Formation has been determined based on graptolites, where the Zone of *Bryograptus kjerulfi* was recognized (González Barry and Alonso, 1984; Albanesi *et al.*, 2008; Maletz *et al.*, 2010). This zone indicates an Upper Tremadocian age, following the bipartite scheme of the Tremadocian, but it has also been correlated with the *Paltodus deltifera* Biozone (Albanesi *et al.*, 2008) and, hence, the age is Middle Tremadocian using the tripartite scheme followed in this paper.

#### 4. SYSTEMATIC PALAEOONTOLOGY

Order Ellesmerocerida Flower *in* Flower and Kummel, 1950  
 Suborder Cyrtocerina Flower, 1964  
 Family Eothinoceratidae Ulrich, Foerste, Miller and Unklesbay, 1944

*Discussion.* The Suborder Cyrtocerina is composed of three families: Eothinoceratidae Ulrich *et al.*, 1944, Bathmoceratidae Gill, 1871 and Cyrtocerinae Flower,

1946, that shared a characteristic siphuncular structure, with connecting rings where one surface protrudes into the lumen as collars or lobes of various shapes, and the other surface is concave facing into the camera (Flower, 1964; Chen and Teichert, 1987). Mutvei (2002) considered that the lobes within the endosiphuncle of *Bathmocerata* are not connecting rings, having a different structure, and that *Bathmocerata* should not be regarded as an ellesmerocerid. If this is the case, it is probable that the lobes present on the siphuncles of the other families of the Cyrtocerina are not connecting rings either and this group should be classified as a different order. At present, with only our own material to hand, it would be impossible to add new information about the connecting rings of the eothinoceratids. Hence, in this work, the family Eothinoceratidae is treated traditionally as belonging in the suborder Cyrtocerina, order Ellesmerocerida. This family was defined by Ulrich *et al.* (1944) and regarded as a monotypic family for a long period (Evans, 2005). Balashov (1962) included the Family Cyrtocerinae of Flower (1946) within the Eothinoceratidae, whilst Furnish and Glenister (1964) considered the Eothinoceratidae a synonym of the Bathmoceratidae. However, the three families are treated separately (Flower, 1964; Evans, 2005, 2007). The Cyrtocerinae are characterized by endogastric, breviconic conchs, whereas the Eothinoceratidae are characterized by straight to gently cyrtoconic

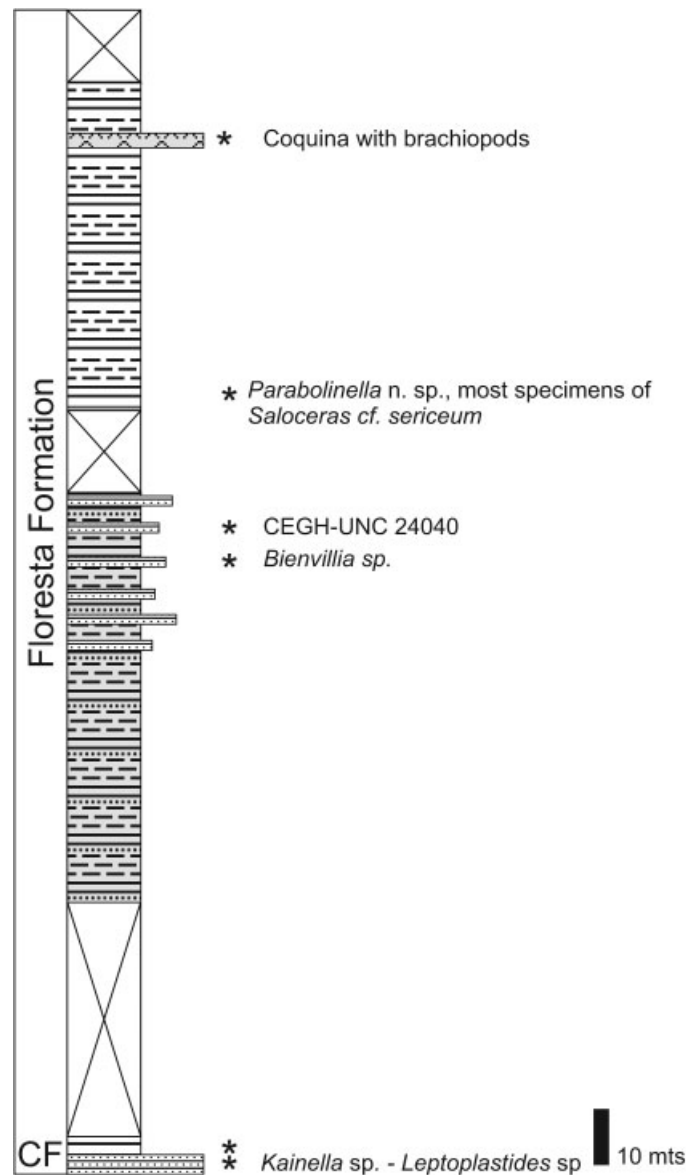


Figure 2. Stratigraphical section of the Floresta Formation at La Cornisa, Sierra de Mojotoro, Cordillera Oriental Argentina, showing the levels where cephalopods were found.

conchs, with generally compressed cross-sections. The Bathmoceratidae is a monogeneric family characterized by connecting rings with inner surfaces that are strongly expanded to form a sequence of adorally directed collars. Externally, siphuncular segments appear to form a series of small cones, superimposed on one another, with the apices pointing toward the aperture (Chen and Teichert, 1987). In the Eothinoceratidae the connecting rings vary in thickness. If the internal structures (in a sagittal section) cannot be seen, it may be rather difficult to differentiate between the Bathmoceratidae and the Eothinoceratidae. However, the siphuncular segments in the Eothinoceratidae are usually more rounded.

#### Genus *Saloceras* Evans, 2005

*Type species. Orthoceras sericeum* Salter in Ramsay, 1866, by original designation, from the Tremadocian of the Garth area, North Wales.

*Saloceras cf. sericeum* (Salter in Ramsay, 1866)

#### Figure 3

1953. *Bathmoceratidae* sp.; Cecioni, p. 74.

1985. *B. cf. australe* Teichert; Cecioni and Flower, p. 345.

*Material examined.* CEGH-UNC 24038-24070, 24071a-b.

*Description.* Small to moderate size (maximum length preserved 83.8 mm), orthoconic to very slightly cyrtconic, longiconic conchs (Figure 3A, C). Due to the strong



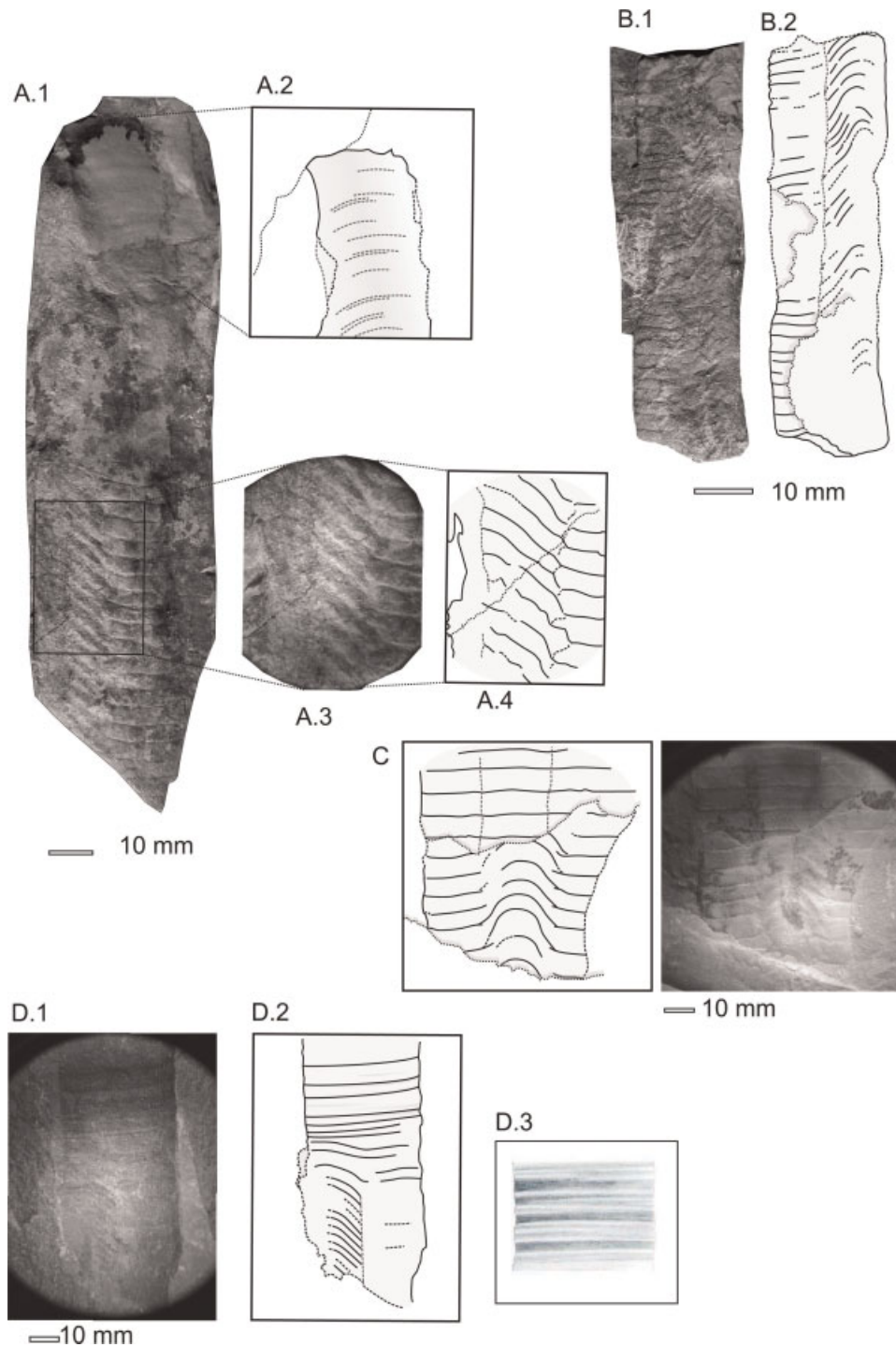


Figure 3. *Saloceras* cf. *sericeum*, from the Middle Tremadocian Floresta Formation, Sierra de Mojotoro, Cordillera Oriental, Jujuy, Argentina. **A.** CEGH-UNC 24039. **A.1.** Preserved specimen compacted laterally; the siphuncle is seen on one side. **A.2.** Schematic of the living chamber with growth lines. **A.3.** Detail of the siphuncle with **A.4** Schematic of it to the right. **B.** CEGH-UNC 24041. **B.1.** Internal mould in lateral view. **B.2.** Schematic of B.1. **C.** CEGH-UNC 24071a in ventral view to the right, with a schematic to the left. **D.** CEGH-UNC 24040 in lateral view. **D.1.** External mould in micaceous sandstone. **D.2.** Schematic of D.1. **D.3.** Schematic of the faint ornamentation. This figure is available in colour online at [wileyonlinelibrary.com/journal/gj](http://wileyonlinelibrary.com/journal/gj)

compaction of the specimens, it is impossible to appreciate the shape of the cross-section of the conch or to measure the apical angle. However, the expansion rate seems to be rather low. Septa are relatively crowded (Figure 3A–C), with the length of the chambers around 2 mm (ranging between 1.6 and 2.7 mm; Table 1). Suture line straight dorsally and laterally (Figure 3A–C), but on the venter it appears to slope adorally forming a rather conspicuous saddle (saddle height of 1–2 chambers). It is not clear if the saddle is an original feature or a taphonomic artifact (Figure 3C), particularly considering the morphology of the siphuncle and the compaction of the conch. It may be also that the traces of the apparent sutures represent the impression of the phragmone wall on the ventral surface of the siphuncle. Siphuncle moderate to large in size, with a width 29–54% that of the width of the compacted conch, and marginal in position (Figure 3A–D). The internal structure of the siphuncle is not visible. The segments are inclined ventrally to the adoral end forming rounded arcs (Figure 3A–C), indicating that the thickening of the connecting rings is asymmetrical. The siphuncular segments have a height equivalent to 1–2 camerae. Where the siphuncle is preserved as an internal mould, the segments can be seen facing convex outwardly into the camerae, representing the infill of the spaces within the thickened connecting rings (Figure 3A.1, 3). When the ectosiphuncle is preserved, the grooves are interpreted as marking the position of the septal foraminae and the ridges would be the connecting rings that may have strongly intruded into the lumen of the siphuncle (Figure 3B, C). In external moulds of the ventral part of the conch (which has the siphuncle impressed), the grooves represent the mould of the concave outline of the connecting rings and the ridges mark the position of the septal foraminae (Figure 3D.1). Septal necks appear to be suborthochoanitic to aneuchoanitic (Figure 3A.4, C), but are difficult to identify. Shell ornament consists of faint transverse striae or lirae (Figure 3A.1–2, D.1–3). The maximum length of the living chamber is 38.45 mm (Figure 3A) and appears to be almost complete at the adoral end.

**Discussion.** The characteristic morphology of the siphuncle in these specimens allows us to assign them to the Family Eothinoceratidae. In particular, the general shape of the conch and its proportions suggest that they belong to the recently described genus *Saloceras* Evans, 2005, from the Upper Tremadocian and Floian of Wales. However, the poor condition of preservation and the impossibility of observing certain characters of the siphuncle, including the presence and disposition of diaphragms, or a longitudinal section of the septal necks and connecting rings, all make their determination at a specific level difficult. Based on a general resemblance with the type species of the genus, we assigned these specimens to *Saloceras* cf. *sericeum*. Although siphonal diaphragms have not been seen in Argentine material, the lack

of preserved apical portions of these specimens may also reflect the presence of them, as this part of the shell may have been preferentially damaged and destroyed after the death of the cephalopods (Evans, 1992, 2005).

Cecioni and Flower (1985) described some species from NW Argentina and southern Bolivia, which, based on the classification of Furnish and Glenister (1964), were assigned to the family Bathmoceratidae. The Argentine species are represented by *Desioceras floweri* Cecioni and *Bathmocer* cf. *australe* Teichert. *Desioceras floweri* was later considered as an eothinoceratid (Chen and Teichert, 1987; Evans, 2005). Cecioni (1953) (p. 74) first mentioned the specimen referred to *Bathmocer* cf. *australe* as *Bathmocer* sp. This specimen was apparently badly preserved and compacted. Cecioni and Flower (1985) did not illustrate this specimen, but gave measurements that are contradictory (e.g. the length of the body chamber is greater than the total length of the fragment, p. 345). Comparisons are therefore difficult. Furthermore, the original material could not be found in the collections at JUY. Although *B. australe* is well illustrated (Teichert, 1939, Figure 3), the original description of the species is based on a single specimen, which was not cut open to expose the internal structure of the siphuncle. Thus, the presence of the inwardly and adorally projections of the connecting rings, typical of *Bathmocer*, cannot be confirmed. Moreover, from an external view, the adoral expansions of the siphuncular segments are rounded rather than acute as seen in other species of this genus (e.g. *Bathmocer* *llanvirnense* (Roberts) in Evans, 2005; *B. linnarsoni* Angelin in Mutvei *et al.*, 2007). Considering these aspects of the siphuncle morphology, *Bathmocer* *australe* could be included in the family Eothinoceratidae. It is interesting to note that at the time of its publication, the Eothinoceratidae had not yet been proposed as a family.

Cecioni and Flower (1985) reported that the specimen described as *Bathmocer* cf. *australe* was found at the locality of Dique La Ciénaga, 39 km from San Salvador de Jujuy to Salta city on National Road No. 9. Cecioni (1953) and Cecioni and Flower (1985) discussed the age of the fossiliferous strata, and considered that they could be Tremadocian, Arenigian or Llanvirnian. Attending the details left by Iglesias (the man who collected the specimen, along with numerous trilobites, in 1949) on the index card of some of the trilobites coming from the same locality, it is concluded here that this locality is the same as that from which the material described here from the Floresta Formation was collected. The index cards indicate that the locality was 13 km from Dique La Ciénaga, on the left margin of the road. That location is consistent with the place where the specimens here assigned to *Saloceras* cf. *sericeum* were recorded. This, and the evidence provided by the trilobites occurring in the same strata, indicate that the age of *Bathmocer* cf. *australe* is also Middle Tremadocian.

Taking into account the resolution of the geographical and stratigraphical provenance of the *Bathmoceras* cf. *australe* described by Cecioni and Flower (1985), and based on its description, we consider it to belong to *Saloceras* cf. *sericeum*, although the original material has not been revised.

Evans (2007) pointed out the close similarity noted by Harrington (1937) between one specimen from the Middle Ordovician of Perú (assigned to the Eothinoceratidae indet. by Evans, 2007) and another from the Late Tremadocian Parcha Formation in NW Argentina (assigned by Harrington to the Endoceratidae). It is possible that the specimen of the Parcha Formation is a further eothinoceratid.

*Desioceras floweri* Cecioni was first considered to be a protocycloceratid by Cecioni (1953), whilst Cecioni and Flower (1985) assigned it to the Bathmoceratidae (considering Bathmoceratidae to be a synonym of Eothinoceratidae, as in the *Treatise of Invertebrate Paleontology*). As noted above, it is now considered to be an eothinoceratid (Chen and Teichert, 1987). It was found in an erratic boulder on the San Lorenzo River and is of an undetermined age. Based on the lithology of the rock containing the fossil, both Llanvirnian and Tremadocian ages were proposed for this specimen. Figure 1.1 of Cecioni and Flower (1985) is an illustration of a longitudinal thin section of the siphuncle, in which the connecting rings are seen protruding into the lumen. This section is not available in the original collections at JUY. Although other supposed type material was studied (JUY-P 40), it has not proved possible to identify any characteristic of the siphuncle that could be related to the eothinoceratids. More material related with this taxon is needed in order to clarify the systematic position of *Desioceras floweri*.

The differences between *Saloceras* cf. *sericeum* and the species of *Margaritoceras* described by Cecioni and Flower from the Floian of Bolivia and NW Argentina (Cecioni and Flower, 1985; Cichowolski and Vaccari, research in progress) are to be found mainly in the proportionate width of the siphuncle and the rate of shell expansion. Comparisons with other eothinoceratids may be found in Evans (2005).

Evans (2005) considered that *Cameroceras* cf. *vertebrale* (Eichwald, 1860), described by Gnoli and Pillola (2002) from the Arenigian of south-east Sardinia (Armorica), belongs to *Saloceras*, even possibly to *Saloceras sericeum*. Evans (2005) also considered *Engonoceras*, as used by Douglas (1933) (p. 354, pl. 29, figures 1 and 2) from the Middle Ordovician of Perú, and *Proterocameroceras contrarium* (Teichert and Glenister, 1954 pl. 14, figure 4) from the Emanuel Limestone of north-west Australia, to be related to *Saloceras*.

*Occurrence.* Middle Tremadocian (*Paltodus deltifer* Conodont Zone), Sierra de Mojotoro, Eastern Cordillera, NW Argentina.

## 5. DISCUSSION

This is the first certain record of the genus *Saloceras* in the Central Andean Basin and, in particular, is the first record in Argentina. This genus would have had a predominantly high latitudes distribution in Gondwana and Perigondwana (Figure 4), although a form with a close resemblance to *Saloceras* was reported from Australia (Evans, 2005). Until now, the occurrence of the family Eothinoceratidae in the Central Andean Basin had been reported for the Floian of Bolivia and the Middle Ordovician of Perú (Cecioni and Flower, 1985; Evans, 2007), and only the enigmatic genus *Desioceras* was known from Argentina, but of uncertain age and provenance. This is the first explicit report of the family in Argentina. This occurrence is documented by many specimens, which probably represent the oldest cephalopods from NW Argentina.

Their importance lies mainly in that they currently represent the oldest records of the family Eothinoceratidae, extending its stratigraphical range into the Middle Tremadocian. Very little is known about the Ordovician radiation of cephalopods in this part of western Gondwana, but, based on our own material from the Floian of NW Argentina and Bolivia, it can be said that this family was well represented during the Early Ordovician at intermediate to high palaeolatitudes. Tremadocian cephalopods of NW Argentina, as currently known, are scarce and very poorly diversified, but during the Floian they appear to undergo a radiation, corresponding to the first global Ordovician diversity peak of Kröger and Zhang (2009). This peak is characterized by the highest Ordovician turnover rates, combining high extinction and high diversification rates (Kröger and Zhang, 2009). In the case of the eothinoceratids from NW Argentina, the genus *Saloceras* is not recorded in the Floian, but the family shows a very important radiation of taxa, with some forms in common with that of Bolivia and some additional new genera endemic to Argentina (Cichowolski and Vaccari, research in progress).

The reported specimens are among the very rare records of cephalopods in the mid Tremadocian (*Paltodus deltifer* Conodont Zone) beyond carbonate platforms depositional environments. Although a deep water environment for the Floresta Formation has been proposed by Moya (1998), the scattered distribution of the outcrop makes it impossible to confirm that assessment. In addition, the morphology of the specimens suggests that they lived in a rather shallow-water environment (Westermann, 1999). Their taphonomic traits, with the rather common presence of at least part of the living chamber, suggest a short period of *post-mortem* drift (Reyment, 1958). However, the presence of these cephalopods within facies dominated by graptolites and trilobites in such ancient siliciclastic rocks is remarkable (Kröger *et al.*, 2009).



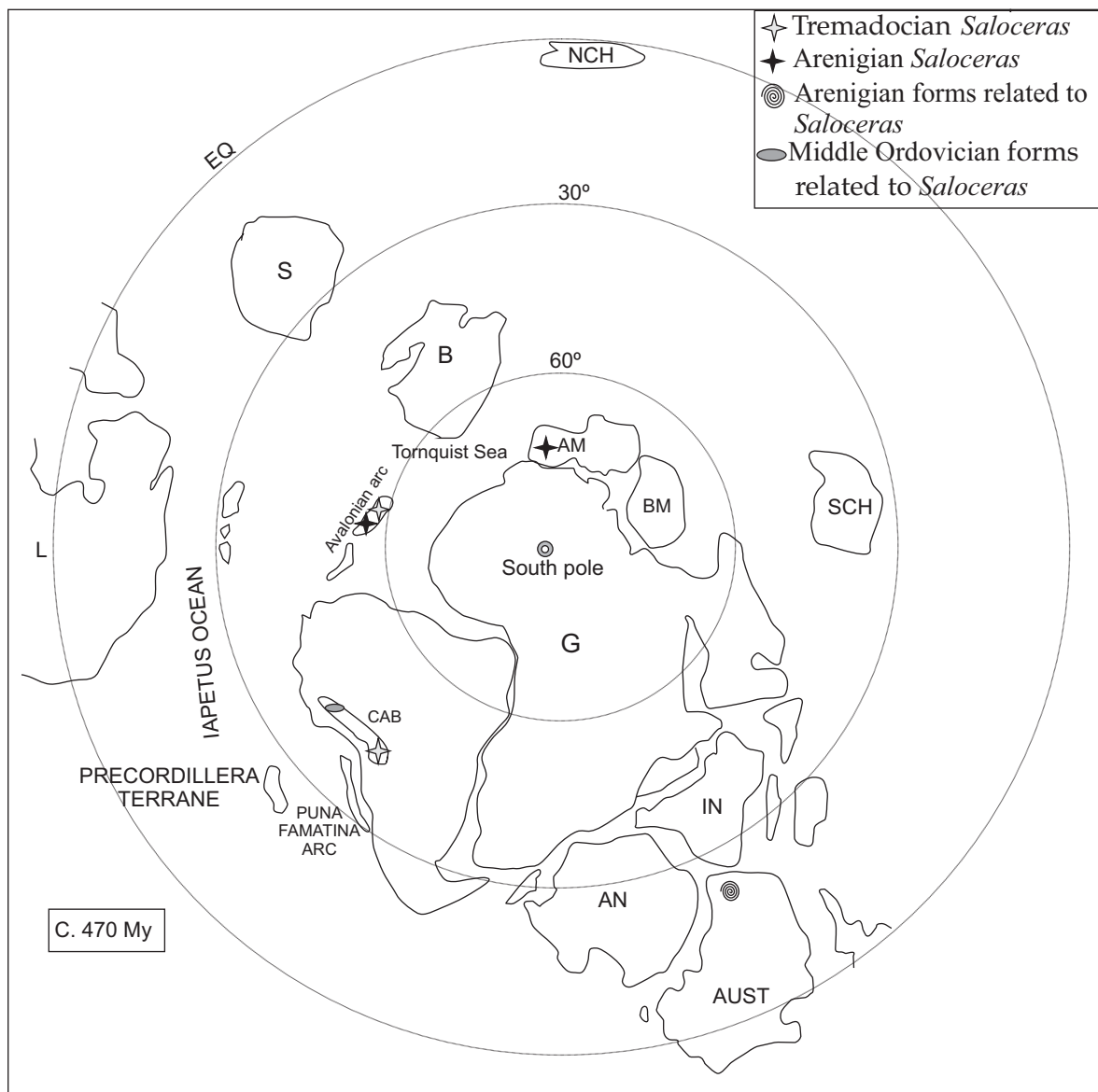


Figure 4. Palaeobiogeographical distribution of *Saloceras* and *Saloceras*-related forms (see text for explanation). AN, Antarctica; AUST, Australia; AM, Armorican Massif; BM, Bohemian Massif; B, Baltica; G, Gondwana; IN, India; L, Laurentia; SCH, South China; NCH, North China; S, Siberia; CAB, Central Andean Basin (palaeogeographical map after Astini *et al.*, 2007).

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#### REFERENCES

- Albanesi, G.L., Ortega, G., Zeballo, F.J. 2008. Faunas de conodontes y graptolitos del Paleozoico Inferior en la Cordillera Oriental Argentina. *Relatorio XVII Congreso Geológico Argentino, Jujuy* 98–118.

- Astini, R.A., Collo, G., Martina, F. 2007.** Ordovician K-bentonites in the upper-plate active margin of Western Gondwana (Famatina Ranges): stratigraphic and palaeogeographic significance. *Gondwana Research* **11**, 311–325.
- Balashov, Z.G. 1962.** Ostryad Ellesmeroceratida. In: *Osnovy Paleontologii Mollyuski-Golovonogie I*, Ruzhentsev, V.E. (ed), Izdatel'stvo Akademii Nauk SSSR: Moskva. [In Russian.]; 73–77.
- Benedetto, J.L., Carrasco, P.A. 2002.** Tremadoc (earliest Ordovician) brachiopods from Purmamarca and the Sierra de Mojotoro, Cordillera Oriental of the northwestern Argentina. *Geobios* **35**, 647–661.
- Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C., Dronov, A. 2009.** The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to  $\delta^{13}\text{C}$  chemostratigraphy. *Lethaia* **42**, 97–107.
- Cecioni, G. 1953.** Contribución al conocimiento de los nautiloideos Eo-Paleozoicos argentinos. Parte I: Protocycloceratidae–Cyclostomiceratidae. *Boletín del Museo Nacional de Historia Natural* **26**, 57–109.
- Cecioni, G. 1965.** Contribución al conocimiento de los nautiloideos Eo-Paleozoicos argentinos. Parte II: Robsonoceratidae, Ellesmeroceratidae, Proterocameroceratidae, Baltoceratidae. *Boletín del Museo de Historia Natural* **29**, 1–24.
- Cecioni, G., Flower, R.H. 1985.** Bathmoceratidae (Nautiloideos, Ordovícico) de Sud América. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **170**, 343–357.
- Chen, J., Teichert, C. 1987.** The Ordovician cephalopod Suborder Cyrtocerininda (Order Ellesmerocerida). *Palaeontologia Cathayana* **3**, 145–229.
- Cichowski, M. 2009.** A review of the endocerid cephalopod *Protocyp-tendoceras* from the Floian (Lower Ordovician) of the Eastern Cordillera, Argentina. *Acta Palaeontologica Polonica* **54**, 99–109.
- Douglas, J.A. 1933.** The geology of the Marcapata Valley in eastern Perú, with an appendix on the graptolites on the Quitari area by O.M.B. Bulman. *Quarterly Journal of the Geological Society of London* **94**, 308–356.
- Eichwald, E. 1860.** *Lethaea Rossica ou paleontology de la Russie. V. I, secondes sectione de l'ancienne période*. Librairie et Imprimerie de E. Schweizerbart. Stuttgart: 681–1657.
- Evans, D.H. 1992.** Phragmocone implosion in Ordovician nautiloids and the function of siphonal diaphragms and endocones. *Palaeontology* **35**, 585–595.
- Evans, D.H. 2005.** The Lower and Middle Ordovician cephalopod faunas of England and Wales. *Monograph of the Palaeontographical Society* **158**(623 for 2004), 1–81.
- Evans, D.H. 2007.** A Middle Ordovician cephalopod fauna from Cuzco Province, southern Perú and its palaeobiogeographical significance. *Geological Journal* **42**, 25–36.
- Flower, R.H. 1946.** Ordovician cephalopods of the Cincinnati Region, Part 1. *Bulletins of American Paleontology* **29**(116): 1–556.
- Flower, R.H. 1964.** The nautiloid order Ellesmeroceratida (Cephalopoda). *New Mexico Institute of Mining and Technology, Memoir* **12**, 1–234.
- Flower, R.H., Kummel, B. 1950.** Classification of the Nautiloidea. *Journal of Paleontology* **24**, 604–615.
- Furnish, W., Glenister, B.F. 1964.** Nautiloidea–Tarphycerida. In: *Treatise on Invertebrate Paleontology. Part K. Mollusca 3. Cephalopoda, General features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea*, Moore, R.C. (ed), Geological Society of America and University of Kansas Press: Boulder and Lawrence; 343–368.
- Gill, T. 1871.** Arrangement of the families of the Mollusca. *Smithsonian Miscellaneous Collections* **227**, 1–49.
- Gnoli, M., Pillola, G.L. 2002.** The oldest nautiloid cephalopod of Sardinia: *Cameroceras* cf. *vertebrale* (Eichwald, 1860) from the Arenig (Early Ordovician) of Tacconis (south east Sardinia) and remarks on the associated biota. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte* **2002**, 19–26.
- González Barry, C., Alonso, R. 1984.** Nuevos graptolites del Tremadociano Superior del norte de Argentina. III Congreso Latinoamericano de Paleontología (México), Memorias, 62–67.
- Harrington, H.J. 1937.** On some Ordovician fossils from northern Argentina. *Geological Magazine* **74**, 97–134.
- Harrington, H.J., Leanza, A.F. 1957.** *Ordovician Trilobites of Argentina*. Department of Geology, University of Kansas: Special Publication; Vol. 1; 276.
- Kröger, B., Zhang, Y. 2009.** Pulsed cephalopod diversification during the Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology* **273**, 174–183.
- Kröger, B., Servais, T., Zhang, Y. 2009.** The origin and initial rise of pelagic cephalopods in the Ordovician. *PLoS ONE* **4**(9): e7262. 10.1371/journal.pone.0007262.
- Maletz, J., Egenhoff, S., Alonso, R. 2010.** The Upper Tremadocian (Ordovician) graptolite *Bryograptus*: taxonomy, biostratigraphy and biogeography. *Palaeontology* **53**, 59–75.
- Moya, M.C. 1998.** El Paleozoico inferior en la Sierra de Mojotoro, Salta-Jujuy. *Revista de la Asociación Geológica Argentina* **52**, 219–238.
- Mutvei, H. 2002.** Nautiloid systematics based on siphuncular structure and position of muscle scars. In: *Cephalopods – Present and Past*, Summesberger, H., Histon, K., Daurer, A. (eds). Abhandlungen Der Geologischen Bundesanstalt Band: Wien. Vol. 57; 379–392.
- Mutvei, H., Zhang, Y., Dunca, E. 2007.** Late Cambrian Plectronocerid nautiloids and their role in cephalopod evolution. *Palaeontology* **50**, 1327–1333.
- Ramsay, A.C. 1866.** The Geology of North Wales, with an appendix of the fossils by J. W. Salter. *Memoir of the Geological Survey of Great Britain* **3**, viii+381.
- Reyment, R.A. 1958.** Some factors in the distribution of fossil cephalopods. *Stockholm Contribution to Geology* **1**, 97–184.
- Sánchez, T.M., Vaccari, N.E. 2003.** Ucumariidae new family (Bivalvia, Anomalodesmata) and other bivalves from the Early Ordovician (Tremadocian) of northwestern Argentina. *Ameghiniana* **40**, 415–424.
- Teichert, C. 1939.** The nautiloid *Bathmoceras* Barrande. *Transactions of the Royal Society of South Australia* **63**, 384–391.
- Teichert, C. 1988.** Main features of cephalopod evolution. In: *Paleontology and Neontology of Cephalopods, The Mollusca 12*, Trueman, E.R., Clarke, M.R. (eds). Academic Press: San Diego; 11–79.
- Teichert, C., Glenister, B.F. 1954.** Early Ordovician cephalopod fauna from northwestern Australia. *Bulletin of American Paleontology* **35**, 153–258.
- Ulrich, E.O., Foerste, A.F., Miller, A.K., Unklesbay, A.G. 1944.** Ozarkian and Canadian cephalopods. Part III: Longicones and summary. *Geological Society of America Special Papers* **58**, 1–226.
- Westermann, G.G.E. 1999.** Life habits of nautiloids. In: *Functional Morphology of the Invertebrate Skeleton*, Savazzi, E. (ed). John Willey and Sons: Chichester; 263–298.
- Zeballos, F.J., Albanesi, G.L., Ortega, G. 2005.** Conodontes y graptolitos de las formaciones Alfarcito y Rupasca (Tremadociano) en el área de Alfarcito, Tilcara, Cordillera Oriental de Jujuy, Argentina. Parte 1: Bioestratigrafía. *Ameghiniana* **42**, 39–46.