C. R. Palevol 14 (2015) 85–93

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General palaeontology, systematics and evolution (Invertebrate palaeontology)

Chronostratigraphy and significance of the Rugosa Group (*Cruziana*, trace fossil) in the Ordovician strata of the South American Central Andean Basin

La chronostratigraphie et l'importance du groupe Rugosa (ichnofossiles) dans l'Ordovicien du bassin des Andes centrales d'Amérique du Sud

Guillermo Aceñolaza[a,*], Susana Heredia[b], Josefina Carlorosi[a]

[a] *INSUGEO – CONICET, Facultad de Ciencias Naturales e I.M.L., Universidad Nacional de Tucumán, Miguel Lillo 205, 4000 Tucumán, Argentina*
[b] *CONICET - Instituto de Investigaciones Mineras, Universidad Nacional de San Juan, Libertador y Urquiza, 5400 San Juan, Argentina*

ARTICLE INFO

Article history:
Received 30 May 2014
Accepted after revision 9 October 2014
Available online 14 January 2015

Handled by Annalisa Ferretti

Keywords:
Trace fossils
Cruziana
Chronostratigraphy
South America

ABSTRACT

Although most trace fossils display long temporal ranges, certain forms as the Paleozoic mostly trilobite trace *Cruziana* have particular biostratigraphic significance. The evolution and replacement of trilobite families during the Paleozoic are reflected by the morphological characteristics of trace fossils that have contributed to interpret ages in the "non-fossiliferous" shallow marine Gondwanan realm. The "*Cruziana* stratigraphy" concept is based on this scheme, where different sets of traces replace each other on the stratigraphical record. The *Cruziana rugosa* Group is part of this scheme, and has been classically mis-referred as an exclusively Lower Ordovician element in the Central Andean Basin of South America. This contribution reevaluates the presence of the *C. rugosa* Group in the Lower to Middle Ordovician strata of the Cordillera Oriental and Subandean ranges of Argentina and in the Lower to Upper Ordovician of the Cordillera Oriental and Subandean ranges of Bolivia, and highlights its original distribution on its type area. The current paper displays a biostratigraphically-supported analysis of its record, also contributing with little known data from the northern sector of the continent, in the Colombian Andes.

Mots clés :
Ichnofossiles
Cruziana
Chronostratigraphie
Amérique du Sud

RÉSUMÉ

Bien que la plupart des ichnofossiles correspondent à de longues tranches de temps, certaines formes, telles l'ichnofossile *Cruziana*, le plus souvent paléozoïque, ont une signification biostratigraphique particulière. L'évolution et le remplacement de familles de trilobites au cours du Paléozoïque se reflètent dans les caractéristiques morphologiques des ichnofossiles, qui ont contribué à une interprétation des âges dans le domaine gondwanien « non fossilifère » de mer peu profonde. Le concept de « stratigraphie *Cruziana* » est basé sur le schéma selon lequel différentes séries de traces se remplacent l'une l'autre dans l'enregistrement stratigraphique. Le groupe *Cruziana rugosa* fait partie de ce schéma et a été classiquement assigné, de manière erronée, à un élément exclusivement Ordovicien inférieur du Bassin andin central d'Amérique du Sud. Cet article réévalue la présence du groupe *Cruziana rugosa* dans de

* Corresponding author.
E-mail addresses: gfacenolaza@gmail.com, insugeohm@tucbbs.com.ar (G. Aceñolaza).

http://dx.doi.org/10.1016/j.crpv.2014.10.003
1631-0683/

les strates l'Ordovicien inférieur à moyen de la Cordillère orientale et des chaînes subandines d'Argentine et dans les chaînes de la Cordillère orientale et des chaînes sub-andines de Bolivie, en mettant en évidence sa distribution originelle dans cette zone type. L'article fournit une analyse corroborée biostratigraphiquement de son enregistrement et contribue à une meilleure connaissance du secteur nord du continent Sud-Américain, dans les Andes colombiennes.

1. Introduction

During the last 60 years, several studies have stressed the significance of the trace fossil distribution in the geological record (Alpert, 1977; Lucas, 2007; Narbonne et al., 1987; Seilacher, 1956 among others), with some pioneer works dating back to the 19th century like the French and Portuguese schools with d'Orbigny (1839, 1842) and Delgado (1885, 1887, 1908). In the last 20 years, their importance was renewed as chronostratigraphic tools taking into account their significance within the evolutionary history of biota (Miller, 2007; Seilacher, 2007, both with references). As expected, living organisms display evolutionary patterns that are reflected in their traces left on the sediments within their environmental settings (Crimes, 1970; Seilacher, 1970, 2007).

Among the different fossils, *Cruziana* is one of the most widely known trace fossils that represents mostly the furrowing activity of trilobites on the Paleozoic shallow marine sandstones (Crimes, 1975; Crimes and Marcos, 1976; Goldring, 1984; Osgood, 1970; Seilacher, 1985). These, were dug at the water-sediment interface and also representing true burrows that were casted on sandstone soles (Seilacher, 1970; Whittington, 1997). *Cruziana* has been used for facies analysis on different sequences worldwide, and particularly has proved to work as a reliable chronostratigraphical element for the "non-fossiliferous" sandstone facies in northern Gondwana (Crimes, 1969, 1970; Seilacher, 1969, 1970, 1994, 2007), and has been proposed as a useful tool in paleogeographical reconstructions (MacNaughton, 2007; Seilacher, 2005).

The ichnogenus *Cruziana* displays over 30 ichnospecies separated by morphology and distribution patterns, generating a "*Cruziana* stratigraphy", with a scheme where several forms replace each other along the chronostratigraphy of 200 million years (Cambrian–Lower Carboniferous; Seilacher, 1970). In Seilacher's original paper, ten different sets of *Cruziana* were identified: the Fasciculata Group (*C. cantabrica* and *C. fasciculata*); the Dispar Group (*C. dispar*, *C. barbata* and *C. grenvillensis*); the Semiplicata Group (*C. arizonensis*, *C. semiplicata*, *C. jenningsi* and *C. carinata*); the Rugosa Group (*C. rugosa*, *C. furcifera* and *C. goldfussi*); the Imbricata Group (*C. imbricata*); the Petraea Group (*C. omanica*, *C. petraea, C. acacensis* and *C. ancora*); the Almadenensis Group (*C. almadenensis, C. flammosa, C. perucca, C. lineata* and *C. pedroana*); the Quadrata Group (*C. cuadrata*, *C. lobosa* and *C.* cf. *cuadrata*); the Pudica Group (*C. pudica*, *C. rhenana* and *C. uniloba*) and the Carleyi Group (*C. polonica*, *C. carleyi*, and *C. dilatata*).

Evolution and behavior of fauna are important elements that could be better explained when interpreting general trends on the successive replacement of trace fossils forms. Even though there are some discussions (Borghi et al., 2003), it is particularly notorious that other traces follow a comparable pattern of evolution supporting the idea of a partial stratigraphical usefulness (e.g., *Arthrophycus*, *Daedalus* and "*Phycodes*"; Seilacher, 2000, 2007).

The current analysis focuses on the South American material of the Rugosa Group, which has been classically referred as characteristic of the Lower Ordovician strata (Seilacher, 2007).

This usefulness of *Cruziana* as a chronostratigraphical element has been always referred to Gondwana and Peri-Gondwana, where recent data highlights a needed analysis of the original distribution of ichnospecies and localities, suggesting a re-evaluation of the scheme for the Ordovician and the western margin of Gondwana (Egenhoff et al., 2007). In addition, as stated by Seilacher (1994), little has been done on the biostratigraphical distribution of *Cruziana* outside the supercontinent, and a great deal of information could be obtained by a detailed analysis of faunal provincialism at an ichnospecific level for testing paleocontinental reconstructions (Knaust, 2004).

The aim of this contribution is to reevaluate the stratigraphical distribution of the *C. rugosa* Group in its type region, the Central Andean Basin of South America, based on outstanding material from northwestern Argentina, the known bibliographical data of Bolivia and to recall the presence of some little known Colombian material. The data presented herein supports the original information given by d'Orbigny (1839, 1842), and provides noteworthy chronological information to discuss on a firm basis the application of the *Cruziana* stratigraphy concept in the western margin of Gondwana.

The range of *C. rugosa* from the most important localities in NW Argentina and Bolivia supports the correction of the biostratigraphical range of *C. rugosa* in the type area, based on outstanding preserved material and well-dated sections with abundant accompanying fauna.

2. The Rugosa Group in the Central Andean Basin

The Lower Paleozoic Central Andean Basin is developed on a large area covering southern Perú, and the Eastern Cordillera and Subandean areas of Bolivia and Argentina. It is lithologically represented by a highly fossiliferous succession of siliciclastic material dominated by sandstones and shales that has been considered as the most prominent Ordovician sequence worldwide, with over 10 km in

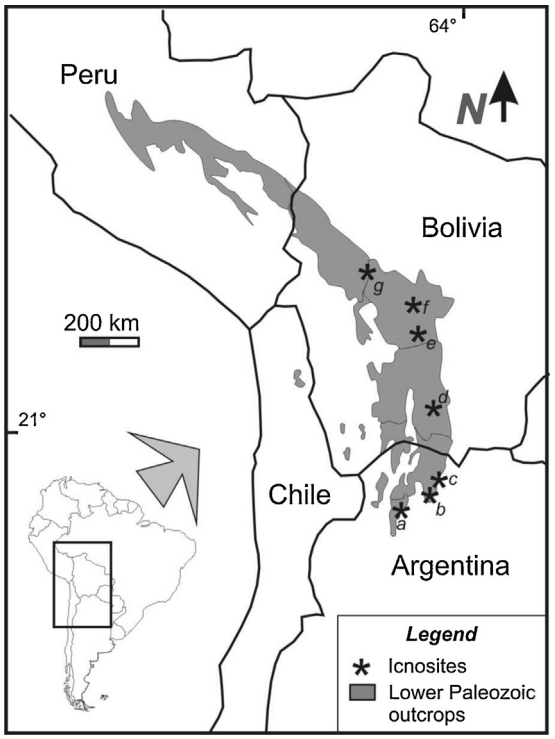

Fig. 1. Location map and geographical distribution of the Rugosa Group in the Central Andean Basin of South America. The gray areas represent Lower Paleozoic sequences. Ichnosites of the Rugosa Group in Argentina: a: Mojotoro Range; b: Los Colorados; c: Zenta Range; in Bolivia; d: Tarija; e: La Ciénaga; f: Tipa Jara; g: Liriuni.

Fig. 1. Carte de localisation et distribution géographique du Groupe Rugosa dans le Bassin andin central d'Amérique du Sud. Les zones en grisé représentent les séquences paléozoïques. Ichnosites du groupe Rugosa en Argentine : a : chaîne de Mojotoro ; b : Los Colorados ; c : chaîne de Zenta ; en Bolivie ; d : Tarija ; e : La Ciénaga ; f : Tipa Jara ; g : Liriuni.

thickness (Egenhoff, 2000; Erdtmann et al., 1995; Suárez-Soruco, 1992) (Fig. 1).

Shallow marine sequences characterize the whole region and were deposited on a general deepening westwards basin. This Ordovician basin was bounded by the Brazilian shield to the east and the Pampean shield to the southeast. Sequences have provided abundant trace fossils whose chronostratigraphical resolution was lacking the needed precision for an accurate international correlation. During the last 20 years an important amount of data has been put together and nowadays, a fairly acceptable general picture of the stratigraphy, fossils and ages is available (Aceñolaza, 2002; Benedetto, 2003; Egenhoff et al., 2004; Erdtmann et al., 1995; Gagnier et al., 1996; Suárez-Soruco, 2000).

Historically, the trace fossils played a prominent role in the early studies of the Cambro-Ordovician strata in South America. *Cruziana* was originally described by the French naturalist Alcide d'Orbigny in Bolivia with detailed descriptions and figures of two members of the Rugosa Group (d'Orbigny, 1842). *C. furcifera* and *C. rugosa* represent dominant forms in this group and were described and figured from the Upper Ordovician strata of the Anzaldo Formation at Liriuni, near Cochabamba, northern Bolivia (d'Orbigny, 1839, 1842). Later, abundant material was located from the Argentinian Cordillera Oriental, with a notorious lack of record in the northern part of the South American Basin (Aceñolaza and Aceñolaza, 2002 with references).

2.1. Localities and chronological aspects of the Rugosa Group in Bolivia

The widespread distributed sequences of shallow marine sandstones in the Eastern Cordillera of Bolivia were sedimented on a shoreface to offshore transitional environment setting, as a response to an early stage rift that evolved to a foreland successor basin (Egenhoff, 2003; Egenhoff et al., 1999; Erdtmann and Suárez-Soruco, 1999). As a tectonically ruled shallow sedimentary basin, a generally decreasing trend of age has been recognized from south to north (Egenhoff et al., 2007; Suárez-Soruco, 1976), with the common record of *Cruziana* in sandstones that represent the more suitable sedimentary facies (Fig. 1d–g).

In the southern Tarija Department (Fig. 1d), the Rugosa Group is well represented in the Rumi Orkho Formation, with the presence of *C. rugosa*, *C. furcifera*, *C. goldfussi* and *C. roualti* (Egenhoff et al., 2007). These are associated to the graptolites *Baltograptus* sp. cf. *B. deflexus* and *B. minutus*, that were included in the *B. minutus* zone of "mid-Arenig" (Egenhoff, 2000; Maletz et al., 1995) or Floian age, in the global standard stages for the Ordovician (Bergström et al., 2008; Cohen et al., 2014; Finney, 2005).

Northwards, a thick succession at La Ciénaga village (nearby Sucre city; Fig. 1e), displays the Capinota and Anzaldo formations with poorly preserved *Cruziana* of the Rugosa Group. Even though the lithological characters of these units, with sandstones, siltstones and mudstones, do not allow a fine preservation of trace fossils, the association of *Cruziana* to conodonts and trilobites provides a clear biostratigraphic framework for the whole sequence. At this locality, *C. furcifera* and *C. goldfussi* are associated to the trilobite *Neseuretus* in the Capinota Formation, suggesting for that interval a Middle Ordovician age. Egenhoff et al. (2007) recovered fragmented conodonts that were interpreted as *Erismodus* cf. *E. quadridactylus*, *Erismodus* sp., *Drepanoistodus*? sp. and *Semiacontiodus* sp. suggesting an Upper Ordovician (Sandbian) age for the Anzaldo Formation. Other age reference for the Anzaldo Formation is the association of graptolites to the ptetaspidomorph fish *Sacabambaspis janvieri*, suggesting a Darriwillian to Sandbian age for the unit (Davies et al., 2007; Suárez-Soruco, 2000; Toro et al., 1990).

A similar age range for the upper sector of the succession cropping out at Tipa Jara has been described by Egenhoff et al. (2007), where the Anzaldo Formation records *Cruziana* cf. *furcifera*, *C. goldfussi* and *C. rugosa* (Fig. 1f). Even though this locality did not provide chronologically important fossils, the overlying San Benito Formation bears Upper Ordovician chitinozoans and brachiopods (Egenhoff et al., 2007; Suárez-Soruco and Benedetto, 1996).

The northern sector of the Bolivian Cordillera Oriental is the type area where d'Orbigny (1842) defined *Cruziana.* There, the association of *C. furcifera*, *C. goldfussi* and *C. rugosa* is common in the upper part of the Anzaldo Formation (Branisa, 1965; d'Orbigny, 1842; Egenhoff et al.,

2007; Steinmann and Hoek, 1912). The suitable lithological features of the upper sector of the unit, dominated by sandstones, has provided outstanding material in association to acritarchs and brachiopods (Gagnier et al., 1996), restricting the age of the trace fossil levels to the late Middle Ordovician to Upper Ordovician (Darriwillian to Sandbian–Katian?) (Fig. 1g).

2.2. Localities and chronological aspects of the Rugosa Group in NW Argentina

Cruziana is a common trace fossil in the Cambro-Ordovician strata of Northwest Argentina (Aceñolaza and Aceñolaza, 2002). Particularly the Rugosa Group has been found in several places, with four main localities recording outstanding traces in Cordillera Oriental and Subandean Ranges of the northern provinces of Salta and Jujuy (Figs. 1 and 2).

Several localities where *Cruziana* was found were searched for conodonts with diverse results. The main sites with conodont data are the Zenta Range and Los Colorados in Jujuy province and the Mojotoro Range in Salta province (Fig. 1a–c). In the first area the trace fossils come from the upper sector of the Ordovician sequence of the Sierra de Zenta in Jujuy province (Fig. 1c and Fig. 2A), and has been taxonomically assigned to the Rugosa Group of Seilacher (1970). The fossiliferous localities of Abra Llana and Laguna Verde display an impressive sequence with well-preserved *Cruziana* in western Gondwana due to the continuity of strata and the abundance and preservation of traces (Aceñolaza and Milana, 2005; Heredia and Aceñolaza, 2005; Fig. 2). Interbedded coquinoid carbonate lenses provided a conodont association integrated by *Trapezognathus diprion* (Lindström), *Erraticodon patu* Cooper and *Baltoniodus triangularis* Lindström among others (Fig. 3A–D), identifying the *B. triangularis* Zone (Carlorosi and Heredia, 2013). This biozone is also recorded in Baltica and South China, suggesting an early Middle Ordovician age (lower Dapingian, Bagnoli and Stouge, 1997; Li et al., 2010). On a recent paper, Voldman et al. (2013: Figs. 2–6, 8, 15, 16, 17, 18) figure well-preserved specimens of *B. triangularis* from the same locality. In Laguna Verde locality, the whole sequence is unconformably overlain by the reddish and whitish sandstones of the Hirnantian Caspalá Formation (Aceñolaza and Milana, 2005; Aráoz et al., 2008), where large sized *C. rugosa* are found associated to *C. furcifera*, *C. goldfussi*, and *C. gutii* (Fig. 2). On the other hand, the strata cropping out westwards at Los Colorados (Jujuy) has provided well-preserved *C. rugosa* material from the Alto del Cóndor Formation (in both members of this unit) (Fig. 1b). At this locality, traces are associated with Dapingian (Middle Ordovician) conodonts of the *B. triangularis* Zone (Fig. 3E–J) (Carlorosi, 2012; Carlorosi et al., 2013). *C. rugosa* is associated with *C. furcifera* and *C. yini*, the latter one being a peculiar Lower Ordovician Chinese form that has been recorded in the northern and western margins of Gondwana (Aceñolaza et al., 2008). The association of conodonts and trace fossils of the Rugosa Group are congruent with the faunal province of the South of China showing a great affinity with this Peri-Gondwanan region (Carlorosi et al., 2013; Li et al., 2010; Wang et al., 2009).

Southwards in the Mojotoro Range of Salta province (Fig. 1a), Ordovician sandstones and siltstones with *C. rugosa* are also well known (Aceñolaza and Aceñolaza, 2002; Borrello, 1966). The Mojotoro Formation is a poorly dated unit bearing *Cruziana* that paraconformably underlies the Santa Gertrudis Formation (Moya, 1998, 2008). This last unit has provided a well-preserved early Middle Ordovician conodont fauna (Fig. 3K–R) (Carlorosi et al., 2011), and has been compared to the Shallow-Sea Realm of the Temperate–Cold Domain (Zhen and Percival, 2003), with typical forms such as *B. triangularis* (Lindström), *T. quadrangulum* Lindström and *E. patu* Cooper. The *C. rugosa* Group at the Mojotoro range is represented by the homonymous form, *C. furcifera, C. goldfussi* and *C. problematica* in soles of quartz-rich sandstone layers. The *Cruziana* association age constraints match with the conodont association suggesting a Middle Ordovician age.

As a general setting, sequences represent shallow water on a tide dominated, marine platform—subtidal to intertidal environments—, with some sectors denoting subaerial exposure that supports the partial erosion of this sector of the Andean basin trough the Lower to Middle Ordovician.

2.3. Other occurrences of Cruziana in South America

The record of *Cruziana* in the northern part of South America is very rare and little is known from its occurrence. Particularly *C. furcifera* has been mentioned several times in the region (Bogotá, 1980, 1983a; Herrera Gálvez and Velásquez, 1978; Therý, 1982; Therý et al., 1986), but has been figured only once from the Chiribiquete Range in the Amazonic region of Colombia (Bogotá, 1983b).

The traces were located on a 210-m-thick section dominated by reddish sandstones in the middle part of the Araracuara Formation cropping out in the Tauraré River, 150 km northwest of Araracuara. A varied acritarch association supports a Lower Ordovician age for the formation (Therý, 1982; Therý et al., 1986), so the lack of precise and detailed data of associated forms of *Cruziana* for this locality precludes a clear analysis on the chronological aspects of this occurrence. This data of *C. furcifera* does not support a clear presence of the Rugosa Group in this part of South America, but deserves to be mentioned because it is the only data of *Cruziana* in Colombia, and could represent the presence of the group in the area. Additional material and the revision of accompanying fauna are needed in order to fully support this suggestion.

The material from Colombia is represented by the unique sample known, actually missing from the paleontological collections of the INGEOMINAS and the Universidad Nacional at Bogotá (personal communication of J.C. Gutiérrez-Marco, Madrid, who searched after the sample in Colombia) (Bogotá, 1983b).

3. General chronostratigraphical considerations

Egenhoff et al. (2007) concluded that *C. furcifera*, *C. goldfussi* and *C. rugosa* occur in the Lower to Upper Ordovician strata of Bolivia, also pointing out that the

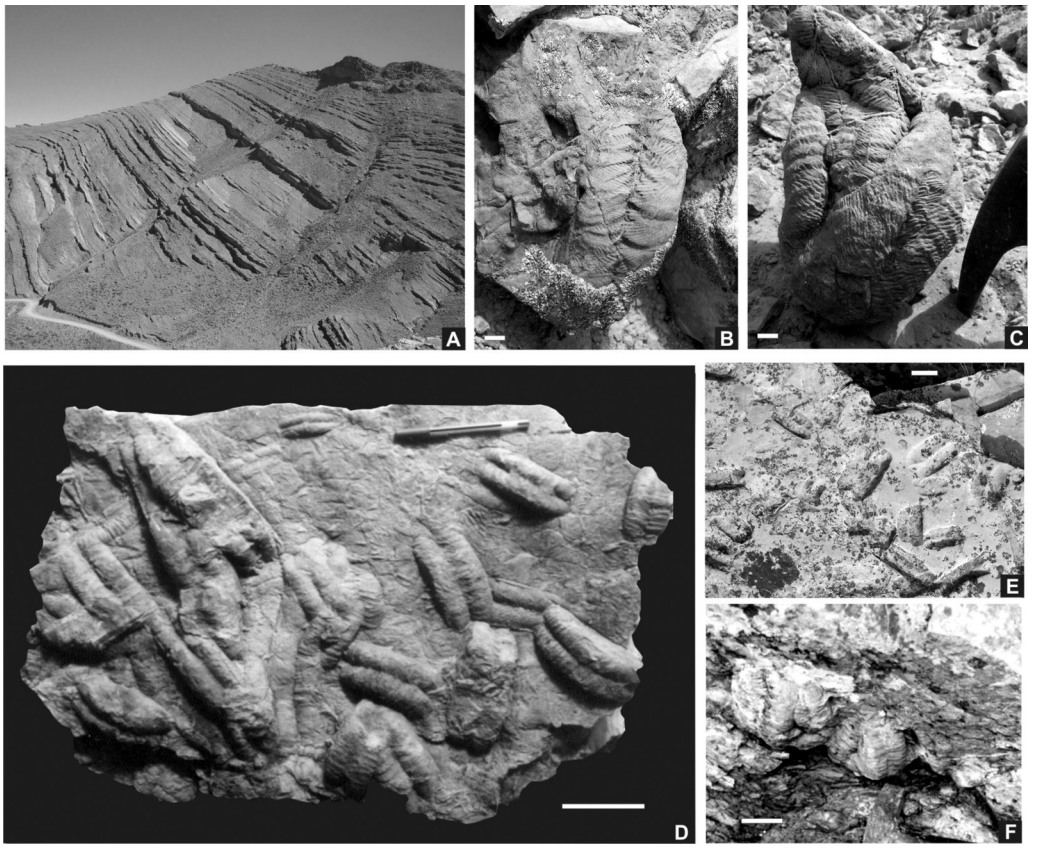

Fig. 2. Lower and Middle Ordovician strata bearing *Cruziana* at Zenta Range (Salta and Jujuy provinces of NW Argentina). A. General view of strata at Abra Llana–Laguna Verde denoting shoaling bars on a shallow water on shore depositional setting. B–F. Association of *Cruziana* soles of sandstone beds (scale bar = 10 cm). B. Well-defined C*ruziana rugosa* from Zenta displaying typical corrugation of lobes (scale bar = 1 cm.). C. Compound structures represented by overimposed traces assigned to C. *rugosa* from Los Colorados (scale bar = 1 cm). D. *C. rugosa*, *C. furcifera* and *C. isp*. in the sole of a 30-cm-thick sandstone level (scale bar = 10 cm.). E. Uncommon preservation of *Cruziana* (dominated by *C. rugosa* and *C. furcifera*) as concave epirelief on the upper surface of sandstones. Traces display a bimodal orientation caused by current direction (scale bar = 5 cm). F. *In situ* material of *C. rugosa* with deep intra-stratal development and well-defined crests defining the type ichnospecies (scale bar = 10 cm.). Figured material is 5 to 10 cm wide, and traces reach down into strata up to 11 cm deep.

Fig. 2. Strates de l'Ordovicien inférieur et moyen comportant *Cruziana* dans la chaîne de Zenta (provinces de Salta et de Jujuy au Nord-Ouest de l'Argentine). A. Vue générale des strates à Abra Llana–Lagune Verde, représentant des barres de haut-fond dans un site de dépôt *on shore* de faible profondeur d'eau. B–F. Association de semelles de lits gréseux à *Cruziana*. B. *Cruziana rugosa* bien définie, en provenance de Zenta, montrant des lobes gaufrés (barre d'échelle = 1 cm). Structures composites représentées par des traces superposées, attribuées à *C. rugosa*, en provenance de Los Colorados (barre d'échelle = 1 cm). *C. rugosa*, *C. furcifera* et *C. isp* dans la semelle d'un épais niveau gréseux (30 cm d'épaisseur) (barre d'échelle = 10 cm). E. Préservation exceptionnelle de *Cruziana* (dominée par *C. rugosa* et *C. furcifera*) sous forme d'un épirelief concave à la surface de grès. Les traces montrent une orientation bimodale due à l'orientation du courant (barre d'échelle = 5 cm). F. Matériau in situ à *C. rugosa*, avec profond développement intra-strate et crêtes bien marquées, définissant le type d'ichnofossile (barre d'échelle = 10 cm). Matériau figuré, in situ, de 5 à 10 cm de large, et traces s'enfonçant dans les strates jusqu'à une profondeur de 11 cm.

Rugosa Group presents a diachronous distribution for the different sectors of the basin. Southwards, in the Sella region (near Tarija) they appear associated with graptolites of Floian age, while in La Ciénaga (Capinota Fm) the Rugosa Group is accompanied with the trilobite *Neseuretus* aff. *sanlucasensis* suggesting a "late Arenig to Llanvirn age" (Darriwillian) but the trilobite does have a doubtful taxonomical assignation. Towards the top of the Anzaldo Formation in La Ciénaga locality, the *Cruziana* association is recorded with a conodont fauna interpreted by Lehnert (in Egenhoff et al., 2007) as *Erismodus* cf. *E. quadridactylus*, *Drepanoistodus* sp. and *Semiacontiodus* sp. pointing out a Sandbian age ("Caradocian"). An analysis of the conodonts shown in the aforementioned paper suggests that the elements assigned to *Erismodus* cf. *quadridactylus* actually belong to *E. patu*. In Egenhoff et al. (2007) the Sb element assigned to *Erismodus* cf. *quadridactylus* ("fig. 8g") resembles figures I, Q and R of our material (Plate 3) which represent an Sb and Sd elements of *E. patu* from Los Colorados region and the Mojotoro Range (Santa Gertrudis Formation). In addition the figures c, d, e and f of Egenhoff et al., 2007 (Plate 8) represent fragmented denticles which could also be attributed to *E. patu*.

The *Erismodus* elements from the Anzaldo Fm. were compared with those of the Santa Gertrudis Fm. (Mojotoro Range), Alto del Cóndor Fm. (Los Colorados region) and Santa Victoria Group (at Zenta Range) in the Argentinian Eastern Cordillera (Albanesi and Astini, 2002; Albanesi et al., 2007; Moya et al., 2003; Sarmiento and Rao, 1987). Recent studies on the conodonts of these units (Carlorosi

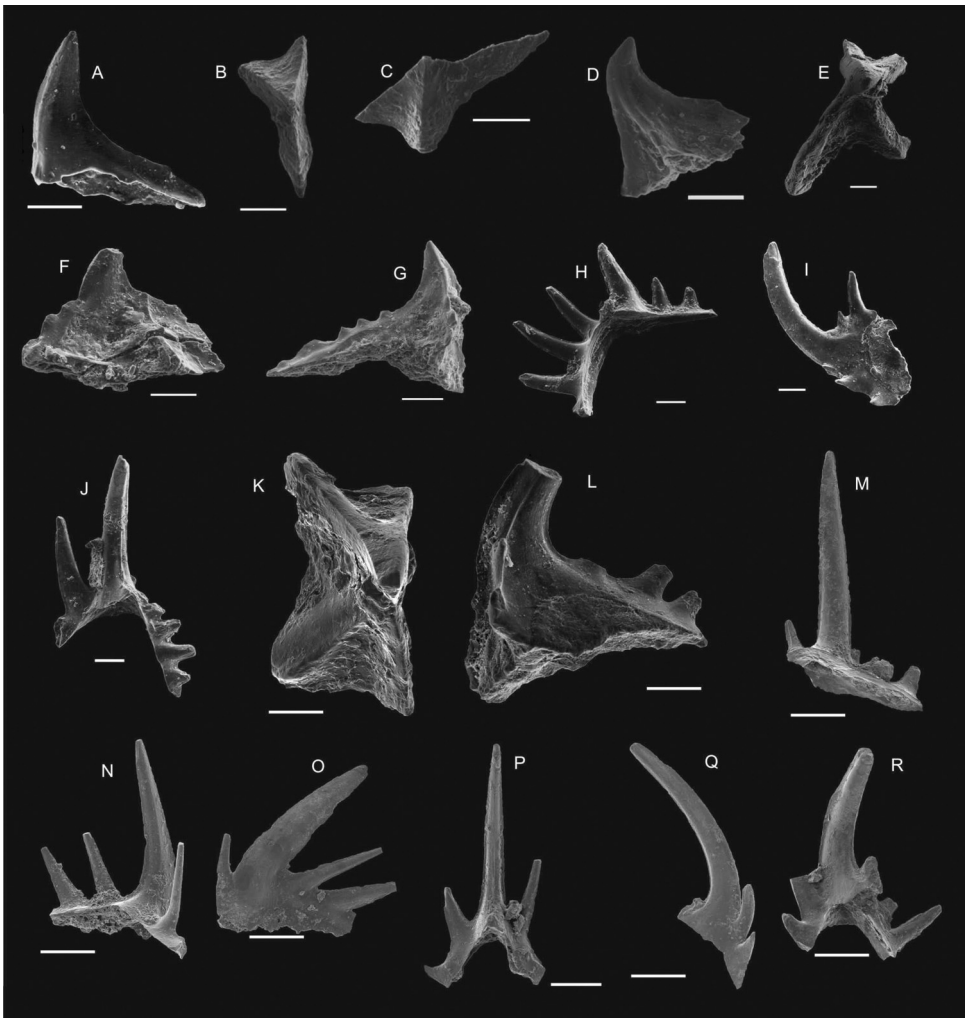

Fig. 3. Scanning electron microscope microphotograph of a late Lower to early Middle Ordovician Conodont association from Zenta Range, Los Colorados region and Mojotoro Range (NW Argentina). All figured elements belong to Dapingian beds of the Eastern Cordillera. The bar indicates 0.1 mm. A–D. Conodonts from Laguna Verde section, Zenta Range. A. *Baltoniodus triangularis*, Lindström, P element, antero-lateral view, CML-C 3002(1). B–C. *Trapezognathus diprion* (Lindström), Pa element, upper and antero-lateral views, CML-C 3001(1, 3). E–J. Conodonts from the Alto del Cóndor Formation, Los Colorados region. E–G. *B. triangularis* Lindström. E. Pa element, upper view, CML-C 5078(1). F–G. Pb elements, postero-lateral views, CML-C 5078(3, 15). H–J. *Erraticodon patu* Cooper. H. Pa element, posterior view, CML-C 5084(1). I. Sb element, lateral view, CML-C 5078(119). J. Sd element, postero-lateral view, CML-C 5078(320). K–R. Conodonts from Santa Gertrudis Formation, Mojotoro Range. K–L. *B. triangularis* Lindström. K. Pa element, upper view, CML-C 7008(1), L. Pb element, postero-lateral view, CML-C 7009(1). M–R. *E. patu* Cooper. M. Pa element, posterior view, CML-C 7001(3). N. Pb element, postero-lateral view, CML-C 7002(1). O. M element, antero-lateral view, CML-C 7003(1). P. Sa element, posterior view, CML-C 7004(1). Q. Sb element, lateral view, CML-C 7005(1). R. Sd element, posterior view, CML-C 7007(2).

Fig. 3. Microphotographie au microscope électronique à balayage d'une association de conodontes de l'Ordovicien fini-inférieur à moyen précoce, en provenance de la chaîne de Zenta, de la région de Los Colorados et de la chaîne de Mojotoro (Nord-Ouest de l'Argentine). Tous les éléments figurés appartiennent aux niveaux dapingiens de la Cordillière orientale. La barre d'échelle indique 0,1 mm. A–D. Conodontes de la coupe de Laguina Verde, dans la chaîne de Zenta. A. *Baltoniodus triangularis*, Lindström, élément P, vue antéro-latérale, CML-C 3002(1). B–C. *Trapezognathus diprion* (Lindström), élément Pa, vues du dessus et antéro-latérale, CML-C 3001(1, 3). E–J. Conodontes de la formation Alto de Condor, région de Los Colorados. E–G. *B. triangularis* Lindström. E. Élément Pa, vue du dessus, CML-C 5078(1). F–G. Éléments Pb, vues postéro-latérales, CML-C 5078(3, 15). H–J. *Erraticodon patu* Cooper. H. Élément Pa, vue postérieure, CML-C 5084(1). I. Élément Sb, vue latérale, CML-C 5078(119). J. Élément Sd, vue postéro-latérale, CML-C 5078(320). K–R. Conodontes de la formation Santa Gertrudis, chaîne de Mojotoro. K–L. *B. triangularis* Lindström. K. Élément Pa, vue du dessus, CML-C 7008(1). L. Élément Pb, vue postéro-latérale, CML-C 5009(1). M–R. *E. patu* Cooper. M. Élément Pa, vue postérieure, CML-C 7001(3). N. Élément Pb, vue postéro-latérale, CML-C 7002(1). O. Élément M, vue antéro-latérale, CML-C 7003(1). P. Élément Sa, vue postérieure, CML-C 7004(1). Q. Élément Sb, vue latérale, CML-C 7005(1). R. Élément Sd, vue postérieure, CML-C 7007(2).

et al., 2011; Heredia and Aceñolaza, 2005; Heredia et al., 2013, and the current paper) record *E. patu* Cooper, *Erraticodon* sp., *Baltoniodus* cf. *B. triangularis* and *B. triangularis*, among others restricting the age of the Last to Late Floian and early Dapingian (Lower–Middle Ordovician).

Egenhoff et al. (2007) pointed out that *Cruziana* in the Anzaldo Formation in Tipa Jara and Liriuni localities are constrained by the fossil record of brachiopods and chitinozoans in the overlying San Benito Formation, assigning this unit to the Upper Ordovician.

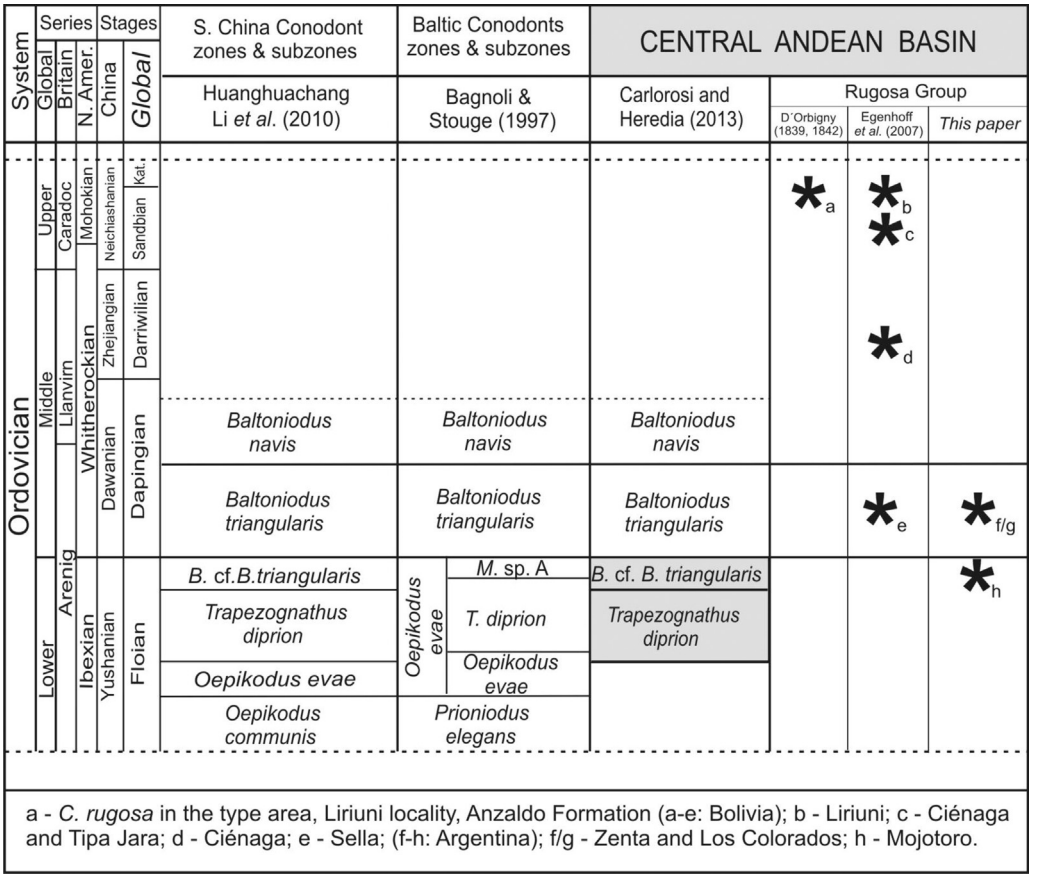

Fig. 4. Biostratigraphy of the Rugosa Group from selected localities in the Lower Paleozoic strata of the Central Andean Basin of South America. The type locality (d'Orbigny, 1839, 1842) and Egenhoff's et al. (2007) data are considered from Bolivia, incorporating the conodont-referenced localities in NW Argentina.

Fig. 4. Biostratigraphie du groupe Rugosa en provenance de localités sélectionnées dans les strates du Paléozoïque inférieur du bassin Andin central d'Amérique du Sud. Les données de la localité type (d'Orbigny, 1839, 1842) et d'Egenhoff et al. (2007) sont considérées comme provenant de Bolivie, incorporant les localités répertoriées pour les conodontes dans le Nord-Ouest de l'Argentine.

The presence of the Rugosa Group in the Argentinian Eastern Cordillera is accompanied by key conodonts that record Late Floian and Early Dapingian ages. This association is constituted mainly by *T. diprion*, *E. patu*, *Baltoniodus* cf. *B. triangularis* and *B. triangularis*. This conodont fauna provides complementary data to the chronological distribution of the *C. rugosa* Group in northern Argentina, and supports the idea of a relative chronostratigraphical utility due to its wide biozonation that includes a time span from the Lower Ordovician (NW Argentina) and reaching up to the Upper Ordovician (N Bolivia) in the Paleozoic Central Andean Basin (Fig. 4).

4. Final considerations

The behavior and evolution of biota through time is properly reflected by the trace fossil record, allowing the identification of certain chronostratigraphical useful ichnofamilies (Seilacher, 2000, 2007). It is also important to note that morphological patterns of fossils display evolutionary modifications along geologic times; meanwhile the trace fossils display wider temporal ranges.

Considering that Rugosa Group members have been classically referred to the Lower Ordovician strata in South America, the presence of the different forms of the Group in the Middle and Upper Ordovician of Argentina and Bolivia highlights the need of a detailed analysis of earlier literature (Branisa, 1965; d'Orbigny, 1839, 1842; Moya, 1998; Steinmann and Hoek, 1912). Even though these findings seem to be new, the type material described by Alcyde d'Orbigny (1842) from the Anzaldo Formation of northern Bolivia has always belonged to the Upper Ordovician aged sequences (Fig. 4).

The presence of archetypical "Lower Ordovician" forms associated with diagnostic Middle and Upper Ordovician conodonts represents the clear extension of the Rugosa Group into the Middle and Upper Ordovician of the Central Andean Basin. As early stated by Aceñolaza and Heredia (2008), the Rugosa Group cannot be regarded as a trustworthy indicator of Lower Ordovician strata, supporting the ideas of Egenhoff et al. (2007).

The presence of the Rugosa Group in the Central Andean Basin is restricted to Argentina and Bolivia, with unknown reliable records in the northern sector of the basin. The

little known and single record of *C. furcifera* from the "Arenigian" Araracuara Formation of Colombia requires additional material in order to interpret it as a Colombian record of a member of the Rugosa Group.

Acknowledgements

Authors acknowledge the insightful revision of Editor and reviewers. María Vergel, Franco Tortello, Juan P. Milana and Lucía Aráoz contributed with enlightening discussions in the field. Financial support was provided by the Universidad Nacional de Tucumán and the CONICET (Argentina).

References

Aceñolaza, F.G., 2002. Aspects of the Ordovician System in Argentina. INSUGEO, Ser. Corr. Geol. 16 (368 p.).

Aceñolaza, G.F., Aceñolaza, F.G., 2002. Ordovician trace fossils of Argentina. In: Aceñolaza, F.G. (Ed.), Aspects of the Ordovician System in Argentina. INSUGEO, Ser. Corr. Geol. 16, 177–194.

Aceñolaza, G.F., Heredia, S., 2008. The status of the *Cruziana* (Trilobite trace fossil) stratigraphy in western Gondwana: the mixing of Lower and Upper Ordovician elements in the Central Andean Basin of South America. In: Rábano, I., Gonzalo, R., García-Bellido, D. (Eds.), Advances in Trilobite Research. Cuad. Mus. Geomin. 9, 13–18.

Aceñolaza, G.F., Milana, J.P., 2005. Remarkable *Cruziana* beds in the Lower Ordovician of the Cordillera Oriental, NW Argentina. Ameghiniana 42 (3), 633–637.

Aceñolaza, G.F., Sá, A.A., Gutiérrez-Marco, J.C., 2008. *Cruziana yini* Yang, a peri-Gondwanan trilobite trace with new records in the Ordovician of South America and Iberia. In: Rábano, I., Gonzalo, R., García-Bellido, D. (Eds.), Advances in Trilobite Research. Cuad. Mus. Geomin. 9, 19–26.

Albanesi, G., Astini, R., 2002. Faunas de conodontes y *Sacabambaspis janvieri* (Vertebrata) en el Ordovícico Medio de la Cordillera Oriental argentina: implicancias estratigráficas y paleobiogeográficas. Octavo Congr. Argent. Paleontol. Bioestratigr. 1, 17.

Albanesi, G., Monaldi, C., Ortega, G., Trotter, J., 2007. The Capillas Formation (Late Darriwillian) of Subandean Ranges, northwestern Argentina: Age, correlation and environmental contraints. Acta Palaeontol. Sinica 46, 9–15.

Alpert, S.P., 1977. Trace fossils and the basal Cambrian boundary. In: Crimes, T.P., Harper, J.C., (Eds.), Trace Fossils 2. Geol. J., Spec. Issue 9, 1–8.

Aráoz, L., Aceñolaza, G., Vergel, M.M., Heredia, S., Tortello, M.F., Milana, J.P., 2008. El Ordovícico del sector central de la Sierra de Zenta (Sistema Interandino de las Provincias de Jujuy y Salta): Cronoestratigrafía y correlación. XVII Congr. Geol. Arg., Jujuy, 1., pp. 339–340.

Bagnoli, G., Stouge, S., 1997. Lower Ordovician, Billingenian–Kunda conodont zonation and provinces based on sections from Horns Udde, North Öland, Sweden. Boll. Soc. Paleont. Ital. 35, 109–163.

Benedetto, J.L. (Ed.), 2003. Ordovician fossils of Argentina. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba (561 p.).

Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C., Dronov, A., 2008. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and $\delta^{13}C$ chemostratigraphy. Lethaia 41, 97–107.

Bogotá, R.J., 1980. Informe preliminar geológico, Secciones 7, 11, 12, 13, 25, 26, LP13. Informe Interno, Cogema, Bogotá (63 p.).

Bogotá, R.J., 1983a. Estratigrafía del Paleozoico Inferior en el área amazónica de Colombia. Geol. Norandina 6, 29–38.

Bogotá, R.J., 1983b. La región de la Amazonia Colombiana. II Reunión del Grupo de Trabajo Internacional IGCP 192. INSUGEO, Ser. Correl. Geol. 1, 119–120.

Borghi, L., Fernández, A., Netto de Carvalho, C., 2003. Diferenciaçao das icnoespécies e variantes de "*Arthrophycus*" e sua utilizaçao problemática em icnoestratigrafia. Rev. Esp. Paleontol. 18, 221–228.

Borrello, A., 1966. Las facies de *Cruziana* en el Ordovícico del Norte Argentino. Ameghiniana 4, 185–188.

Branisa, L., 1965. Los fósiles guías de Bolivia. I Paleozoico. Serv. Geol. Bolivia, Bol. 6, 1–282.

Carlorosi, J.M.T., (PhD Thesis) 2012. Bioestratigrafía y taxonomía de conodontes de la Formación Sepulturas (Ordovícico), Cordillera Oriental de Jujuy. Universidad Nacional de Tucumán, Tucumán (310 p. [unpublished]).

Carlorosi, J., Heredia, S., 2013. The Ordovician conodont Trapezognathus Lindström, 1955 in the Andean Basin, Argentina. Neues Jahrb. Geol. P-A 267, 309–321.

Carlorosi, J., Heredia, S., Aceñolaza, G., 2013. Middle Ordovician (Early Dapingian) conodonts in the Central Andean Basin of NW Argentina. Alcheringa 37, 1–13.

Carlorosi, J., Heredia, S., Sarmiento, G., Moya, M.C., 2011. Reworked conodonts in the Upper Ordovician Santa Gertrudis Formation (Salta, Argentina). In: Gutiérrez-Marco, J.C, Rábano, I. and García-Bellido, D. (Eds.), Ordovician of the World. Cuad. Mus. Geominero 14, 83–88.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.X., 2014. The ICS International chronostratigraphical chart. Episodes 36, 199–204.

Crimes, T.P., 1969. Trace fossils from the Cambro-Ordovician rocks of North Wales and their stratigraphic significance. Geol. J. 6, 333–338.

Crimes, T.P., 1970. The significance of trace fossils in sedimentology, stratigraphy and palaeoecology with examples from Lower Palaeozoic strata. In: Crimes, T.P., Harper, J.C. (Eds.), Trace Fossils. Geol. J., Spec. Issue 3, 101–126.

Crimes, T.P., 1975. Trilobite traces from the Lower Tremadocian of Tortworth. Geol. Mag. 112, 33–46.

Crimes, T.P., Marcos, A., 1976. Trilobite traces and the age of the lowest part of the Ordovician reference section for NW Spain. Geol. Mag. 113, 349–356.

d'Orbigny, A., 1839. Voyage dans l'Amérique méridionale, Tome 8 (Atlas). Pitois-Levrault et Levrault, Paris and Strasbourg (no pagination).

d'Orbigny, A., 1842. Voyage dans l'Amérique méridionale. In: Paléontologie, Tome Troisième, 4 Partie. Pitois-Levrault et Levrault, Paris and Strasbourg (188 p.).

Davies, N., Sansom, I., Albanesi, G., Céspedes, R., 2007. Ichnology, palaeoecology and taphonomy of a Gondwanan early vertebrate habitat: insights from the Ordovician Anzaldo Formation, Bolivia. Palaeogr., Palaeoclimatol., Palaeoecol. 249, 18–35.

Delgado, J.F.N., 1885. Estudo sobre os bilobites e outros fosseis das quartzites da base do Systema Silurico de Portugal. Mem. Sec. Trab. Geol. Portugal, Lisboa (111 p.).

Delgado, J.F.N., 1887. Terrains Paléozoiques du Portugal. Étude sur les Bilobites et autres fossiles des quartzites de la base du Système Silurique du Portugal – (supplément). Mem. Sec. Trab. Geol. Portugal, Lisboa (76 p.).

Delgado, J.F.N., 1908. Système Silurique du Portugal. Étude de stratigraphie paléontologique. Mem. Comun. Serv. Geol. Portugal, Lisboa (245 p.).

Egenhoff, S., 2000. Sedimentologie und Beckenentwicklung im Ordovizium in Südbolivien. Berliner Geowiss. Abh. A207, 1–173.

Egenhoff, S., 2003. Review of the Ordovician basin evolution in southern Bolivia. INSUGEO, Ser. Corr. Geol. 17, 409–412.

Egenhoff, S., Maletz, J., Erdtmann, B.D., 1999. Upper Ordovician basin evolution in southern Bolivia. Acta Univ. Carolinae 43, 131–133.

Egenhoff, S., Maletz, J., Erdtmann, B.D., 2004. Lower Ordovician graptolite biozonation and lithofacies of southern Bolivia: relevance for paleogeographic interpretations. Geol. Mag. 141, 287–299.

Egenhoff, S., Webber, B., Lehnert, O., Maletz, J., 2007. Biostratigraphic precision of the *Cruziana rugosa* Group: a study from the Ordovician succession of southern and central Bolivia. Geol. Mag. 144, 289–303.

Erdtmann, B.D., Kley, J., Müller, J., Jacobshagen, V., 1995. Ordovician basin dynamics and new graptolite data from the Tarija region, Eastern Cordillera. South Bolivia. In: Cooper, J., Droser, M., Finney, S.C. (Eds.), Ordovician Odyssey: Short Papers for the Seventh International Symposium on the Ordovician System. The Pacific Section Society for Sedimentary Geology (SEMP), Book, Fullerton, California, pp. 69–73 (77).

Erdtmann, B.D., Suárez-Soruco, R., 1999. The Ordovician tectonostratigraphy of Bolivia. Acta Univ. Carolinae 43, 127–130.

Finney, S., 2005. Global Series and Stages for the Ordovician System: a progress report. Geol. Acta 3, 309–316.

Gagnier, P.Y., Bliek, A., Emig, C., Sempere, T., Vachard, D., Vanguestaine, M., 1996. New paleontological and geological data on the Ordovician and Silurian of Bolivia. J. South Am. Earth Sci. 9, 329–347.

Goldring, R., 1984. The formation of the trace fossil *Cruziana*. Geol. Mag. 122, 65–72.

Heredia, S., Aceñolaza, G., 2005. The *Trapezognathus diprion* conodont Zone and correlation of an outstanding occurrence of the *Cruziana rugosa* Group (Trace fossils) in the Lower Ordovician of western Gondwana. In: Pankhurst, J., Veiga, G. (Eds.), Gondwana 12 Geological and Biological heritage of Gondwana. Academia Nacional de Ciencias, Córdoba, p. 197.

Heredia, S., Carlorosi, J., Mestre, A., Soria, T., 2013. Stratigraphical distribution of the Ordovician conodont *Erraticodon* Dzik in Argentina. J. South Am. Earth Sci. 45, 224–234.

Herrera Gálvez, A., Velásquez, B.E., (Tesis del Departamento de Geociencias, Facultad de Ciencias) 1978. Estratigrafía de la sección de Araracuara (Amazonas). Universidad Nacional de Colombia, Colombia (82 p.).
Knaust, D., 2004. Cambro-Ordovician trace fossils from the SW-Norwegian Caledonides. Geol. J. 39, 1–24.
Li, Z., Stouge, S., Chen, X., Wang, C., Wang, X., Zen, G., 2010. Precisely compartmentalized and correlated Lower Ordovician *Oepikodus evae* Zone of the Fuluoian in the Huanghuachang section, Yichang, Hubei Province. Acta Palaeont. Sinica 49, 108–124 (in Chinese with English abstract).
Lucas, S.G., 2007. Tetrapod footprint biostratigraphy and biochronology. Ichnos 14, 5–38.
MacNaughton, R.B., 2007. The application of trace fossils to biostratigraphy. In: Miller III., W. (Ed.), Trace Fossils Concepts, Problems, Prospects. Elsevier, Amsterdam, pp. 135–148.
Maletz, J., Kley, J., Reinhardt, M., 1995. New data on the palaeontology and biostratigraphy of the Ordovician in southern Bolivia. Newsl. Stratigr. 32, 163–173.
Miller III., W., 2007. Trace Fossils Concepts, Problems, Prospects. Elsevier, Amsterdam, (512 p.).
Moya, M.C., 1998. El Paleozoico Inferior en la Sierra de Mojotoro, Salta-Jujuy. Rev. Asoc. Geol. Argent. 53, 219–238.
Moya, M.C., 2008. El Paleozoico Inferior en el Noroeste Argentino, evidencias, incógnitas, propuestas para la discusión. In: Coira B., Zappettini, E. (Eds.), Geología y Recursos Naturales de la Provincia de Jujuy. Publ. Esp. Asoc. Geol. Argent. 1, 74–84.
Moya, M.C., Monteros, J.A., Malanca, S., Albanesi, G., 2003. The Mojotoro Range, Eastern Cordillera, Salta Province. INSUGEO, Miscelánea 11, 17–22.
Narbonne, G., Myrow, P.M., Anderson, M., 1987. A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. Can. J. Earth Sci. 24, 1277–1293.
Osgood, R.J., 1970. Trace fossils of the Cincinnati area. Palaeont. Am. 6, 277–444.
Sarmiento, G.N., Rao, R.I., 1987. *Erismodus quadridactylus* (Conodonta) en la Formación Santa Gertrudis (Ordovícico); Provincia de Salta, Argentina. In: IV Congr. Latinoam. Paleont., Mem. 1, pp. 89–95.
Seilacher, A., 1956. Der Beginn des Kambriums als biologische Wende. Neues Jahr. für Geol. Paläont., Abh. 103, 155–180.
Seilacher, A., 1969. Sedimentary rhythms and trace fossils in Paleozoic sandstones of Libya. In: Kanes, W.H. (Ed.), Geology, Archaeology and Prehistory of the southwestern Fezzan, Libya. In: Petroleum Exploration Society of Libya, 11th annual field conference, pp. 117–123.
Seilacher, A., 1970. *Cruziana* stratigraphy of "non-fossiliferous" Paleozoic sandstones. In: Crimes, T.P., Harper, J.C. (Eds.), Trace Fossils. Geol. J., Spec. Issue 3, 447–476.
Seilacher, A., 1985. Trilobite palaeobiology and substrate relationship. Trans. R. Soc. Edinb. 76, 231–237.
Seilacher, A., 1994. How valid is *Cruziana* stratigraphy? Geol. Rundschau. 83, 752–758.
Seilacher, A., 2000. Ordovician and Silurian Arthrophycid Ichnostratigraphy. In: Sola, M.A., Worsley, D. (Eds.), Geological Exploration in the Murzuq Basin. Elsevier, Amsterdam, pp. 237–258.
Seilacher, A., 2005. Silurian trace fossils from Africa and South America: mapping a trans-Gondwanan seaway. Neues Jahrb. Geol. Paläont. 3, 129–141.
Seilacher, A., 2007. Trace Fossil Analysis. Springer-Verlag, Berlin, Heidelberg (226 p.).
Steinmann, G., Hoek, H., 1912. Das Silur und Cambrium des Hochlandes von Bolibia und ihre fauna. Neues Jahrb. Min., Geol. Paläont. 34, 176–252.
Suárez-Soruco, R., 1976. El Sistema Ordovícico en Bolivia. I Congr. Argent. Paleontol. Bioestratigr. 1, pp. 133–148.
Suárez-Soruco, R., 1992. El Paleozoico Inferior de Bolivia y Perú. In: Gutiérrez-Marco, J.C., Saavedra, J., Rábano, I. (Eds.), Paleozoico Inferior de Ibero-América. Universidad de Extremadura, Extremadura, pp. 225–240.
Suárez-Soruco, R., 2000. Compendio de geología de Bolivia. Rev. Téc. YPFB 18, 1–210.
Suárez-Soruco, R., Benedetto, J.L., 1996. Primeros datos sobre la fauna de braquiópodos de la Formación San Benito en la Cordillera de Tunari, Cochabamba, Bolivia. In: 12 Congr. Geol. Boliviano 1, pp. 211–216.
Therý, J.M., (Unpublished Doctoral Thesis) 1982. Constitution du Nord–Ouest du continent Sud-Américain avant les Tectoniques andines, 3 tomes. Université Bordeaux III, Bordeaux (221 fig., 20 planches hors textes).
Therý, J.M., Peniguel, T., Haye, G., 1986. Descubrimiento de acritarcos del Arenigiano cerca a Araracuara (Caquetá–Colombia). Ensayo de reinterpretación de esta región de la Saliente del Vaupés. Geol. Norandina 9, 3–17.
Toro, M., Paredes, M., Miranda, R., 1990. Nuevos registros de peces para la Formación Anzaldo (Ordovícico) Dpto. de Cochabamba y algunas consideraciones sobre su edad. Rev. Técn. Yac. Petr. Fisc. Bolivianos 11, 309–311.
Voldman, G., Albanesi, G., Zeballo, F., Monaldi, C., 2013. Early Ordovician (Late Floian) conodonts from the Zenta Range, Cordillera Oriental, NW Argentina. Asoc. Paleont. Argent., Spec. Publ. 13, 123–128.
Wang, X., Stouge, S., Chen, X., Li, Z., Wang, C., Finney, S., Zeng, Q., Zhou, Z., Chen, H., Erdtmann, B., 2009. The global stratotype section and point for the base of the Middle Ordovician Series and the Third Stage (Dapingian). Episodes 32, 96–113.
Whittington, H.B., 1997. Mode of life, habits and occurrence. In: Kaessler, R. (Ed.), Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita. Revised. Geological Society of America and University of Kansas, Boulder, pp. 74–84.
Zhen, Y., Percival, I.G., 2003. Ordovician conodont biogeography – reconsidered. Lethaia 36, 357–369.