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The late Givetian (Middle Devonian) ammonoid *Epitornoceras* Frech, 1902 from Argentina (southwestern Gondwana)

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ABSTRACT
During the Early to Middle Devonian, southwestern Gondwana was characterized by circumpolar marine environments with striking phases of increased endemism and near absence of typical Paleozoic groups (mainly conodonts, graptolites and stromatoporoids), which defined the Malvinoxhosan (Malvinokaffric) Realm. One of these clades is the Ammonoida. They are extremely rare: only a few occurrences were reported in Bolivia and Argentina in deposits ranging from early Eifelian to early Frasnian. The taxonomy of the only Devonian ammonoid species known from Argentina, *Tornoceras baldisi* Leanza, 1968, was revised based on type material and new specimens from the type area (Chigua Formation, Precordillera, western Argentina). The stratigraphic polarity of the sedimentary succession was reinterpreted, and ammonoid fossils occur in the uppermost interval of the Chigua Formation. *Tornoceras baldisi* is herein assigned to the genus *Epitornoceras* Frech, 1902, and consequently a late Givetian age is proposed for those levels. These occurrences better constrain the age of the upper part of the Chigua Formation (Chavela Member), which is now considered younger than the Belén and Huamampampa formations from Bolivia and possibly coeval to the upper part of the Iquiri Formation. Although the ammonoids indicate a biogeographic dilution of the Malvinoxhosan signature during the late Middle Devonian, the realm is still recognizable on the basis of endemic trilobites as typical indicators.

KEY WORDS
Ammonoids,
Middle Devonian,
South America,
Argentina,
Precordillera,
Chigua Formation,
Gondwana.

RÉSUMÉ
L'ammonoïde Epitornoceras *Frech, 1902 du Givétien supérieur (Dévonien moyen) d'Argentine (sud-ouest du Gondwana).*
Pendant le Dévonien inférieur et moyen, le sud-ouest du Gondwana était caractérisé par des environnements circumpolaires marins, associés à des phases d'endémisme accru et à la quasi-absence de groupes typiques du Paléozoïque (conodontes, graptolites et stromatopores), qui définissaient le domaine Malvinoxhosan (Malvinokaffric). Les Ammonoida constituent l'un de ces clades. Ils sont extrêmement rares : seulement quelques occurrences ont été reportées en Bolivie et en Argentine dans des dépôts datant de l'Eifélien inférieur au Frasnien inférieur. La taxonomie de l'unique espèce d'ammonoïde dévonien connue en Argentine, *Tornoceras baldisi* Leanza, 1968, a été révisée sur la base du matériel type et de nouveaux spécimens provenant de la localité type (Formation Chigua, Précordillère, ouest de l'Argentine). La polarité stratigraphique de la succession sédimentaire a été réinterprétée, et les fossiles d'ammonoïdes proviennent de l'intervalle le plus haut. *Tornoceras baldisi* est assigné au genre *Epitornoceras* Frech, 1902, et par conséquent un âge Givétien supérieur est proposé pour ces niveaux. Ces occurrences contraignent mieux l'âge de la partie supérieure de la Formation Chigua (Membre Chavela), qui est désormais considérée comme étant plus récente que les formations Belén et Huamampampa de Bolivie, et possiblement équivalente à la partie supérieure de la Formation d'Iquiri. Bien que la présence d'ammonoïdes indique une dilution biogéographique du domaine Malvinoxhosan à la fin du Dévonien moyen, le domaine est toujours reconnaissable sur la base de trilobites endémiques constituant des indicateurs typiques.

MOTS CLÉS
Ammonoïdes,
Dévonien moyen,
Amérique du Sud,
Argentine,
Précordillère,
Formation Chigua,
Gondwana.

INTRODUCTION

During the Early to Middle Devonian, the southern circumpolar region of Gondwana hosted a marine fauna with a particular biogeographic signature. The high proportion of endemism in certain clades, particularly trilobites and brachiopods, and the virtual absence of some other major groups, let the recognition of a major biogeographic unit of the Devonian known as the Malvinoxhosan realm (formerly Malvinokaffric, see Penn-Clarke & Harper 2021; Fig. 1). This biochorema is recognized in southern South America, Antarctica and southern Africa and it is characterized by a low diversity fauna dominated by trilobites, brachiopods, hyolithids and conulariids. Among the most relevant absences are stromatoporoids, some brachiopod orders and some of the most important Paleozoic biostratigraphic groups such as conodonts and graptolites (Dowding & Ebach 2018). In this scenario, ammonoids also constitute a clade relevant for the definition of the Malvinoxhosan realm, as they are very scarce and only represented by a few taxa (Leanza 1968; Hünicken *et al.* 1980; Babin *et al.* 1991; Kullmann 1993; Troth *et al.* 2011). Their near absence was interpreted as evidence of low influx of tropical waters, while their immigration to Malvinoxhosan basins was considered as indication of the



FIG. 1. — Early Devonian simplified paleogeographic reconstruction showing the Malvinoxhosan (Malvinokaffric) Realm (**red circle**) indicating the location of the Precordillera (modified from Cocks & Torsvik 2006). Old Red Sandstone continents in Laurussia and Gondwana indicated in **light yellow**; terrane names are **labeled**. The localities with *Epitornoceras* Frech, 1902 are indicated by a **white star**: Morocco, Germany (**RH**, Rheno-Hercynian Terrane), North America, Argentine Precordillera.

end of the biogeographic barriers that accounted for the high endemism (Dowding & Ebach 2018). However, while some evidence suggests the end of the Malvinoxhosan realm near the earliest Givetian (Bosetti *et al.* 2011), immigration of ammonoids into Malvinoxhosan basins is known to occur as early as earliest Eifelian, i.e., *c.* 9 Ma earlier (Troth *et al.* 2011). Therefore, in order to understand the demise of the Malvinoxhosan realm, the precise timing of immigration in these basins needs to be better constrained. The few occurrences of Devonian ammonoids from the Malvinoxhosan realm are limited to South America (no records from southern Africa; Penn-Clark, 2022 pers comm.). Four genera and possibly seven species have been reported: 1) *Tornoceras baldisi* Leanza, 1968 from Argentina (Leanza 1968); 2) *Tornoceras bolivianum* (Kullmann, 1980) from Bolivia (Hünicken *et al.* 1980); 3) *Tornoceras* sp., *Tornoceras* "*simplex*", *Sporadoceras* sp. and *Agoniatites* sp. from Bolivia (Babin *et al.* 1991); and 4) *Mimotornoceras*? sp. from Bolivia (Troth *et al.* 2011). However, according to Troth *et al.* (2011), the material identified as *Tornoceras bolivianum* by Hünicken *et al.* (1980) and the specimen identified by them as *Mimotornoceras*? sp. would correspond to the same species that should be assigned to the genus *Mimotornoceras* Klug, 2002.

The first Devonian ammonoid record from South America came from central-west Argentina and was based only on two specimens. Based on them, Leanza (1968) recognized the genus *Tornoceras* Hyatt, 1884 and erected the new species *Tornoceras baldisi*. The material was found in the Chigua Formation, in the Precordillera of the San Juan province (central western Argentina).

A Late Devonian age was originally attributed to the Chigua Formation, but the bearing levels were subsequently considered to range from latest Early to Middle Devonian, according to trilobites and palynological information (Baldis 1967; Baldis & Longobucco 1977; Amenábar 2009; Amenábar *et al.* 2009).

Subsequently, other ammonoid species were documented in South America. Kullmann (in Hünicken *et al.* 1980) described *Tornoceras bolivianum* from the Huamampampa Formation in Bolivia, while Babin *et al.* (1991) reported the occurrence of three ammonoid genera (*Tornoceras*, *Sporadoceras* Hyatt, 1884 and *Agoniatites* Meek, 1877) also from Devonian deposits of Bolivia although lacking further stratigraphic information.

More recently, *Tornoceras bolivianum* was also recognized by Troth *et al.* (2011) in its type locality (basal part of the Huamampampa Formation, at Campo Redondo, Bolivia). However, Troth *et al.* (2011), stated that *T. bolivianum* needs to be removed from the genus *Tornoceras* because several characters of the new discovered specimen suggest affinities with *Mimotornoceras* Klug, 2002 (Troth *et al.* 2011: 13). This proposed reassignment agrees with the early Eifelian age of the basal Huamampampa Formation suggested by the palynoflora (Troth *et al.* 2011). Furthermore, it raises the question on whether other South American material originally assigned to *Tornoceras*, such as *T. baldisi*, might actually belong to *Mimotornoceras*, constraining the deposits to the Eifelian.

Based on the original material and new specimens recently collected from the type area of the Chigua Formation, we reinvestigated the taxonomy of the Argentinian ammonoid *Tornoceras baldisi*. Our study enabled us to better constrain the age of the ammonoid bearing levels, evaluate the potential correlation of the few well-known ammonoid records from South America and shed light onto the biogeographic ammonoid dynamics in the context of the main events characterizing the history of the Malvinoxhosan Realm.

GEOLOGICAL SETTING

The study area (Fig. 2) is located in the Argentine Precordillera, an intraplate fold-and-thrust belt located at the southern end of the Central Andes foreland basin. The Precordillera has traditionally been divided into western, central and eastern domains, based on stratigraphy and structural features (Furque & Cuerda 1979). In the Western Precordillera, early to middle Paleozoic rocks are typically separated from the Carboniferous glacial and post-glacial beds of the Paganzo Group by a regional angular unconformity (Baldis & Sarudiansky 1975; Furque 1979; Pazos 2002; Balseiro *et al.* 2009). Mostly, this type of contact has been attributed to the Chanic Orogeny, alternatively related to the collision of the Cuyania terrane during the Devonian (e.g. Astini 1996; Ramos 2004) or resulting from a contractional event in a subduction tectonic setting (Dahlquist *et al.* 2021).

This study was conducted in the context of Western Precordillera, focusing on the Middle Devonian marine Pircas Negras and Chigua formations, in a belt that extends to the east of the Blanco River, on the western slope of the Punilla and the Volcán ranges (Furque & Baldis 1973; Baldis & Sarudiansky 1975; Fig. 3). The Chigua Formation is in tectonic contact with the Pircas Negras Formation (Furque & Baldis 1973) and is separated by an angular unconformity from the overlying Late Tournaisian?-Early Visean (Mississippian) Malimán Formation (Scalabrini Ortiz 1972; Amenábar 2009; Amenábar *et al.* 2009). A main concern on the Pircas Negras and Chigua formations involves the interpretation of the stratigraphic polarity of the layers and the geological structure of the type area. In pioneer contributions, Furque (1956, 1963) interpreted a normal stratigraphic arrangement of these units, i.e., the Chigua Formation overlying the Pircas Negras Formation and the Chavela Member overlying the Ramadita Member in the Chigua Formation. In this initial proposal, the ammonoid bearing levels of the Chavela Member which are located immediately below the angular discordance with the overlying Mississippian Malimán Formation, were the uppermost and youngest. However, in following contributions – based on interpretations raised from the licentiate thesis work of Sarudiansky (1971) – Furque & Baldis (1973) and Baldis & Sarudiansky (1975) proposed an anticline structure and an inverse relationship in the succession of ages of the Pircas Negras and Chigua formations. Significantly, in this interpretation, the ammonoid bearing levels would be located at the base of the Chigua Formation. This scheme was adopted by later authors including Amenábar *et al.* (2009), which had implications on the stratigraphic position of palyniferous samples with biostratigraphic significance.

Our field stratigraphic observations in the type area of the Chigua Formation (Fig. 2) allowed us to reinterpret the structure and stratigraphic relationships of this formation (Vaccari *et al.* 2016). Based on the polarity of sandstone beds in the Ramadita Member, we interpret the succession as exhibiting normal polarity in an overall homocline disposition of layers (in spite of some local tectonic deformation), with ages progressively younger to the east (Fig. 3A-D). This interpretation is in accordance with the original proposal of Furque (1956). Hence, according to our stratigraphic interpretation, the ammonoid fossils come from the uppermost part of the Chavela Member of the Chigua Formation (Fig. 4).

As already reported by Baldis (1967) and Baldis & Longobucco (1977), the same fossiliferous interval also records trilobites preserved inside nodules, including *Punillaspis argentina* (Baldis, 1967), "*Phacops*" *chavelai* Baldis & Longobucco, 1977, and "*Acanthopyge*" *balliviani* (Kozlowski, 1923), among others. Additional paleontological records from the Chavela Member account for conulariids, orthoconic nautiloids, bivalves, corals, hyoliths, gastropods and fishes mainly from nodules (Vaccari *et al.* 2016; Fig. 4). The flora is represented by the herbaceous lycophytes "*Haplostigma*" *furquei* Frenguelli, 1952, "*Haplostigma*" *baldisii* Gutiérrez, 1996 and ?*Cyclostigma* sp. (Gutiérrez 1996).

The Chigua Formation (Middle Devonian) is a siliciclastic unit that reaches *c.* 450 m in thickness, formally divided into the Ramadita and Chavela members (Furque & Baldis 1973; Baldis & Sarudiansky 1975; Figs 3; 4). This unit is strongly deformed due to its proximity to the faults that juxtapose the Pircas Negras Formation over the Chigua Formation, as well as the extensive network of Miocene intrusive dikes associated with it. The Ramadita Member is characterized by the greatest proportion of sandstones (Figs 3; 4). It shows a heterolithic facies with an alternation of laminated silt-claystones, massive/

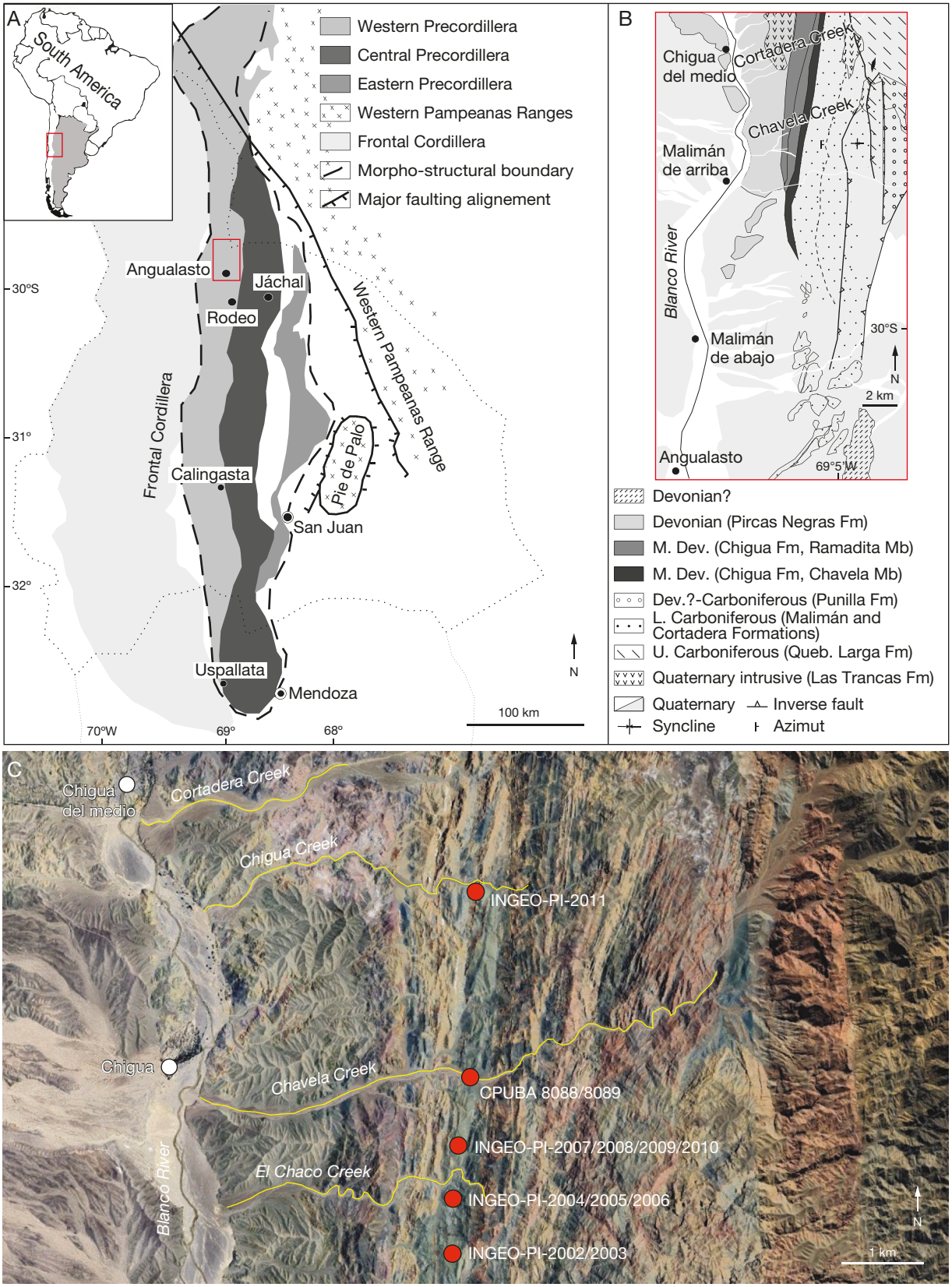


FIG. 2. — Geological maps of the study area (**A**, **B**, modified from Amenábar 2009), and satellite image showing the location of the ammonoid fossils (**C**, from Google Earth).

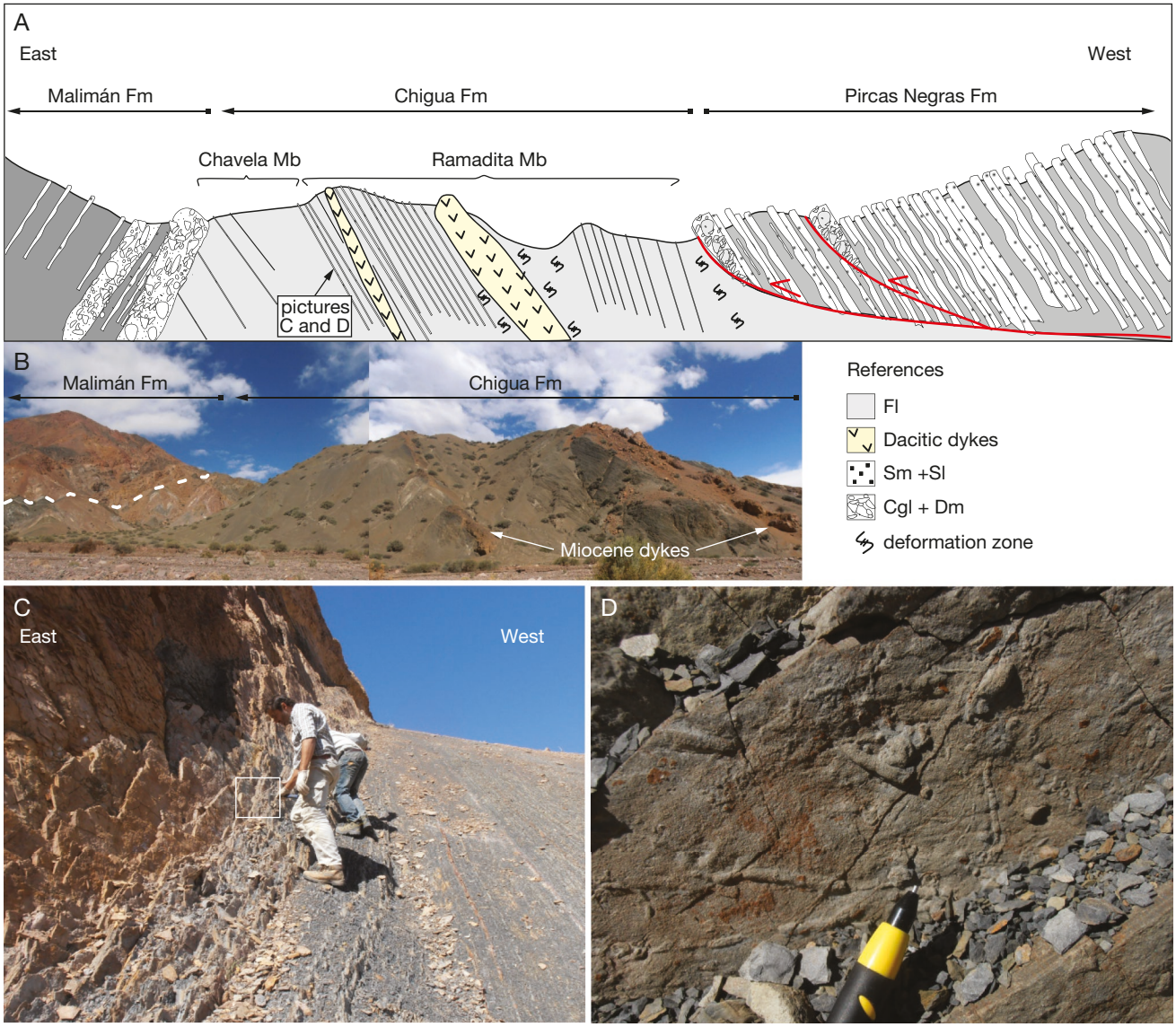


FIG. 3. — The Chavela Creek: **A**, **B**, structural cross-section of the Chavela Creek, showing the tectonic relation between the Chigua and Pircas Negras formations, and the angular unconformity from the overlying Malimán Formation (Mississippian); **arrows** point towards younger deposits; the **white box** (in **A**) indicates the location of pictures C and D; **C**, overturned psammitic beds, younger deposits towards the East; **D**, Ichnofossils indicating the base of beds.

laminated sandstones and occasional carbonate sandstones. Plant remains and scarce, poorly preserved trilobites have been reported from this member (Baldis & Sarudiansky 1975). It would correspond to a middle platform, with a predominance of settling processes and periodic arrival of tractive flows.

The overlying Chavela Member is distinguishable from the Ramadita Member by its more greenish to brown color in the landscape (fresh rock being darker), and by its minor sand content. It is an overall fine-grained interval integrated by laminated to massive greenish-dark fossiliferous silt-claystones or shales with sparse nodules and calcareous lenses, and occasional massive/laminated sandstones noticeably thinner than in the lower member. It is interpreted as deposits from the middle to distal platform, with predominance of settling processes.

Concerning the age of the unit, the trilobite "*Acanthopyge*" *balliviani,* also recorded in the Devonian of Bolivia, suggested an Emsian or Eifelian age (Ahlfeld & Branisa 1960; Baldis 1967; Wolfart & Voges 1968; Baldis & Longobucco 1977). In turn, the former recognition of the ammonoid as *Tornoceras* (according to the original assignment by Leanza in 1968) indicated a Givetian or Frasnian age considering records from Euramerica (Kullmann 1993). Hence, Baldis & Sarudiansky (1975) considered ages spanning from the Emsian-Eifelian boundary to the Givetian-Frasnian boundary on the basis of the co-occurrence of *A. balliviani* and *Tornoceras baldisi*, thus proposing a more probable Givetian age for the Chavela Member of the Chigua Formation.

In the 2000s, Amenábar and collaborators sampled the shaly Chavela Member of the Chigua Formation for palynomorph analyses. Palynological data, although lacking vertical completeness of sampling throughout the unit, accounted for ages ranging from the Emsian to the Givetian-Frasnian boundary

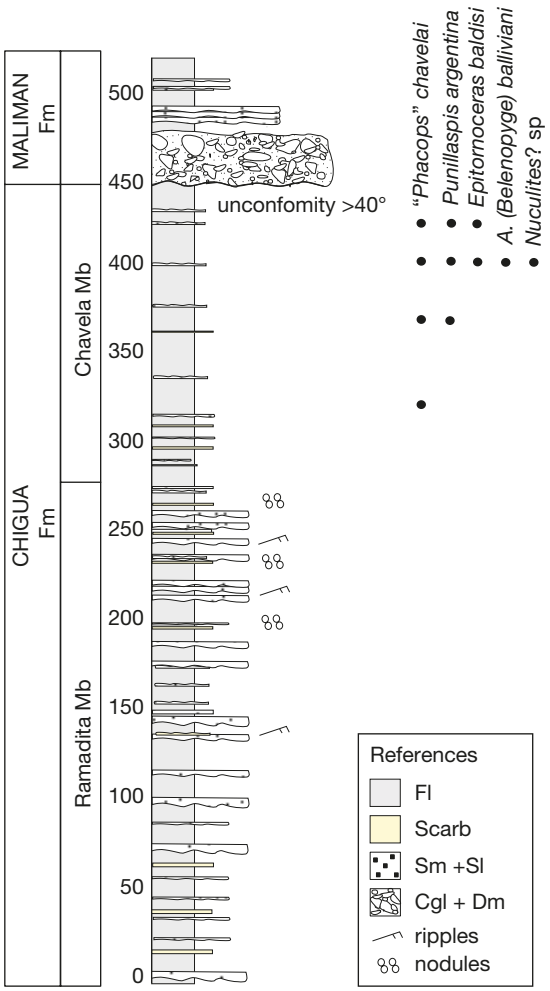


Fig. 4. — Stratigraphic section of the Chigua Formation showing the distribution of the identified taxa within the Chavela Member (ammonoid, trilobites, bivalve). Note the angular unconformity (>40°) between the Chigua and Malimán formations.

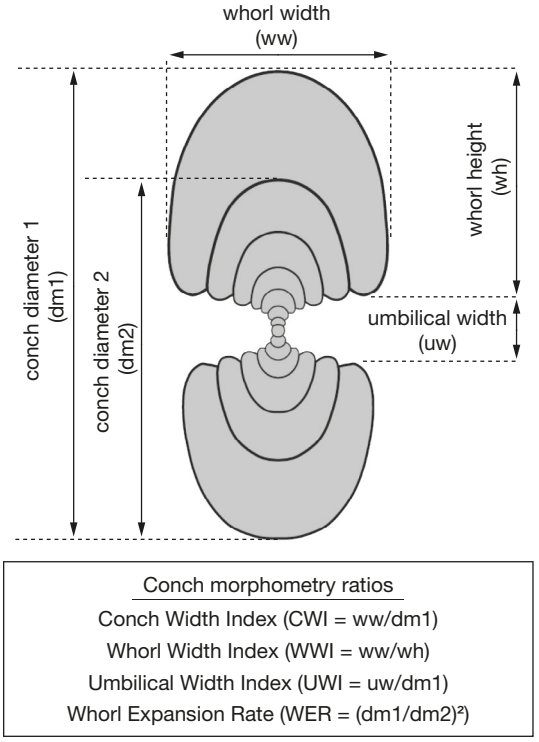


Fig. 5. — Morphological terms used in the description of the ammonoid conchs.

for the Chavela Member of the Chigua Formation (Amenábar *et al.* 2006, 2007, 2009; Amenábar 2009). Lithological and stratigraphic position consistent with the noduliferous shales of the upper part of the Chavela Member, would reliably correspond only to palyniferous samples of Amenábar *et al.* (2009) interpreted as Givetian in age.

The taxonomic reinterpretation of the ammonoids made in the present work allows us to recognize the genus *Epitornoceras* Frech, 1902 and thus constrain with certainty the uppermost levels of the Chavela Member of the Chigua Formation to the late Givetian, implying that the Ramadita Member should be older.

MATERIAL AND METHODS

The two specimens of *Tornoceras baldisi* from Leanza (1968; the holotype and an additional specimen) are stored in the collection of Paleontology of the University of Buenos Aires (UBA) as CPUBA 8088 and 8089. They were revised and re-illustrated through new pictures provided by the curator Marian Tanuz. We noticed that these specimens were not fully prepared prior to photography in the original publication.

A number of additional specimens mentioned in a subsequent contribution on the type area by Baldis & Sarudiansky (1975: fig. 5), could not be found after checking the "Baldis collection" from the Chigua Formation housed at the University of San Juan (USJ) and are presently considered lost.

Ten new specimens described here are stored in the collection of the Geological Research Institute Dr Emiliano Pedro Aparicio at USJ, numbered from INGEO-PI-2002 to 2011. These new specimens were collected in the type area including the Chigua, Chavela, and El Chaco creeks (Fig. 2).

The stratigraphic interval surveyed corresponds to the uppermost part of the Chigua Formation (in this paper) composed of noduliferous greenish brown to dark siltstones and shales, which is located below the angular unconformity with the overlying mainly Tournaisian (Mississippian) Malimán Formation (Figs 3; 4). All specimens are preserved in slightly carbonaceous nodules of dark grey to black color, included in a greenish-dark fine-grained interval. As said, accompanying biota includes trilobites, conulariids, gastropods, bivalves, nautiloids, corals, hyoliths, fishes and lycophytes.

Fossils were prepared using pneumatic jacks and needles. Latex casts of external molds and natural internal molds were inked and whitened with ammonium chloride (NH_4Cl) for taking pictures under raking light using a Canon Power Shot S50 digital camera mounted on a Leica MZ75 binocular loupe. The suture lines were drawn under a stereomicroscope with a camera lucida.

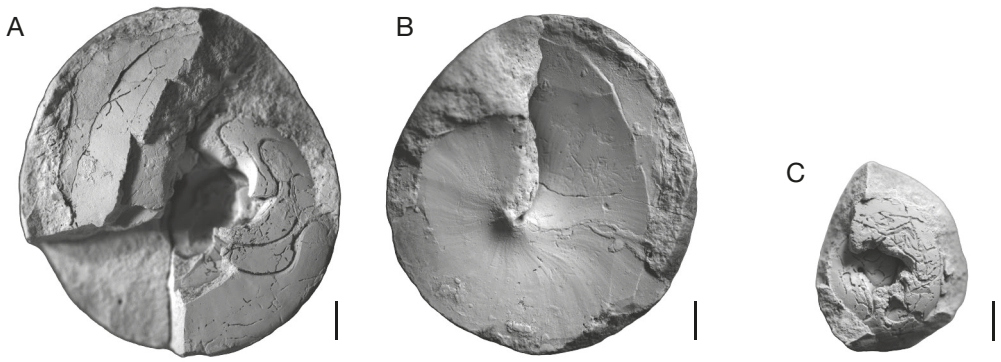


Fig. 6. — Historical material of *Epitornoceras baldisi* (Leanza, 1968), identified as *Tornoceras baldisi* Leanza, 1968 by Leanza (1968), from the Chavela Creek ("Quebrada de la Chavela"), Chavela Member, Chigua Formation (San Juan Province, Argentina): **A**, **B**, holotype CPUBA 8088 (part and counterpart showing the external mold of the conch); **C**, additional specimen CPUBA 8089. Scale bars: 2 mm.

The description of the material follows the scheme for Paleozoic ammonoids outlined by Korn (2010) and (Klug *et al.* 2015a) (Fig. 5).

Abbreviations

A lobe	adventive lobe;
E lobe	external lobe;
CWI	conch width index (ww/dm);
dm	conch diameter;
uw	umbilical width;
UWI	umbilical width index (uw/dm);
WER	whorl expansion rate = $(dm1/dm2)^2$;
wh	whorl height;
ww	whorl width;
WWI	whorl width index (ww/wh).

SYSTEMATIC PALEONTOLOGY

Class CEPHALOPODA Cuvier, 1795
Subclass COLEOIDEA Bather, 1888
Superorder AMMONOIDA Haeckel, 1866
Order GONIATITIDA Hyatt, 1884
Suborder TORNOCERATINA Wedekind, 1914
Superfamily Tornoceratoidea von Arthaber, 1911
Family Tornoceratidae Hyatt, 1884
Subfamily Tornoceratinae von Arthaber, 1911
Genus *Epitornoceras* Frech, 1902

Epitornoceras baldisi (Leanza, 1968)
(Figs 6; 7)

Tornoceras baldisi Leanza, 1968: figs 1-4.

non *Tornoceras* (*Tornoceras*) cf. *baldisi* House, 1978: pl. 6, figs 9, 10.

Type material. — **Holotype. Argentina** • Specimen CPUBA 8088 designed by Leanza (1968), stored at the University of Buenos Aires (re-illustrated here, see Fig. 6).

Diagnosis. — *Epitornoceras* reaching at least 50 mm conch diameter. Extremely discoidal and involute adult stage (CWI *c.* 0.25; umbilicus closed at 30 mm dm); whorl profile strongly compressed (WWI *c.* 0.40 at 30 mm dm). Flanks weakly convex, convergent, umbilical margin continuously rounded. Without any ventrolateral grooves. Suture line with broadly rounded, nearly symmetric adventive lobe with convergent flanks; adventive lobe wider than deep.

Type locality and horizon. — Uppermost part of the Chavela Member, uppermost part of the Chigua Formation, Chinguillos Group, north of Angualasto town, San Juan province, Argentina.

Occurrence. — The species is known only from the type locality (Chavela Member, Chigua Formation, San Juan province, Argentina), late Givetian.

Material. — Ten specimens, INGEO-PI-2002 to 2011.

Description

The conch is extremely discoidal (CWI *c.* 0.25) with a strongly compressed whorl section (WWI *c.* 0.40) in the subadult stage (30-50 mm dm); its umbilicus is completely closed (specimens INGEO-PI-2011, INGEO-PI-2007 and INGEO-PI-2004; Fig. 7A-C, I). The flanks are weakly convex and convergent, and the venter is narrowly rounded; the umbilical margin is continuously rounded. At a smaller diameter (20-30 mm dm), the conch is also discoidal, but has a slightly opened umbilicus (specimens INGEO-PI-2005 and INGEO-PI-2002; Fig. 7F-H). At about 20 mm dm, the coiling rate is very high (WER *c.* 2.35). Based on specimen INGEO-PI-2003 (Fig. 7Q, L), the morphology of the earlier whorls can be investigated by the use of latex casts: around 10-15 mm dm, the conch is thinly discoidal (CWI *c.* 0.35-0.40) with a weakly compressed whorl section (WWI *c.* 0.50-0.60) and a high whorl expansion rate (WER *c.* 2.10). Surprisingly, the umbilicus appears to be entirely closed.

In most specimens, partially preserved suture lines or septal surfaces are visible. The entire suture line can be reconstructed for specimen INGEO-PI-2007 (Fig. 7C, E); at wh *c.* 18 mm, it consists of a narrow and deep external lobe, a narrow and subacute E/A saddle, a broadly rounded, wide and deep nearly symmetric adventive lobe with convergent flanks, followed by a similarly broadly rounded and deep but wider saddle. Suture lines are also relatively well preserved in specimen INGEO-PI-2004 (Fig. 7D, I); the shape of the adventive lobe and the following saddle is similar to specimen INGEO-PI-2007 (Fig. 7E); the external lobe and the ventrolateral saddle are

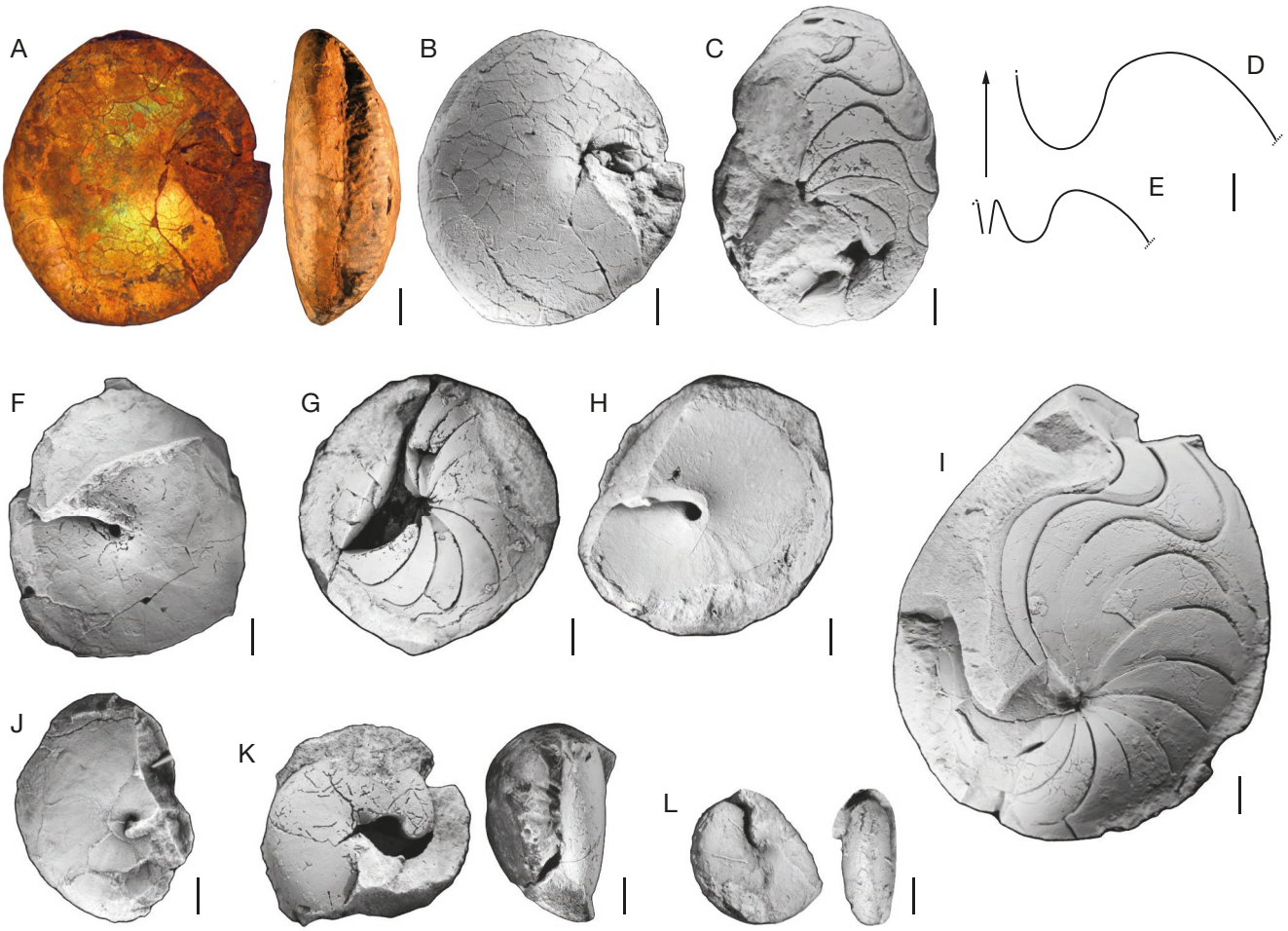


FIG. 7. — New specimens of *Epitornoceras baldisi* (Leanza, 1968) from the type area of the Chigua Formation (San Juan Province, Argentina): **A**, **B**, specimen INGEO-PI-2011; **C**, specimen INGEO-PI-2007; **D**, suture line of specimen INGEO-PI- 2004 at wh *c.* 33 mm; **E**, reconstructed suture line based on specimen INGEO-PI-2007 at wh *c.* 18 mm; **F**, specimen INGEO-PI-2005 (counterpart showing the external mold of the conch); **G**, **H**, specimen INGEO-PI- 2002 (part and counterpart showing the external mold of the conch); **I**, specimen INGEO-PI-2004; **J**, specimen INGEO-PI-2006; **K**, **L**, specimen INGEO-PI-2003 (L corresponds to latex cast of internal whorl). Scale bars: 2 mm. The pictures of some specimens have been flipped (A, B, and K).

not visible. Interestingly, the larger specimens show a septal thickening when comparing with smaller ones (i.e., increase in thickness of the septal wall when it meets the shell; compare the wideness of the suture lines of specimens INGEO-PI-2007 and INGEO-PI-2004, Fig. 7C, I, with specimen INGEO-PI-2002, Fig. 7G). This trend of increasing septal thickness toward adulthood (see Klug *et al.* 2015b) was already documented in several ammonoids (Westermann 1971) as in modern nautilids (Collins & Ward 1987).

Although cracked, the shell is partially preserved in one specimen (INGEO-PI-2011, Fig. 7A); it exhibits iridescent colors. Growth lines are not visible.

REMARKS

This material fits well with the description of Korn & Bockwinkel (2022) defining the genus *Epitornoceras* Frech, 1902 with a compressed and involute conch, a completely closed umbilicus in the pre-adult stage but slightly opened in the juvenile stage, sutural formula E A L I with broadly rounded adventive lobe, narrow and subacute ventrolateral saddle. *Epitornoceras* differs from the other genera of the subfamily Tornoceratinae by its very narrow and subacute ventrolateral saddle (Korn & Bockwinkel 2022).

Four other species of *Epitornoceras* have been described: *Epitornoceras mithracoides* (Frech, 1888) from the Rhenish Mountains of Germany (Bockwinkel *et al.* 2013; Bockwinkel & Korn 2015; Korn & Bockwinkel 2022), *Epitornoceras transmediterraneum* Korn & Bockwinkel, 2022 from the Anti-Atlas of Morocco (Bockwinkel *et al.* 2009, 2013, 2017; Bockwinkel & Korn 2015; Korn & Bockwinkel 2022), *Epitornoceras peracutum* (Hall, 1876; holotype described by Miller 1938) and *Epitornoceras dennisoni* Kirchgasser, Baird & Brett, 2020 reported from North America (see Table 1 for a comparison of the morphological characters of the different species). House (1965, 1978) also identified forms showing affinities with *Epitornoceras peracutum* (refigured in House & Kirchgasser 2008).

As a general observation, the conch of *E. baldisi* appears to be more slender (i.e., extremely discoidal, see Table 1) at the adult stage than in all other *Epitornoceras* species (by excluding *E. peracutum* from the comparison, for which the conch shape is not well known; the description of this species is almost only based on its suture line, see Miller 1938).

TABLE 1. — Comparison of the morphological characteristics of the different species belonging to the genus *Epitornoceras* Frech, 1902. Abbreviations: **CWI**, conch width index; **UWI**, umbilical width index; **WER**, whorl expansion rate; **WWI**, whorl width index.

Morphological characters at the adult stage (*c.* 30-50 mm dm)	***Epitornoceras baldisi*** **(Leanza, 1968)**	***Epitornoceras mithracoides*** **(Frech, 1888)**	***Epitornoceras transmediterraneum*** **Korn & Bockwinkel, 2022**	***Epitornoceras dennisoni*** **Kirchgasser, Baird & Brett, 2020**	***Epitornoceras peracutum*** **(Hall, 1876)**
Conch geometry	Extremely discoidal (CWI *c.* 0.25)	Thinly discoidal (CWI *c.* 0.35)	Thinly discoidal (CWI *c.* 0.35)	Thinly discoidal (CWI *c.* 0.35)	Conch probably discoidal
	Whorl profile strongly compressed (WWI *c.* 0.40)	Whorl profile compressed (WWI *c.* 0.65)	Whorl profile compressed (WWI *c.* 0.65)	Whorl profile compressed (WWI *c.* 0.65)	Whorl profile shape unknown
	Umbilicus closed at 30 mm dm	Umbilicus closed at 50 mm dm	Umbilicus closed at 50 mm dm	Diameter of umbilical closure unknown	Diameter of umbilical closure unknown
	Umbilical margin continuously rounded	Umbilical margin continuously rounded	Umbilical margin obliquely flattened (funnel-shaped)	Umbilical margin continuously rounded	Umbilical margin continuously rounded
	Flanks weakly convex, convergent	Flanks weakly convex, convergent	Flanks nearly parallel	Flanks weakly convex, convergent	Flanks weakly convex
Suture line	Narrow E lobe	V-shaped E lobe	V-shaped E lobe	Wide E lobe with convex flanks	Wide E lobe with concave flanks
	Nearly symmetric A lobe, wider than deep	Asymmetric A lobe, as deep as wide, convergent flanks	Nearly symmetric A lobe, deeper than wide, parallel flanks	Asymmetric A lobe, slightly wider than deep	Asymmetric A lobe, very deep, deeper than wide
	–	–	–	Flat-topped dorsolateral saddle	Dorsolateral saddle less wide

Epitornoceras baldisi differs from *E. transmediterraneum* in the shape of the umbilicus: the umbilical wall is obliquely flattened caused by an umbilical shell thickening in *E. transmediterraneum* (i.e., funnel-shaped umbilicus), while in *E. baldisi* the umbilical margin is continuously rounded (as in all others species, see Table 1). The two species also differ when comparing the suture line. The suture line of *E. baldisi* possesses a narrower external lobe, in *E. transmediterraneum* the E lobe is V-shaped and wider. Furthermore, the A lobe is considerably deeper in *E. transmediterraneum*, and the flanks are nearly parallel (Korn & Bockwinkel 2022). In the latter, the A lobe is deeper than wide (Korn & Bockwinkel 2022), while in *E. baldisi* the A lobe is slightly wider than deep (Fig. 7D, E).

Epitornoceras baldisi and *E. mithracoides* are close in terms of conch shape (see Table 1). However, differences can be seen in the suture line: in *E. mithracoides*, the A lobe is asymmetric and as wide as it is deep (Korn & Bockwinkel 2022), while in *E. baldisi*, the A lobe is nearly symmetric (and wider than deep), furthermore the L saddle is deeper and considerably wider (Fig. 7D, E).

Epitornoceras baldisi mainly differs from the North American species (*E. peracutum* and *E. dennisoni*) in its suture line (see Table 1). *Epitornoceras peracutum* possesses an E lobe much wider (with concave flanks), and an A lobe much deeper and more asymmetric, furthermore, the dorsolateral saddle is comparatively less wide (Miller 1938). *Epitornoceras dennisoni* also possesses an E lobe much wider (with convex flanks), and a flat-topped dorsolateral saddle (Kirchgasser *et al.* 2020).

The type material of *E. baldisi* was originally attributed to the genus *Tornoceras*. Two specimens were described: the holotype CPUBA 8088 and CPUBA 8089, re-illustrated here in Fig. 6. The conch of the holotype is involute with an entirely closed umbilicus (Fig. 6A, B); suture lines are visible (see Leanza 1968: fig. 4) and their shape is characteristic of the genus *Epitornoceras* Frech, 1902. The counterpart of the specimen shows the external mold with imprints of the growth lines (Fig. 6B). As indicated by Leanza (1968), they have a biconvex course (characteristic of the genus *Epitornoceras*; see Korn & Bockwinkel 2022). The holotype and the new specimens described herein share very similar characteristics and came from the same levels and localities, so they most likely correspond to the same species. The additional specimen of Leanza (1968), CPUBA 8089, consists of a poorly preserved internal mold (Fig. 6C) of an involute conch; the internal whorl shows a slightly opened umbilicus (pre-adult stage).

The specimen from Bolivia identified as *Tornoceras* (*Tornoceras*) cf. *baldisi* by House (1978: pl. 6, figs 9, 10) has a much stouter conch than *E. baldisi*. Thus, it can be neither identified as *E. baldisi* nor as *E.* cf. *baldisi*.

In Morocco, the genus *Epitornoceras* occurs from the topmost middle Givetian (*Pharciceras* aff. *amplexum* Zone) to the topmost late Givetian (*Petteroceras errans* Zone) deposits (Becker & House 2000; Bockwinkel *et al.* 2009, 2013, 2015, 2017; Aboussalam & Becker 2011; Becker *et al.* 2013; Aboussalam *et al.* 2018). In Germany, *Epitornoceras* was reported in one late Givetian biozone (*Pseudoprobeloceras pernai* Zone; Korn & Bockwinkel 2022). In North America, *Epitornoceras was* recognized in the lower part of the late Givetian (i.e., *E.* aff. *peracutum*; upper part of the Geneseo shale, House 1965, 1978) and in early Frasnian rocks (i.e., *E. dennisoni*; Kirchgasser *et al.* 2020). *Epitornoceras* was also reported in early Famennian deposits from Australia (Petersen 1975). House (1978), however, stated that the specimens



FIG. 8. — Artistic reconstruction of the ammonoid *Epitornoceras baldisi* (Leanza, 1968) during the Middle Devonian. Paleoartist: H. Santiago Druetta (CICTERRA, Universidad Nacional de Córdoba, Argentina).

identified there as *Epitornoceras peracutum* by Petersen (1975) must be assigned to a different genus. Therefore, the Argentinian *Epitornoceras* most likely indicates a late Givetian age (see also Discussion section below for more details about biostratigraphic correlations).

The specimen whose shell shows iridescent colors (INGEO-PI-2011; Fig. 7A) is the subject of further investigations. Chemical analyses and SEM observations will be performed to understand the origin of these colors, and the results will be presented in a future study.

DISCUSSION

Biostratigraphy and correlation

Previous assessments of the age of the Chigua Formation based on the macrofaunal (Baldis 1967; Baldis & Sarudiansky 1975) and palynological (Amenábar *et al.* 2009; Amenábar 2009) content suggested an age ranging from the late Emsian to the Givetian-Frasnian boundary. The new taxonomic assignment of the species *Tornoceras baldisi* Leanza, 1968, now considered to belong to the genus *Epitornoceras*, allows us to refine the age of the Chavela Member of the Chigua Formation for the first time, as the stratigraphic range of the genus *Epitornoceras* is much more restricted (i.e., topmost middle Givetian to earliest Frasnian; Becker & House 2000; Aboussalam *et al.* 2018; Kirchgasser *et al.* 2020; Korn & Bockwinkel 2022). This biostratigraphic data is in agreement with the age of the youngest palynological assemblage described by Amenábar (2009; a time span around the Givetian-Frasnian boundary) and with the inferences of Givetian ages based on combined records of ammonoids and the co-occurring trilobite "*Acanthopyge*" *balliviani* (Baldis 1967; Baldis & Longobucco 1977).

It is worth noting that the trilobite "*Acanthopyge*" *balliviani*, should be considered as *Belenopyge balliviani*, which is an endemic Malvinoxhosan genus according to the taxonomic revision made by Van Viersen (2021). *Belenopyge balliviani* has been interpreted as a relevant regional biostratigraphic marker for South America since its early recognition (Kozlowski 1923; Baldis 1967; Baldis & Longobucco 1977). Indeed, it has been used to correlate the Chavela Member of the Chigua Formation with the Upper Member of the Belén Formation in Bolivia (Baldis 1967; Baldis & Longobucco 1977; Van Viersen 2021). While the age of these units remained unconstrained for many years, recent studies have dated the Huamampampa Formation from Bolivia (laterally equivalent to the Upper Member of the Belén Formation, following Racheboeuf *et al.* (1993) as Eifelian, based on key palynological markers and the presence of *Mimotornoceras* (Troth *et al.* 2011). However, our data indicates that the Chavela Member of the Chigua Formation is significantly younger (most likely late Givetian) and cannot be correlated to those units, but more probably with the lower distinctive dark grey organic matter rich (AOM) mudstone/shale package in the upper part of the Iquiri Formation (Troth *et al.* 2011). These results, in addition, warn that the temporal range of "*Belenopyge*" *balliviani* might be much larger (probably Emsian-Givetian) than previously thought and suggest that this trilobite species should not be used for detailed correlations across basins.

In addition, *Epitornoceras* has been indicated as a typical ammonoid that radiated during the last interval of the Taghanic biocrisis and immediately after the crisis (Aboussalam & Becker 2011). The end of the Taghanic biocrisis is marked by a sharp transgression (known as the Geneseo transgression or IIa-Gen, see Aboussalam & Becker 2011) in its type area (Northern Appalachian basin, Zambito *et al.* 2012) and across the paleotropics (Aboussalam & Becker 2011). As mentioned above, in the Precordillera, the contact between the Ramadita and Chavela members of the Chigua Formation is marked by a contrasting lithological change, where shallower sand-rich facies are overlain by fine shales. Such a stratigraphic pattern, associated with the presence of *Epitornoceras* in the Chavela Member, could be indicative of the Geneseo transgression in the Argentine Precordillera. This would extend the recognition of this important transgression far from the paleotropics where it has been previously recognized (Aboussalam & Becker 2011), and further supports the occurrence of this eustatic event in western Gondwana (Troth *et al.* 2011).

Paleobiogeography

During the Early Devonian, the southern circumpolar region hosted a highly endemic fauna, defining the Malvinoxhosanic realm, a major paleobiogeographic unit (Penn-Clarke & Harper 2021). While its definition and origins have been studied in detail (Boucot & Racheboeuf 1993; Benedetto & Sánchez 1996; Dowding & Ebach 2018, 2019; Penn-Clarke & Harper 2021), its demise is less understood (Sedorko *et al.* 2021). In spite of significant isolation supporting this major biochorema, a number of nearly cosmopolitan or extra-Malvinoxhosanic taxa indicated exchange even during the Early Devonian in the Argentine Precordillera. Some examples include the phacopid trilobites *Reedops* and *Echidnops* (Holloway & Rustán 2012; Rustán & Balseiro 2016), the bactritoid cephalopods *Bactrites* and *Devonobactrites*? (Cichowolski & Rustán 2017), the lamellorthoceratid cephalopod *Arthrophyllum* (Cichowolski & Rustán 2020) and virtually all bryozoan genera recorded (Carrera *et al.* 2019).

It has been claimed that the ingression of warm waters, and the consequent common immigration of taxa from low paleolatitudinal regions to the circumpolar basins was the cause for the disappearance of the Malvinoxhosan realm, with most compelling evidences precisely during the late middle Devonian (Penn-Clarke 2019).

Epitornoceras is present in North Africa, and in the Rhenish-Bohemian and Appalachian basins; its diversification and the acquisition of its wide geographic distribution took place after the late middle Givetian Taghanic biocrisis (Aboussalam & Becker 2011). Hence, the occurrence of *Epitornoceras* during the late Givetian in southernmost western Gondwana is not surprising, as there is a well-recorded pattern of immigrants from tropical regions in circumpolar basins after the Taghanic biocrisis (Melo 1988; Boucot *et al.* 1983; Boucot & Theron 2001; Dowding & Ebach 2018). The post-Taghanic interval is considered to be a time of global dispersion causing a decrease in biogeographic endemisms (Zambito *et al.* 2012). Consistent evidence from the Paraná basin in Brazil suggests that the Malvinoxhosan fauna disappeared through the Givetian (Bosetti *et al.* 2011; Sedorko *et al.* 2021). However, despite their very low diversity, calmoniids and other typical Malvinoxhosan endemic trilobite genera like *Belenopyge* (Baldis 1967; Baldis & Longobucco 1977), occur together with *Epitornoceras* in the Chigua Formation (Fig. 8). Therefore, although the identity and extension of the faunal realm might have decreased during the Middle Devonian, the persistence of hallmark Malvinoxhosan taxa until the late Givetian suggests that endemic nature of the fauna had not totally vanished.

CONCLUSIONS

The Chavela Member of the Chigua Formation in the Precordillera of the San Juan province of Argentina overlies the Ramadita Member. The ammonoid-bearing levels correspond to the uppermost interval of the entire stratigraphic succession.

The taxonomic reinterpretation made herein implies that the species *Tornoceras baldisi* (Leanza, 1968) actually belongs to the genus *Epitornoceras.* This is the first South American record of this genus, which otherwise is recorded in North America, North Africa and Europe.

According to the stratigraphic range of the other *Epitornoceras* species (*E. mithracoides*, *E. peracutum*, *E. transmediterraneum* and *E. dennisoni*), we conclude that the uppermost levels of the Chavela Member of the Chigua Formation are late Givetian.

The Chigua Formation in Argentina would be younger than the Belén Formation in Bolivia, based on the occurrence of the ammonoid *Mimotornoceras* that indicates an Eifelian age.

The transition from the sand-rich Ramadita Member to the fine-shale Chavela Member most probably reflects the Geneseo transgression (also known as the IIa-Gen transgression), which is a major eustatic event otherwise recognized in paleotropical regions.

Epitornoceras is a cosmopolitan genus, which diversified after the Taghanic biocrisis of the late middle Givetian, according to Appalachian, Moroccan and European records. Its presence in southernmost western Gondwana suggests immigration from tropical regions to the cold Malvinoxhosan Realm during the late Givetian.

In spite of the record of cosmopolitan ammonoids in the Argentine Precordillera, the co-occurring trilobite family Calmoniidae along with additional endemic genera like *Belenopyge,* support that the Malvinoxhosan (Malvinokaffric) realm is still identifiable during the late Givetian in southernmost western Gondwana as a major biogeographic unit, on the basis of their typical diagnostic elements.

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