



Mid-Late Devonian assemblages of herbaceous lycophytes from northern Argentina and Bolivia: Age assessment with palynomorphs and invertebrates and paleobiogeographic importance



Mercedes Di Pasquo ^{a,*}, Sol Noetinger ^b, Peter Isaacson ^c, George Grader ^c, Daniel Starck ^d, Eduardo Morel ^e, Heidi Anderson Folnagy ^f

^a Laboratorio de Palinoestratigrafía y Paleobotánica, CICYTTP-CONICET, Dr. Materi y España S/N, Diamante, E3105BWA, Entre Ríos, Argentina

^b Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"- CONICET, Angel Gallardo 470, Ciudad A. de Buenos Aires, C1405DJR, Argentina

^c University of Idaho, Geological Sciences, Moscow, ID, USA

^d Tecpetrol S.A., Della Paolera 299-Piso 21, C1001ADA, Buenos Aires, Argentina

^e División Paleobotánica, Museo de La Plata-UNLP y CIC Prov, Buenos Aires, Argentina

^f University of Montana Western, Dillon, MT, USA

ARTICLE INFO

Article history:

Received 12 March 2015

Received in revised form

19 June 2015

Accepted 28 June 2015

Available online 4 July 2015

Keywords:

Lycophyte plant fossils

Palynology

Invertebrates

Mid-Late Devonian

Argentina

Bolivia

ABSTRACT

Implications of a new collection of lycophytes of the genera *Haplostigma* Seward and *Paleostigma* Kräusel and Dolianiti from southern Bolivia and northern Argentina are presented. Fragmented herbaceous stems of lycophytes preserved as compressions, impressions and casts come from the Middle and Late Devonian Pescado (Huamampampa), Los Monos and Iquiri formations at Mataral, Yesera, Angosto del Pescado and Balapuca. The interbedded shales and siltstones bearing the lycophytes were also examined for palynology. They yielded mostly terrestrial palynomorphs with *Grandispora pseudoreticulata* and other Eifelian to Givetian species and fewer microplanktonic species (i.e., acritarchs, prasinophytes, chitinozoans). At Yesera, diagnostic spores and elements of the microplankton suggest a Givetian-Frasnian up to early Famennian age for the *Haplostigma* beds. Moreover, presence of the same brachiopod taxon in the *Haplostigma* intervals at Yesera Dique (palynologically barren) and Yesera Centro supports their correlation. This new information supports terrestrial connections between these Bolivian and Argentine areas and other regions of South America in the Eifelian – Givetian Afrosouthamerican Subrealm, which extended up to the early Famennian.

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1. Introduction

Megafloras from the Middle to Late Devonian of southern Bolivia and northern Argentina are not well understood, mainly due to the scarcity of records and the uncertainty over the identification of *Haplostigma* Seward 1932 and *Paleostigma* Kräusel and Dolianiti 1957 species. This relates to poor preservation of fossil plant remains in many cases. Newly discovered specimens provide important taxonomic information at the generic and specific level, and on the biodiversity and the succession of floristic events. This

* Corresponding author.

E-mail addresses: medipa@cicytpp.org.ar (M. Di Pasquo), noetinger@macn.gov.ar (S. Noetinger), isaacson@uidaho.edu (P. Isaacson), georgewgrader@prisemgeoconsulting.com (G. Grader), Daniel.Starck@tecpetrol.com (D. Starck), heidi.anderson@umwestern.edu (H.A. Folnagy).

includes its paleobiogeographic distribution (di Pasquo et al., 2009; Moisan et al., 2011). To date, we have well documented specimens from the Balapuca section published by di Pasquo (2007), while those illustrated by Ahlfeld and Branisa (1960) and Branisa (1965) have been lost. The *Centro de Información de Hidrocarburos YPFB* (Santa Cruz de la Sierra, Bolivia), allowed M. di Pasquo to visit the repository where the Branisa's specimens should have been housed. Neither specimens of *Haplostigma* nor other plant species were found there nor at the Museum in Cochabamba where Drs. Ramiro Suárez Soruco and Ramiro Suárez might have had unpublished specimens. Hence, to improve knowledge the current biostratigraphy (Limachi et al., 1996), of particular importance are the new records of *Haplostigma* presented herein. These were collected from southern Bolivia (Balapuca, Mataral and Yesera areas) and northern Argentina (Balapuca and Angosto del Pescado, Figs. 1 and 2). Their age is provided by palynology and

invertebrates, associated with these plants (Fig. 3), and their paleobiogeographic importance is also addressed.

2. Geological setting

The Devonian deposits in South America constituted marine sedimentary basins (Fig. 1) that were interconnected during transgressive intervals. Terrestrial connections are also based on common paleontological records (Grahm, 2005; di Pasquo et al., 2009). To the east of the Puna Highlands, the Peru–Bolivia

Master Basin was a foreland basin where siliciclastics were deposited during the Silurian and Devonian. In the latest Devonian the structure of the basin changed perhaps due to the docking of the Chilenia terrane to the south causing an unconformity between the Devonian rocks and the overlying Carboniferous attributed to the Chanic Orogeny (Starck et al., 1993b; Starck, 1995; Sempere, 1995; Tankard et al., 1995; Ramos, 2008).

Devonian rocks of the Tarija Basin are known from northern Argentina cropping out in the areas of the Cordillera Oriental, western Subandean Ranges and Santa Barbara System, and they

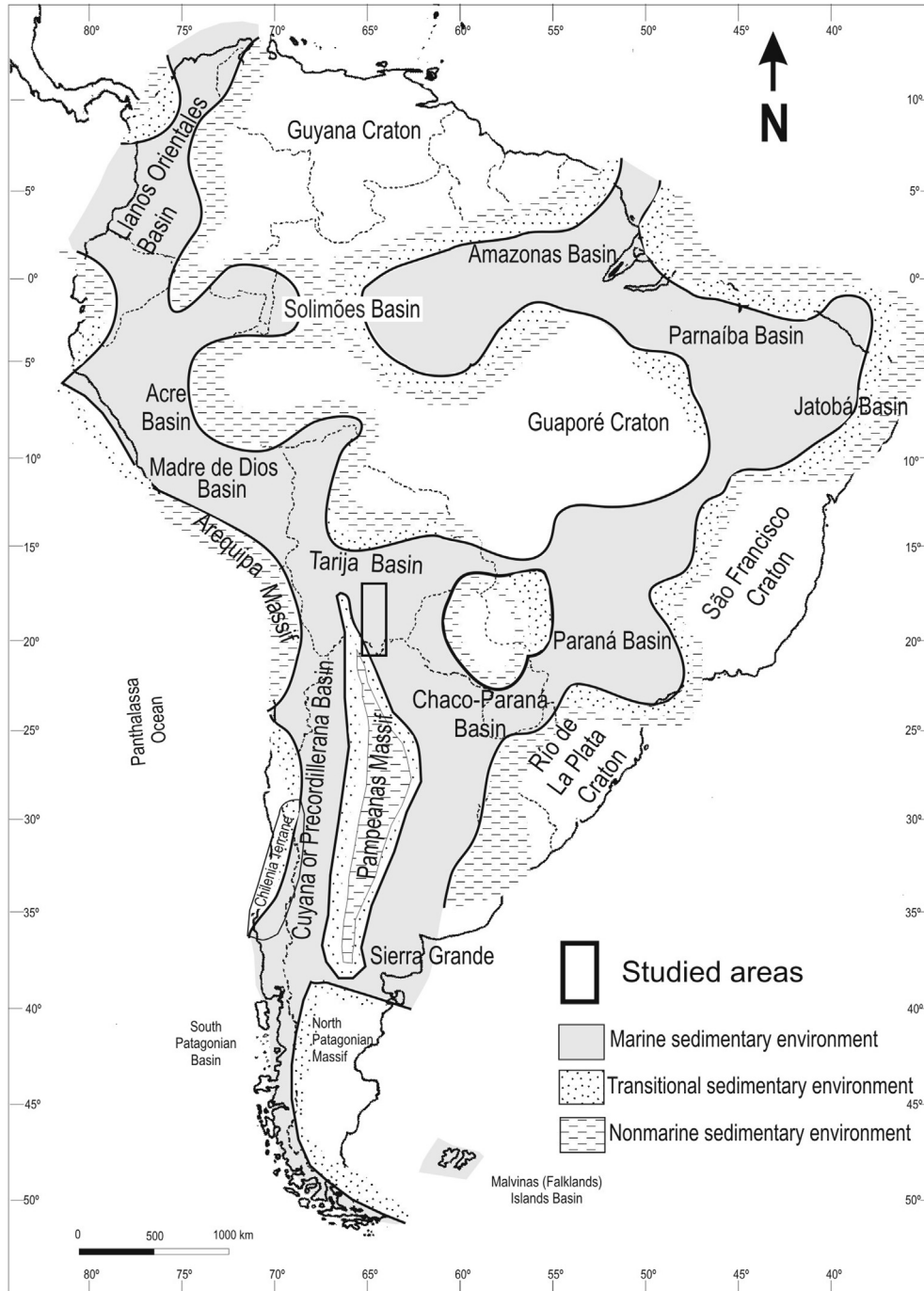


Fig. 1. Location of the Tarija Basin in South America within the paleogeographic map at Givetian-Frasnian time (modified from di Pasquo et al., 2009).

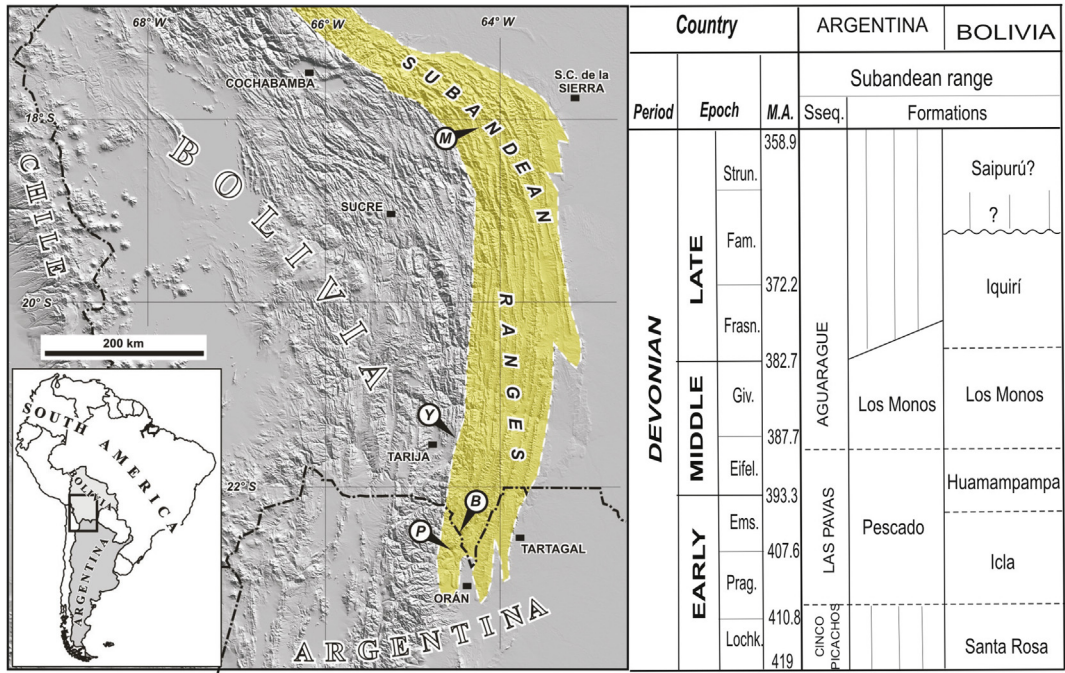


Fig. 2. (1). Location map for the studied sections along the Subandean Ranges: M: Mataral, Y: Yesera, B: Balapuca, P: Angosto del Pescado. (2). Simplified correlation chart of the Devonian stratigraphic units in northern Argentina and Bolivia (see text for references).

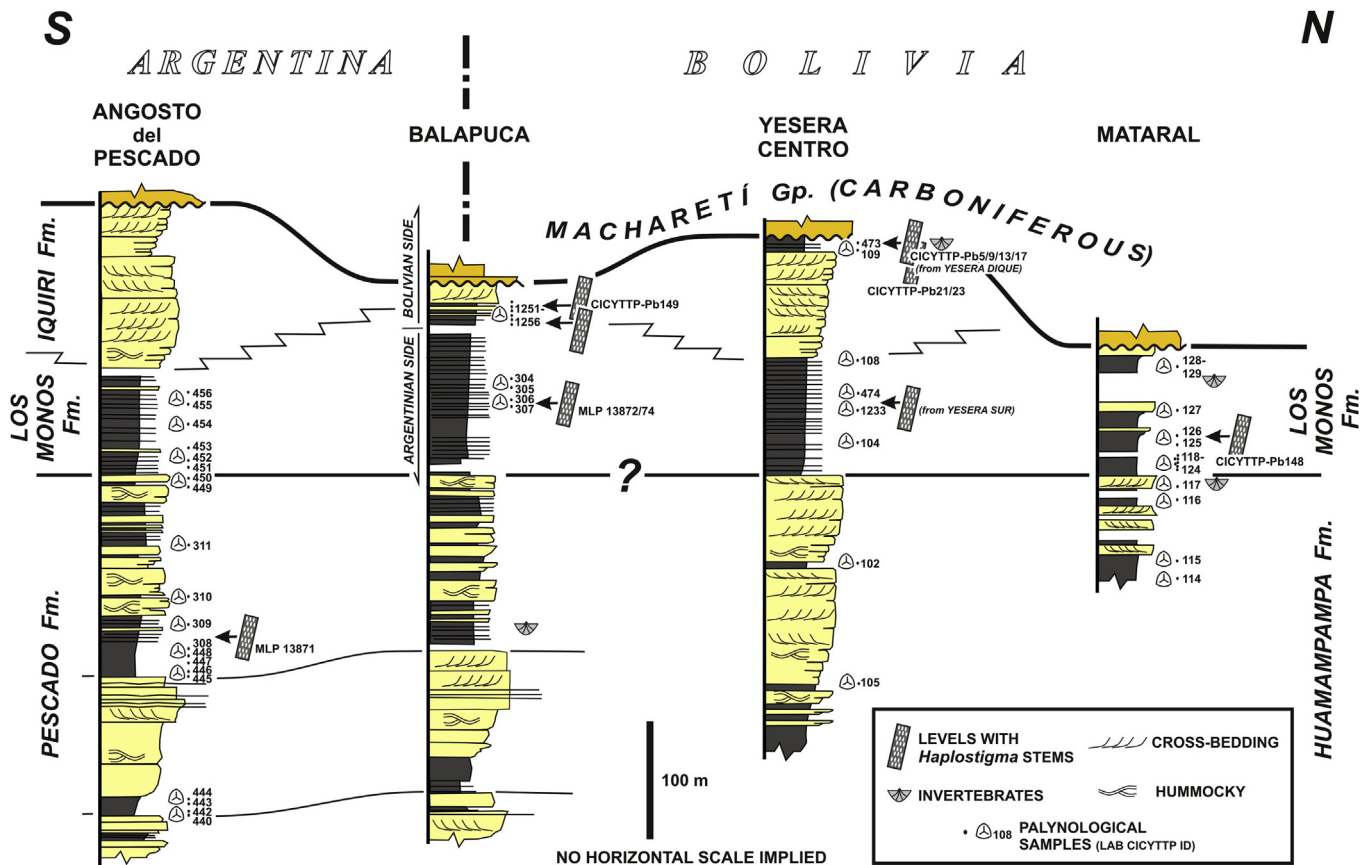


Fig. 3. Stratigraphic correlation of the plants bearing units (location of the stratigraphic sections in Fig. 2).

extend into the central and southern Bolivia as well as in subsurface to the east in the Subandean Ranges up to the Chaco Plain and northwestern Paraguay. The Devonian mudstone sections are proved source rocks in the basin, whereas the sandy (mainly quartzitic) beds behave as reservoirs in structural traps in the subandean anticlines. Therefore, these basins have been studied multidisciplinary for exploration purposes based on information from subsurface and surface. However, they are mostly unpublished reports of the oil companies involved, while some work has been published (Vistalli, 1989, 1999; Starck et al., 1992, 1993a, 1993b; Starck, 1999; Suárez Soruco, 2000; Albariño et al., 2002; Alvarez et al., 2003).

The middle to upper Paleozoic succession in northern Argentina and southern Bolivia consists of marine Devonian sandstone and mudstone units (Fig. 2.2) unconformably overlain by Carboniferous and Permian continental deposits (Starck et al., 1993a, 1993b; Suárez Soruco, 2000; di Pasquo, 2003; Starck and del Papa, 2006). The Silurian to Devonian record, separated by regional unconformities from the preceding and succeeding ones, led to the definition, in Bolivia, of the “Cordilleran Cycle” (see Suárez Soruco, 2000). Within this major cycle, three supersequences (Cinco Picachos, Las Pavas and Aguaraquíe), have been defined. These supersequences comprise several hundreds of meters coarsening upward sections, separated by sharp flooding surfaces (Starck et al., 1993b; Starck, 1995, 1996). In Argentina, the Cinco Picachos Supersequence includes the Silurian Lipeón Formation and a Lower Devonian succession (Baritú and Porongal formations). In Bolivia this supersequence involves the Kirusillas, Tarabuco and Santa Rosa formations. The Las Pavas Supersequence is represented in Argentina by the Pescado formation (Pragian-Eifelian), outcropping in the Subandean Ranges. In the Cordillera Oriental, the mudstone basal section is known as Piedras (or Cerro Piedras) formation. The Bolivian counterparts for the Las Pavas Supersequence are the Icla and Huamampampa formations. The Aguaraquíe Supersequence involves the Los Monos Formation (Eifelian - Frasnian/Famennian), which is transitionally overlain by the Iquiri Formation that records an increase of sandstone. The age of all these units are independently based on palynomorphs (e.g., Ottone, 1996; Grahn, 2002; di Pasquo, 2007; Noetinger, 2010; Noetinger and di Pasquo, 2010, 2011) and invertebrates (e.g., Isaacson, 1977, 1993; Isaacson and Perry, 1977; Dalenz Farjat, 1993), but still, there are few studies that integrate information from different paleontological groups (e.g., Branisa, 1965; Blicek et al., 1996; Limachi et al., 1996; Alvarez et al., 2003; di Pasquo and Noetinger, 2008; Troth et al., 2011; Noetinger et al., 2015a, b).

The basal mudstones of the Los Monos Formation appear to be related to a regional Kačák flooding event occurring during the late Eifelian (Marshall et al., 2007; Troth et al., 2011; Bosetti et al., 2011; Horodyski et al., 2013). The Givetian was characterized by shallow siliciclastic marine environments frequently influenced by storms and the Frasnian represented a transgressive interval; this is supported by an increase in the marine palynomorphs as part of the palynoassemblages documented in northern Argentina and southern Bolivia (Ottone, 1996; di Pasquo, 2007; Noetinger, 2010, 2014; Noetinger and di Pasquo, 2011, and references therein). These assemblages are composed of many cosmopolitan index species that support a partial correlation with Brazilian and Euramerican zonations resulting from the effects of paleolatitude and the configuration of land and sea for that time, with a narrow Rheic Ocean between northern Gondwana and Euramerica (di Pasquo et al., 2009). The fossil plants, subject of this contribution, were mainly collected from the upper supersequence, except one specimen coming from the upper levels of the Las Pavas Supersequence.

3. Materials and methods

3.1. Geological information and precedence of the fossil assemblages

Plant remains of lycophyte affinity, invertebrates and palynomorphs, with different degrees of preservation, were recovered from different mudstone/fine grained-sandstone levels of the Devonian succession at four localities in Argentina and Bolivia (Figs. 2.1 and 3). Lithostratigraphy and location of fossils in the outcrops are presented in Fig. 3 and is summarized below. Figs. 4–8 present a selection of field sections with plant specimens, lycophytes, invertebrate and palynomorphs mentioned in the text.

3.1.1. Balapuca and Angosto del Pescado sections

The Pavas Range (or Pescado Range) is part of the Subandean Ranges in northern Salta Province, Argentina (Fig. 2.1). It extends

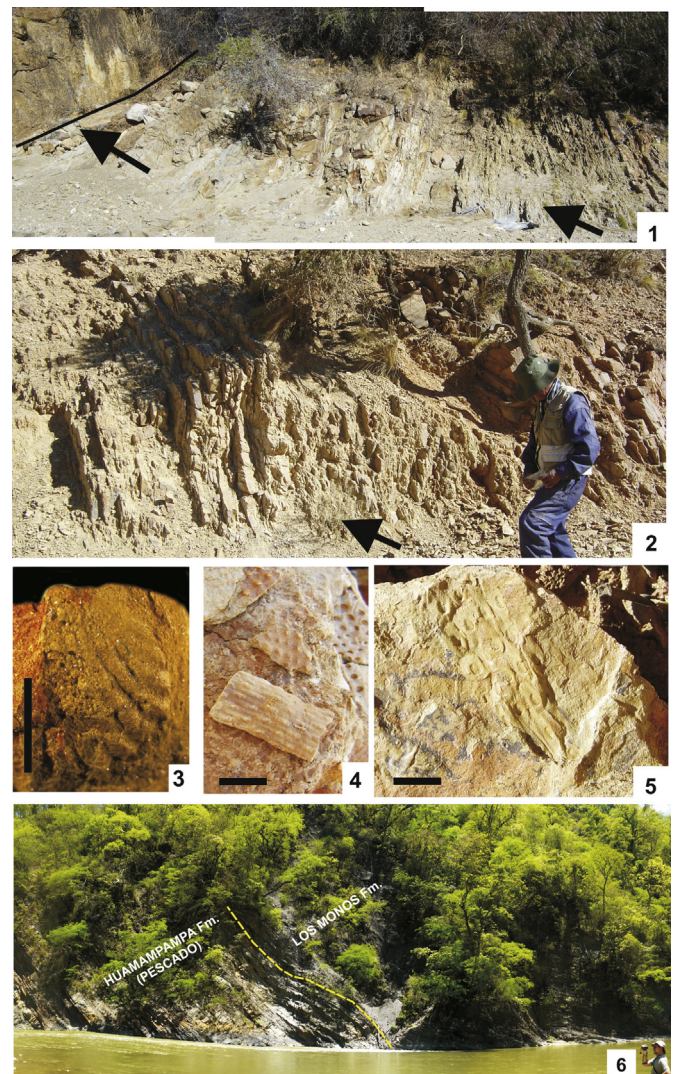


Fig. 4. (1, 2) Upper Devonian sections outcropping at Yesera Centro (1), and at Yesera Dique (2), levels bearing lycophyte stems and single species of a brachiopod marked with an arrow. (3) Indeterminate brachiopod (fragmented external mold) (CICYTTP-In1) from Yesera Dique (see Fig. 4.2). Scale bar 0.5 cm (4, 5) Outcrop photograph of indeterminate species of *Haplostigma* (CICYTTP-Pb 9, cast; CICYTTP-Pb 17, stems) from Yesera Dique (see Fig. 4.2). Scale bar 1 cm. (6) Huamampampa-Los Monos formations contact at Balapuca (Argentinian margin), the MLP13872/74 *Haplostigma* specimen was collected slightly outside of the right margin of the photograph.

for about 60 km from slightly south of the Iruya to the Bermejo River, to Bolivia, where it is known as San Telmo Range. From the structural point of view it consists of an anticline heading SSW–NNE, cored in Devonian levels. The Bermejo (Balapuca section) and Pescado rivers cut narrow valleys across the structure of the Pescado Range, hence these outcrops were surveyed. From the Angosto del Pescado section (W 64° 34.4' and S 22° 41.2') one nicely preserved lycophyte stem, 21 samples for palynology and many specimens of shelly fauna deposits (not studied yet), were collected by D. Starck in 1990 (Figs. 3 and 6). The invertebrate fauna of the Pescado river was the subject of publications as early as 1933 (Feruglio, 1933).

The Balapuca (or Angosto de Balapuca) section is located along the Argentinian-Bolivian boundary, defined by the Bermejo River (W 64° 30' and S 22° 30'). A paved national road runs along the Bolivian margin of the river, providing an easy access (especially to the Bolivian margin) to the section. From this margin, a new

collection of plant material (compressions and impressions) and crinoid stems (invertebrates) were obtained by M. di Pasquo in 2007 from the Los Monos Formation (Fig. 5). A previous collection of these materials was presented by di Pasquo (2007), who established an Eifelian-Givetian age for the interval with lycophytes based on the palynological analysis.

From the Argentinian margin D. Starck in 1990 collected one specimen of a lycophyte stem and 20 samples for palynology from the Los Monos Formation at Balapuca (Figs. 3 and 6). From the plant interval four samples were selected and processed in 2012 (Mdp) to establish its palynological age. As in the Angosto del Pescado section, invertebrate remains have been collected and classified (YPF unpublished reports). In both sections the most fossiliferous levels (in terms of macrofauna) are located in lower stratigraphic levels

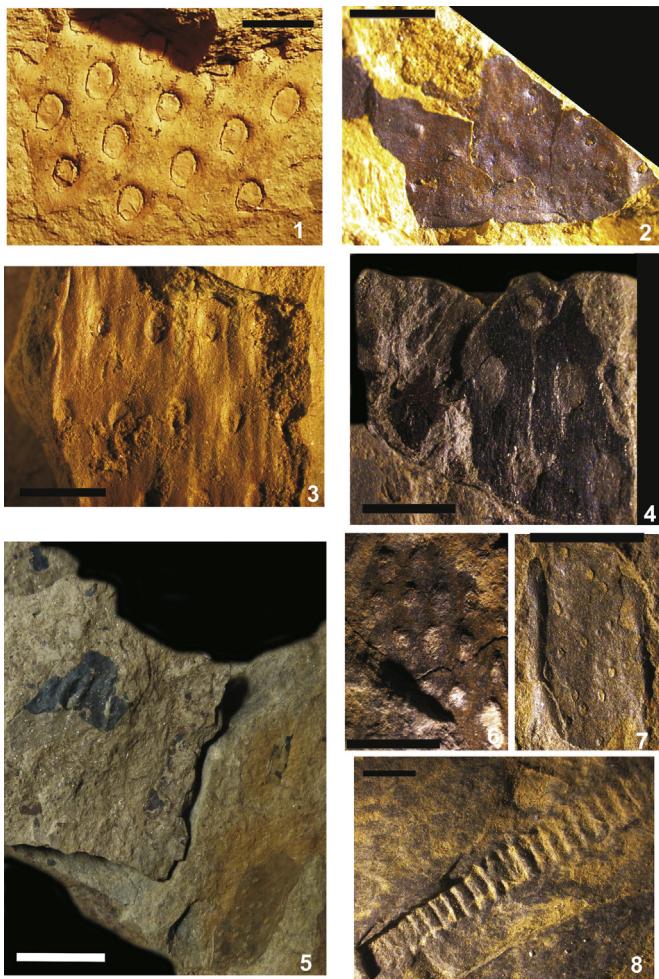


Fig. 5. (1) Detail of the scars, rib and furrows on stem of indeterminate species of *Haplostigma* (CICYTTP-Pb 5) from Yesera Dique. Scale bar 0.4 cm (2) Detail of the disposition of the scars of *Paleostigma* sp. (CICYTTP-Pb 13, cuticle preserved) from Yesera Dique. Scale bar 0.4 cm (3) Detail of the scars, rib and furrows on stem of indeterminate species of *Haplostigma* (CICYTTP-Pb 23) from Yesera Centro. Scale bar 0.4 cm (4) Detail of the scars, rib and furrows on stem of indeterminate species of *Haplostigma* (CICYTTP-Pb 21, cuticle preserved) from Yesera Centro. Scale bar 0.4 cm (5) Detail of the disposition of the scars on stem of indeterminate species of *Haplostigma* (CICYTTP-Pb 148, partially compression) and *Paleostigma* sp. (CICYTTP-Pb 147, right) from Mataral. Scale bar 1 cm. (6) *Haplostigma* sp. (CICYTTP-Pb 150) from Balapuca, Bolivia. Scale bar 1 cm (7) Detail of the disposition of the scars of *Paleostigma* sp. (CICYTTP-Pb 149) from Balapuca, Bolivia. Scale bar 0.5 cm (8) Impression of crinoid column (CICYTTP-In 4) from Balapuca, Bolivia. Scale bar 0.3 cm.

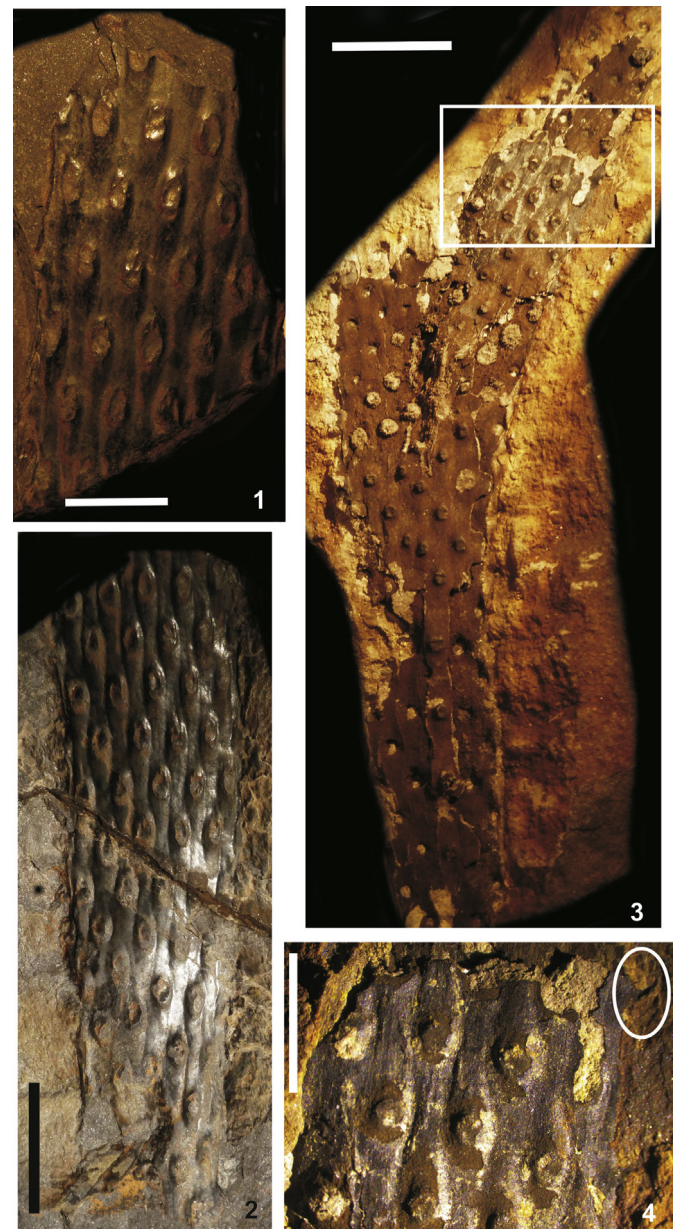


Fig. 6. (1, 2) Detail of the scars, rib and furrows on stem of indeterminate species of *Haplostigma* (MLP 13874 and 13872) from Balapuca, Argentina. Scale bar 1 cm. (3) *Haplostigma* sp. (MLP 13871 a), bifurcate stem with spiny lateral appendages from Angosto del Pescado. Scale bar 1 cm. (4) Detail of the square section in (3) where scars, ribs, furrows and spiny lateral appendages (circles) are observed.

than the lycophyte bearing ones. These levels have not been included in the correlation (Fig. 3).

3.1.2. Yesera

The Yesera area (W 64° 30' and S 21° 20–30') is located to the northeast of Tarija city in southern Bolivia (Fig. 2.1). Several Devonian sections were surveyed for this study in different parts of this area called Yesera Dique, Centro and Sur (Fig. 3). At Yesera Centro lycophyte stems (compressions and impressions), a single species of invertebrate (external molds of poorly preserved shells), and samples for palynology were collected (MdP in 2007) from the Iquiri Formation (Fig. 3), beneath the unconformable contact with the Carboniferous Tupambi Formation (Fig. 4.1). Downward in the Yesera Centro section palynological assemblages were recorded from the Los Monos and Huamampampa formations (di Pasquo, 2013). From the latter several levels mostly with invertebrates have been documented (not included in Fig. 3).

At Yesera Dique, the same brachiopod impressions found in the Iquiri Formation at Yesera Centro associated with lycophyte stems were collected ca. 3 m beneath the unconformable contact with the Carboniferous Tupambi Formation (Figs. 3 and 4). Two green yellowish mudstones were barren for palynology due to weathering.

At Yesera Sur, lycophyte remains similar to the collected ones, were recognized in the Los Monos Formation but only one sample (CICYTTP-PI 1233) from this interval was collected for palynology (H. Anderson in 2007), ca. 69 m below the unconformity with the Carboniferous diamictites (Fig. 3).

3.1.3. Mataral

This section is located in the Abra de Quiña (W 64°15'43.4" and S 18°8'47.3"), southwest of Santa Cruz de la Sierra (Fig. 2.1). Lycophyte stems poorly preserved (Fig. 5) and sixteen samples for palynology were collected by M. di Pasquo and G. Grader in 2007 from the Los Monos Formation. Invertebrates and trace fossils were also observed at this outcrop (Fig. 3).

3.2. Methods and repositories

All the sections were investigated for palynology (Fig. 3) and fifty eight samples were processed since 2011 at the Laboratory of the Palynostratigraphy and Paleobotany in the *Centro de Investigaciones Científicas y Tecnológicas de Transferencia a la Producción* (CICYTTP-CONICET), Diamante. Although the standard methodology (Traverse, 2007) was followed, HCl was not used to start the processing of the samples as they were not calcareous. Hence, HF was directly applied to the crushed sediment and maintained for two days. The neutralization was achieved by settling after four washings with distilled water. The residue obtained was sieved with a mesh of 25 microns and mounted with glycerine jelly for the first microscopic analysis. Productive samples were improved using other treatments (i.e., HF second time, HCl boiled, KOH, ZnCl) and more permanent slides were mounted to be studied and catalogued under the acronym CICYTTP-PI, housed in the palynological repository of the laboratory (see above; di Pasquo and Silvestri, 2014). Palynomorphs were studied and illustrated in a trinocular transmitted light microscope bearing a video camera (*Leica DM500* and *Leica EC3*, 3.0 Mp).

All the plant and invertebrate megafossils from Bolivia are housed in their respective repositories of Paleobotany (CICYTTP-Pb) and Invertebrate (CICYTTP-In) at the CICYTTP (di Pasquo and Silvestri, 2014). The Argentinian specimens from Balapuca and Angosto del Pescado (collected by D.S.) were housed at the *División Paleobotánica, Facultad de Ciencias Naturales y Museo*, University of La Plata, under the acronym LPPB (Morel et al., 2015). All materials were cleaned carefully and illustrated with a *Panasonic Lumix DMC-*

ZS7 (12 Mp) digital camera and under a *Leica* stereoscope 58APO with a videocamera *Leica DFC 295* (5 Mp.), at the CICYTTP.

4. Results

We present the relevant palynological and invertebrate information obtained from the stratigraphic units bearing new records of lycophytes at each locality (Fig. 2.1), which dated and correlated them (Fig. 3).

4.1. Approaches on the fossil plant assemblages

The plant assemblages are mostly composed of herbaceous stems preserved as compressions (with preserved cuticles). Impressions and few casts were also found (Figs. 4–6). They are indeterminate species of *Haplostigma* and *Paleostigma* (Gutiérrez, 1996; Moisan et al., 2011; Matsumura et al., 2013), based on two different morphologies observed in the material (Figs. 4–6): a) *Haplostigma* stems show false leaf scars that are helically arranged (pseudosigillaroid-sigillaroid phyllotaxis), bearing spiny appendages in some specimens (Fig. 6.4) and being larger than 1 cm in width, and b) *Paleostigma* stems are smaller than 1 cm in width and scars are irregularly distributed. Concerning the taxonomic assignment to specific level of these lycophyte stems, it is beyond of the scope of this paper. A detailed morphological and taxonomical study (i.e., assignment of species) is in progress, through a direct comparison of the collection of *Haplostigma* and *Paleostigma* species documented in the Ponta Grossa Formation by Matsumura as part of his Ph.D. (currently in progress, see Matsumura and Iannuzzi, 2013; Matsumura et al., 2013). This comparison includes morphologic study of their cuticles under optical and SEM microscopes, which is essential in determining species. Another method that will assist in species determination and taxonomic separation between those two genera is Spectroscopy analysis (functional groups and semi-quantitative data) by Fourier transform infrared (FTIR) spectroscopy. This was applied to the Brazilian *Spongiophyton* and *Palaeostigma* plant material presented by Matsumura et al. (2015). The chemical differences recognized between them confirmed their taxonomic separation previously proposed on the basis of their morphology and geochemistry (carbon and hydrogen composition) by Guerra Sommer et al. (1996).

It deserves to be mentioned here that specimens illustrated by Branisa (1965) as *Haplostigma furquei* from Finca Carlazo in the East of Tarija (his plate 51, Figs. 2, 3), and *Haplostigma* cf. *furquei* from Sicasica (his plate 50, Figs. 1–3) from Bolivia, are not available anymore (lost). Others were only mentioned in the literature, such as *Haplostigma furquei* from the Huamampampa, Los Monos and Iquiri formations at Campo Redondo (Suárez Riglos, 1975) and Lajas (Wood, 1995), and other localities of southern and central Bolivia (Suárez Soruco, 1988; Limachi et al., 1996). The same situation occurs in Brazil, with *Haplostigma irregularis* described from the Pimenteira Formation, Parnaíba Basin by Suárez Riglos (1975). Hence, they cannot be further studied in detail and therefore, our *Haplostigma* specimens from northern Argentina and southern Bolivia constitute the first curated collections at two institutions in Argentina (di Pasquo and Silvestri, 2014; Morel et al., 2015). This assures to researchers access to these materials in the future for further taxonomic analysis and comparison.

4.2. Characteristics and age of the fossil assemblages at each locality

4.2.1. Angosto del Pescado

The plant specimen collected from one level corresponds to the palynological sample CICYTTP-PI 309 (Fig. 3). The stem consists of a

bifurcated specimen of 1.2 cm in width, 8 cm in length attributed to the genus *Haplostigma* (indeterminate species) based on its pseudosigillaroid phyllotaxis with few spiny lateral appendices (Fig. 6.4). The plant interval was dated through the palynologic analysis of 15 samples from the Pescado and Los Monos formations (Fig. 3). The palynoassemblages include both continental and marine elements of Eifelian to Givetian age due to the presence of some diagnostic species such as *Acinosporites acanthommillatus*, *Dibolisporites eifeliensis*, *Emphanisporites annulatus*, *Geminospora lemurata*, *Grandispora pseudoreticulata*, *Leiotriletes balapucensis*, *Verrucosporites scurrus* and various species of phytoplankton without stratigraphic value (e.g. *Ammonidium* spp., *Arkonites bilixus*, *Exochoderma* spp., *Multiplicisphaeridium* spp.

Tunisphaeridium spp.). Some chitinozoans such as *Lagenochitina* sp. cf. *Lagenochitina praeavelinoi*, *Ancyrochitina morzadeci*, *Spinachitina* aff. *Spinachitina biconstricta* and *Ramochitina stiphrospinata* support the age assigned by spores (Figs. 7–9). Also remarkable is the presence of new forms in the associations, possibly endemic that are together with others cosmopolitans, would correspond to the Afrosouthamerican Subrealm (Fig. 10; Noetinger et al., 2015a).

4.2.2. Balapuca (Argentina and Bolivia)

In Bolivia, stems of indeterminate species of *Paleostigma* sp. were found associated to *Haplostigma* and crinoid stems (Fig. 3), as part of the new collection that enlarges the prior one (di Pasquo, 2007; di Pasquo et al., 2009). The palynological analysis

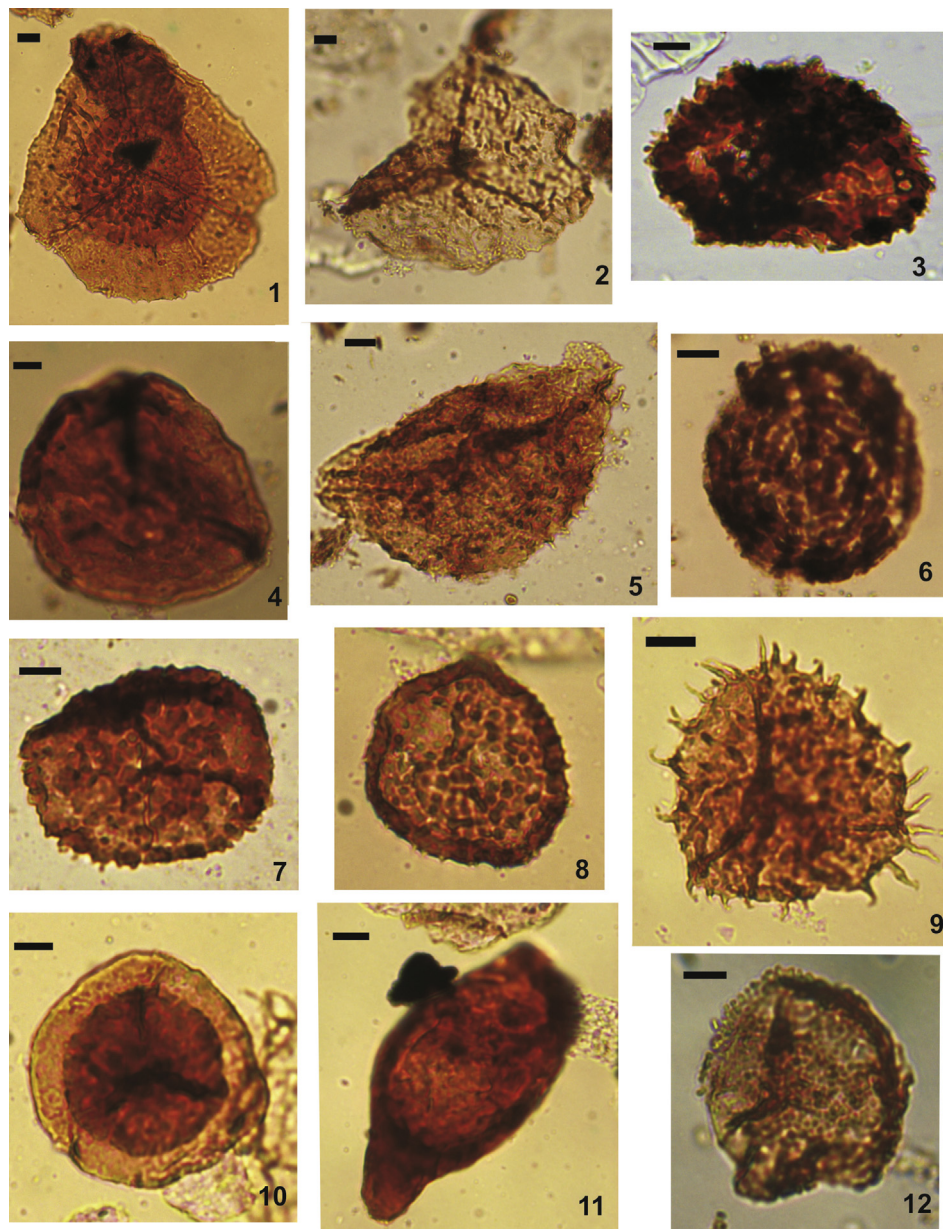


Fig. 7. Selected species of palynomorphs from the Los Monos and Iquiri formations recorded at the studied localities (see Fig. 3). (1) *Grandispora pseudoreticulata* (Menéndez and Pöthe de Baldis) Ottone. CICYTTP-PI 473(1): S13/0. (2) *Leiotriletes balapucensis* di Pasquo. CICYTTP-PI 104(1): P32/1. (3) *Densosporites inaequus* (McGregor) McGregor and Camfield. CICYTTP-PI 102(1): J44/1. (4) *Geminospora lemurata* Balme emend. Playford. CICYTTP-PI 104(1): O44/1. (5) *Samarisporites triangulatus* Allen. CICYTTP-PI 109(1): R48/0. (6) *Chomotriletes vedugensis* Naumova. CICYTTP-PI 106(1): S50/3. (7) *Acinosporites eumammillatus* Loboziak, Strel, Burjack. CICYTTP-PI 109(1): W51/0. (8) *Geminospora piliformis* Loboziak, Strel, Burjack. CICYTTP-PI 473(1): E43/0. (9) *Ancyrospora langii* (Taugourdeau-Lantz) Allen. CICYTTP-PI 473(1): N54/3. (10) *Auroraspora macra* Sullivan. CICYTTP-PI 473(1): E53/1. (11) *Cornispora* sp. CICYTTP-PI 473(1): F57/4. (12) *Endoculeospora altobellii* di Pasquo. CICYTTP-PI 473(1): Z50/0. Scale bar = 10 μ m.

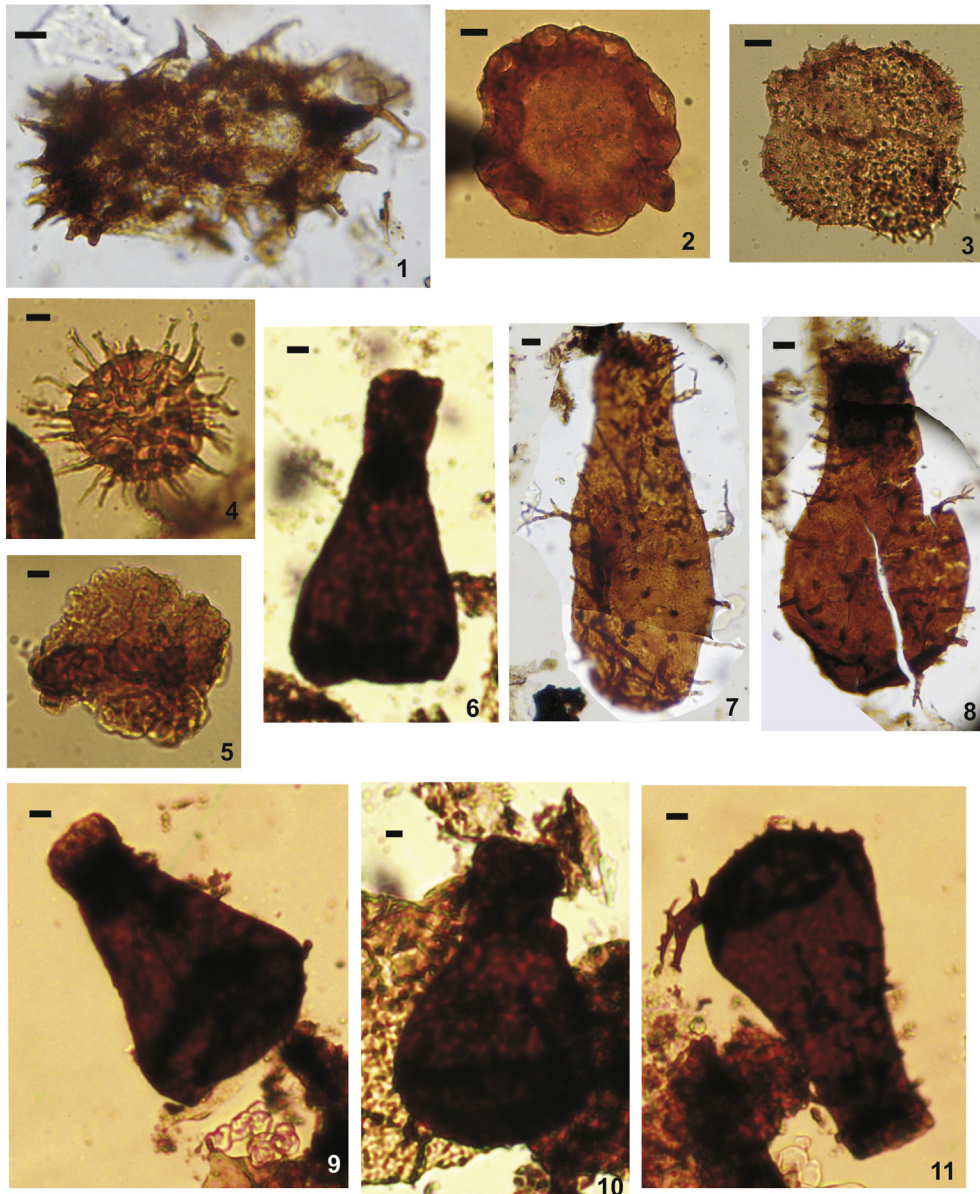


Fig. 8. Selected species of palynomorphs from the Los Monos and Iquiri formations recorded at the studied localities (see Fig. 3). (1) *Crystisporites horridus* (Hacquetard) McGregor and Camfield. CICYTTP-PI 1233(1): Y47/1. (2) *Maranhites mosesii* (Sommer) Brito. CICYTTP-PI 473(1): B45/1. (3) *Quadrisporites horridus* Hennelly ex Potonié and Lele. CICYTTP-PI 473(1): A44/3. (4) *Gorgonisphaeridium furcillatum* Wicander and Playford. CICYTTP-PI 473(1): E49/1. (5) *Botryococcus*. CICYTTP-PI 473(1): K57/4. (6) *Belonechitina hofeltzii* Ottone. CICYTTP-PI 106(1): T58/0. (7) *Ramochitina boliviensis* Grahn. CICYTTP-PI 1233(1): T40/1. (8) *Ramochitina ramosi* Sommer and van Boekel. CICYTTP-PI 1233(1): Z52/1. (9) *Ramochitina autasmirimense* Grahn and Melo. CICYTTP-PI 311(1): E38/4. (10) *Angochitina galarzae* Ottone. CICYTTP-PI 106(1): U38/0. (11) *Ramochitina stiphrospinata* Grahn and Melo. CICYTTP-PI 311(1): E38/4. Scale bar = 10 μ m.

presented by di Pasquo (2007) support the Middle Devonian age of this plant interval in the Los Monos Formation, based on the stratigraphic distribution of diagnostic palynomorphs. Two assemblages (A1 and A2, Fig. 3), contained abundant plant debris (cuticles, tracheids, other brown to black phytoclasts) and amorphous organic matter, where the proportion of major palynological groups (spores, acritarchs, prasinophytes, chitinozoan, others) is variable in different samples. The A1 (mid-late Eifelian) is dominated by terrestrial palynomorphs, and spore species of *Grandispora* are abundant associated with scarce marine palynomorphs, represented by chitinozoans and prasinophytes/acritarchs (sphaeroidal forms without processes). Molds of crinoid stems are also documented (see Fig. 5.7, and di Pasquo et al., 2009, Fig. 4). A shallow marine shelf was interpreted for this section based on the

presence of invertebrates and other marine microplankton. This interpretation agrees with the general framework presented by Albariño et al. (2002), whereby the Balapuca section during late Emsian to late Givetian time is located at the margin of the marine basin. These data provided more information on the paleogeography of the Givetian of these regions, with new information on locations of the emergent areas (i.e., continental or at least transitional areas, di Pasquo et al., 2009; see Fig. 1).

The overlying palynoassemblage A2 is very similar but slightly more diverse, comprising spore species along with scarce prasinophytes/acritarchs (sphaeroidal forms without processes) and chitinozoans. Abundant but poorly preserved debris of the same lycophyte are recorded in these beds along with microscopic tracheids, cuticles, charcoal and many specimens of *Grandispora* and

4.2.4. Mataral

Some poorly preserved stems of indeterminate species of *Haplostigma* and *Paleostigma* (Fig. 5) were obtained from the Los Monos Formation at Mataral (Fig. 3). Two assemblages of invertebrates were observed at the top of the Los Monos Formation (In-M1, *Nuculites oblongatus*), and at the top of the Huamampampa Formation (In-M2, *Conularia quichua*, indeterminate gastropod). In Bolivia, *Nuculites oblongatus* was identified from the Emsian *Conularia quichua* Zone Limachi et al. (1996), up to the Frasnian (Dalenz-Farjat, 1993; Blicke et al., 1996). Thirteen (of sixteen) samples yielded spores and marine planktonic groups (acritarchs, prasinophytes, chitinozoans) variable in abundance and preservation that allowed constraining the age of the units to the Eifelian and Givetian respectively (e.g., spores *Acinosporites acanthomammillatus*, *Grandispora protea*, acritarchs *Maranhites insulatus*, *Estiastra rhytidia*, *Exochoderma arca*).

5. Biostratigraphic discussion and correlation

The plant fossil record from Middle to Late Devonian in South America and especially in Bolivia and northern Argentina (e.g. Limachi et al., 1996; di Pasquo et al., 2009; Edwards et al., 2009; Matsumura et al., 2013, 2014) is poorly known. There appear to be many hiatuses in between the plant assemblages documented up to now (Fig. 9). Plant remains are often found in mudstones to fine-grained sandstones in general. These lithologies occur in our sections as well (see Fig. 3). The limited reports of Devonian plants in southern South America are probably due to a combination of several factors such as, a) not many paleontologists/paleobotanists have searched for plants, b) morphological features of the Devonian plants are not easily preserved (e.g. they are mostly herbaceous), c) taphonomic problems prevented their preservation (e.g. long distance transport, high energy depocenters). This poor record contrasts with the Devonian plant record from northern Hemisphere (Fig. 9) as summarized by Edwards et al. (2000). Interestingly, fewer differences are recognized between the palynozones on chitinozoans and spores from North America and Europe and South America as discussed by Grahn (2005) and di Pasquo et al. (2009).

The ages and correlation of the stratigraphic units with new records of lycophytes in each locality (Fig. 3) were derived from occurrences of relevant palynological and invertebrate information presented above. A preliminary information was presented by di Pasquo et al. (2013) that summarised the palynological results from the shales and siltstones bearing *Haplostigma* at Mataral, Yesera, and Balapuca. They yielded mostly terrestrial palynomorphs with *Grandispora pseudoreticulata* and other Eifelian (i.e. *Densosporites inaequus*, *Leiotriletes balapucensis*, *Verrucosporites scurris*) to Givetian species (e.g. *Geminospora lemurata*, *Archaeozonotriletes variabilis*, *Chomotriletes vedugensis*, *Verruciretusispora ornata*, *Chelinospora ligurata*, *Samarisporites triangulatus*), with fewer microplanktonic species (i.e. acritarchs, prasinophytes, chitinozoans). Among chitinozoans, *Ramochitina autasmirimense*, and *R. stiphrospinata*, are mainly found at Angosto del Pescado, while *R. ramosi* and *R. boliviensis* at Yesera. The endemic chitinozoans *Belonechitina holfeltzii* and *Angochitina galarzae* (Givetian-Frasnian in Ottone, 1996) are also present at Yesera. These assemblages are related to the late Eifelian up to earliest Frasnian *Grandispora permulta* (Per) and *Geminospora lemurata*-*Chelinospora* ex *Gr. ligurata* (LLi) and *S. triangulatus* (Trg) Zones Melo and Loboziak (2003) from Brazil and *R. ramosi* to *Ancyrochitina taouratinensis* Zones Grahn (2005) from Bolivia (Fig. 9).

Haplostigma was found in the Iquiri Formation only at Yesera Centro, and it was associated with the spores *Acinosporites eumammillatus*, *Ancyrospora langii*, *Auroraspora macra*, *Cornispora* sp., *Endoculeospora altobellii*, *Geminospora piliformis*, and the

acritarchs *Maranhites insulatus*, *Ammonidium garrasinoi*, *Crucidia camirensis*, *Verhyachium pannuceum*, *Gorgonisphaeridium furcillatum*, *Gorgonisphaeridium ohioense*. This assemblage suggests a Givetian-Frasnian up to early Famennian age in comparison to similar palynofloras in Brazil and elsewhere (Fig. 9; see Grahn, 2005; di Pasquo et al., 2009). Noticeably, *Quadrisporites horridus* and *Botryococcus* (green algal remains) occur in the Iquiri Formation. From Yesera Dique the samples for palynology were barren. Thus, the presence of the poorly preserved and incomplete brachiopod likely related to *Rhipidothyris ava* associated to *Haplostigma* in this section and at Yesera Centro supported their correlation (Fig. 3). These chronological data confirmed a Givetian age for most of the occurrences of the deposits bearing *Haplostigma* and extended them up to the early Famennian in the studied sections in Bolivia and northern Argentina (Figs. 9 and 10). Possible Eifelian occurrences are not discarded but they need new recoveries.

6. Paleobiogeography

From the Middle to Late Devonian (Eifelian to Frasnian), herbaceous lycopsids grouped in the genus *Haplostigma* became dominant during the Eifelian/Givetian interval in South America (di Pasquo et al., 2009; Moisan et al., 2011). Hence, the *Haplostigma* Flora Limachi et al. (1996) developed in Bolivia (Fig. 9) is characterized by low diversity herbaceous lycophytes (mainly *Haplostigma* morphospecies). These are floras typical in high latitudes but with a more complex morphology than the *Cooksonia*-like taxa from late Silurian-Early Devonian in this region (Fig. 9). Based on the reconstruction of the paleoclimatic zones here, reproduced from Scotese in Cingolani et al. (2002; see Fig. 10), these floras appear to have developed around 55°–75° S palaeolatitude in Southern Gondwana mostly during the Eifelian – Givetian (Argentina, Bolivia, Brazil, South Africa, Antarctica, Australia). Frasnian records are known from the marginal region of southern Gondwana (Argentina, Bolivia, Chile, South Africa, Antarctica, Australia). In contrast, Early Famennian records are described in Chile (Moisan et al., 2011) and South Africa (Anderson and Anderson, 1985), as well as in Bolivia at Yesera (Figs. 2.1, 3, 10), based on the current and prior information summarised by Cingolani et al. (2002), di Pasquo et al. (2009) and Moisan et al. (2011). The Afrosouthamerican Subrealm (Fig. 10) should be extended to include the Antarctica records that are found at palaeolatitudes higher than ca. 50°S (Fig. 10), although more studies and collections are needed, because some compositional differences are locally documented along southern Gondwana (Edwards, 1990; Cingolani et al., 2002). Australian occurrences of *Haplostigma lineare* are the exception to those high latitude records, as it is found at ca. 30° South paleolatitude into a slightly more diverse plant assemblage so it could be maintained outside of the subrealm till having more studies (see di Pasquo et al., 2009).

A comparison with the floras from the northern equatorial zone, during the Eifelian-Early Famennian shows that more than one endemic floral realm (Fig. 9), which appeared to be climatically (latitudinally) influenced (Berry, 1996; Edwards et al., 2000). These differences with the *Haplostigma* Flora include the fossil plant records from northern South America and Africa, where the lycophyte *Haskinsia* Grierson and Banks from Venezuela and other related species confirm that several paleofloristic realms existed (Berry and Edwards, 1996; see also Cingolani et al., 2002). Possible terrestrial connections between northern and southern Hemispheres may have existed, based on coeval palynology that suggests a narrow Rheic Ocean between Gondwana and Euramerica at least since the Lochkovian (Steemans et al., 2007), based on palynological evidence from Saudi Arabia. Scotese et al. (1999) explained that during the “Hot House” periods, the warm and cool temperate belts

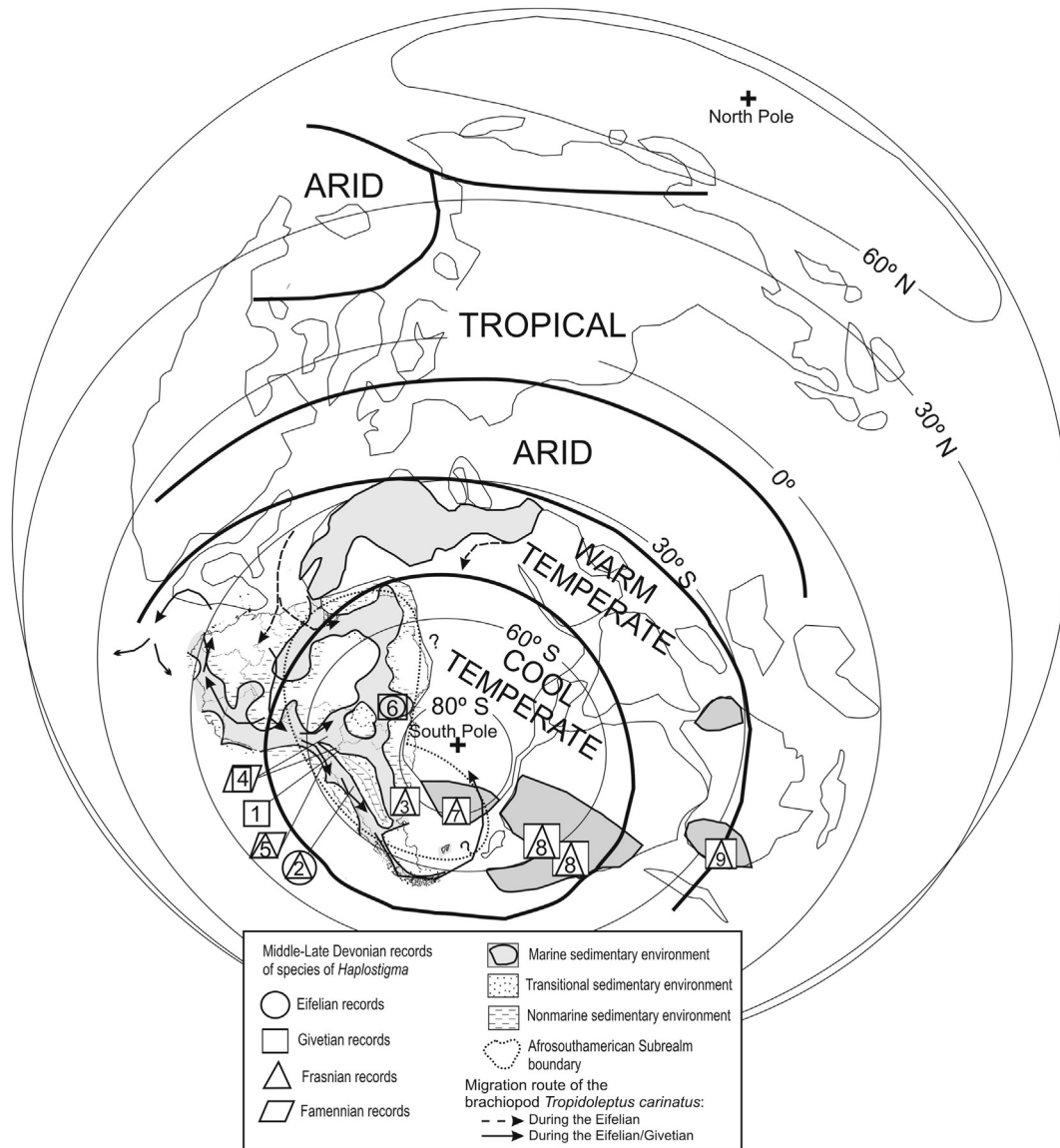


Fig. 10. Selected records of the genus *Haplostigma* (Lycophyte) documented in South America and elsewhere in Gondwana in the Middle Devonian paleogeography illustrated by di Pasquo et al. (2009) and Moisan et al. (2011). The position of the Afrosouthamerican Subrealm and land – sea distribution of deposits in Gondwana is modified from di Pasquo et al. (2009). References: **Argentina** (1–3). **1.** Tarija Basin. **1.A.** Angosto del Pescado, Pescado and Los Monos formations (Givetian, this study). **1.B.** Balapuca, Los Monos Formation (Givetian, this study). **2.** Precordillera. **2.A.** Punta Negra Formation (Eifelian–Givetian; Baldis and Peralta, 2000). **2.B.** Chigua Formation (Eifelian–early Frasnian; Gutiérrez, 1996; Gutiérrez and Archangelsky, 1997; di Pasquo et al., 2009; Amenábar et al., 2009). **3.** Sierras Australes, Lolén Formation (Givetian–early Frasnian; Cingolani et al., 2002). **4.** **Bolivia**, Tarija Basin. **4.A.** Sella, Huamampampa Formation (Finca Carlazo, Branisa, 1965). **4.B.** Yesera, Los Monos (Givetian) and Iquiri (Frasnian–early Famennian) formations (this study). **4.C.** Balapuca, Los Monos Formation (Givetian, di Pasquo, 2007 and this study). **4.D.** Mataral, Los Monos Formation (Givetian, Limachi et al., 1996 and this study). **5.** **Chile**, Antofagasta region, El Toco Formation (indefinite Late Devonian, Moisan et al., 2011). **6.** **Brazil**, Paraná Basin, Ponta Grossa e Sao Domingos formations (Eifelian–Givetian; Kräusel, 1960; Bosetti et al., 2011; Grahn et al., 2013; Matsumura et al., 2013, 2014, 2015). **7.** **South Africa**, Cape Basin (Givetian–?Famennian; Seward, 1932; Plumstead, 1967; Anderson and Anderson, 1985). **8.** **Antarctica** (Givetian–Frasnian; Grindley et al., 1980; Edwards, 1990; McLoughlin and Long, 1994; Bradshaw, 2013). **9.** **Australia**, New South Wales (Givetian–Frasnian; McLoughlin and Long, 1994).

extended to the pole and the polar climate zone did not exist. Our *Haplostigma* assemblages are found in association with palynomorphs (di Pasquo, 2005, 2007, 2013; di Pasquo et al., 2009, 2013), characterized by abundant species of *Grandispora*, particularly the endemic *G. pseudoreticulata*. Both endemic forms along with others (e.g. *Leiotriletes balapucensis*, *Belonechitina holfeltzii*) were also used to define the Afrosouthamerican Subrealm (di Pasquo et al., 2009). Nevertheless, the occurrences of some Euramerican spore species in the assemblages of the cooler Afrosouthamerican Subrealm (see di Pasquo et al., 2009, their database Chart 1a–c), support the development of terrestrial connections used for exchanging of cosmopolitan species, more tolerant to

different paleoclimatic conditions in both regions (McGregor and Playford, 1992; Streele and Loboziak, 1996). Streele and Loboziak (1996) used several endemic taxa such as *Archaeoperisaccus* (e.g. Braman and Hills, 1985; Streele et al., 1990; Hashemi and Playford, 2005), to delimit the Northern Euramerica phytogeographical province. In northern Argentina *Archaeoperisaccus* was scarcely documented in Givetian–Frasnian deposits (Ottone, 1996) and as part of the Devonian reworked group of palynomorphs from the Pennsylvanian Macharetí Group in northern Argentina (di Pasquo, 2003). This exchange of species showing connection with equatorial regions is also suggested by brachiopod occurrences, such as *Tropidoleptus carinatus* (Fonseca and Melo, 1987; Isaacson and

Perry, 1977) and several microplankton species (Figs. 9 and 10; Quadros, 1999; di Pasquo et al., 2009). Even our tentatively identified species of brachiopod associated with *Haplostigma* in the Iquiri Formation at Yesera Centro and Dique are only comparable to *Rhipidothyris* due to their fragmentary condition. The occurrence of an equivalent to *Rhipidothyris ava* stratigraphically above *Tropidoleptus* in Libya is like their occurrences in Bolivia as well. This further supports the suggestion of a marine connection with Libya, via the Amazonas Basin in Givetian - Frasnian time and supports the paleogeographical reconstruction presented by Heckel and Witzke (1979) used by several authors (Streel et al., 1990; Wood, 1995; Cingolani et al., 2002; di Pasquo et al., 2009) to map Givetian-Frasnian phytogeography with a very narrow Rheic Ocean (Fig. 10).

7. Conclusions

New collections of herbaceous lycophytes come from Middle to Late Devonian Pescado, Los Monos and Iquiri formations in northern Argentina (Angosto del Pescado, Balapuca) and Bolivia (Balapuca, Yesera, Mataral; Figs. 2.1 and 3), and the specimens collected constitute curated collections of two institutions in Argentina.

The plant assemblages are composed of herbaceous stems of lycophytes preserved as compressions (with preserved cuticles). Impressions and a few casts, with two different morphologies were observed in the collections. The differences are mainly related to the phyllotaxis and width of the stems that supported the recognition of indeterminate species of *Haplostigma* and *Paleostigma* (Figs. 4–6), in agreement with current literature (Gutiérrez, 1996; Moisan et al., 2011; Matsumura et al., 2013). Their taxonomic assignment to specific level is beyond of the scope of this paper.

Associated to these plant intervals in each locality (Fig. 2.1), relevant palynological and invertebrate information allowed its dating from the Late Eifelian Givetian up to the earliest Famennian (Figs. 3 and 9).

Terrestrial connections between the localities presented here, and other regions in South America bearing similar Eifelian – Frasnian terrestrial palynofloras and floras, are part of the Afro-southamerican Subrealm, whose age now extends up to the early Famennian based on the new records at Yesera (Figs. 2.1 and 10).

A significant question remains: Why are so few/scarce plant species recorded as part of the *Haplostigma* Flora, when spores from terrestrial plants (associated in the same levels) are so diverse? A simple or even single explanation is unlikely, but we suggest that the *Haplostigma* plants, as well as other herbaceous remains (e.g. *Spongiophyton* Kräusel, *Paleostigma*), could have lived close to the marine shoreline. Most of their records are found in marine deposits (mainly storm beds) associated with marine fossils (invertebrates, microplankton). So, if they were transported, it was not for long distances causing their deterioration (i.e., preventing their weathering in soils and fragmentation and biological degradation by microorganisms). However, the majority of the land plants that should have been established inward (farther from the shoreline), could not reach marine environments. The poorly preserved molds of invertebrates in our samples suggest they were transported into a shallow marine environment (shoreward from below storm wave shelf), and deposited together with lycophyte remains that were transported from proximal terrestrial environments.

Acknowledgments

A special acknowledgment is made to Drs. Jaime Oller and Luis Albariño, who helped M. di Pasquo in the stratigraphic work during

field trips in 2000 around Bolivia, and it is extensive to Drs. Ramiro Suárez Soruco and Mario Suárez for their contribution looking for plant specimens in their collections (2007). We thank to the reviewers (Drs. E. Ottone, M. Vergel, and anonymous) and the Editor, whose suggestions allowed the improvement of the manuscript. This research was supported with funds from *Consejo Nacional de Investigaciones Científicas y Técnicas* CONICET PIP 5518 (2005–2007), PIP 0305 (2011–2013), UBACYT X428 (2008–2010) and CGL2006-07376/BTE (2006–2009).

List of taxa with authority mentioned in the text.

Plants

Haplostigma lineare (Walkom) Mc Longhlin and Long 1994
Haplostigma furquei (Frenquelli) Gutiérrez 1996

Palynomorphs

Acinosporites acanthomammillatus Richardson 1965
Acinosporites apiculatus (Streel) Streel 1967
Acinosporites eumammillatus Loboziak, Streel, Burjack 1988
Ammonidium garrasinoi Ottone 1996
Ancyrochitina langei Sommer, Boekel 1964
Ancyrospora langii (Taugourdeau-Lantz) Allen 1965
Angochitina galarzae Ottone 1996
Apiculatasporites adavalensis (de Jersey) Balme 1988
Apiculatasporites microconus (Richardson) McGregor, Camfield 1982
Apiculatisporis grandis Menéndez, Pöthe de Baldis 1967
Apiculiretusispora laxa Amenábar, di Pasquo, Carrizo, Azcuy 2006
Archaeozonotriletes variabilis Naumova emend. Allen 1965
Auroraspora macra Sullivan 1968
Belonechitina holfeltzii Ottone 1996
Chelinospora ligurata Allen 1965
Chomotriletes vedugensis Naumova 1953
Contagisporites optivus (Chibrikova) Owens 1971
Corystisporites horridus (Hacquebard) McGregor, Camfield 1976
Corystisporites multispinosus Richardson 1965
Crucidia camirensis (Lobo Boneta) Ottone 1996.
Densosporites inaequus (McGregor) McGregor, Camfield 1976
Dibolisporites uncatatus McGregor, Camfield 1982
Endoculeospora altobellii di Pasquo 2007
Estiastra rhytidia Downie 1963
Exochoderma arca Wicander, Wood 1981
Geminospora lemurata Balme emend. Playford 1983
Geminospora piliformis Loboziak, Streel, Burjack 1988
Grandispora protea (Naumova) Moreau-Benoit 1980
Gorgonisphaeridium furcillatum Wicander, Playford 1985
Gorgonisphaeridium ohioense (Winslow) Wicander 1974
Grandispora douglstownense McGregor 1973
Grandispora inculta Allen 1965
Grandispora megaformis (Richardson) McGregor 1973
Grandispora pseudoreticulata (Menéndez, Pöthe de Baldis) Ottone 1996.
Leiotriletes balapucensis di Pasquo 2007
Maranhites insulatus Burjack, Oliveira 1989
Maranhites moesii (Sommer) Brito 1967 emend. Burjack, Oliveira 1989
Quadrisporites horridus Hennelly ex Potonié, Lele 1961
Ramochitina autasmirimensis Grahn, Melo 2004
Ramochitina boliviensis Grahn 2002
Ramochitina ramosi Sommer, Boekel 1964
Ramochitina stiphrospinata Grahn, Melo 2004

Retusotriteles maculatus McGregor, Camfield 1976
Samarisporites triangulatus Allen 1965
Verhyachium pannuceum Wicander, Loeblich 1976
Verruciretusispora ornata (Menéndez, Pöthe de Baldis) Pérez Leyton ex di Pasquo 2005.
Verrucosporites scurrus (Naumova) McGregor, Camfield 1982

Invertebrates

Conularia quichua (Ulrich in Steinmann and Döderlein 1890)
Nuculites oblongatus (Conrad 1841)
Rhipidothyris ava (Isaacson 1993)
Tropidoleptus carinatus (Conrad 1839)

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