The nautiloid Family Eothinoceratidae from the Floian of the Central Andean Basin (NW Argentina and South Bolivia)

MARCELA CICHOWOLSKI[1]*, BEATRIZ G. WAISFELD[2], NORBERTO E. VACCARI[2] and LARISA MARENGO[3]

[1] *Instituto de Estudios Andinos 'Don Pablo Groeber' (IDEAN), CONICET and Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pab. 2, C1428EGA, Buenos Aires, Argentina*
[2] *Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), CONICET and Centro de Investigaciones Paleobiológicas (CIPAL), Universidad Nacional de Córdoba, Córdoba, Argentina*
[3] *Fagnano 90, B° Gral. Mosconi (9005), Comodoro Rivadavia, Chubut, Argentina*

A single confidently dated species of cephalopod is so far known in the Tremadocian of the southern Central Andean Basin (NW Argentina and southern Bolivia). This species belongs to the Eothinoceratidae and has a strong affinity mainly with Avalonia. During the Floian, a notable increase in diversity took place, with the appearance of a variety of families represented by several genera, in particular, within the Family Eothinoceratidae. In addition to the previously described species from southern Bolivia, we evaluate the other records of that family from the Central Andean Basin, and propose the following new taxa: *Saloceras sikus* sp. nov., *Saloceras quena* sp. nov., *Mutveiceras* gen. nov., and *Mutveiceras cienagaensis* sp. nov. We also describe *Margaritoceras diploide*, *Margaritoceras* sp., and *Mutveiceras* sp. From a palaeogeographic perspective, the cephalopod fauna shows affinities mainly with those of England, Wales, and the Montagne Noire (cold water Gondwana and peri-Gondwana). As with other cephalopod faunas of mid to high palaeolatitudes, eothinoceratids occur along with other cephalopods forming assemblages of low morphological diversity. We interpret the forms described here as demersal with a subvertical poise, but capable of making rapid buoyancy changes, living in a wide spectrum of shallow offshore to shoreface settings. Copyright © 2014 John Wiley & Sons, Ltd.

1. INTRODUCTION

After their origin in the Late Cambrian, during the Ordovician the cephalopods underwent a major diversification. A wealth of new morphotypes evolved and expanded differentially into almost all marine environments (Frey *et al.*, 2004).

Ordovician cephalopods from the southern Central Andean Basin (NW Argentina and Bolivia) remain poorly known. The most important contributions to our knowledge of these faunas are those of Cecioni (1953, 1965) and Cecioni and Flower (1985). These describe several cephalopod taxa including ellesmerocerids, orthocerids, and endocerids. However, mainly as a consequence of deficiencies in the illustrations and descriptions, combined with the uncertainty regarding the precise age of these faunas, previously described species

*Correspondence to: M. Cichowolski, Instituto de Estudios Andinos 'Don Pablo Groeber' (IDEAN), CONICET and Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pab. 2, C1428EGA, Buenos Aires, Argentina. E-mail: mcicho@gl.fcen.uba.ar

are in need of revision. Recently, Cichowolski (2009) revised the endocerid genus *Protocyptendoceras* Cecioni from the Floian of Purmamarca area (Cordillera Oriental, Jujuy, Argentina), and Cichowolski and Vaccari (2011) reported the presence of the Family Eothinoceratidae from the Middle Tremadocian of the Sierra de Mojotoro (Cordillera Oriental, Jujuy). Previous reports on Ordovician Eothinoceratidae of the Central Andean Basin are summarized in Table 1.

Kröger and Evans (2011) noted that intermediate to high palaeolatitude cephalopod assemblages are of relatively low diversity and characterized by the presence of members of the family Eothinoceratidae. Based on these eothinoceratid-dominated assemblages, they suggested the presence of a '*Saloceras* realm' that may have extended along the margins of East and West Gondwana, at least into intermediate latitudes. However, Kröger (2013) pointed out that from a nomenclatural viewpoint the term '*Saloceras* realm' does not follow the recommendations proposed by Westermann (2000) for the definition of biogeographic units, and discussed the existence of a peri-Gondwana Realm,

Table 1. Previous research on Eothinoceratidae from the Ordovician of the Central Andean Basin.

Taxon	*Margaritoceras margaritae* Cecioni and Flower	*Margaritoceras diploide* Cecioni and Flower	*Margaritoceras* sp.	*Eothinoceras renatae* Cecioni and Flower	*Saloceras* cf. *sericeum* (Salter)	*Desioceras floweri* Cecioni and Flower	Eothinoceratidae gen. et sp. indet.
Locality	San Lucas, southern Bolivia	San Lucas and Sella, southern Bolivia, Los Colorados–Chamarra, NW Argentina	San Lucas, southern Bolivia	Sella, southern Bolivia	Dique La Ciénaga = La Cornisa, Cordillera Oriental, Jujuy, Argentina	Río San Lorenzo, Jujuy, Argentina	To the west of Quince Mil (valleys of the Río Yuscamayo and Río Yanahurco) southern Perú
Age (according to the original paper)	Arenigian	Arenigian	Arenigian	Arenigian	Dubious	Uncertain (within an erratic boulder)	Middle or late Llanvirn
Revised age assignment	Probable mid-late Floian	Mid–late Floian	Probable mid–late Floian	Probable mid Floian	Middle Tremadocian	Probable Darriwilian (cf. Chen and Teichert, 1987; Evans, 2005)	–
Observations	–	Described herein upon Argentine material	–	–	*Bathmoceras* cf. *australe* Teichert (Cecioni and Flower, 1985) and *Bathmoceras* sp. (in Cecioni, 1953), referred to *Saloceras* cf. *sericeum* by Cichowolski and Vaccari (2011)	Part of type material (including the thin section of the siphuncle) is lost	Considered to be closely related to *Saloceras*, *Margaritoceras* and *Sacerdosoceras*
References	Cecioni and Flower (1985)	Cecioni and Flower (1985), this report	Cecioni and Flower (1985)	Cecioni and Flower (1985)	Cecioni and Flower (1985), Cichowolski and Vaccari (2011)	Cecioni and Flower (1985), Chen and Teichert (1987)	Evans (2007)

probably since the Middle Tremadocian to the Floian, to make reference to associations of slender eothinoceratids and proterocameroceratids of high latitudes and peri-Gondwanan regions.

In NW Argentina, only *Saloceras* cf. *sericeum* (Salter) is present in Tremadocian rocks (Cichowolski and Vaccari, 2011), but during the Floian eothinoceratids become increasingly diverse and are characterized by the appearance of new species of *Saloceras* Evans, the presence of *Margaritoceras* Cecioni and Flower, and *Mutveiceras* gen. nov.

This report describes the Floian eothinoceratid assemblages of the southern part of the Central Andean Basin (NW Argentina and southern Bolivia). Besides, their palaeoautoecological characteristics and palaeobiogeographical significance are discussed.

2. MATERIAL AND METHODS

A total of 24 cephalopod specimens from Lower Ordovician horizons in Argentina and Bolivia (Figs. 1 and 2) were studied. All material from Argentina is housed at the CIPAL (Centro de Investigaciones Paleobiológicas, Córdoba, Argentina), under the prefix CEGH-UNC (Cátedra de Estratigrafía y Geología Histórica, Universidad Nacional de Córdoba, Córdoba, Argentina). The Bolivian specimens are housed at the Museo de Historia Natural Alcide d' Orbigny, Cochabamba, Bolivia, under the prefix MHNC. The specimens have been collected over several field seasons during the last decade.

The preservation of the specimens differs according to localities. With the exception of the specimens from Los Colorados and La Ciénaga, in which shell material is preserved, all other material is preserved as internal and external moulds. Those specimens in which the shell material was preserved were cut longitudinally and polished with aluminum oxide in order to study the internal structures. The specimen from Los Colorados (CEGH-UNC 23886) was polished on a naturally broken surface (on the siphuncular side of the conch), and the surface could not be completely smoothed (Fig. 3 A_2).

In some specimens the conch—at least the phragmocone—is preserved as a 3-D external mould with the siphuncle preserved as a sediment-filled rod (MHNC 13539a from Sella, CEGH-UNC 25641 from Portillo, Fig. 3B–C). Most specimens include part of the living chamber, but some consist of phragmocone only. No specimens with preserved apical part of the conch have been recovered. Deformation of some specimens as a consequence of sedimentary loading, combined with the presence of strongly cemented matrix adhering to some specimens means that it is difficult to obtain accurate measurements in some cases.
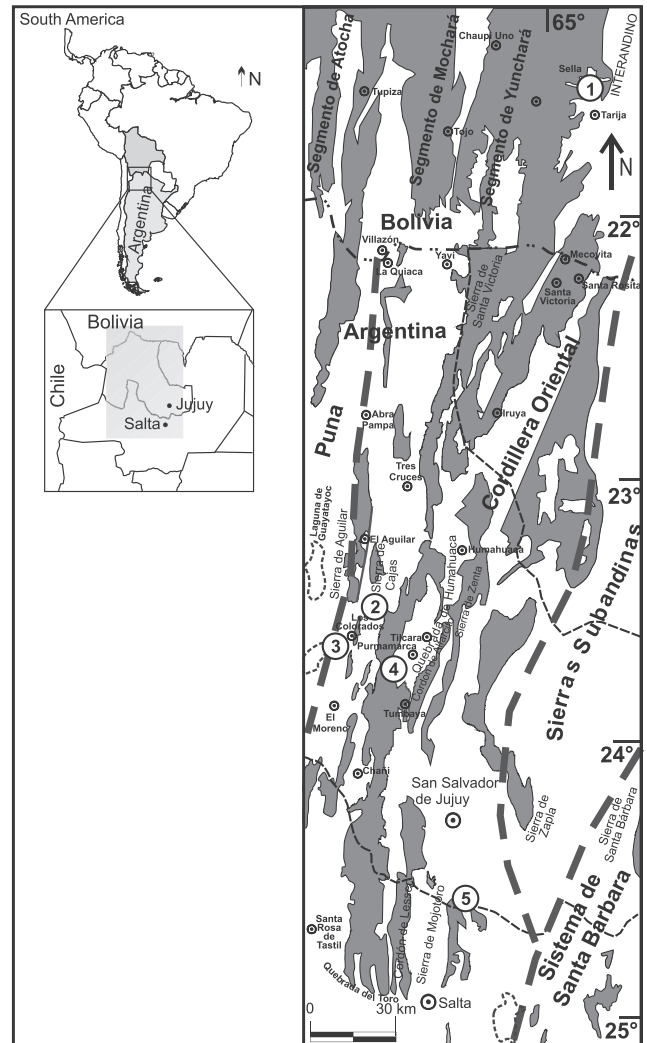

Figure 1. Map showing the location of fossil localities. The outcrops of Cambro-Ordovician rocks are indicated in grey. (1) Sella, (2) Portillo (south of Sierra de Cajas), (3) Los Colorados–Chamarra, (4) La Ciénaga, (5) La Cornisa.

The terminology used in the descriptions is that explained in the Treatise on Invertebrate Paleontology (Moore, 1964, Part K, Mollusca 3, p. K16-17).

The characters measured are set out in the explanation of Tables 2 and 3. All measurements were taken using digital calipers with a resolution of 0.1 mm. With the exception of the cut and polished specimens (which were photographed submerged in ethylic alcohol), and those preserved as moulds of the siphuncle and the living chamber (MHNC 13539a and CEGH-UNC 25641), all specimens were coated with ammonium chloride and then were photographed using a Canon PowerShot SX20 IS. Details of the internal aspect of the siphuncle were recorded with a reflected light binocular microscope, Nikon SMZ 1500, equipped with an AxioCam HRc Zeiss ccd camera.

3. GEOLOGICAL SETTING AND STRATIGRAPHIC FRAMEWORK

The Central Andean Basin is a large autochthonous Gondwanan basin that extended from central Perú to Northwestern Argentina. The southern part of the Central Andean Basin is exceptionally exposed in the Cordillera Oriental of northwestern Argentina and Bolivia, where siliciclastic successions were deposited along the western Gondwanan margin of South America (Benedetto and Sánchez, 1996). The Cordillera Oriental is interpreted as a forebulge, where platform deposits developed into a low gradient ramp-like setting influenced by a large scale prograding deltaic system from the east, and by an active volcanic arc complex in the west (present in the Puna region) (Bahlburg, 1990, 1991; Bahlburg and Furlong, 1996; Astini, 2003).

The cephalopods were collected from different litostratigraphical units (Fig. 2). In the Los Colorados–Chamarra region (Fig. 1), *Margaritoceras* and *Saloceras* were recovered from the Acoite Formation. In La Ciénaga (Fig. 1), *Mutveiceras* gen. nov. was recovered from the Acoite Formation. In Sella (Fig. 1), southern Bolivia, *Margaritoceras* was collected from the Sella Formation.
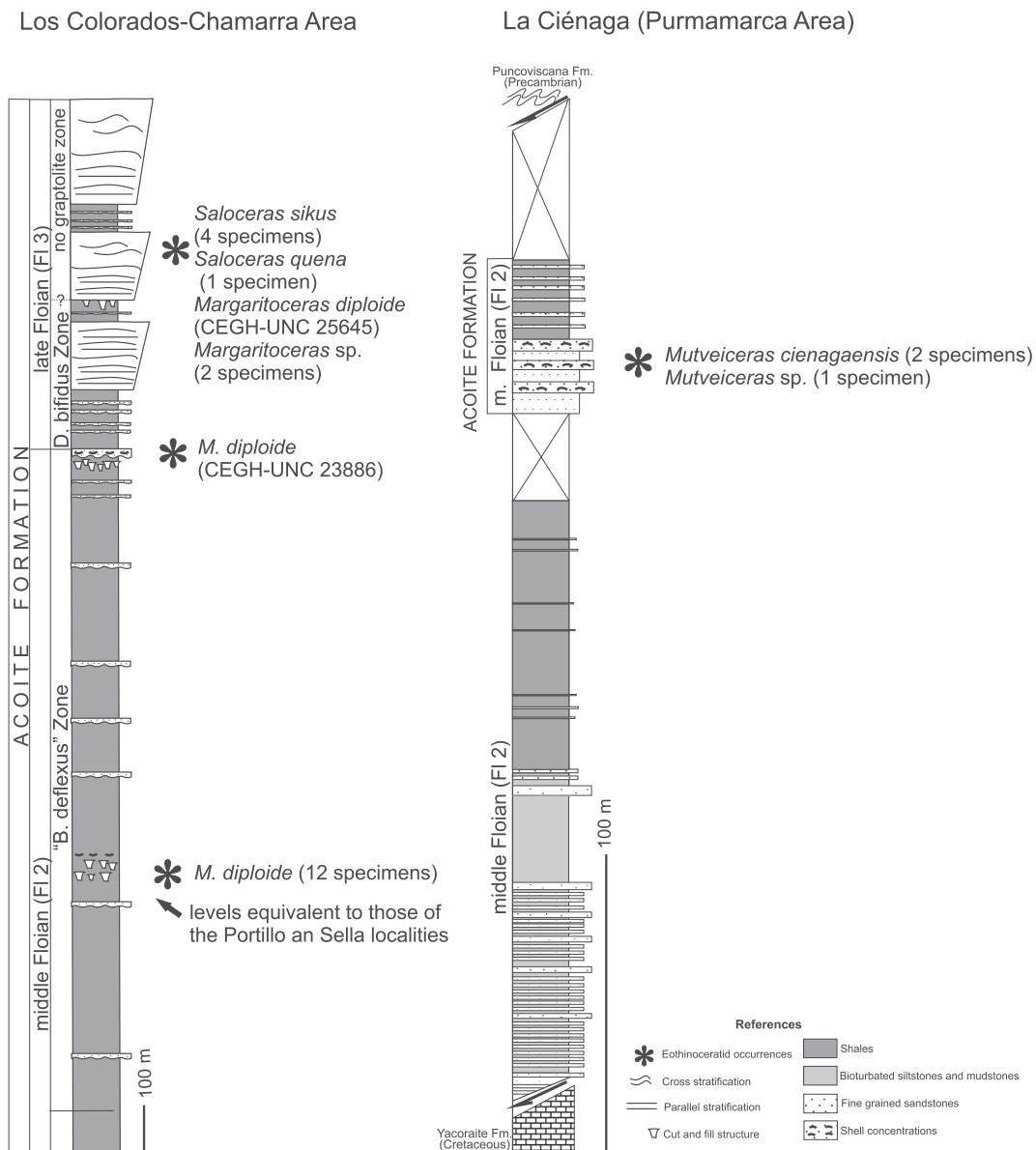

Figure 2. Stratigraphic sections at Chamarra–Los Colorados Area (to the left) and La Ciénaga, Purmamarca Area (to the right), Cordillera Oriental, Argentina, with nautiloid occurrences indicated.

3.1. Outcrops in Argentina

3.1.1. Los Colorados–Chamarra area

It is located approximately 28 km northwest of Purmamarca Village, in Jujuy Province (Fig. 1). The Portillo section lies about 15 km northwest of this section, on the eastern flank of the Sierra de Cajas. The sedimentary succession exposed in the area ranges from Lower Ordovician to Devonian in age (Astini *et al*., 2004). The cephalopods studied here come from the Early Ordovician Acoite Formation, which together with the Santa Rosita Formation (late Cambrian–Tremadocian) comprise the Santa Victoria Group (Turner, 1960); superbly exposed in the Cordillera Oriental. The material was recovered from three sections (Fig. 1): Los Colorados (one specimen), Quebrada de Chamarra (10 specimens), and Portillo (five specimens) (see Fig. 2). The age of
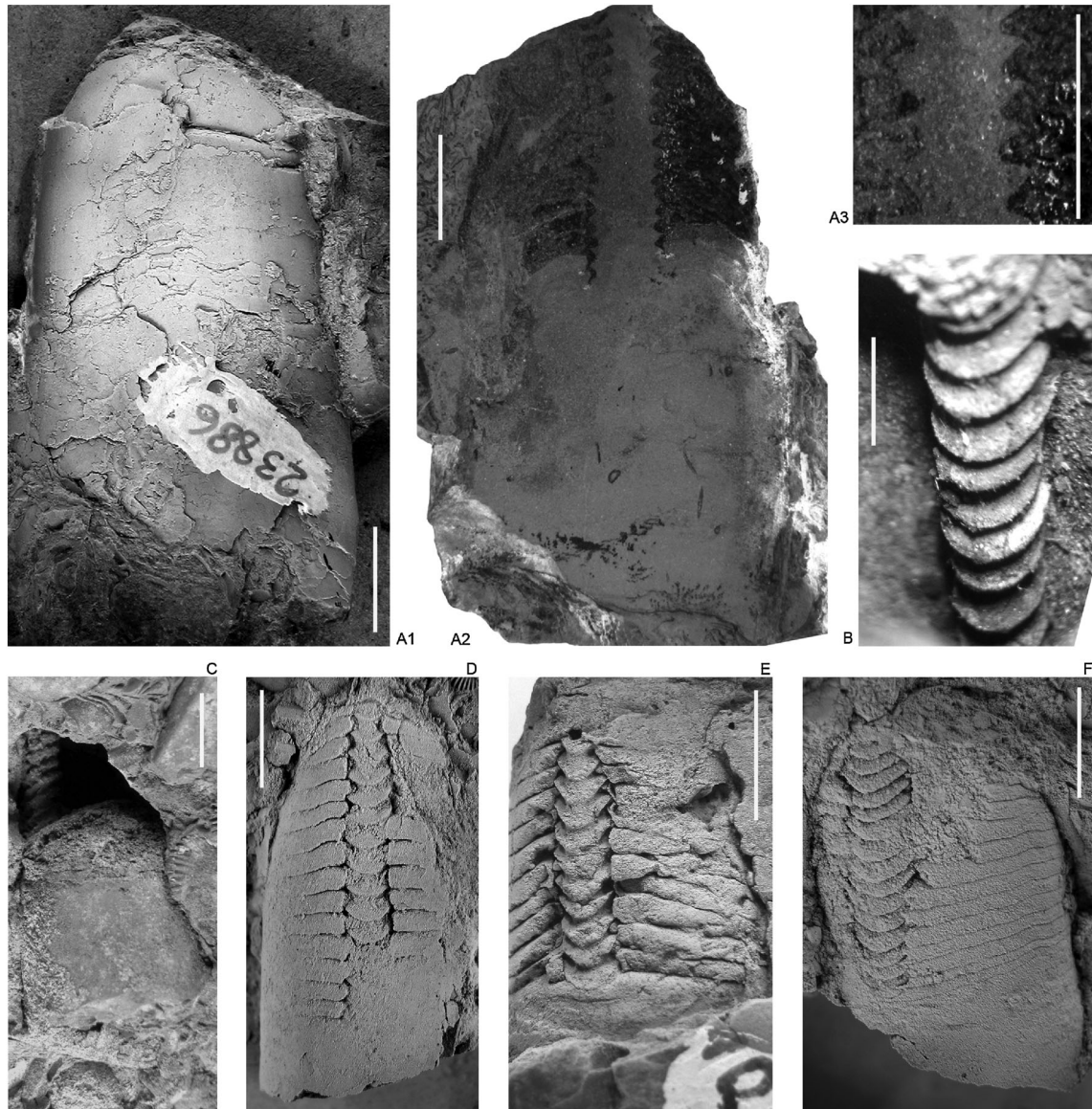

Figure 3. Eothinoceratids from the Floian of the southern Central Andean Basin. **A–E**. *Margaritoceras diploide* Cecioni and Flower. **A**. Specimen CEGH-UNC 23886, Acoite Formation, Los Colorados. **A$_1$**. External view of the specimen. **A$_2$**. Polished section of a tangential naturally cut of the siphuncular side of the conch. **A$_3$**. Detail of part of the siphuncle, showing the thickened connecting rings. **B**. Specimen CEGH-UNC 25641, Acoite Formation, Portillo, showing the siphuncle within the empty space left by the removed septa. **C.** Specimen MHNC 13539a, Sella Formation, Sella, lateral view showing the living chamber with part of the siphuncle within the empty space left by the removed septa. **D**. Specimen CEGH-UNC 25642a, Acoite Formation, Portillo, external view of the siphuncular side showing the concave and arched segments of the siphuncle, the sutures, and a small part of the living chamber. **E**. Specimen CEGH-UNC 25642a, Acoite Formation, Quebrada de Chamarra, external view of the siphuncular side showing the siphuncle, the sutures, and a small part of the living chamber. **F**. *Margaritoceras* sp., specimen CEGH-UNC 25644a, upper part of the Acoite Formation, Quebrada de Chamarra, external view of the specimen showing the siphuncle, the sutures and a small part of the living chamber. The scale bars are 10 mm long throughout the figure.

the Acoite Formation in the area is biostratigraphically constrained between the *Tetragraptus phyllograptoides* (early Floian) and the *Didymograptellus bifidus* (late Floian) graptolite zones (Toro, 1997; Toro and Maletz, 2008).

The uppermost part of the Acoite Formation lacks biostratigraphically diagnostic elements, although the presence of some trilobite species that are present in underlying levels suggests a late Floian age for the upper part of the Acoite Formation. The nautiloids were recovered from both the '*B. deflexus*' Zone, and the *D. bifidus* Zone, as well as from the uppermost part of the unit.

The Acoite Formation reaches a thickness of approximately 2500 m in the Los Colorados–Chamarra area, and it is interpreted as a storm-dominated shallow marine succession that displays stacked, large-scale shallowing-upward cycles, encompassing shelf to shoreface settings. The lower half of the Acoite Formation is composed of black and grey shales deposited in a largely disoxic shelf environment, below normal wave base. The middle and upper parts of the Acoite Formation are characterized by several upward thickening and coarsening cycles with abundant wave-generated structures deposited in an increasingly shallow shelf environment, which indicates shoreline progradation (Astini and Waisfeld, 1993).

Most of the material assigned to *Margaritoceras diploide* Cecioni and Flower comes from bioclastic concentrations preserved in gutter casts. These structures are particularly abundant in a 15–20 m thick muddy interval in the middle part of the Acoite Formation interpreted as a lower offshore setting (Fl 2, '*B. deflexus*' Zone). They are especially well represented at Chamarra and Portillo sections, where interval with gutter-casts represents a good stratigraphic marker for the unit (Astini and Waisfeld, 1995). The range of *M. diploide* (represented by a single specimen (CEGH-UNC 25645)) extends into the upper part of the Acoite Formation, interpreted as shoreface deposits strongly influenced by storm and wave activity. This specimen comes from storm-induced shell concentrations that occur in coarse sandy packages exhibiting abundant hummocky cross-stratification structures. *Margaritoceras* sp., *Saloceras sikus* sp. nov., and *S. quena* sp. nov. also come from the shell beds in the uppermost portion of the Acoite Formation.

The accompanying macrofauna is mainly composed of trilobites with subordinate rynchonelliformean brachiopods, ostracods, and bivalves. In one coquina we also found conodonts (CEGH-UNC 25639). Other cephalopods found in the same outcrops of the Los Colorados–Chamarra area consist largely of undescribed protocycloceratids and endocerids. Concerning the trilobite faunas, its taxonomy (Waisfeld and Vaccari, 2003, and references therein), biostratigraphy (Waisfeld and Vaccari, 2008), palaeoecology (Waisfeld *et al.*, 2003; Balseiro and Waisfeld, 2013), and biogeography (Vaccari *et al.*, 2006; Benedetto *et al.*, 2009)

are relatively well understood. The trilobite assemblages form part of the *Famatinolithus* Fauna (Waisfeld *et al.*, 1999, 2003), which apart from the ubiquitous *Famatinolithus* includes asaphids and subordinate calymenids, raphiophorids, pliomerids, and olenids. The *Famatinolithus* Fauna developed across a relatively wide spectrum of environmental zones, from the lower offshore to the upper shoreface, showing a clear decline in diversity into shallower waters. This fauna extended into the Floian successions of South Bolivia with a broadly similar generic composition and patterns of abundance.

3.1.2. *Purmamarca area*

The material studied was collected from beds of Floian age at the locality of La Ciénaga, about 5 km west of Purmamarca, Tumbaya Department, Jujuy Province, in the Cordillera Oriental of Argentina (Fig. 1). The Early Ordovician sedimentary 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 study area, the succession is composed of discontinuous shale packages containing occasional interbedded calcareous sandstone beds, informally referred to the 'Cieneguillas Shales' by Harrington and Leanza (1957). It is overlain by a similar succession (also including intercalated calcareous lenses), referred to the 'Sepulturas Limestones' by the same authors (Fig. 2). Vaccari *et al.* (2006) suggested that these two 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, 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 (Fig. 2). Aceñolaza (2003) suggested a Floian age on the basis of the association of the trilobite *Pliomeridius sulcatus* and the conodont *Gothodus crassulus andinus* (Rao *et al.*, 1994). Waisfeld and Vaccari (2008) correlated the shale succession exposed at La Ciénaga with the upper levels of the Acoite Formation at Santa Victoria on the basis of shared trilobite taxa, constraining it to the upper part of the '*B. deflexus*' Zone. The relatively thick shale packages with occasionally interbedded thin, tabular sandstone beds deposition in a lower offshore setting. Eothinoceratids occur in the same beds as proterocameroceratids (especially *Protocyptendoceras*) as well as other undescribed ellesmerocerids (see Cichowolski, 2009).

3.2. *Outcrops in Bolivia*

Sella area. The material studied was collected from the upper part of the Sella Formation, exposed in the Quebrada Rumi Orkho, 4 km east of Sella, 16 km NE of Tarija city,

Table 2. Measurements of *Margaritoceras diploide* Cecioni and Flower and *Margaritoceras* sp. from the Floian of the Acoite and Sella Formations

Species, specimen number and locality	*Margaritoceras diploide* CEGH-UNC 23886 Los Colorados	*Margaritoceras diploide* CEGH-UNC 25640a Portillo	*Margaritoceras diploide* CEGH-UNC 25641 Portillo	*Margaritoceras diploide* CEGH-UNC 25640b Portillo	*Margaritoceras diploide* CEGH-UNC 25642a Chamarra	*Margaritoceras diploide* MHNC 13539a Sella	*Margaritoceras* sp. CEGH-UNC 25644a Chamarra
LF (mm)	55.5	34.7	42 *	20.7	18.8	32.6*	29
WF$_{or}$ (mm)	29.5	–	–	–	–	–	–
WF$_{ap}$ (mm)	22.6	–	–	–	–	–	–
WS (%)	24	–	–	–	–	–	–
Dv Dia$_{or}$ (mm)	–	23.5*	18.3	–	–	–	–
Lat. Dia$_{or}$ (mm)	–	22.5*	18.5	21.5	22.2*	21.6	24.5*
Dv Dia$_{ap}$ (mm)	–	–	–	–	–	–	–
Lat. Dia$_{ap}$ (mm)	–	–	–	–	17.2*	–	–
LM (mm)	48	34.7	34.7	–	18.8	–	–
Dep. I.	–	0.96*	1.01	–	–	–	–
Si. Dia. (%)	–	23*	26	19	22	22.13	21*
L. Cham. (mm)	2–2.3	1.7–2.1	–	–	1.6–2.1	–	1.7–1.8
Cham./Conch Dia	17[a]	13	–	–	11	–	14
L. Li. Cham. (mm)	31	6.6	–	–	–	19.32	13.4
L. Phrag. (mm)	24	28.1	–	–	18.8	13.28	15.6
Dv Exp.	–	–	–	–	–	–	–
AA dv (°)	–	–	–	–	–	–	–
Lat. Exp.	–	–	–	–	0.26	–	–
AA lat. (°)	–	–	–	–	14.9	–	–
Sep. Dep. (%)	–	–	–	–	–	–	–
Cam. Dep. (%)	–	–	–	–	8	–	7*

LF, length of fragment; **WF$_{or}$**, adoral width of fragment; **WF$_{ap}$**, adapical width of fragment; **WS**, preserved width of the siphuncle in relation to the preserved width of the conch at the same point of growth (as a percentage), when it is not possible to measure the siphuncle diameter because of the taphonomic compaction; **Dv Dia$_{or}$**, dorsoventral diameter at adoralmost preserved end; **Lat. Dia$_{or}$**, lateral diameter at adoralmost preserved end; **Dv Dia$_{ap}$**, dorsoventral diameter at adapicalmost preserved end; **Lat. Dia$_{ap}$**, lateral diameter at adapicalmost preserved end; **LM**, length over which measured (measures above); **Dep. I.**, depression index: Lat. Dia./ Dv Dia. at the same point of growth; **Si. Dia.**, siphuncle diameter (ratio of the siphuncle diameter to the conch diameter, expressed as a percentage); **L.Cham.**, length of the camerae, measured as the distance between two adjacent suture lines. Usually a range of measures is considered (a maximum and a minimum value); **Cham./Conch. Dia**, number of camerae within a distance equivalent to the maximum preserved conch diameter; **L.Li.Cham.**; Length of the preserved fragment of the living chamber; **L.Phrag.**, length of the preserved fragment of phragmocone; **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 expansion rate, calculated in the same form as for the Dv Exp. but using Lat. Dia.); **AA lat.**, Apical angle based on lateral expansion rate; **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); **Cam. Dep.**, cameral depth (ratio of the distance between adjacent sutures—the media—, and the conch diameter, expressed as a percentage).

[a]In this case is Cham./WF$_{or}$.

*Asterisks indicate approximate measures due to bad preservation or breakage.

Table 3. Measurements of *Saloceras quena* sp. nov., *Saloceras sikus* sp. nov., *Mutveiceras cienagaensis* gen. et sp. nov., and *Mutveiceras* sp. from the Floian of the Acoite Formation

Species, specimen number and locality	*Saloceras quena* CEGH 25639b Chamarra	*Saloceras sikus* CEGH 25639c Chamarra	*Saloceras sikus* CEGH 25639d Chamarra	*Mutveiceras cienagaensis* CEGH-UNC 23837a La Ciénaga	*Mutveiceras cienagaensis* CEGH-UNC 25646 La Ciénaga	*Mutveiceras* sp. CEGH-UNC 23837b La Ciénaga
LF (mm)	37.3	49	48	31.47	21	21.23
Dv Dia$_{or}$ (mm)	–	–	–	21.25	15	18.14*
Lat. Dia$_{or}$ (mm)	23*	31	29*	21.7*	–	18.46
Dv Dia$_{ap}$ (mm)	–	–	–	18.1	–	13.52*
Lat. Dia$_{ap}$ (mm)	–	24.4*	25*	18*	–	14.4*
LM (mm)	–	34	28	31.47	–	18.3*
Dep. I.	–	–	–	1.02*	–	1.03*
Si. Dia. (%)	20–27*a	22–35*a	22–37*a	20	34	22*
L. Cham. (mm)	1.66–2.17	1.5–1.9	1.7–2.07	1–1.34	1–1.4	1.27–1.42
Cham./Conch Dia	12	10	10	16	13	13
L. Li. Cham. (mm)	12.6*	11.2	2*	25	–	–
L. Phrag. (mm)	25*	37.8*	46*	5.47	21	21.23
Dv Exp.	–	–	–	0.1	–	0.25*
AA dv (°)	–	–	–	5.7	–	14.3*
Lat. Exp.	–	0.2	0.14	0.11*	–	0.22*
AA lat. (°)	–	11	8	6.7*	–	12.6*
Sep. Dep. (%)	–	–	–	23.5	31.8	18
Cam. Dep. (%)	8	5	6	5.5	7.7	9.1

Abbreviations are the same as in Table 2.

aNote that on these specimens the relative siphuncle diameter was estimated measuring the width of the siphuncle visible on the ventral side of the conch because of their mouldic condition.

*Asterisks indicate approximate measures due to bad preservation or breakage.

South Bolivia (Fig. 1). The Sella Formation is composed of green, bioturbated shales, interbedded with fine sandstone beds, which become coarser and more frequent upward. The unit was interpreted as a deltaic-influenced, shallow marine platform with frequent storm events (Schönian, 2003). This unit was traditionally considered to be Llanvirnian in age, based mainly upon the trilobite and brachiopod faunas (Přybil and Vaněk, 1980; Havlíček and Branisa, 1980). The largely similar trilobite fauna of the Sella and Acoite formations, has led the Bolivian unit to be regarded as Floian in age (e.g. Waisfeld, 1998; Aceñolaza *et al.*, 1999). Trilobite species associated with *M. diploide* from the Sella Formation are under study; however, preliminary results suggest that most taxa resemble trilobite assemblages limited to the 'B. deflexus' Zone of the Acoite Formation. In Sella, eothinoceratids co-occur with protocycloceratids.

4. SYSTEMATIC PALAEONTOLOGY

Class CEPHALOPODA Cuvier, 1797
Subclass NAUTILOIDEA Agassiz, 1847
Order ELLESMEROCERIDA Flower in Flower and Kummel, 1950
Suborder CYRTOCERININA Flower, 1964
Family EOTHINOCERATIDAE Ulrich, Foerste, Miller and Unklesbay, 1944
Genus *MARGARITOCERAS* Cecioni and Flower, 1985

Type species. Margaritoceras margaritae Cecioni and Flower, 1985, from the Arenig of San Lucas, Bolivia, by original designation.

Emended diagnosis. Orthoconic and relatively rapidly expanding shells, with circular to moderately depressed cross-section. Septa closely spaced. Suture line very slightly sinuous, with shallow lateral lobes and a narrow ventral saddle, sometimes within a shallow ventral lobe. Medium size siphuncle, marginal in position, in contact with shell wall. Septal necks achoanitic to loxochoanitic. Connecting rings concave and thickened, protruding into siphuncle. At present, diaphragms unknown.

Margaritoceras diploide Cecioni and Flower, 1985
(Fig. 3A–E, Table 2)
1985 *Margaritoceras diploide* Cecioni and Flower: p. 351, fig. 2 (1–3).
  Holotype. Specimen nº 12, designated by Cecioni and Flower (1985, pg. 354), from the Arenig of San Lucas, Bolivia, and housed at the New Mexico Museum of Natural History and Science, Albuquerque.
  Material examined. Fourteen specimens CEGH-UNC 23886 from Los Colorados, CEGH-UNC 25640 a–d, and 25641 from El Portillo, CEGH-UNC 25642a, 25643 and 25645 from Quebrada de Chamarra, and MHNC 13539a–e from Sella (Bolivia).

Emended diagnosis. Orthoconic conchs with expansion rate of approximately 15°; conch cross-section circular to moderately depressed; external surface apparently smooth, with faint growth lines; length of phragmocone chambers varying from ca. 1.6 to 2.3 mm; sutures simple, with small ventral saddle, sometimes within a shallow ventral lobe; siphuncle marginal, with diameter approximately of 25 % that of the conch; septal necks achoanitic to loxochoanitic, siphuncle segments concave outward.

Description. Orthoconic conchs with maximum length preserved of 55 mm. Relatively high angle of expansion (apical angle measured in the lateral plane of CEGH-UNC 25632a is 14.9°). Due to bad preservation it is not possible to estimate the depression index, the cross-section of the conch seems to be subcircular to moderately depressed. The septa are relatively crowded (Fig. 3 A$_2$, D–E), phragmocone chambers being 1.6 to 2.3 mm in length (though they vary with relative position to the living chamber and are sometimes approximated toward the living chamber). Suture lines are simple, with shallow lateral lobes and small ventral saddles, sometimes within a shallow ventral lobe (Fig. 3D–E). The ventral saddle is not always clear, and may be confused with the arched segments of the siphuncle. The siphuncle is marginal in position, in contact with ventral shell wall (Fig. 3C–E). Siphuncular diameter is approximately 25 % of that of the conch diameter. The siphuncular segments are concave, with the connecting rings protruding into the lumen of the siphuncle (Fig. 3 A$_2$–A$_3$, B–E). The septal necks appear to be achoanitic to loxochoanitic (Fig. 3 A$_2$–A$_3$), although they are not easily visible in our material. The mould of the siphuncular segments show ridges that are adorally arched on the ventral side, but adapically on the dorsal side (Fig. 3B–E), indicating the asymmetrical thickening of the connecting rings. Endosiphuncular diaphragms are not known, but the absence of the apical part of the conchs might reflect their presence (Evans, 1992). No wholly complete living chamber is preserved, but it seems to be simple in form (Fig. 3A, C). The shell surface is smooth.

Discussion. The general conch shape and the type and proportions of the siphuncle lead us to assign these specimens to the genus *Margaritoceras* Cecioni and Flower. The rate of expansion, the shape of the suture, and the length of the phragmocone chambers suggest they should be assigned to *Margaritoceras diploide* Cecioni and Flower. *M. margaritae* Cecioni and Flower has a higher angle of expansion than *M. diploide*. Sutures

in *M. diploide* are more sinuous than in species of *Eothinoceras* Ulrich *et al*. *Margaritoceras* differs from *Bathmoceras* Barrande in having rounded saddles instead of acute. *Saloceras* Evans exhibits a higher relative siphuncle diameter and a lower angle of expansion.

We were not able to study the original material described by Cecioni and Flower (1985). They figured one specimen (Cecioni and Flower, 1985, p. 353, fig. 2.1–3) and it is not clear how many specimens were studied and assigned to *M. diploide*. But it seems probable that it was based on the figured specimen and perhaps one other. Their diagnosis indicates that the cross-section of the conch was strongly depressed, but their description indicates that it was 'a bit depressed', which is in contradiction. The images, however, indicate that the cross-section was subcircular to moderately depressed, as shown also in specimens described here.

Although in only one of the five Bolivian specimens (MHNC 13539a) here assigned to *M. diploide* is the 'eothinoceratid type' siphuncle clearly visible (Fig. 3C), the external form of the conch and the proportions of the chambers in the other specimens from the same coquina suggest they belong to the same taxon.

Occurrence. Sella Formation, localities of San Lucas (Cecioni and Flower, 1985) and Sella, southern Bolivia; Acoite Formation, localities of Los Colorados, Quebrada de Chamarra and Portillo, Jujuy Province, Northwestern Argentina. Middle–late Floian ('*B. deflexus*' and *D. bifidus* zones).

In proposing *Margaritoceras,* Cecioni and Flower (1985) described *M. margaritae* Cecioni and Flower (type species), *M. diploide* Cecioni and Flower, and *Margaritoceras* sp. indet. The species were reported from the 'upper part of the Lower Canadian or the lower part of the Upper Canadian (Arenigian)' (see p. 352, 354 in Cecioni and Flower, 1985) of San Lucas, Chuquisaca Region, in southern Bolivia. Most of the material described by Cecioni and Flower (1985) was not collected by them and hence, the stratigraphic position and age of several taxa are dubious. The age of the horizons yielding these species is controversial. Havlíček and Branisa (1980) and Přybil and Vaněk (1980) indicated a 'Llanvirn' age for the brachiopods and trilobites described from this locality. The brachiopod *Paralenorthis immitatrix,* reported by Havlíček and Branisa (1980) from the San Lucas locality has also been reported from the lower part of the San José Formation (SE Perú) by Gutiérrez-Marco and Villas (2007), where it is associated with probably late Floian conodonts. Thus, a similar age for the horizons bearing *P. immitatrix* levels in Bolivia may be suggested. However, it remains uncertain as to whether the cephalopods originated from the same horizons as the brachiopod fauna. In this respect, our studies based on the collection of additional material from type localities, may be significant in resolving the status and stratigraphic distribution of some of these species. The occurrence of *Margaritoceras diploide* in the Acoite Formation (NW Argentina) ranges from the '*Baltograptus deflexus*' graptolite Zone (cf. revision by Toro and Maletz, 2008) to the *Didymograptellus bifidus* Zone, indicating a mid–late Floian age (Fl2–Fl3) for the species. Records of this species (Cecioni and Flower, 1985) from San Lucas indicate a similar age for the southern Bolivian occurrence. Furthermore, the occurrence of *M. diploide* in the Sella locality reported herein makes possible correlation between Bolivian localities, and the Acoite Formation in NW Argentina.

Margaritoceras sp.
(Fig. 3F, Table 2)

Material. Two specimens CEGH-UNC 25644a–b from Quebrada de Chamarra, Upper part of the Acoite Formation. *Description.* The specimen CEGH-UNC 25644a consists of an internal mould of part of a phragmocone 29 mm long, and a small portion (13.4 mm) of the living chamber. The external face of the mould of the siphuncle is visible, and has a width of *ca*. 4.3 mm. At CEGH-UNC 25644a, the expansion rate seems to be rather high. The phragmocone chambers are 1.7 to 1.8 mm long, with 13 camerae preserved. Camerae are shorter adorally (Fig. 3F), probably indicating septal approximation and the maturity of the organism. The sutures are relatively straight, with wide lateral lobes and wide ventral saddles (Fig. 3F). The dorsal surface of the conch is not visible. CEGH-UNC 256644b is a small portion of phragmocone from which no measurements could be made.
Discussion. The general shape of the conch and the expansion rate allow us to assign these specimens to the genus *Margaritoceras*. As the state of preservation of the specimens does not allow assignment to a species, they are left in open nomenclature within *Margaritoceras* until additional material becomes available for study. The specimens differ from *M. diploide* mainly in the shorter length of the camerae, and probably also in the larger relative diameter of the siphuncle. It seems probable that the expansion rate of these specimens is slightly higher. In this last feature, they are similar to *M. margaritae*, but the camerae are shorter in our specimens. Here described *Margaritoceras* sp. is not conspecific with *Margaritoceras* sp. *sensu* Cecioni and Flower (1985), which possesses a smaller apical angle and it is slightly cyrtoconic (Cecioni and Flower, 1985, fig. 2, 4–6).
Occurrence. Upper part of the Acoite Formation. Quebrada de Chamarra localitity, Los Colorados area, Cordillera Oriental, Jujuy Province, Argentina. From

horizons lacking graptolites, nevertheless, the trilobite assemblage indicates a late Floian age.

Genus SALOCERAS Evans, 2005

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

Emended diagnosis. Orthoconic eothinoceratids with circular to slightly depressed cross-section and moderate angle of expansion; sutures straight and directly transverse with ventral saddle over siphuncle; siphuncle marginal, most forms with diameter 0.2–0.5 of corresponding phragmocone cross-section, less frequently smaller; septal necks achoanitic to weakly orthochoanitic; siphuncular segments strongly concave with connecting rings asymmetrically thickened, protruding into the siphuncle; siphonal diaphragms present. *Saloceras* differs from other orthochonic eothinoceratids mainly in having usually wider siphuncle, lower angle of expansion, and siphuncular segments more pronouncedly arched (after Kröger and Evans, 2011).

Saloceras sikus sp. nov.
(Fig. 4A–B, Table 3)

Etymology. The sikus (Aymara) is a traditional Andean panpipe, typically played within the Andean populations.
Holotype. CEGH-UNC 25639c, from the Quebrada de Chamarra, upper part of the Acoite Formation, Floian Stage.
Other material (paratypes). Three specimens CEGH-UNC 25639a, d, f, from the Quebrada de Chamarra, upper part of the Acoite Formation, Floian Stage.
Type locality and horizon. Quebrada de Chamarra, Los Colorados Area, western border of the Cordillera Oriental of Jujuy, Argentina. Upper part of the Acoite Formation, Floian.
Diagnosis. Smooth *Saloceras* with siphuncle of moderate to large relative diameter, siphuncular segments compacted and roundly arched, externally pointing to the aperture, sometimes becoming shorter and wider in that direction; internal structure and diaphragms unknown.
Description. The available specimens are mainly internal moulds. The conch is straight, with circular to subcircular cross-section and an angle of expansion ranging from 8 to 11° (measured on lateral diameter, see Table 3). The camerae are short, from 1.5 to 2.1 mm, and shorter adorally in CEGH-UNC 25639c, probably due to septal approximation at maturity. There are *ca*. 10 camerae in a length similar to phragmocone diameter. The siphuncle is marginal and wide. The width of the siphuncle in contact with the conch wall appears to increase toward the base of the living chamber (Fig. 4A–B), ranging between 22 to 35 % the

width of the conch in CEGH-UNC 25639c, and from 22 to 37 % in CEGH-UNC 25639d. Externally, the segments are inclined to the adoral end forming compacted and roundly arcs, indicating that the thickening of the connecting rings is asymmetrical. Sometimes they become shorter adorally, reflecting the septal approximation in coincidence with the shortening of camerae (Fig. 4A). Suture lines are transverse laterally, with a broad and relatively shallow saddle over the siphuncle. Septal necks are difficult to identify, but appear likely to be very short. Relicts of shell preserved show smooth surface.

Discussion. The general shape of the conchs and their proportions suggest that they belong to the genus *Saloceras* Evans, 2005. *S. sikus* sp. nov. differs from other late Tremadocian and Floian species (*S. chinianense* (Thoral), *S. murvielense* Kröger and Evans, *S. pradense* (Thoral)) from the St. Chinian and La Maurerie formations of the Montagne Noire, France. In these species the siphuncle is narrower and the conch wall is annulated or shows constrictions. *S. sikus* sp. nov. differs from the type species, *S. sericeum*, from the Tremadocian–Floian of the Welsh Borderland, in possessing more rounded and shallower traces of the ventral side of the septal foraminae. The camerae are probably shorter in *S. sikus*, whilst the siphuncle diameter is generally larger. The expansion of the siphuncle towards the base of the living chamber in *S. sikus* differentiates it from all others previously assigned to the genus. If this character is found to be present in future collected specimens of the species, it could be sufficiently important to separate it in a different genus.
Occurrence. Upper part of Acoite Formation, Quebrada de Chamarra, Los Colorados area, Cordillera Oriental, Jujuy Province, Argentina. From horizons lacking graptolites, nevertheless, the trilobite assemblage indicates a late Floian age.

Saloceras quena sp. nov.
(Fig. 4C, Table 3)

Etymology. The quena (from Quechua) is a traditional flute of the Andes.
Holotype. Specimen CEGH-UNC 25639b from the Quebrada de Chamarra, upper part of the Acoite Formation, Floian Stage.
Type locality and horizon. Quebrada de Chamarra, Los Colorados Area, western border of the Cordillera Oriental of Jujuy, Argentina. Upper part of the Acoite Formation, Floian.
Material. Holotype only.
Diagnosis. Small and apparently smooth *Saloceras* with siphuncular segments arched and rounded, and probably

expanding adorally; shape of septal necks not known.

Description. The holotype is a portion of a phragmocone and a small part of the living chamber with a total length of 37.3 mm and a lateral diameter of 23 mm (Fig. 4C). The conch cross-section appears to be subcircular to slightly depressed. The angle of expansion seems to be relatively low to moderate, although no measurements could be taken due to deformation and incompleteness of the specimen. The length of the camerae is between 1.6 and 2.2 mm, with 12 camerae in a length similar to that of the conch diameter. The suture line is only visible on siphuncular side and presents a small saddle over the siphuncle (Fig. 4C). The siphuncle is marginal. The mould of the siphuncular segments shows constrictions that culminate in the adoral portion of each segment, indicating that the connecting rings are asymmetrically thickened (Fig. 4C). The relative diameter of the siphuncle inflates rapidly towards the base of the living chamber (Fig. 4C), being the width of its ventral part between 20 and 27 % that of the phragmocone diameter at different points of measurement (see Table 3).

Discussion. The general conch shape and proportions led us to assign this specimen to the genus *Saloceras*. Despite only the holotype is available, the specimen shows species-specific characters, which differ from all other species of the genus.

Saloceras quena sp. nov. differs from species reported from the Montagne Noire (Kröger and Evans, 2011) and *S. sericeum* in the relative siphuncle diameter and in the shape of the segments. *S. quena* differs from the Montagne Noire species in lacking annulations and constrictions. It differs from *S. sikus* sp. nov. in having relative thinner siphuncle, less compacted segments and probably lower angle of expansion. They share the apparent relative widening of the siphuncle in an adoral direction. Since we have only one specimen to analyse, no proper conclusion can be made about this feature, but as mentioned above, this character should be deeply studied in the future as a possible signature for the erection of a new genus.

Occurrence. Upper part of the Acoite Formation, Quebrada de Chamarra, Los Colorados Area, Cordillera Oriental, Jujuy Province, Argentina. *S. quena* was found in a coquina together with *S. sikus*, and is therefore probably also late Floian in age.

Genus MUTVEICERAS gen. nov.

Etymology. Dedicated to Harry Mutvei (Stockholm).
Type species. Mutveiceras cienagaensis gen. et sp. nov., from the Acoite Formation, Floian Stage. La Ciénaga, Cordillera Oriental, Jujuy Province, Argentina.

Species included. Mutveiceras cienagaensis, Mutveiceras sp.

Diagnosis. Small and very slightly cyrtoconic exogastric conchs with low to moderate angle of expansion, ornamented with faint lirae; cross-section subcircular; sutures directly transverse, usually with a narrow saddle on the convex side of the conch; camerae very short, around 15 sutures in a distance equal to the corresponding phragmocone diameter; siphuncle marginal to slightly submarginal at convex side of the conch curvature, with a diameter between 0.2 to 0.35 of phragmocone diameter; septal necks loxochoanitic; siphuncular segments concave with connecting rings thickened and protruding into the siphuncle. Diaphragms unknown.

Discussion. Mutveiceras shows thickened connecting rings that protrude into the siphuncle, and should be considered a member of the Eothinoceratidae. Although generally similar to *Sacerdosoceras* Evans, from the Llanvirnian (Darriwillian) of Wales (Evans, 2005) in the shape of the conch and siphuncle, cameral depth is higher in *Sacerdosoceras*, as is probably the degree of conch curvature, whilst the conch cross-section in *Sacerdosoceras* is more compressed. It is not possible to judge whether the living chamber contracts toward the aperture as is suggested for *Sacerdosoceras*. Siphuncular diaphragms are currently unknown in *Mutveiceras*. The connecting rings of *Mutveiceras* protrude more strongly into the siphuncle than those of *Sacerdosoceras*. *Mutveiceras* gen. nov. differs from *Margaritoceras* Cecioni and Flower, in its lower angle of expansion, the slight curvature of the conch, and the shorter camerae. It differs from *Saloceras* Evans in the generally smaller siphuncle, shorter camerae, and shallower sutural saddles over the siphuncle. *Mutveiceras* differs from *Eothinoceras* Ulrich *et al.* (1944), in the more undulatory suture of the former genus and the shorter camerae. Chinese genera belonging to Eothinoceratidae (*Protothinoceras*, *Mesothinoceras*, and *Conothinoceras*, Chen and Teichert, 1987) have a submarginal siphuncle of a larger relative diameter, are usually more strongly curved than *Mutveiceras* and are endogastric. The enigmatic genus *Desioceras* Cecioni, found in an erratic block from Jujuy, Argentina (age unknown) differs from *Mutveiceras* mainly in the possession of an annulate conch.

Mutveiceras cienagaensis sp. nov.
(Fig. 4D–E, Table 3)

Etymology. From the locality of La Ciénaga (Purmamarca area, Jujuy, Argentina).
Syntypes. Specimens CEGH-UNC 23837a and 25646 from La Ciénaga, Purmamarca Region, Acoite Formation.
Type locality and horizon. La Ciénaga, about 5 km west of Purmamarca, Jujuy Province, Eastern Cordillera of Argentina. Acoite Formation, Middle Floian ('*Baltograptus deflexus*' Zone).
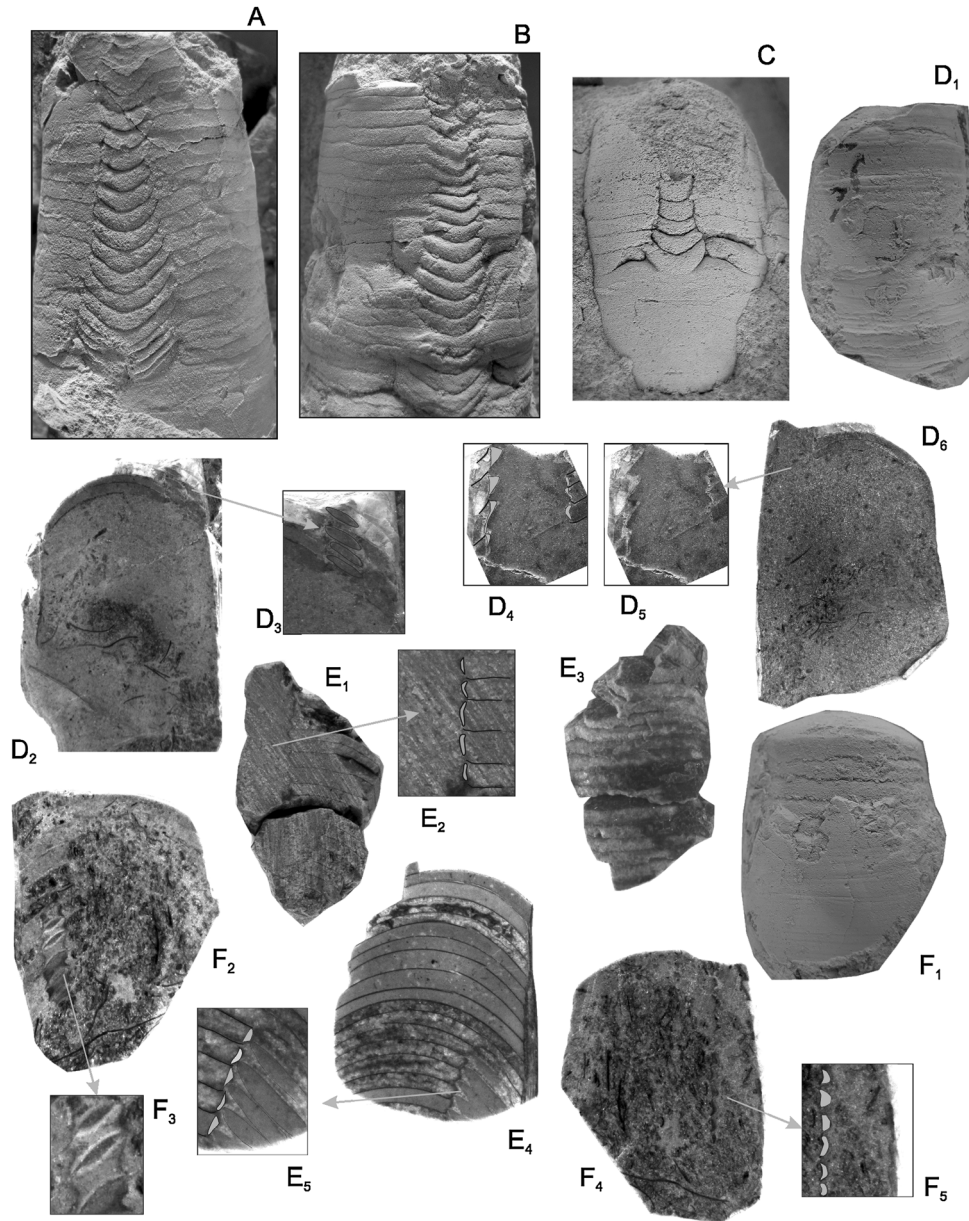
Figure 4. Eothinoceratids from the Floian of the southern Central Andean Basin. **A–B**. *Saloceras sikus* sp. nov. from the upper part of the Acoite Formation, Quebrada de Chamarra. **A**. Specimen CEGH-UNC 25639c, external view of the siphuncular side showing the arched segments of the siphuncle, the sutures, and a small part of the living chamber. **B**. Specimen CEGH-UNC 25639d, external view of part of the phragmocone showing part of the siphuncle and the sutures. **C**. *Saloceras quena* sp. nov., specimen CEGH-UNC 25639b, upper part of the Acoite Formation, Quebrada de Chamarra, external view of the specimen showing the inflated segments of the siphuncle, the sutures and a small part of the living chamber. **D–E**. *Mutveiceras cienagaensis* sp. nov., Acoite Formation, La Ciénaga, Purmamarca. **D**. Specimen CEGH-UNC 23837a. D_1. External lateral view of part of the living chamber with a very small fragment of phragmocone, showing the growth lines of the shell. D_2. Polished longitudinal section of part of the living chamber and a few phragmocone chambers with the siphuncular segments. D_3. Detail of the siphuncular segments with a schematic interpretation over the photograph. D_4. Detail of the polished section of the siphuncle (from D_6 but before being silvered) showing the concave segments, the protruding connecting rings and the loxochoanitic septal necks in a schematic drawing superimposed to the picture. D_5. Same detail as in D_4 (without the schematic interpretation of the characters). D_6. Polished longitudinal section of part of the living chamber and a few phragmocone chambers (counterpart of D_2). Note that it was silvered to be studied under the SEM and then lacks details. **E**. Specimen CEGH-UNC 25646. E_1. Cut but unpolished section of two adjacent parts of the phragmocone showing short camerae and the siphuncular segments with thickened connecting rings and loxochoanitic septal necks. E_2. Detail of the siphuncle. E_3. External view of E_1, showing the sutures. E_4. Cut and polished section of part of the phragmocone showing the short camerae, the deep septa and the siphuncle with concave segments, thickened connecting rings and loxochoanitic septal necks. E_5. Detail of the siphuncle from E_4. **F**. *Mutveiceras* sp., specimen CEGH-UNC 23837b, Acoite Formation, La Ciénaga, Purmamarca. F_1. External lateral view of part of the phragmocone showing the sutures and the shape of the conch. F_2. Cut and polished off-medial section of part of the phragmocone, showing the siphuncular segments concave outward and some broken septa. It can also be seen the sedimentary fill full of ostracod valves. F_3. Detail of the siphuncle in F_2. F_4. Unpolished longitudinal section showing the thickened connecting rings of the siphuncle protruding into the lumen. F_5. Detail of the siphuncle from F_4 with a schematic interpretation of the connecting rings. Scales: with the exception of the details of siphuncle, A, B, C and D are x 1.5, and E and F are x 2.

Material. Syntypes only.

Diagnosis. *Mutveiceras* with low angle of expansion (approximately 6°); shell ornamented with faint lirae; low cameral depth but rather high septal depth; sutures with a small saddle on the ventral side of the conch; siphuncle marginal to slightly submarginal, near the ventral side of the conch, with asymmetrically thickened connecting rings that protrude into the lumen.

Description. CEGH-UNC 23837a consists of a 31.5 mm long fragment consisting of a living chamber and four camerae (Fig. 4 D_2, D_6). Externally, the living chamber shows faint radial transverse lirae approximately each 0.6 mm apart (Fig. 4D_1). The dorsoventral diameter at the adoral end is 21.2 mm and 18.1 mm at the adapical end, giving a rate expansion of 5.7°. The living chamber appears to be weakly cyrtoconic (Fig. 4 D_2, D_6). Camerae are short (from 1 to 1.34 mm) but the septa are relatively deep (septal depth 23.5 %). The sutures are not visible. The siphuncle diameter is 20 % that of the conch diameter and is located slightly away from the side of the conch with a convex curvature. Because of the orientation of the section, two different perspectives of the siphuncle are seen (Fig. 4 D_3–D_5). In both cases it appears to be faintly submarginal; however, this could be an artifact of the view, if the section is not medial. On one side (Fig. 4 D_3), the structures that are seen are interpreted as the sediment fill of the siphuncular segments in an off-medial plane. The other section (Fig. 4 D_{4-5}) is located nearer the median plane, and the sediment fill of the siphuncle is visible with the connecting rings expanding asymmetrically into the lumen, and protrude more deeply those of the ventral than of the dorsal side (Fig. 4 D_{4-5}). The septal necks seem to be loxochoanitic (Fig. 4 D_{4-5}). CEGH-UNC 25646 consists of a portion of phragmocone 21 mm long (Fig. 4 E_1, E_{3-4}), with a dorsoventral diameter of 15 mm adorally. The conch cross-section is subcircular. It was cut and polished on one side only (Fig. 4 E_4). The sutures (Fig. 4 E_3) are transverse with a small ventral saddle one camera in height. The camerae are very short (1 to 1.4 mm, cameral depth 7.7%) and the septal depth is rather high (31%). The siphuncle diameter is approximately 34 % that of the conch. It is very close to the shell margin. The polished section (Fig. 4 E_4) shows a siphuncle distant from the shell margin, but as the cut is not in a median plane it is not conclusive. Fig. 4 E_5 shows the sediment fill of the siphuncular segments in an off-medial plane, and the connecting rings protruding into the lumen and thickest toward the adapical end of the segments. The unpolished section, which broke whilst being cut, consists of two portions of phragmocone (Fig. 4 E_1, E_3). The ventral part of the siphuncle is difficult to interpret here, but on the dorsal surface the connecting rings are seen to protrude into the lumen (Fig. 4 E_2). The septal necks are loxochoanitic (Fig. 4 E_2, E_5). Externally, the ventral surface of the conch in the polished sample is covered with an indeterminate laminated calcitic epizoan (Fig. 4 E_4).

Discussion. This species is founded on two incomplete and imperfectly preserved individuals. Additional material is needed in order to resolve uncertainties regarding the position of the siphuncle and the shape of the living chamber. At present, the small size of the phragmocone, its low angle of expansion and the very short camerae are characteristic features of *M. cienagaensis.*

Occurrence. Acoite Formation, La Ciénaga, about 5 km west of Purmamarca, Jujuy Province, Cordillera Oriental, Argentina. Middle Floian ('*Baltograptus deflexus*' Zone).

Mutveiceras sp.
(Fig. 4F, Table 3)

Material. Specimen CEGH-UNC 23837b from La Ciénaga.

Description. The specimen consists of a portion of a phragmocone 21 mm in length, in which the camerae are imperfectly preserved (Fig. 4 F_2, F_4). Part of the shell wall is preserved, and shows very faint transverse lirae (Fig. 4 F_1). The conch is slightly convex on one side and slightly concave on the opposite (Fig. 4 F_1, F_4), indicating that it is slightly cyrtoconic. The lateral apical angle is approximately 12.6° and 14.3° dorsoventrally. There is a slight alteration of the expansion rate at a point 8 mm adorally from the most apicad septum (Fig. 4 F_1, F_4). This does not seem to be a taphonomic effect. The cross-section is subcircular. The sutures are not completely visible, being transverse on the lateral surfaces and shows the edges of a small lobe on the ventral and dorsal sides (Fig. 4 F_1). It is possible that on the convex side of the conch, the lobe includes a small medial saddle. The distance between the sutures varies from 1.3 to 1.4 mm giving a cameral depth of approximately 9 % that of the phragmocone diameter. The septal depth is 18 % the phragmocone diameter. The siphuncle shows different views in both sections of the cut specimen. On the unpolished portion (Fig. 4 F_4–F_5), the thickened connecting rings can be seen protruding into the lumen, and the siphuncle appears to be marginal. It is interpreted as being an almost medial plane and the diameter is 16 to 22 % that of the conch diameter. In the polished section (Fig. 4 F_2–F_3), the siphuncle appears to be submarginal, and it is interpreted as an off-medial cut, so that only the cameral facing surfaces of the connecting rings are visible. For this same reason, the position of the siphuncle appears to be submarginal and the septal necks are not visible. In both sections a high amount of ostracod valves can be seen within the sediment fill of the phragmocone.

Discussion. The moderate angle of expansion, the small size, short cameras and size of the siphuncle suggest this specimen should be assigned to *Mutveiceras* gen. nov. This specimen differs from *M. cienagaensis* sp. nov.

mainly in the slightly longer camerae and shallower septal depth. The possible alteration of the rate of expansion may supply another distinction. In addition, the position of the siphuncle, which is probably marginal in *Mutveiceras* sp., is slightly submarginal in *M. cienagaensis* sp. nov.

However, the state of preservation is such that there is insufficient detail to justify the erection of a new species. The possible presence of a break in the rate of expansion, the shape of the living chamber, and the form of the sutures, amongst others, are all characters that require further resolution.

Occurrence. Acoite Formation, La Ciénaga, about 5 km west of Purmamarca, Jujuy Province, Cordillera Oriental, Argentina. Middle Floian ('*Baltograptus deflexus*' Zone).

5. REMARKS ON PALAEOAUTOECOLOGY AND PRESERVATION

Differences in the structure of the siphuncle, and particularly that of the connecting rings, reflect different functional specializations of the osmotic regulation of cameral liquid across the siphuncular wall (Mutvei, 1996). Since the initial conception of Ellesmerocerida, which was very inclusive (Flower, 1964, Furnish and Glenister, 1964), this order has become progressively eroded through the separation of different families (Kröger and Mutvei, 2005). Although Mutvei (1964, 2002) proposed that the main part of the thick 'connecting rings' in the family Bathmoceratidae represents a special type of endosiphuncular deposit, and, probably along with the Cyrtocerinidae, should not be included in the order Ellesmerocerida, until now genera belonging to Cyrtocerinina have been always been assigned to the Ellesmerocerida, even in recent taxonomic works (e.g. Evans, 2005; Kröger and Evans, 2011; Kröger and Lefebvre, 2012). It is likely that the Eothinoceratidae has the same type of siphuncular structure as other families of the Cyrtocerinina (Cyrtocerinidae and Bathmoceratidae), since they share those lobate structures expanding from the siphuncle wall into the lumen, whether they are considered to be connecting rings or deposits. Those siphuncular structures have been interpreted as beneficial for rapid buoyancy change and sensitive buoyancy regulation because of the enhanced surface area available for exchange of cameral liquid (e.g. Mutvei, in press, in Kröger and Lefebvre, 2012). According to Westermann (1999), in the absence of effective counterweights for neutral equilibrium, the poise of most Ellesmerocerida was subvertical, an attitude well suited for pelagic vertical migrants as well as for 'hopping' bottomfeeders. According to their morphologies, with densely spaced and weakly concave septa, along with a rather wide siphuncle, they were probably habitants of rather shallow water environments (Westermann, 1999). According to these,

and considering the moderate angle of expansion of most of them, we suggest that eothinoceratids of the Floian of the Cordillera Oriental of NW Argentina and southern Bolivia lived demersally with a subvertical poise but were capable of rapid buoyancy changes when needed.

The strata containing these cephalopods are here interpreted as having been deposited in a shallow shelf environment, below fair-weather wave-base but periodically affected by storms. Many specimens were also found in shoreface facies. These are in agreement with the interpretation of the conch morphology.

Cephalopod shells studied here were mainly found in storm generated sediments. Most shells are preserved as a portion of the phragmocone combined with a partially complete living chamber. No apical parts of the conch were found. The relatively large siphuncle makes for rapid flooding of the phragmocone chambers, which along with the presence of part of the living chamber, suggests an absent or short period of *post-mortem* drifting (Reyment, 1958; Boston and Mapes, 1991). However, the frequent fragmentation of the conchs indicates some reworking or transport of the shells, probably as a consequence of the storm-wave action. The cephalopod assemblage is therefore interpreted as parautochthonous.

Those cases where the conchs are preserved as three-dimensional external moulds in the middle of which the siphuncle is preserved (Fig. 3B–C) with no traces of the chambers or of the phragmocone wall are interpreted as cases in which the phragmocones were first invested with cement and the siphuncle with sediment. The dissolution of carbonates of the cement at a later stage would result in external moulds of the conchs with the internal moulds of the siphuncles inside. The sedimentary infill of many phragmocone chambers of specimens deposited in the shoreface subenvironment, along with the relative completeness of the conchs (besides lacking apical parts) may be explained by rapid burial in a high-energy environment and a high rate of sedimentation, which allowed the conchs to be filled with sediment during burial, but prevented them from further breakage once buried.

Therefore, the Floian eothinoceratids from the Central Andean Basin probably had a demersal mode of life with a subvertical poise ('hopping' bottom feeder) in a relatively proximal shelf environment. After death, the conchs were subject to some degree of transport, evidenced by their fragmentation. The storm events that frequently tracked over the platform probably deposited the nautiloids along with many other skeletal remains in the tempestites and associated units.

6. PALAEOGEOGRAPHIC CONSIDERATIONS

During the Early Ordovician, the Central Andean Basin was at intermediate latitudes, at around 45° S, and constituted

part of the temperate to cold water platforms of western Gondwana (Benedetto, 2003, 2007; Benedetto *et al*., 2009). In contrast with cephalopod faunas associated with warm water platforms, and similar to other basins located at the same or higher paleolatitudes, cephalopod faunas from the Central Andean Basin are of relatively low morphological diversity (low disparity), mainly composed of orthocones and weakly cyrtoconic forms. However, they can be relatively diverse taxonomically (e.g. Evans, 2005; Kröger and Evans, 2011, Kröger and Lefebvre, 2012).

General affinities of the Early Ordovician cephalopods from NW Argentina were analysed by Cichowolski (2009) based on the taxonomic studies of Cecioni (1953, 1965). It was found that most taxa described for this basin indicate warm water faunal influences, with the exception of a few genera that are endemic of the region. In particular, *Protocyptendoceras* Cecioni was found to be related to proterocameroceratids from Eastern Gondwana, in agreement with the affinities of some trilobites coming from the same locality as these cephalopods (Vaccari *et al*., 2006). With the recent contributions in relation to the Lower Ordovician cephalopods from the Montagne Noire (Kröger and Evans, 2011) and Morocco (Kröger and Lefebvre, 2012), it is now known that proterocameroceratids like *Protocyptendoceras* are additional elements of a peri-Gondwana Realm (Kröger, 2013), in which *Saloceras* or related eothinoceratids dominated the associations along the margins of east and west Gondwana, at least into mid latitudes (Kröger and Evans, 2011, fig. 5).

The cephalopod association described herein is mainly characterized by the presence of endemic forms. *Margaritoceras*, by far the most abundant eothinoceratid in the Acoite Formation (NW Argentina) is otherwise only known from other localities within the Central Andean Basin such as South Bolivia. *Mutveiceras* is another endemic eothinoceratid so far restricted to the Acoite Formation. In addition, Floian species of *Saloceras* are at present known only from the Central Andean Basin. However, at generic level, the records of *Saloceras*, occurring since the Middle Tremadocian (Cichowolski and Vaccari, 2011) within the basin, support the perigondwanan signature of the cephalopod association. As noted above, the occurrence of *Protocyptendoceras*, of wider geographic distribution than previously thought, also reinforces this signature. Kröger and Evans (2011) considered that *Lobendoceras* (common in Australia, Teichert and Glenister, 1954), present in the Lower Ordovician of the Montagne Noire, could be a synonym of *Protocyptendoceras* or, at least, a much closely related form. Interestingly, Kröger and Lefebvre (2012) reported one broken specimen from the Floian of Morocco that was assigned to *Protocyptendoceras*.

Although a detailed taxonomic revision of the whole Ordovician cephalopod faunas of the Central Andean Basin is still required in order to achieve a complete framework of their palaeogeographical affinities, the presence of representatives of Protocycloceratidae in several localities is indicative of some connections with warm water faunas at least for some groups (Kröger and Evans, 2011).

The Tremadocian cephalopod fauna reported from NW Argentina is monospecifically represented by *Saloceras* cf. *sericeum* (Cichowolski and Vaccari, 2011), and probably represents one of the first pulses of immigration of cephalopods to this region of the Iapetus Ocean. In contrast, the Floian cephalopod fauna is characterized by the presence of several families, and in particular, the Eothinoceratidae. This family seems to have diversified within the basin giving rise to the endemic forms described here. The faunal affinities of the Eothinoceratidae from the southern Central Andean Basin suggest cold water Gondwanan links, mainly with Avalonia and the Montagne Noire, based upon the presence of *Saloceras* and the resemblance of *Margaritoceras* to *Sacerdosoceras*.

It is interesting to note that Suarez-Soruco (1992) listed some Ordovician cephalopods from Bolivia and reported their Mediterranean similarities. However, as the taxonomy is in need of revision and most specimens were neither illustrated nor described, it is not possible to compare them with the material under discussion. The affinities noted here are largely based on material from San Lucas (the same locality from which material described by Cecioni and Flower, 1985, was collected). Future taxonomic revision of recently and previously collected material should increase our knowledge of the palaeogeographic affinities of cephalopod faunas of this part of the world. The presence of the Eothinoceratidae also in the Middle Ordovician of Perú (northern part of the basin) (Evans, 2007) suggests that members of this family had a wide distribution within the basin and probably reached an important diversification along its margins. The report of the species *Eothinoceras renatae* from Bolivia by Cecioni and Flower (1985) would add the presence of an almost cosmopolitan genus, not restricted to Gondwanan margins.

Interestingly, this biogeographic scenario is in broad agreement with that of the associated trilobite fauna. Trilobite affinities support a biogeographic context consistent with the position of the South American margin at intermediate latitudes (Benedetto *et al*., 2009 and references therein). Low diversity Late Tremadocian to early Floian trilobite assemblages, currently included in the *Thysanopyge* Fauna (Harrington and Leanza, 1957; Waisfeld *et al*., 1999), are mainly dominated by endemic forms (mostly asaphids) whereas biogeographically sensitive elements account for warm water affinities (Waisfeld and Vaccari, 2008). During the middle Floian and late Floian biogeographic affinities

become more complex. A new suite of endemic trilobites belonging to several families (e.g. Asaphidae, Pliomeridae, Trinucleidae) appeared, and were associated with several widespread forms (*Famatinolithus* Fauna, Waisfeld *et al.*, 2003). In summary, endemism among various groups supports a certain degree of isolation; meanwhile provincially significant elements exhibit a mixture of affinities with both, western Gondwana and warm water areas.

Although the Eothinoceratidae as a family is not restricted to cold regions, it is worth mentioning its apparent absence in the Precordillera. The Precordillera terrane of Argentina was rifted as a lithospheric block from the Ouachita embayment of southeastern Laurentia and accreted to western Gondwana (Benedetto, 1993; Astini *et al.*, 1995; Thomas and Astini, 1996). The Lower Ordovician cephalopods from San Juan, Argentina, are known mainly through its orthoceridan faunas (Kröger *et al.*, 2007), which when combined with previous work (Aceñolaza *et al.*, 1977; Aceñolaza and Beresi, 2002), and our own material, indicate that no representatives of the Cyrtocerinina have so far been found in the Precordillera Basin. The San Juan Formation, the main Lower Ordovician unit where cephalopods were recovered, was deposited in a relatively low latitude passive margin carbonate platform (Waisfeld *et al.*, 2003 and references cited therein). Therefore, it would not be expected to find representatives of the peri-Gondwana Realm there, although other forms of Cyrtocerinina might well be present. Apart from the publication by Kröger *et al.* (2007), much work is still required in order to achieve a complete framework for the cephalopod faunas from Precordillera.

We consider of interest the fact that the eothinoceratids from the Central Andean Basin occur in different settings of the onshore–offshore gradient. Although most specimens assigned to *Margaritoceras diploide* and those defined as *Mutveiceras* were recovered from a lower offshore setting, the new species of *Saloceras* and some specimens of *Margaritoceras* were found in onshore settings, in the high-energy, wave- and storm-dominated shoreface of the upper part of the Acoite Formation. These records are of particular relevance as they widen the environmental range of the peri-Gondwanan cephalopod associations otherwise reported to occur in more offshore settings such as in the Montagne Noire, Morocco, and Wales (Evans, 2005; Kröger and Evans, 2011; Kröger and Lefebvre, 2012). It is also remarkable that in the shoreface setting *Saloceras* occurs in the same shell beds with biogeographically significant trilobites such *Nesueretus* and *Ogyginus*, key elements in inshore settings of perigondwanan areas (cf. Fortey and Morris, 1982). Interestingly, Evans (personal communication, 2013) indicated that species of *Saloceras* co-occur with *Neseuretus* in some early Floian localities of the Welsh Basin. Hence, members

of these assemblages appear to thrive also in shallower depositional settings in some areas of West Gondwana.

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