A review of the endocerid cephalopod *Protocyptendoceras* from the Floian (Lower Ordovician) of the Eastern Cordillera, Argentina

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Ordovician cephalopods from Western Gondwana are still poorly known and published data is in need of systematic and stratigraphical revision. In this work, the endocerid proterocameroceratid *Protocyptendoceras* from the Floian of the Eastern Cordillera of Argentina is revised using new material from La Ciénaga, 5 km upstream from Purmamarca. The species *P. corvalani* and *P. teicherti* are considered to be junior synonyms of *P. fuenzalidae*, which is redescribed in detail and reillustrated. Specimens preserve adapical parts of isolated siphuncles, related here to the presence of endocones in a posterior portion. Evidently *P. fuenzalidae* had a nektobenthic mode of life in a shallow water environment, oriented horizontally. Its palaeobiogeographical affinities are mainly with Floian proterocameroceratids from Eastern Gondwana, such as *Anthoceras decorum* and the related genera *Lobendoceras*, *Ventroloboceras*, and *Notocycloceras*.

Key words: Cephalopoda, Endocerida, Proterocameroceratidae, Floian, Ordovician, Eastern Cordillera, Argentina.

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Introduction

Ordovician cephalopod faunas from the Eastern Cordillera of Argentina are still poorly known, the main contributions being by Cecioni (1953, 1965) and Cecioni and Flower (1985). Recently, Aceñolaza and Beresi (2002) listed previously studied and new material from the Ordovician of Argentina but did not offer any substantial taxonomic revision.

Cecioni (1965) described several species collected from what he supposed to be Tremadocian and lower Darriwillian strata of northwestern Argentina (see Table 1). Among other taxa, he proposed and described three species of the new proterocameroceratid genus *Protocyptendoceras* Cecioni, 1965: *P. fuenzalidae* Cecioni, 1965, *P. corvalani* Cecioni, 1965, and *P. teicherti* Cecioni, 1965. Both *P. fuenzalidae* and *P. corvalani* came from outcrops located on the Purmamarca River, about 4 km upstream from Purmamarca, and were regarded as being of early Tremadocian age. In contrast, *P. teicherti* was described from erratics, without a precise geographical or stratigraphical provenance.

The main purpose of this paper is to revise the endocerid *Protocyptendoceras* from the Floian of the Eastern Cordillera of Argentina, evaluating the validity of the species included in it, and providing new data on its age and morphology.

Institutional abbreviations.—CIPAL, Centro de Investigaciones Paleobiológicas, Córdoba, Argentina; CEGH-UNC, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina; JUY-P, Museo de Geología, Mineralogía y Paleontología de la Universidad Nacional de Jujuy, San Salvador de Jujuy, Argentina.

Material and methods

A total of forty-eight cephalopods were studied. Forty-four of the studied specimens are housed at the CEGH-UNC. These were collected by Juan L. Benedetto and Teresa M. Sánchez (CIPAL, CEGH-UNC) from the locality La Ciénaga during the summer of 2004, as part of the project "The Ordovician faunal radiation in western Gondwana". Rock samples containing the specimens consist of bioclastic concentrations in a fine-grained matrix, the packing of the bioclasts being dense in some places. Macrofauna includes trilobites, bivalves, and brachiopods. Most of the cephalopods are represented by incomplete phragmocones (CEGH-UNC 23118b, 23120a, 23121c, 23123a, b, 23126a–c, 23131, 23132a–j, 23134a–d, 23137a–c, 23140, 23141, 23145, 23148, 23182a, b), sometimes with parts of the recrystallised shell preserved. Twelve specimens consist of isolated siphuncle fragments (CEGH-UNC 23117, 23122, 23125, 23127, 23133, 23136, 23138a, b, 23139, 23143, 23146, 23147), and only one is an incomplete living chamber (CEGH-UNC 23145). Nine specimens were cut and polished in order to investigate the inner structures of the phragmocones and siphuncles (CEGH-UNC 23126c, 23127, 23132d, 23134a, b, 23136, 23146, 23147, 23182a).

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The remaining four studied specimens correspond to the type material studied by Cecioni (1965) (JUY-P 28–31) and are housed at the JUY-P.

Other cephalopods mentioned by Cecioni (1965) from the same outcrops as the studied material are *Robsonoceras compressum* Cecioni, 1965, *Purmamarcoceras kobayashii* Cecioni, 1965 and *Clarkoceras argentinum* Cecioni, 1965 (see Table 1).

The cephalopods were described using some of the quantitative measurements outlined by Kröger (2004) and Evans (2005) (see Table 2 and Fig. 1). The measurements were taken with digital calipers with a resolution of 0.1 mm.

Table 1. List of species described by Cecioni (1953, 1965), with locality and age data taken from the original papers, and their state of systematic revision.

Species	Fossil locality	Age (according to the original paper)	Reference	Revision state of the taxon
Protocycloceras stefaninni Cecioni, 1953	Garrapatal Creek / Las Capillas river (Zapla Range)	Llanvirnian	Cecioni, 1953	not revised
Protocycloceras harringtoni Cecioni, 1953	Las Capillas river (Zapla Range)	Llandeilian	Cecioni, 1953	not revised
Protocycloceras cfr. *harringtoni* Cecioni, 1953	Las Capillas river (Zapla Range)	Llanvirnian	Cecioni, 1953	not revised
Protocycloceras bonarelli Cecioni, 1953	Las Capillas river (Zapla Range)	Llanvirnian	Cecioni, 1953	not revised
Protocycloceras sp. 1	Las Capillas river (Zapla Range)	Llanvirnian	Cecioni, 1953	not revised
Protocycloceras sp. 2	Las Capillas river (Zapla Range)	Llanvirnian	Cecioni, 1953	not revised
Protocycloceras sp. 3	Las Capillas river (Zapla Range)	Llanvirnian	Cecioni, 1953	not revised
Desioceras floweri Cecioni, 1953	Erratic at the San Lorenzo river, Ledesma (Jujuy)	?	Cecioni, 1953	under revision by MC
Cyclostomiceras depressius Cecioni, 1953	Quebrada de Coquena, Purmamarca	Arenigian	Cecioni, 1953	Family revised by King 1998, considering Cecioni's descriptions
Paracyclostomiceras floweri Cecioni, 1953	Las Capillas river (Zapla Range)	Llanvirnian	Cecioni, 1953	Family revised by King 1998, considering Cecioni's descriptions
Paracyclostomiceras depressum Cecioni, 1953	Garrapatal Creek (Zapla Range)	Llanvirnian	Cecioni, 1953	Family revised by King 1998, considering Cecioni's descriptions
Purmamarcoceras kobayashii Cecioni, 1965	Purmamarca river	Early Tremadocian	Cecioni, 1965	not revised
Clarkeoceras argentinum Cecioni, 1965	Purmamarca river	Early Tremadocian	Cecioni, 1965	not revised
Protocyptendoceras fuenzalidae Cecioni, 1965	Purmamarca river	Early Tremadocian	Cecioni, 1965	revised in this work
Protocyptendoceras corvalani Cecioni, 1965	Purmamarca river	Early Tremadocian	Cecioni, 1965	revised in this work
Protocyptendoceras teicherti Cecioni, 1965	Erratic at Tilcara	?	Cecioni, 1965	revised in this work
Cyptendocerina (?) *floweri* Cecioni, 1965	Quebrada de Coqueta, Purmamarca	Early Tremadocian	Cecioni, 1965	not revised
Baltoceras paucistriatum Cecioni, 1965	Las Capillas river (Zapla Range)	Early Llanvirnian	Cecioni, 1965	not revised
Baltoceras americanum Cecioni, 1965	Las Capillas river (Zapla Range)	Early Llanvirnian	Cecioni, 1965	not revised
Baltoceras multistriatum Cecioni, 1965	Las Capillas river (Zapla Range)	Early Llanvirnian	Cecioni, 1965	not revised
Belloceras milleri Cecioni, 1965	Garrapatal Creek (Zapla Range)	Early Llanvirnian	Cecioni, 1965	not revised
Bathmoceras cf. *australe* Teichert, 1939	Dique La Ciénaga, along the National Road no 9	could be Tremadocian to Llanvirnian	Cecioni, 1953 and Cecioni and Flower, 1985	under revision by MC
Robsonoceras compressum Cecioni, 1953	Purmamarca river	Early Tremadocian	Cecioni, 1953	not revised

Table 2. Measurements of the specimens. Abbreviations: LF, length of the fragment; Or. Dv Dia., adoral dorsoventral diameter; Ap. Dv Dia., apicad dorsoventral diameter; Or. Lat. Dia., adoral lateral diameter; Ap. Lat. Dia., apicad lateral diameter; LM, length over which measured (measures above); Dv Exp., dorsoventral expansion rate (rate of expansion of the conch in the dorsoventral plane, calculated as [Dv Dia. 1-Dv Dia. 2]/distance between 1 and 2); AA dv, apical angle based on dorsoventral expansion rate (tangents $^{-1}$ of the expansion rate); Lat. Exp., lateral rate of expansion of phragmocone, calculated in the same form as for the Dv Exp. but using Lat. Dia.); AA lat., Apical angle based on lateral expansion rate; Comp.: compression ratio (calculated as the ratio of dorsoventral diameter to lateral diameter); Cam. Dep., cameral depth (ratio of the distance between adjacent sutures to the dorsoventral conch diameter expressed as a percentage); Sep. Dep., septal depth (ratio of the distance between the plane of the suture and the culmination of the septum to the diameter of the phragmocone expressed as a percentage); VL Dep., depth of ventral lobe relative to phragmocone diameter; Si. Dia, Siphuncle diameter (ratio of the siphuncle diameter to the dorsoventral conch diameter expressed as a percentage). Asterisk indicates approximate measurements, due to deformation of specimens. See also Fig. 1.

	JUY-P			CEGH-UNC									
Specimen number	29	28	30	23132a	23132b	23132d	23132e	23132f	23132g	23132h	23132i	23132j	23118b
LF (mm)	23.4	37.8	27.3	35	37.3	34.2	–	–	–	–	–	–	20.1
Or. Dv Dia. (mm)	–	7*	10,2*	–	8.9	–	10.4*	5*	10.1*	9.4*	–	7.6	–
Ap. Dv Dia. (mm)	6.9	5,1*	9.2*	–	–	7.6	–	–	–	–	5.7	–	3.9
Or. Lat. Dia. (mm)	9.1	8.7*	9.9*	6.8	8.9	–	9.4*	4.6*	11.8*	13.2*	–	8.7	–
Ap. Lat. Dia. (mm)	8.1	7.6*	–	7	–	–	–	–	–	–	6.2	–	4.5
LM (mm)	23	28.5	16.8	–	–	–	–	–	–	–	–	–	–
Dv Exp. (°)	–	0.066	0.06	–	–	–	–	–	–	–	–	–	–
AA dv (°)	–	3.8	3.4	–	–	–	–	–	–	–	–	–	–
Lat. Exp. (°)	0.043	0.038	–	–	–	–	–	–	–	–	–	–	–
AA Lat. (°)	2.5	2.2	–	–	–	–	–	–	–	–	–	–	–
Comp.	0.85	0.8/0.67	1.03	0.97	1	–	1.1	1.08	0.85	0.71	0.92	0.87	0.86
Cam. Dep. (%)	24	22	19	25	21	24	–	–	–	–	–	–	30
Sep. Dep. (%)	–	–	–	–	–	16	–	–	–	–	–	–	–
VL Dep. (%)	13	–	10	–	–	–	–	–	–	–	–	–	–
Si. Dia. (%)	39	45	31	50	40	33	33	52	39	27	54	44	48

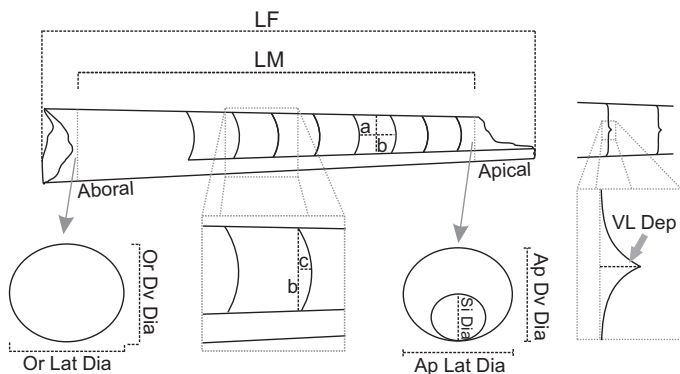| Specimen number	CEGH-UNC											
	23182a	23182b	23145	23137c	23134a	23134b	23134c	23134d	23121c	23123a	23126c	23148
LF (mm)	8.1	11.8	35.7	14.7	22.6	37.3	–	9.3*	28.5	17.7	27.9	30.8
Or. Dv Dia. (mm)	7*	6*	18.2*	8.5*	–	11.4*	–	–	10.7*	11.9*	–	10.9
Ap. Dv Dia. (mm)	–	–	17.7*	–	14.3*	5.7*	4.5*	5.6*	–	–	9.2*	9.4*
Or. Lat. Dia. (mm)	7*	6.9	19.3*	9.2	–	11.4*	–	–	11*	12.3*	–	11.3
Ap. Lat. Dia. (mm)	–	–	18.1*	–	14.3*	6.2*	4.5*	6.4*	9*	–	–	9.8
LM (mm)	–	–	16.4	–	–	37.3	–	–	14*	–	–	9.9
Dv Exp. (°)	–	–	0.03	–	–	0.15	–	–	–	–	–	0.15§
AA dv (°)	–	–	1.7	–	–	8.6	–	–	–	–	–	8.6§
Lat. Exp. (°)	–	–	0.07	–	–	0.14	–	–	0.14	–	–	0.15§
AA Lat. (°)	–	–	4	–	–	8	–	–	8.1	–	–	8.6§
Comp.	1	0.87	0.94/0.97	0.92	1	0.92/1	1	0.87	0.97	0.96	–	0.96
Cam. Dep. (%)	22	23	–	17	15	31	–	30	23	16	25	22
Sep. Dep. (%)	–	–	–	–	–	–	–	–	–	–	–	–
VL Dep. (%)	–	–	–	12	–	–	–	–	–	–	–	10
Si. Dia. (%)	47	50	–	51	37	54	46	50	37	38	47	42

Fig. 1. Explanation of some of the measurements indicated in Table 2: a, distance between adjacent sutures; b, dorsoventral conch diameter; c, distance between the plane of the suture and the culmination of the septum. (a/b).100 = Cam. Dep. (c/b).100 = Sep. Dep. For abbreviations see epigraph of Table 2.

Geological setting

The material studied was collected from beds of Floian age at the locality La Ciénaga, about 5 km west of Purmamarca, Tumbaya Department, Jujuy Province, in the Eastern Cordillera of Argentina (Fig. 2).

The Central Andean Basin is the southern continuation of the extended Andean belt that also comprises the Eastern Cordillera of Peru, as well as the Eastern and Central Cordillera of Bolivia (Waisfeld et al. 1999). The southern part of this basin is exceptionally exposed in the Eastern Cordillera in northwestern Argentina. Siliciclastic successions of the Eastern Cordillera of Argentina and Bolivia were deposited along the western Gondwanan margin of South America (Benedetto and Sánchez 1996). The Early Ordovician successions in the Purmamarca area occur as tectonically truncated packages within several thrust sheets developed during the Andean orogenic cycle in the Tertiary (Vaccari et al. 2006 and references therein). In the studied area, the sequence begins with a discontinuous shale succession containing occasional interbedded calcareous sandstone units, referred to the "Cieneguillas Shales" in Harrington and Leanza (1957). It is overlain by a similar sequence (also including intercalated calcareous lenses), referred to as the "Sepulturas Limestones" in Harrington and Leanza (1957) (Fig. 3). Aceñolaza (2003) considered that these greyish cal-

careous limestones cropping out in the La Ciénaga-El Patacal area represent the stratotype of the Sepulturas Formation. Vaccari et al. (2006), however, pointed out that these units cannot be distinguished in the field and are broadly similar to the Acoite Formation, which is widespread in other parts of the basin, and hence, they referred the succession exposed at La Ciénaga to the Acoite Formation. The cephalopod material studied here was collected from the upper part of the section ("Sepulturas Limestones" of Harrington and Leanza 1957). Aceñolaza (2003) suggested a Floian age on the basis of the association between *Pliomeridius sulcatus* Leanza and Baldis, 1975 and the conodont *Gothodus crassulus andinus* (Rao et al. 1994).

Although there are no detailed lithofacies studies of the locality at La Ciénaga, the facies resemble those of the Los Colorados area (30 km NW of Purmamarca) and correspond to inner shelf sediments deposited below fair-weather wave-base, periodically affected by storm events (Astini et al. 2004). Cephalopods, as well as trilobites, bivalves and brachiopods, are found in the tempestites formed by such storms (Astini and Waisfeld 1993).

Systematic palaeontology

Order Endocerida Teichert, 1933

Family Proterocameroceratidae Kobayashi, 1937

Genus *Protocyptendoceras* Cecioni, 1965

Type species: *Protocyptendoceras fuenzalidae* Cecioni, 1965, by original designation. Floian Stage. La Ciénaga, about 5 km west of Purmamarca, Jujuy Province, Eastern Cordillera of Argentina.

Emended diagnosis.—Straight and longiconic shell with circular to subcircular section. Almost straight suture line, with a narrow ventral lobe. Growth lines on the surface, ornamentation absent. Moderate to large size circular siphuncle, in contact with ventral shell wall. Subholochoanitic septal necks combined with thick connecting rings. Endocones generally droplet shaped in cross section, but sometimes simply rounded.

Remarks.—In his original definition, Cecioni (1965) did not explicitly indicate the presence of endocones, but he observed secondary calcite in an adapical position in the siphuncles, which could correspond to recrystallised endosiphuncular deposits. These are well preserved in the new collected material studied here. The presence of endocones is a key feature permitting assignment of the genus to the Endocerida. Furthermore, the "layered" connecting rings noted by Cecioni (1965) are probably a diagenetic structure, as Mutvei (1997) noted when studying endocerid material using SEM.

Cecioni (1965) compared his new genus *Protocyptendoceras* with others that do not belong to the same family, or even to the same order, such as *Cyptendoceras* Ulrich and Foerste, 1936, *Clarkoceras* Ruedemann, 1905, and *Quebecoceras* Foerste, 1925. Based on the present studies of better-preserved new material, other comparisons can be made
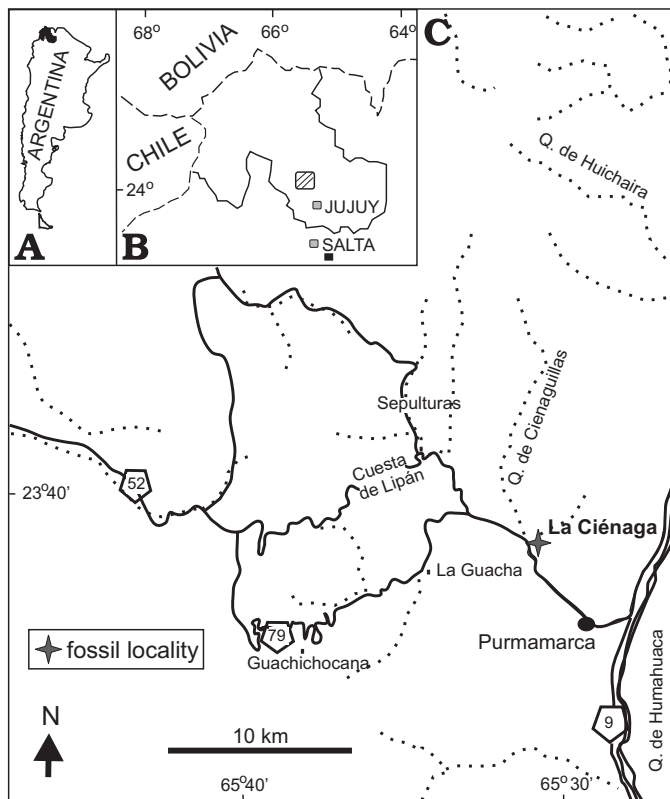

Fig. 2. **A**. Map of Argentina with the Jujuy region in black. **B**. Jujuy region with the study are indicated. **C**. Location map of the fossil locality (La Ciénaga), 5 km northwest of Purmamarca.
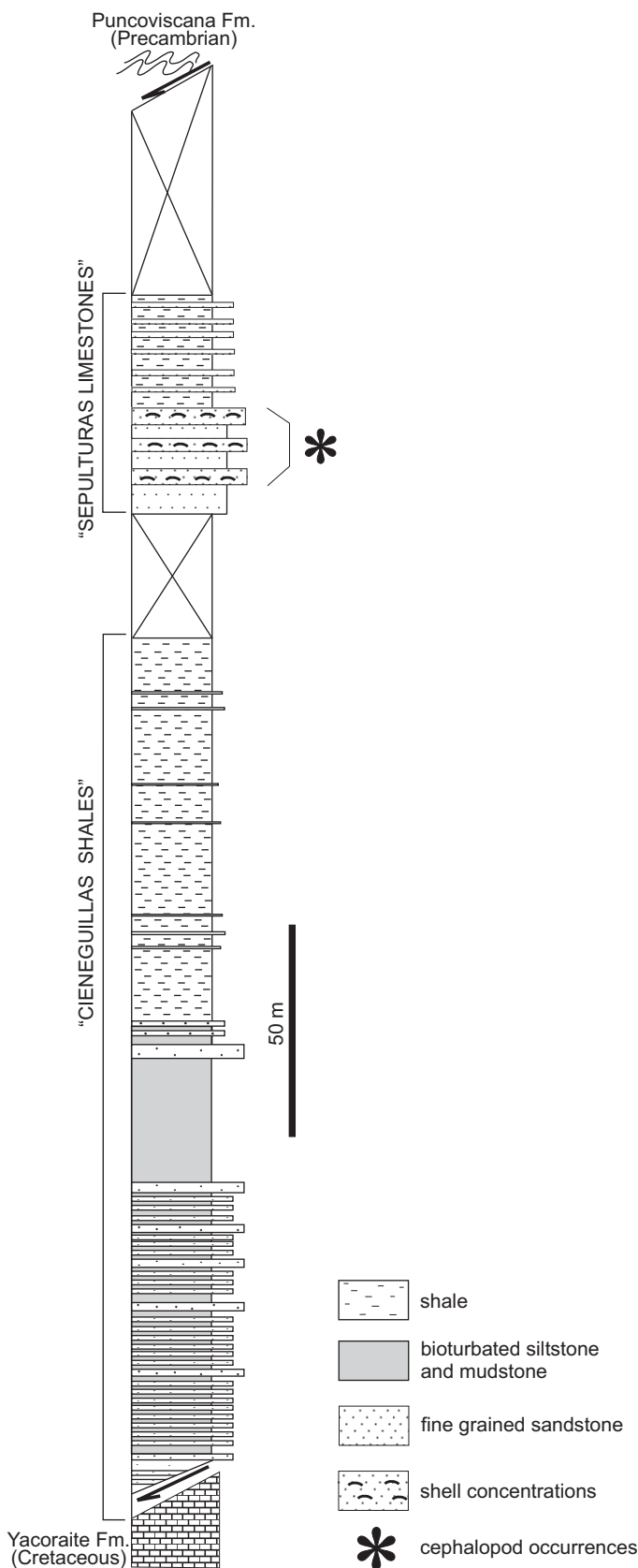
Fig. 3. Stratigraphic column at La Ciénaga, 5 km northwest of Purmamarca, indicating the beds containing cephalopods.

which help in the identification of this western Gondwanan genus.

Protocyptendoceras is very similar to *Anthoceras* Teichert and Glenister, 1954, from the Lower Ordovician of North America, NW Australia, Baltica, and Siberia, in the general conch shape and the siphuncle structure; however, *Anthoceras* is distinguished by having an annulated shell. Furthermore, some species of *Anthoceras* have larger dimensions at mature stage than *Protocyptendoceras*, such as *A. vaginatum* (Schlotheim, 1820) (see Mutvei 1997). *Protocyptendoceras* differs from *Proterocameroceras* Ruedemann, 1905, from the Lower Ordovician of North America, Greenland, Siberia, and NW Australia, mainly in having longer septal necks and in the structure of the endosiphuncular deposits (*Proterocameroceras* has three endosiphuncular blades) (Teichert 1964). *Protocyptendoceras* is usually smaller than *Lobendoceras* Teichert and Glenister, 1954, from the Lower Ordovician of NW Australia and Siberia, and has an elliptical cross section in later ontogenetic stages, rather than circular as in *Lobendoceras*. *Proendoceras* Flower, 1955, from the Lower Ordovician of North America and China, has a smaller siphuncle and a wider range of variability in the length of the septal necks compared with the genus studied here. *Protocyptendoceras* differs from *Paraendoceras* Ulrich and Foerste, 1936 from the Lower Ordovician of North America and Siberia in having longer septal necks and a lower angle of expansion. *Cotteroceras* Ulrich and Foerste, 1936, from the Lower Ordovician of the USA and Siberia, has a compressed cross section instead of a depressed one. *Protocyptendoceras* differs from *Ventroloboceras* Teichert and Glenister, 1954, from the Lower Ordovician of Western Australia, in having a larger siphuncle and shorter septal necks. *Catoraphiceras* Ulrich and Foerste, 1936, from the Lower Ordovician of the USA, Canada, Estonia, and Australia, differs from *Protocyptendoceras* mainly in having an annulated shell.

Protocyptendoceras fuenzalidae Cecioni, 1965

Fig. 4.

1965 *Protocyptendoceras fuenzalidae* sp. nov.; Cecioni, 1965: 9, pl. 2: 1–3.

1965 *Protocyptendoceras corvalani* sp. nov.; Cecioni, 1965: 11, pl. 2: 11–13.

1965 *Protocyptendoceras teicherti* sp. nov.; Cecioni, 1965: 12, pl. 3: 1–5.

Material examined.—Types: Holotype of *Protocyptendoceras fuenzalidae* (JUY-P 29 by original designation) (Fig. 4F₁–F₃). Other material examined: Paratypes JUY-P 30 (Fig. 4G) and JUY-P 31 (only a saggital cut) of *P. fuenzalidae*. Furthermore, the specimen (JUY-P 28) designed as the holotype for *P. corvalani* by Cecioni 1965—here considered to be a junior synonym of *P. fuenzalidae*—was analyzed (Fig. 4H). Forty four specimens from the Sepulturas Formation of La Ciénaga: CEGH-UNC 23117, 23118b, 23120a, 23121c, 23122, 23123a, b, 23125, 23126a–c, 23127, 23131, 23132a–j, 23133, 23134a–d, 23136, 23137a–c, 23138a, b,

23139, 23140, 23141, 23143, 23145, 23146, 23147, 23148, and 23182a, b.

Diagnosis.—As for the genus.

Description.—Orthoconic longiconic conch. Cross section is circular to subcircular, slightly depressed, in particular in later ontogenetic stages, with a compression ratio ranging from 0.67 to 1.1 (Fig. $4A_2$, F_1, J). Maximum diameter at the living chamber: 18 mm. Maximum diameter at the phragmocone: 13.2 mm. Apical angle variable, mean approximately 5.35°, with a maximum of 8.6° and a minimum of 1.7° (this was measured based both on dorsoventral expansion rate and lateral expansion rate, obtaining almost identical values, see Table 2). Shell surface only with growth lines (Fig. 4I). Mean cameral depth (expressed as a percentage of the dorsoventral diameter): 22.88 (max: 31, min: 15, see Table 2). In specimen CEGH-UNC 23132a, a general cameral length of 2–2.5 mm was measured, descending adorally to 1.8 mm, septal approximation indicates the maturity of the individual (Fig. $4A_1$). Suture almost straight, with a shallow, narrow ventral lobe (with a depth approximately 10% of the dorsoventral conch diameter) being well preserved in specimen CEGH-UNC 23137c and in the holotype (Fig. 4C, F_3). Septal depth was calculated only in specimen CEGH-UNC 23132d (which was longitudinally cut and polished), being 16% of the dorsoventral diameter. Moderate to large siphuncle, diameter varying from 27 to 54% of the dorsoventral diameter (mean: 41.7%). This parameter does not seem to change proportionally with ontogeny but it probably varies intraspecifically (see Table 2). The position of the siphuncle is marginal, being in contact with the ventral shell wall (Fig. $4A_1$, F_1, J). Septal necks subholochoanitic and connecting rings thick (Fig. $4K_1$, K_2). External shape of the siphuncle shows oblique lateral ridges and grooves that form an adoral ventral projection and an adapical dorsal sinus reflecting the positions and orientation of the septal foraminae (Fig. $4L_1$, M). Endocones weakly asymmetrical, with the endosiphotube being slightly closer to the ventral side. Cross section generally droplet-shaped (Fig. $4L_2$, N), but sometimes rounded (Fig. $4A_2$). Endosiphuncular deposits often recrystallised (Fig. 4D, E), although in specimen CEGH-UNC 23148 they are very well preserved (Fig. 4N). Spiculum 3 mm in maximum diameter and between 5 and 7 mm in length (Fig.

4D, E). A single endosiphotube is preserved, apparently without internal structures (Fig. 4D). Apical parts are rarely preserved, however one example of a probable external mould is present (CEGH-UNC 23132b). The first 5 chambers estimated as being 2.8 mm in length, while the width of the probable first chamber is estimated as being 1.1 mm.
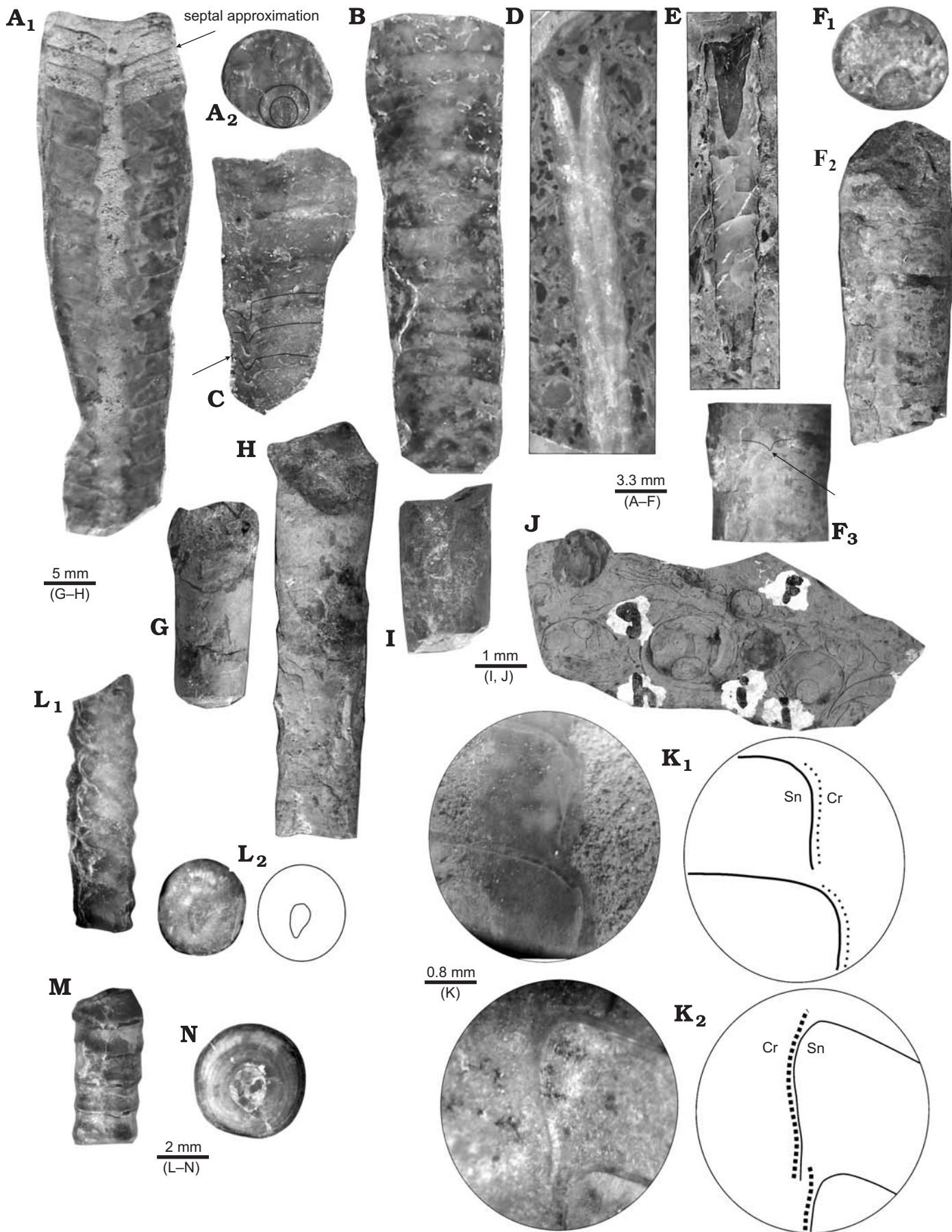
No specimens with a complete living chamber are preserved. A 35 mm long fragment is illustrated, however this shows neither muscle attachment scars nor the shape of the aperture (Fig. 4I).

Discussion.—Based on a revision of Cecioni's (1965) original material, and a detailed study of the recently collected specimens from La Ciénaga, it may be concluded that only one species belonging to the genus *Protocyptendoceras* occurs in the Purmamarca region. The senior synonym of the species is *P. fuenzalidae* Cecioni, 1965.

Cecioni (1965) stated that his material (with the exception of specimens assigned to *P. teicherti* Cecioni, 1965) was found in early Tremadocian strata, on the right margin of the Purmamarca River, 4 km upstream of Purmamarca. However, he also stated that these fossils came from the "Chañarcito Limestones" of Harrington and Leanza (1957). There is some discrepancy between the geographical location and the stratigraphical age and formation to which Cecioni's (1965) material has been assigned. The Chañarcito Formation (Tremadocian) crops out near Purmamarca railway station (Harrington and Leanza 1957), east of the Río Grande (Quebrada de Humahuaca) (see Fig. 2), and far from the Purmamarca River locality. Furthermore, no nautiloid cephalopods have been found in these horizons, which are not limestones but essentially black shales (Harrington and Leanza 1957). It is here concluded that the specimens assigned by Cecioni (1965) to *P. fuenzalidae* and *P. corvalani* were collected from La Ciénaga, and on the evidence of the associated fauna are Floian in age.

P. teicherti was described based on erratic material (apparently a single specimen), without a precise geographical or stratigraphical provenance. Nowadays, the use of specimens for taxonomic descriptions that lack accurate provenance data is discouraged. In this paper, and based on Cecioni's (1965) description, *P. teicherti* is considered as a junior synonym of *P. fuenzalidae*. The original material should be revised in or-

Fig. 4. Endocerid cephalopod *Protocyptendoceras fuenzalidae* Cecioni, 1965, from the Floian of La Ciénega, Purmamarca, Eastern Cordillera of Argentina. →
A. CEGH-UNC 23132a in ventral view [arrow points to the septal approximation (A_1)], and in posterior view showing the most apical part preserved, with the outline of the siphuncle and endocones retouched (A_2). **B**. CEGH-UNC 23134b in dorsal view. **C**. CEGH-UNC 23237c in ventral view, with the suture line retouched in part. Arrow points to the ventral lobe. **D**. CEGH-UNC 23127, polished section of isolated siphuncule, showing the endosiphotube, spiculum and recrystallised endocones. **E**. CEGH-UNC 23136, polished section of isolated siphuncle showing the spiculum and recrystallised endocones. **F**. JUY-P 29 (holotype of *P. fuenzalidae* Cecioni, 1965), transverse section of the most apical portion preserved (F_1), and in ventral view (F_2 and F_3), with the detail of the suture line on the ventral surface retouched to indicate the ventral lobe (F_3). **G**. JUY-P 30 (paratype of *P. fuenzalidae* Cecioni, 1965) in lateral view. **H**. JUY-P 28 (holotype of *P. corvalani* Cecioni, 1965) in ventral view. **I**. CEGH-UNC 23145, broken living chamber in lateral view. **J**. CEGH-UNC 23132, cross section of the rock sample. Note the siphuncle position in the specimens and the relation between the siphuncle and shell diameter. **K**. Detail of the septal necks. K_1, CEGH-UNC 23132a, detail of the siphuncular structure from a ventral view of the entire conch (lacking external shell wall). Note subholochoanitic septal necks and thick connecting rings; K_2, CEGH-UNC 23132d, detail of the siphuncular structure from a longitudinal view of a cut and polished specimen, showing subholochoanitic septal necks, in both cases with a graphical scheme to the right (Sn, septal neck; Cr, connecting ring). **L**. CEGH-UNC 23146, isolated siphuncle in lateral view (L_1), and in polished cross section, showing the droplet shape of the endocones to the right (L_2) (ventral side downward). **M**. CEGH-UNC 23147, isolated siphuncle in dorsal view. **N**. CEGH-UNC 23148, detail of the siphuncle in polished cross section, showing the preserved structure of the endocones (not recrystallised). Ventral side downward.

septal approximation

A_1 A_2 B C D E F_1 F_2 F_3 G H I J K_1 K_2 L_1 L_2 M N

3.3 mm
(A–F)

5 mm
(G–H)

1 mm
(I, J)

0.8 mm
(K)

2 mm
(L–N)

Sn Cr

Cr Sn

der to provide a more definitive conclusion. However, to date this has not been found in the Cecioni's Collection at the JUY-P.

The main differences between the three species described by Cecioni (1965) lie in chamber spacing, and rather dubiously, the form of the suture line. In his description of the three species, Cecioni (1965) made reference to the number of chambers present in an interval equivalent to the lateral diameter of the conch, but omitted mention of the ontogenetic stage at which the shell diameter was measured. Given the preservational differences between the specimens, it may be that Cecioni did not consider giving comparative measurements. In any case, the supposed variability of the material under study may be considered as intraspecific (see Table 2). With regard to the suture, Cecioni (1965) did not make specific mention of the differences between *P. fuenzalidae* and *P. corvalani*, but indicated that a difference could exist. Subsequently, he mentioned that in *P. teicherti* the suture presented a more prominent ventral saddle. Again, this degree of variability is common within a single species. Considering these observations, it is concluded that the recognition of three separate taxa is not justified.

The differences in the suture between the newly described material and the specimens described by Cecioni (1965) may be found in the ventral part, where a lobe should be present instead of a saddle. However, study of specimen JUY-P 29 (holotype of *P. fuenzalidae*) shows that a shallow ventral lobe is present (Fig. 4F$_3$), with a very similar aspect to that present in specimen CEGH-UNC 32137c (Fig. 4C).

In the newly described material the layering of the connecting rings mentioned by Cecioni (1965) for *P. fuenzalidae* is not evident (Fig. 4N). Mutvei (1997), when studying the siphuncular structure of some endocerid genera using SEM, noted that the connecting ring is a continuation of the spherulitic-prismatic layer, one of three structural layers of the septal neck present in this order. He mentioned that the structural differentiation of the connecting ring reported by previous authors (Flower 1941, 1964; Teichert and Glenister 1954) probably results from diagenesis. Furthermore, the siphuncular structure in endocerids agrees in detail with that of living *Spirula* and *Nautilus* (Mutvei 1997).

The conical endosiphuncular deposits (endocones) were secreted by the siphuncular epithelium (Mutvei 1964). Regarding the shape of these deposits, some variability exists in the studied species (Fig. 4A$_2$, L$_2$, N). Most specimens show a droplet shape in cross section, but some of them have a rounded contour. However, Mutvei (1997) stressed the intraspecific variability of these structures, advising caution with regard to their use in the definition of species.

With respect to the length of the septal necks, Cecioni (1965: 8), in the diagnosis of the genus, wrote: "long septal necks, of approximately one third of the chambers length". But in the description of the species *P. fuenzalidae*, he mentioned that septal necks were of approximately three-quarters of chamber length. Although the diagrams shown in Cecioni's plates are not clear, it appears that the septal necks are rather

long (e.g., Cecioni 1965: pl. 2: 7; pl. 3: 5). In the material studied here it can be seen that the septal necks are subholochoanitic (Fig. 4K$_1$, K$_2$). The differences observed in this character could be due to ontogenetic variability, as in other genera of the same family (e.g., *Proendoceras* Flower, 1955).

Aceñolaza et al. (1977) reported the presence of *Cyptendoceras* sp. in the Lower Ordovician of the Precordillera (San Juan Province, Argentina). Based on the description of the single studied specimen (considered by Aceñolaza et al. 1977 to be a proterocameroceratid), it is similar to the material described here in most aspects, although the presence of endocones is not mentioned. However, the calcite infilling of the siphuncle suggests that they may be present in a recrystallised state.

Finally, it is worth noting the similarities between this genus and forms such as *Anthoceras* Teichert and Glenister, 1954, in view of the equivalent age assigned to cephalopod assemblages from Western Australia.

Stratigraphical and geographical distribution.—Sepulturas Formation, Floian Stage. La Ciénaga, about 5 km west of Purmamarca, Jujuy Province, Eastern Cordillera of Argentina.

Comments on preservation and autoecology

As mentioned above, the facies at La Ciénaga resemble those of the Los Colorados area (Astini et al. 2004), and represent inner shelf sediments deposited below fair-weather wave-base, periodically affected by storm events. Cephalopods, as well as trilobites, bivalves and brachiopods, are found in the tempestites formed by such storms (Astini and Waisfeld 1993). Rock samples containing the specimens consist of bioclastic concentrations in a fine-grained matrix, the packing of the bioclasts being dense in some areas.

Specimens assigned to *Protocyptendoceras fuenzalidae* Cecioni, 1965, are preserved in a rather homogeneous way. Living chambers are very rarely preserved and, when present, they are broken (Fig. 4I). Apical parts are rarely preserved, apart from one example of a probable external mould (CEGH-UNC 23132b). Most phragmocone chambers are filled with calcite, but some, generally those in an adoral position, are filled with fine-grained sediment (Fig. 4A$_1$).

The siphuncle is usually infilled with sediment in the adoral part (Fig. 4A$_1$); adapically, the endocones are very rarely preserved with their original structure, usually appearing as amorphous calcite filling the apices. Sediment has also filled the last-formed endocone (forming the spiculum) and the endosiphotube (Fig. 4D, E). Many isolated fragments of siphuncle are preserved (e.g., Fig. 4D, E, L, M), which are always infilled with calcite. This fact, together with the diameter of the fragments, suggests that these are infilled with endosiphuncular deposits, indicating that they represent the apical parts of siphuncles. The very common presence of these isolated siphuncles in the studied species suggests that

the apical chambers were particularly susceptible to damage. Evans (1992) proposed that if apical chambers (or the chambers adjacent to endocones) were empty at the time of death, water could not easily enter because of the presence of deposits. This may be valid for the specimens studied here too. When the adoral chambers were water-filled, and calcite cement accumulated, the apical chambers were empty and then more susceptible to failure by implosion or by collision with other clasts. In polished specimens CEGH-UNC 23127 and 23136 (Fig. 4D, E), siphuncles are preserved adorally just at the end of the endosiphocone, probably indicating a particular point of weakness. The adoral parts of the siphuncle are never preserved in isolation, but are only observed within the phragmocones.

Some aspects of the functional morphology of cephalopods inferred by Westermann (1999 and references cited therein) could be applied to *Protocyptendoceras fuenzalidae*. The SSI (septal strength index) of Westermann (1973) was calculated for the polished specimen CEGH-UNC 23132d. The thickness of the septa was measured by use of a magnifying glass and its radius of curvature was estimated by graphic methods. Each of the nine preserved septa was approximately equivalent to one subdivision of the rule of the magnifying glass, which corresponds to 0.045 mm. The radius of curvature of the nine septa is approximately 6.5 mm (diameter of the circumference being between 12.85 to 13.28 mm). Therefore, the SSI was calculated as $(\delta/R) \times 1000 = (0.045mm/6.5mm) \times 1000 = 6.9$. This index corresponds to an implosion depth of ca. 200 m (based on the calibrating curve of Westermann 1973). Following Westermann (1999), the safety factor between maximal habitat depth and implosion depth is 2 in shallow-water fossil nautiloids; therefore the habitat depth for *Protocyptendoceras* would be approximately 100 m.

It is interesting to note the similarities between this index and that indicated by Westermann (1973) for *Anthoceras* and *Proterocameroceras*. The SSI is 7 for *Anthoceras decorum* Teichert and Glenister, 1954, and 5.5 for *Proterocameroceras contrarium* Teichert and Glenister, 1954, both species from the Lower Ordovician of Western Australia.

Concerning the swimming orientation of the species, the presence of endosiphuncular deposits in the apical part would have acted as a "counterweight" to the body chamber. The centres of mass and buoyancy would coincide in the vertical plane, so that a horizontal orientation would be moderately stable for swimming, with the marginal and wide siphuncle preventing rotation (Westermann 1999).

Paleobiogeographical affinities

The palaeobiogeographical affinities of Ordovician cephalopods from the Eastern Cordillera of Argentina are poorly known. Nevertheless, Crick (1993) identified the Floian–Dapingian as the interval showing the greatest diversity and lowest degree of endemism for endocerids in his study of the biogeography of Early and Middle Paleozoic nautiloids
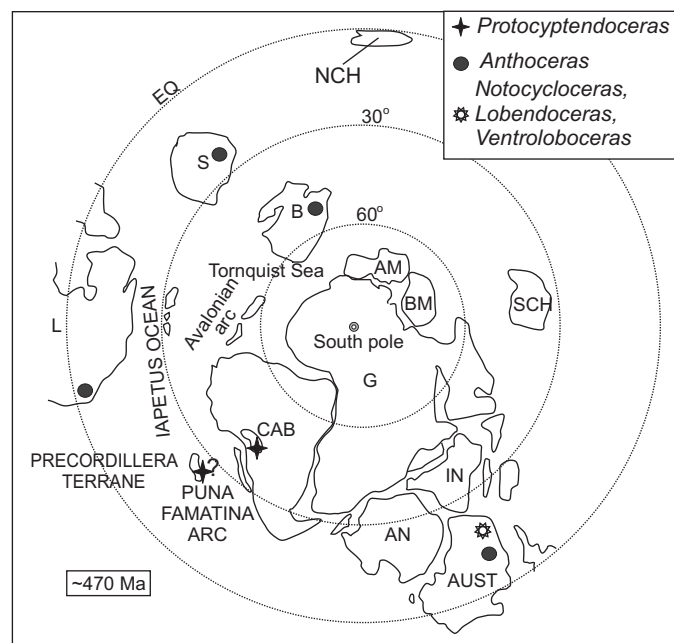

Fig. 5. Paleobiogeographical distribution of *Protocyptendoceras* and the related genera *Anthoceras* Teichert and Glenister, 1954, *Notocycloceras* Teichert and Glenister, 1954, *Lobendoceras* Teichert and Glenister, 1954 and *Ventroloboceras* Teichert and Glenister, 1954 (see text for explanation). 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, Argentinian part of the Central Andean Basin (paleogeographical map after Astini et al. 2007).

which did not include data from the Ordovician of Western Gondwana.

Given the present revision of the genus *Protocyptendoceras* Cecioni, 1965, it is worth discussing some features of its distribution and affinities. At present, *Protocyptendoceras* is known with certainty from the Floian of the Eastern Cordillera of Argentina; however, close similarities exist with *Cyptendoceras* sp. (Aceñolaza et al. 1977) from the Lower Ordovician of the Argentine Precordillera (Cuyania terrane), which at that time was located near the Western Gondwana margin, between the equator and 30°S (Benedetto 2003; Astini et al. 2007). Nevertheless, *Protocyptendoceras* resembles proterocameroceratids from the Floian of Eastern Gondwana, including the Australian species *Anthoceras decorum* Teichert and Glenister, 1945 and related forms such as *Lobendoceras* Teichert and Glenister, 1945, *Ventroloboceras* Teichert and Glenister, 1945, and *Notocycloceras* Teichert and Glenister, 1945, considered by Dzik (1984) to be synonyms of *Anthoceras*. Other species referred to *Anthoceras* are recorded from Siberia (*Anthoceras angarense* Balashov, 1960, *A. bajkitense* Balashov, 1960, and *A. sibiricum* Balashov, 1962), Laurentia (*A. arrowsmithense* Stait and Laurie, 1984), and Baltica [*A. vaginatum* (Schlotheim, 1820)]. Hence, *Protocyptendoceras* shows palaeobiogeographical affinities mainly with warm water faunas (Fig. 5). Close affinities with Eastern Gondwana were also determined for Floian trilobites from the same locality studied here (Vaccari et al. 2006).

Even though most of the taxa described by Cecioni (1953, 1965) are still in need of systematic revision (see Table 1), it is interesting to consider additional data regarding the biogeographical affinities of the Early Ordovician cephalopods from Western Gondwana. *Purmamarcoceras* Cecioni, 1965, along with *Protocyptendoceras*, is only known from the Eastern Cordillera of Argentina. *Robsonoceras* Ulrich and Foerste, 1936, was recorded from the Argentine Precordillera (Aceñolaza et al. 1977) and Laurentia (Flower 1964), whereas *Clarkoceras* Ruedemann, 1905 was recorded from Laurentia (Flower 1964), China (Kobayashi 1931), and Siberia (Balashov 1962). *Cyclostomiceras* Hyatt in Zittel, 1900, and *Cyptendocerina* Ulrich, Foerste, Miller and Unklesbay, 1944, were described from Laurentia (Ulrich et al. 1944; King 1998). Although these general palaeobiogeographical affinities indicate a warm water faunal influence, preliminary studies on the family Eothinoceratidae Ulrich, Foerste, Miller, and Unkelesbay, 1944, from the Tremadocian of NW Argentina and the Floian from NW Argentina and southern Bolivia (including *Bathmoceras* cf. *australe* and *Desioceras floweri*, see Table 1), suggest a predominant distribution of this taxon along the margins of western and northern Gondwana [from the Central Andean Basin to Avalonia and Armorica (Evans 2007)]. This fact indicates that Early Ordovician cephalopod faunas of the Eastern Cordillera of Argentina include both regionally distributed taxa and warm water related taxa.

Genera described by Cecioni (1953, 1965) from the Middle Ordovician of NW Argentina are *Protocycloceras* Hyatt in Zittel, 1900, *Paracyclostomiceras* Cecioni, 1953, *Baltoceras* Holm, 1897 and *Belloceras* Cecioni, 1965. Only *Belloceras* is an endemic genus. *Paracyclostomiceras* is recorded from Baltica (King 1998) and *Baltoceras* from Baltica and Laurentia (Flower 1964), whereas *Protocycloceras* has a cosmopolitan distribution (Furnish and Glenister 1964).

Future field collecting in the Central Andean Basin of Argentina, along with the revision of the original material studied by Cecioni (1953, 1965), is expected to improve our knowledge of the palaeobiogeographical affinities of the Early and Middle Ordovician cephalopods from this region.

Acknowledgments

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