Revista Brasileira de Paleontologia, 28(1):e20250485, 2025
A Journal of the Brazilian Society of Paleontology

doi:10.4072/rbp.2025.1.0485

Article

FIRST MACROFAUNAL EVIDENCE IN THE DEVONIAN CODO FORMATION FROM ARGENTINA AND INSIGHTS INTO THE YOUNGEST CALMONIID TRILOBITE RECORDS

JUAN JOSÉ RUSTÁN
Centro de Investigaciones en Ciencias de la Tierra (CICTERRA: CONICET-UN Córdoba). Av. Vélez Sarsfield 1611, CP X5016GCA, Córdoba, Argentina.
juan.jose.rustan@unc.edu.ar (Corresponding author)

JULIÁN DAVID ROLAN
Instituto de Geocronología y Geología Isotópica, Caba, Argentina.
julianrolan@gmail.com

JONATAN ARIEL ARNOL & NORBERTO JAVIER URIZ
División Geología, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata. Paseo del Bosque s/n, B1900FWA, La Plata, Buenos Aires, Argentina.
arnoljonatan@gmail.com, *norjuz@gmail.com*

ABSTRACT – We report the discovery of macrofauna in the Devonian Codo Formation, from the Precordillera of the San Juan Province, Argentina, based on a poorly preserved calmoniid trilobite. The cephalic remains resemble *Punillaspis argentina* previously reported in the late Givetian Chigua Formation, considered the lateral equivalent of the Codo Formation to the north. However, the thorax most closely resembles acastomorph calmoniids like *Pennaia* and relatives, widely distributed in the Early and Middle Devonian of Southwestern Gondwana (Malvinoxhosanic = Malvinokaffric Realm). Taking into account previous palynological evidence and the youngest stratigraphic records of calmoniid trilobites, the evidence supports most probably late Givetian age for the Codo Formation.

Keywords: calmoniids, trilobites, Malvinoxhosan Realm, Devonian, Argentina, Brazil.

INTRODUCTION

Lower to Middle Devonian trilobites from southern South America, South Africa and Antarctica have proven to be critical for elucidating geographic distribution patterns in order to recognize a major biogeographic Devonian unit known as the Malvinoxhosan (= Malvinokaffric) Realm (Clarke, 1913; Richter & Richter, 1942; Eldredge & Ormiston, 1979; Boucot & Racheboeuf, 1993; Penn-Clarke & Harper, 2021, 2023). Corresponding to cold waters of the austral circumpolar region of Southwestern Gondwana, some emblematic groups, like the family Calmoniidae Delo, 1935, are entirely endemic Malvinoxhosan and display one of the most spectacular diversifications in the history of trilobites (*e.g.*, Eldredge & Braniša, 1980; Abe & Lieberman, 2009, 2012).

However, due to the high endemism and the absence of marker groups (remarkably, graptolites and conodonts), Devonian basins of SW Gondwana lack biostratigraphic precisions based on macrofauna, and accurate stratigraphic correlations have become difficult sometimes even at regional to local scale. Palynostratigraphy has, therefore, become the main tool for supporting revised biostratigraphic schemes during the last few decades. This approach now provides a more robust framework for studying the geographic and stratigraphic distribution of macrofauna (*e.g.*, Amenábar & di Pasquo, 2008; Amenábar *et al*., 2009; Grahn *et al*., 2013; García Muro *et al*., 2017, 2018). Thus, a number of issues have finally been resolved, such as the problem about the diachronism of the classical biozone of the brachiopod *Scaphiocoelia* in the Lower Devonian (Dalenz Farjat *et al*., 2024).

In the particular case of Argentina, the record of trilobites has been highlighted by Baldis (1975) as relevant for developing local to regional biostratigraphic schemes, although just very preliminary insights have been considered up to date (*e.g.*, Rustán, 2016).

The bulk of Argentine Devonian trilobites comes from the Precordillera Basin, in western Argentina, mainly from the Lower Devonian Talacasto Formation (Padula *et al*., 1967), of the San Juan and La Rioja provinces (Baldis, 1975; Rustán *et al*., 2011). In turn, the Middle Devonian Chigua Formation from the San Juan Province also shows relatively diverse trilobite records (Baldis, 1967; Baldis & Longobucco, 1977; Amenábar *et al*., 2009; Allaire *et al*., 2024).

In this context, we report a Devonian calmoniid trilobite remain from the Codo Formation (Guerstein *et al*., 1965; Sessarego *et al*., 1990) in the Precordillera of the San Juan Province, a lithostratigraphic unit otherwise lacking macrofaunal

records. Although very poorly preserved, this discovery allows for preliminary comparison to some trilobites of the probably equivalent Chigua Formation and the older Talacasto Formation in the Precordillera. Stratigraphic distribution of calmoniids trilobites provides new precision into ages previously considered for the Codo Formation based on palynomorphs. Some remarks on the youngest records of calmoniids trilobites, on the basis of former Brazilian evidence and the new Argentinian ones, are also provided.

GEOLOGICAL SETTING AND STRATIGRAPHY

The Argentine Precordillera corresponds to a fold-thrust belt with a preponderant eastward vergence, forming the foothills of the Andean Mountain range between 29–33°S (Ramos *et al*., 1986; Allmendinger *et al*., 1990). Its stratigraphy is mainly composed of a thick Paleozoic sedimentary succession, with a marked absence of volcanic and pyroclastic deposits (Furque & Cuerda, 1979; Astini *et al*., 1995). The recorded sedimentary fill is initially linked with the development of a Cambro–Ordovician passive margin, evidenced by the presence of a widespread carbonate platform (*e.g*., Keller, 1999), overlain by Ordovician, Silurian and Devonian clastic sequences deposited in a foreland basin context (see Astini *et al*., 2005; Arnol *et al*., 2020).

The Western Precordillera (*sensu* Baldis & Chebli, 1969; Ortiz & Zambrano, 1981) is characterized by the presence of slope and platform deposits intercalated with oceanic basement volcanic rocks of Ordovician age (Boedo *et al*., 2021). Above these, strongly deformed marine clastic successions of Silurian-Devonian age are recorded (Von Gossen, 1997; Ariza *et al*., 2018, among others).

One of the most representative units of Devonian sedimentation within the context of the Western Precordillera is the Codo Formation (Guerstein *et al*., 1965; Sessarego *et al*., 1990). Outcrops of this unit occur on both margins of the San Juan River, near the town of Calingasta, where its type locality was defined along the Km 116, 117 and Del Tigre creeks (Figure 1). In the study area, the basal section of the unit does not outcrop, as the unit is in tectonic contact through the Alto de los Pajaritos Thrust with the Ordovician Don Polo Formation (Figure 1). Its top underlies in angular unconformity with Carboniferous sediments corresponding to the Del Ratón Formation (Guerstein *et al*., 1965; Sessarego, 1988; Baldis & Peralta, 1999; Amenábar & di Pasquo, 2008; Colombo *et al*., 2014; Gallastegui *et al*., 2014; Rolan *et al*., 2023a, b). The unit is composed of two main components: (i) fine to medium, and rarely coarse, sandstones of greenish to greenish-brown shades intercalated with (ii) siltstones and claystones of the same coloration (Sessarego *et al*., 1990). One of the most significant characteristics of the Codo Formation is its high degree of penetrative deformation evidenced by folding and thrusting (Alonso *et al*., 2008 Amenábar & di Pasquo, 2008; Gallastegui *et al*., 2014; Rolan *et al*., 2023a). Paleontological records found to date are scarce and limited to trace fossils (*i.e*., *Chondrites* according to Baldis, 1970) and palynological records (Amenábar & di Pasquo, 2008). These records mainly consist of acritarchs (*Lophosphaeridium* spp. and *Cerastum* sp.) and sparse and poorly preserved spores (*Apiculiretusispora* and *Cyclogranisporites*). The age of the unit was initially defined as Carboniferous (Guerstein *et al*., 1965). Later, based on a fertile palynological sample, stratigraphic relationships, and the presence of Visean age intrusions the age was referred to the Middle–Late Devonian (Sessarego, 1988; Sessarego *et al*., 1990). Further studies on palynomorphs (Amenábar & di Pasquo, 2008) supported a Givetian to Frasnian age.

MATERIAL AND METHODS

The Codo Formation is virtually devoid of macrofossils, our exceptionally rare trilobite finding was made only after several collecting trips to the locality. The specimen was found in the middle section of the unit, exposed on the southern side of Provincial Route 149, prior to reaching the Km. 117 Creek (Figure 1), within a fine-grained muddy dark greenish-gray siliciclastic interval (GPS 31°15'14.4" S/69°19'48.12" W).

The trilobite remain is about 1.5 cm long (exsagittal) and 1cm wide (transversely), including the left side of the cephalon poorly preserved and a few anterior (up to 7–8), outstretched, articulated, partial thoracic segments preserving light-colored exfoliated carapace (Figure 2A–F).

This specimen is housed in the collection of the Geological Research Institute Dr. Emiliano Pedro Aparicio at Universidad Nacional de San Juan, numbered as INGEO-PI-2305.

Two additional *Punillaspis argentina* (Baldis, 1967) calmoniid trilobite specimens (thoraces), coming from nodules of the upper part of the Chavela Member of the Chigua Formation at its type-area near Chigua, to the north of Malimán town, are illustrated for comparison herein (Figure 2L–N, P–R) and housed in the same collection. INGEO-PI- 2306 comes from the Chavela Creek at GPS 29°53'37.5" S/69°06'14.28" W. INGEO-PI- 2307 comes from the Don Justo Creek at GPS 29°54'25.8" S/69°06'25.3" W. These *Punillaspis* specimens are late Givetian in age, since they co-occur with the goniatite *Epitornoceras baldisi* (Leanza, 1968), as stated by Allaire *et al*. (2024).

A couple of specimens of the acastomorph calmoniid *Pennaia verneuili* (d´Orbigny, 1842), coming from the Middle Devonian of Bolivia are also illustrated for facilitating comparisons (Figure 2G–K, O–S). They are housed in the collection of the Centro de Investigaciones Paleobiológicas (**CIPAL**) at the CICTERRA building, under the prefix CEGH-UNC. Both represent infaunal molts preserved in nodules, as previously reported by Rustán *et al*. (2015). The specimen CEGH-UNC 27687 probably comes from the upper Belén Formation (most probably Middle Devonian) near Belén. It is important to note that after the recognition of goniatites in the base of the Huamampampa Formation at Campo Redondo, Bolivia (Troth *et al*., 2011), the laterally equivalent upper part of the Belén Formation yielding *Pennaia* should be considered not older than Eifelian.

CEGH-UNC 27688 comes from the overlying Sicasica Formation (Middle Devonian), near La Paz.

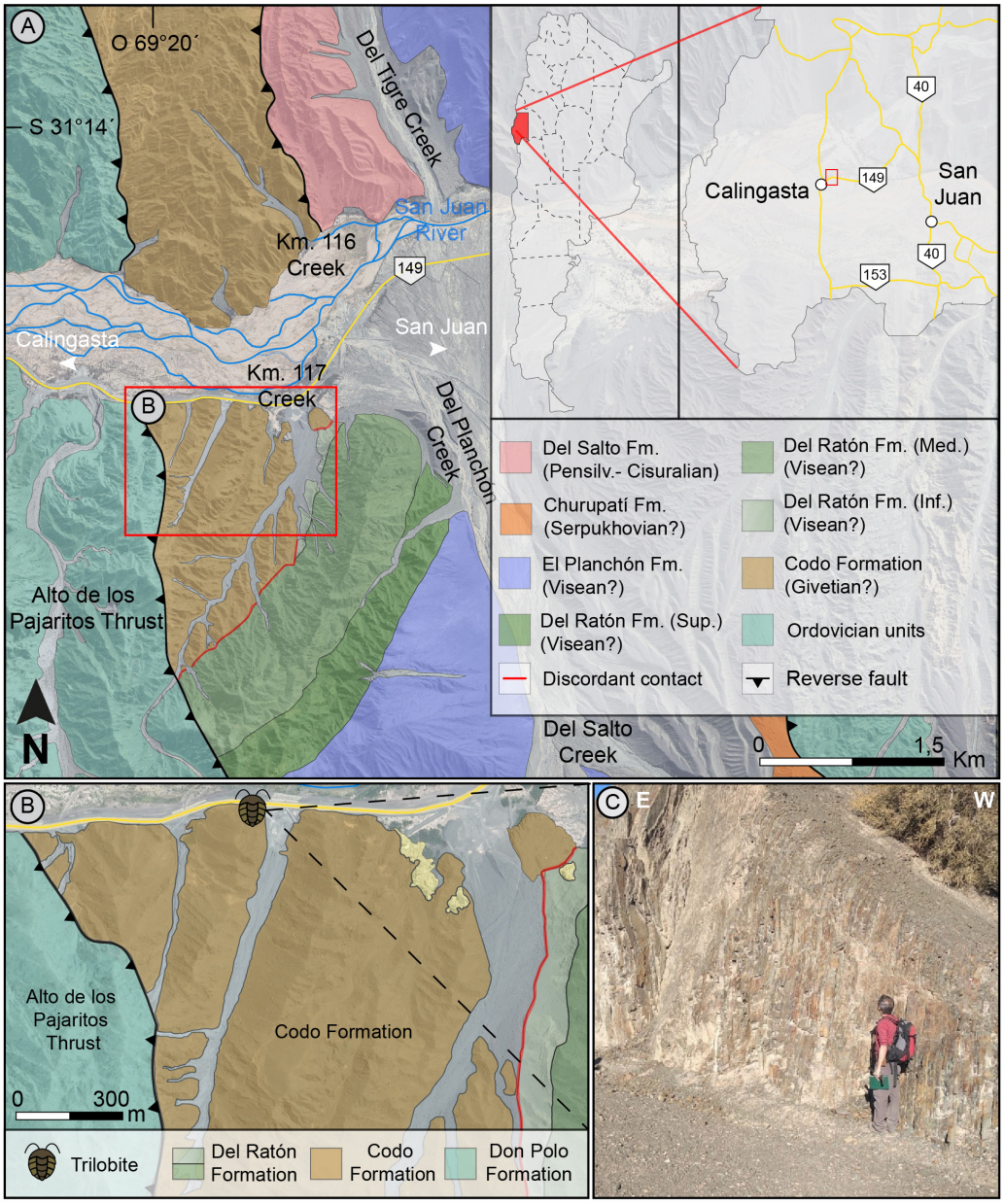

Figure 1. A, geological map and general stratigraphy of the study area located on the south margin of the San Juan River, next to the Route 149 linking San Juan and Calingasta, Argentina. **B**, detailed geological map showing fossil locality in the Codo Formation. **C**, general aspect of the Codo Formation of the fossil-bearing interval.

Fossils were prepared using pneumatic jacks and needles and then inked and whitened with ammonium chloride (NH_4Cl) sublimate, or reproduced in black latex casts of external molds, when necessary, for taking pictures under raking light using a *Canon* Power Shot S50 digital camera mounted on a *Leica* MZ75 binocular loupe.

SYSTEMATIC PALEONTOLOGY

Technical terms are abbreviated as traditional in trilobite descriptions: transversal/transversely (**tr.**), sagittal/sagittally (**sag.**), exsagittal/exsagittally (**exsag.**). Morphological terminology follows Whittington & Kelly (1997).

Superfamily ACASTOIDEA Delo, 1935
Family CALMONIIDAE Delo, 1935

Calmoniidae indet.
(Figure 2A–F)

Referred material. INGEO-PI-2305, a fragmentary thorax, Codo Formation, Givetian? (Middle Devonian), San Juan Province, Argentina.

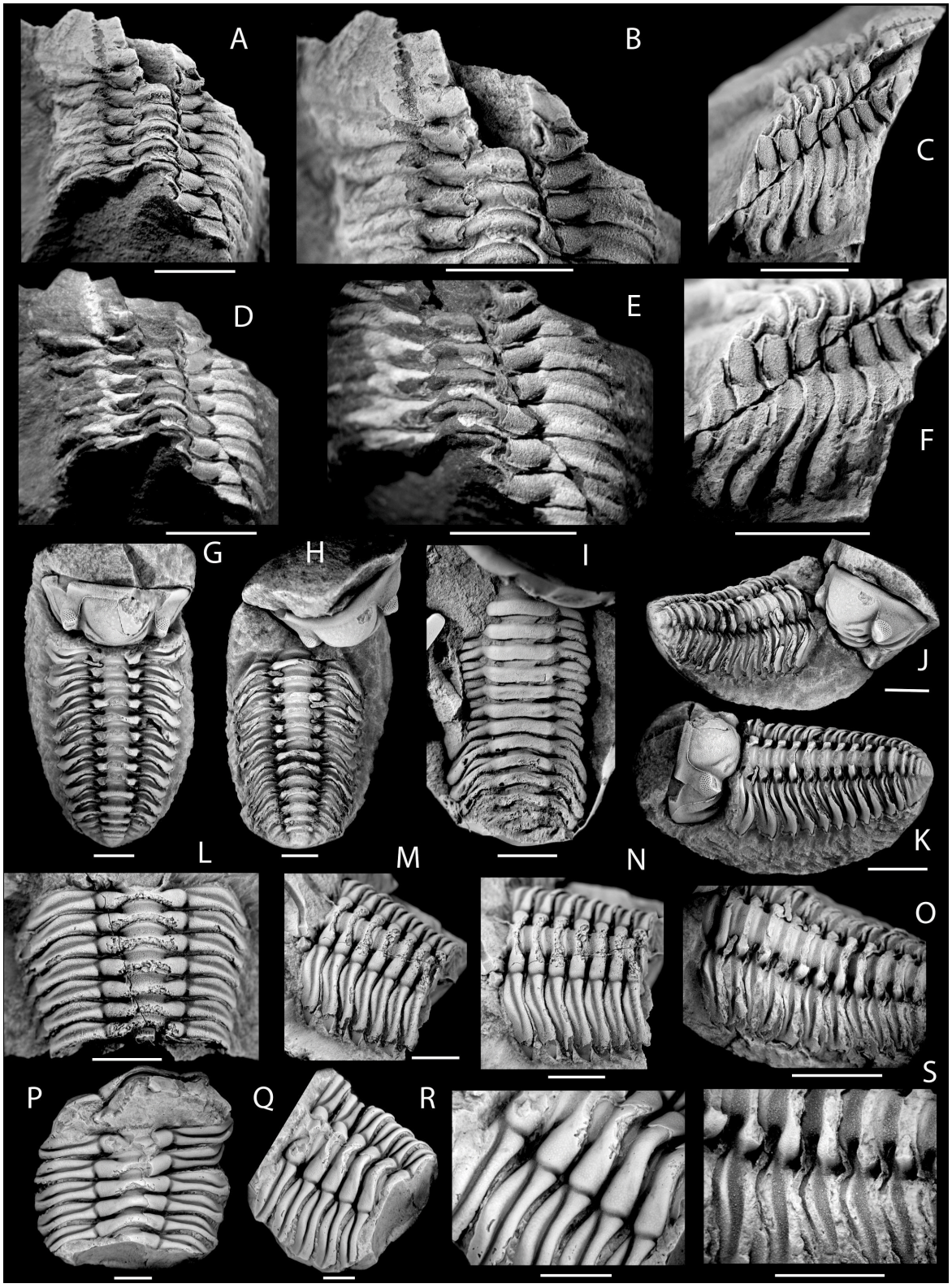

Figure 2. A calmoniid trilobite specimen, the first macrofaunal record of the Devonian Codo Formation, San Juan Province, Argentina, and some similar taxa for comparison. **A–F**, partial cephalon and thorax of the calmoniid specimen from the Codo Formation, INGEO-PI-2305; **A–E**, dorsal view (**D** and **E** without whitening in order to show exfoliation); **C** and **F** latero-dorsal view. **G–K, O, S**, the acastomorph calmoniid *Pennaia verneuili* (d'Orbigny, 1842), from the Middle Devonian of Bolivia; **G, K**, CEGH-UNC 27688, from the Sicasica Formation, near La Paz; **H–J, O, S**, CEGH-UNC 27687, from the upper part of the underlying Belén Formation, near Belén. **L–N, P–R**, the calmoniid *Punillaspis argentina* (Baldis, 1967), from the upper Givetian (Middle Devonian) of the upper part of the Chigua Formation (Chavela Member) in its type-area, San Juan Province, Argentina; **L–N**, INGEO-PI-2306, part of a thorax partially decorticated, from the Chavela Creek, **L**, dorsal view, **M–N**, latero-dorsal view; **P–R**, INGEO-PI-2307 part of a thorax preserving carapace, from the Don Justo Creek, **P**, dorsal view; **Q-R** latero-dorsal view. Scale bars = 5 mm.

DISCUSSION

Taxonomic remarks

Thoracic segments of our specimen do not suggest a trilobite referrable to Phacopidae, especially when taking into account their proximal pleural region (in between the axial furrow and fulcrum). For example, each thoracic segment does not show typical phacopid features as the anterior and posterior margin of each proximal part of pleurae nearly straight (when exfoliated), with a ridge-like anterior pleural band narrower than the posterior one, and pleural furrow deeply incised. In contrast, the proximal part of each pleurae shows the anterior margin gently convex forward, anterior and posterior pleural bands of similar height and width (exsag.), separated by a shallow and wide (exsag.) pleural furrow. In addition, although poorly preserved, the distal (external to fulcrum) region of pleurae appears to be narrow and elongated (exsag.), thus differing from the wide and rounded common morphology of Phacopidae, which develops a wide paddle-like articulating facet.

Conversely, such characters, in combination with the very wide axis, the very narrow (tr.) proximal pleural region, and the distal morphology and orientation of pleurae, indicate a calmoniid trilobite. Furthermore, the posterior left part of the preserved cephalon appears to show the typical S1 and L1 morphology of an acastid or acastomorph calmoniid.

In addition, within calmoniids, the seemingly very wide lateral and post-ocular fixigenal area suggests minute eyes. This character is typical of the calmoniid *Punillaspis argentina* (Baldis, 1967) only known from the Chigua Formation, in the San Juan Province, a lithostratigraphic unit interpreted as a lateral stratigraphic equivalent of the Codo Formation (Amenábar & di Pasquo, 2008). However, we consider that a reliable taxonomic assignment is not possible since a preservational artifact should not be excluded. Furthermore, the thorax of *Punillaspis* appears to differ from our specimen in having a proportionally narrower (tr.) axis, wider (tr.) proximal pleural region, lateral lobe of the axial ring more inflated and without an apodemal notch posteriorly located, and proximal portion of posterior pleural band adjacent to axial furrow more inflated and higher than the anterior pleural band. *Punillaspis* has, otherwise, been interpreted as a member of the derived *Metacryphaeus* group (Lieberman, 1993; Carbonaro *et al*., 2018). For comparative purposes, we provide illustrations of some *Punillaspis* thoraces coming from its type-area (Figure 2L–N, P–R).

Regarding other possible affinities for the new material we present, Edgecombe (1993) highlighted thoracic similarities between the basal acastomorph calmoniid *Andinacaste* Eldredge & Braniša, 1980, from the Silurian–Devonian transition of Bolivia and Argentina, and the secondarily convergent acastomorph *Pennaia* Clarke, 1913, particularly in the absence of spinous processes and presence of notches in the distal tips of pleurae behind of a slender articulating facet in the last thoracic segments.

The thoracic morphology of *Andinacaste* is however not well-illustrated, particularly in the case of the Argentinian *Andinacaste espejensis* Edgecombe, Waisfeld & Vaccari, 1994, from the Ludlow of the Los Espejos Formation, San Juan Province. The better-known thoracic morphology of *Andinacaste legrandi* Eldredge & Braniša, 1980, from the Lochkovian uppermost part of the Catavi Formation from central Bolivia, appears to differ from *Pennaia* and from our specimen in its slightly wider (tr.) axial lobe, without conspicuous lateral expansions, and pleurae with anterior pleural bands slightly shorter (tr.) and more fusiform in dorsal view. Coaptative structures, particularly nodes, and notches related to the articulating facet in the terminal portion of pleurae, cannot be observed in our specimen due to decortication so that a comparison is not warranted.

Pennaia represents another possibility. *Pennaia* (particularly species from the Devonian of Bolivia) had previously been assigned to *Acastoides* Delo, 1935. However, Eldredge & Braniša (1980) convincingly demonstrated that *Acastoides* is absent from the Devonian of Gondwana, since taxa referred to it are convergent with Silurian–Devonian Laurussian "true" *Acastoides* (also see Edgecombe, 1994, p. 56).

The taxonomic concept of *Pennaia* is somewhat vague due to the original diagnosis of Clarke (1913, p. 132). In addition, taxonomic assignments were usually supported on comparisons with similar genera, especially *Oosthuizenella* Cooper, 1982, *Phacopina* Clarke, 1913, *Calmonia* Clarke, 1913, and *Kozlowskiaspis* Braniša & Vaněk, 1973 (see Eldredge & Braniša, 1980; Cooper, 1982; Edgecombe, 1993). In some instances, assignments referred to earlier illustrations rather than to the presence of autapomorphies or diagnostic combinations of characters. The only mention of *Pennaia* in Argentina is by Waisfeld *et al*. (1994, p. 32), from uncertain levels of the Lower Devonian Talacasto Formation at Cerro El Peñón locality, San Juan Province.

All in all, the thorax of our specimen most closely resembles *Pennaia pupillus*, from the Devonian of the Bokkeveld Group, South Africa, as reported by Cooper (1982, fig. 53); *Pennaia pauliana* Clarke, 1913, from the Devonian of Brazil, and especially *Pennaia verneuili* (d'Orbigny, 1842), which is commonly found in the Pragian to Middle Devonian of the Icla, Belén and Sicasica formations from Bolivia. For a more direct comparison to *P. verneuili*, consult Edgecombe (1994, pl. 9) and see herein external and internal molds of specimens from the Belén Formation (Figure 2G–K, O–S).

The monotypic *Oosthuizenella*, from the Devonian of South Africa and Malvinas Islands, has been considered sister taxon to *Pennaia*. *Oosthuizenella ocellus* (Lake, 1904) was compared to *Pennaia* by Cooper (1982) and Edgecombe (1994) but differs from our specimen in having a more inflated lateral part of the axial ring; anterior pleural band adjacent to the axial furrow narrower (tr.) than the posterior one, more fusiform in shape; and pleural furrow narrower (exsag.), deeper and straighter.

Although *Phacopina* Clarke, 1913, is also a typical acastomorph calmoniid very close to *Pennaia*, its thoracic morphology (consider *P. convexa* Eldredge & Braniša, 1980, fig. 22) subtly differs from *Pennaia* and from our specimen in having bigger apodemal notches posterior to the lateral part of the semiarticulating half-ring (visible in internal molds) and a

wider (sag.) axial ring, which also appears to be slightly more gently expanded laterally.

Calmonia is widely distributed in the Lower to Middle Devonian of South America. However, the type species *C. signifer* Clarke, 1913 from Brazil, differs from our specimen in having a proportionally wider (tr.) pleural region (*i.e*., proportionally wider axial lobe), axial rings seemingly more gently and gradually expanding laterally, and distal pleural region not so inclined laterally external to the fulcrum.

Kozlowskiaspis Braniša & Vaněk, 1973 (particularly *K. superna*, see Eldredge & Braniša, 1980, fig. 27) differs in having a more inflated lateral part of axial rings, anterior pleural band narrower (tr.) than the posterior one adjacent to the axial furrow, and pleural furrow narrower (exsag.), deeper and straighter, more posterolaterally directed and distal pleural region not so inclined external to the fulcrum.

Hence, we preliminary hypothesize our specimen might possibly correspond to *Punillaspis* according to cephalic characters, although thoracic ones seem to resemble acastomorph calmoniids close to *Pennaia*.

Some insights into the stratigraphic range of calmoniid trilobites

Calmoniid trilobites have a confirmed Silurian to upper Middle Devonian stratigraphic range, with a single mention of a lower Upper Devonian record in Brazil. Earliest records derive from the Llandovery to Wenlock of the Lipeón Formation, northwestern Argentina (Baldis *et al*., 1976; Rubinstein & Toro, 2006); the Ludlow of the Los Espejos Formation, western Argentina (Edgecombe *et al*., 1994); and the Prídolí to probably Lochkovian of the El Carmen Formation from eastern Bolivia (Edgecombe & Fortey, 2000).

In turn, based on palynomorphs and stratigraphic correlation provided by Grahn *et al*. (2010, 2013), the youngest records of calmoniid trilobites derive from the Middle–Late Devonian transition from the Paraná Basin in Brazil (Carbonaro *et al*., 2016, 2018). These records include: (i) *Metacryphaeus australis* (Clarke, 1913) from the lithostratigraphic Unit 4 of the Chapada Group (Alto Garças Sub-Basin, in the north) and also from the equivalent upper part of the São Domingos Formation (Apucarana Sub-Basin, in the south); and (ii) *Metacryphaeus tuberculatus* (Kozlowski, 1923) from the uppermost levels of the Unit 4 of the Chapada Group.

The records of *Metacryphaeus australis,* however, appear to be no younger than Givetian. On one hand, the stratigraphic position of the record of *M. australis* from the lithostratigraphic Unit 4 of the Chapada Group is lower than the interval that possibly ranges into the Frasnian according to Carbonaro *et al*. (2016, p. 561). On the other hand, following Grahn *et al*. (2013, p. 36) "The highest outcropping strata of the São Domingos Formation in the Apucarana Sub-basin are early Givetian (Sequence E) ...". Hence, a Late Devonian (early Frasnian) age would be possible to assume only for the record of the two *M. tuberculatus* specimens derived from the uppermost levels of the Unit 4 of the Chapada Group, at the locality of Doverlândia, as reported by Carbonaro *et al*. (2016). However, a Frasnian age has not been positively confirmed for *M. tuberculatus* in such locality but inferred from the Givetian–early Frasnian stratigraphic range of the palynomorph of the fossil-bearing interval.

One putative late Fammenian *Metacryphaeus* record has been reported from the Longá Formation, Parnaíba Basin, northeastern Brazil (see Carvalho & Ponciano, 2015). Specimens consist of a cephalon and a pygidium supposedly from the lower part of the unit cropping out at the Barreiras Farm, Elesbão Veloso street, Valença do Piaui City, Piauí State. This is the only one faunal fossiliferous locality of the unit. This record has been interpreted as dubious due to the Strunian age interpreted for the bearing levels. Therefore, we consider this locality merits further investigation in order to discard a stratigraphic misinterpretation. Consequently, we suggest that Late Devonian records of calmoniid trilobites should be considered putative or questionable for the moment.

In this biostratigraphic scenario, *Punillaspis argentina* from the Chigua Formation, western Argentina (Baldis, 1967; Baldis & Longobucco, 1977), seems to be one of the best dated youngest calmoniid occurrences. The Chigua Formation was interpreted as a lateral stratigraphic equivalent of the Codo Formation (Amenábar & di Pasquo, 2008), cropping out nearly 155 km to the north of the locality studied in this paper, to the north of Malimán town in the San Juan Province (Baldis, 1967). The *Punillaspis*-bearing levels of the Chigua Formation are located in the uppermost part of the unit (the upper part of the Chavela Member) which reliably corresponds to the upper Givetian based on the recent revision of the ammonoid *Epitornoceras baldisi* (Leanza, 1968) by Allaire *et al*. (2024).

Therefore, although Amenábar & di Pasquo (2008) suggested Givetian to Frasnian ages for the Codo Formation on the basis of palynomorphs, the new calmoniid record would suggest ages older than Late Devonian, at least for the trilobite-bearing level. We hypothesize that a (probably late) Givetian age is the most probable one for the trilobite record reported herein, supporting a correlation with the upper part of Chigua and São Domingos formations and the upper part of Unit 4 of the Chapada Group.

DATA AVAILABILITY STATEMENT

Data will be available upon request.

ACKNOWLEDGEMENTS

Reviewers greatly improved this paper. The National Scientific and Technical Research Council (CONICET), the National University of Córdoba, and the National University of La Plata provided support and facilities through their research institutes CICTERRA, INGEIS, and the Geology Division of the La Plata Museum. Alejandra Dalenz Farjat, Renato Pirani Ghilardi, and Cameron Penn-Clarke helped us discard unpublished data on Late Devonian calmoniid records.

FUNDING

The authors thank financial support provided by project PPID N044 (UNLP), granted to N. J. Uriz, PICT-2021-I-A-00968, granted to D. Balseiro, and PIP 11220200103192CO to B. Waisfeld.

AUTHOR CONTRIBUTIONS

Juan José Rustán: writing – original draft, conceptualizations, investigation, taxonomic and biostratigraphic analysis. Julián David Rolan: writing – review, editing; conceptualization, formatting. Jonatan Ariel Arnol: review, conceptualization. Norberto Javier Uriz: review, conceptualization. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have not used AI-assisted technologies to create, review, or any part of this article.

ETHICS

This work fulfills collecting authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

REFERENCES

Abe, F.R. & Lieberman, B.S. 2009. The nature of evolutionary radiations: a case study involving Devonian trilobites. *Evolutionary Biology*, **36**:225–234. *doi:10.1007/s11692-009-9060-0*.

Abe, F.R. & Lieberman, B.S. 2012. Quantifying morphological change during an evolutionary radiation of Devonian trilobites. *Paleobiology*, **38**:292–307. *doi:10.1666/10047.1*.

Allaire, N.; Rustán, J.J.; Korn, D.; Vaccari, N.E.; Ezpeleta, M. & Balseiro, D. 2024. The late Givetian (Middle Devonian) ammonoid *Epitornoceras* from Argentina (southwestern Gondwana). *Geodiversitas*, **46**:327–341. *doi:10.5252/geodiversitas2024v46a7*.

Allmendinger, R.W.; Figueroa, D.; Snyder, D.; Beer, J.; Mpodozis, C. & Isacks, B.L. 1990. Foreland shortening and crustal balancing in the Andes at 30 S latitude. *Tectonics*, **9**:789–809. *doi:10.1029/TC009i004p00789*.

Alonso, J.L.; Gallastegui, J.; García-Sansegundo, J.; Farías, P.; Rodríguez Fernández, L.R. & Ramos, V.A. 2008. Extensional tectonics and gravitational collapse in an Ordovician passive margin: the Western Argentine Precordillera. *Gondwana Research*, **13**:204–215. *doi:10.1016/j.gr.2007.05.014*.

Amenábar, C.R. & di Pasquo, M. 2008. Nuevos aportes a la palinología, cronología y paleoambiente de la Precordillera Occidental de Argentina: formaciones El Planchón, Codo (Devónico) y El Ratón (Mississippiano). *Acta Geológica Lilloana*, **21**:3–20.

Amenábar, C.R.; di Pasquo, M. & Azcuy, C.L. 2009. Palynofloras of the Chigua (Devonian) and Malimán (Mississippian) formations from the Precordillera Argentina: age, correlation and discussion of the D/C boundary. *Revista Española de Micropaleontología*, **41**:217–239.

Ariza, J.P.; Boedo, F.L.; Sánchez, M.A.; Christiansen, R.; Lujan, S.B.P.; Vujovich, G.I. & Martínez, P. 2018. Structural setting of the Chanic orogen (Upper Devonian) at central-western Argentina from remote sensing and aeromagnetic data. Implications in the evolution of the proto-Pacific margin of Gondwana. *Journal of South American Earth Sciences*, **88**:352–366. *doi:10.1016/j.jsames.2018.08.021*.

Arnol, J.A.; Uriz, N.J.; Cingolani, C.A.; Basei, M.A.S. & Abre, P. 2020. Provenance analysis of Devonian peripheral foreland basins in SW Gondwana, case of the Gualilán Group, Precordillera Argentina. *International Journal of Earth Sciences*, **109**:2467–2494. *doi:10.1007/s00531-020-01914-9*.

Astini, R.A.; Benedetto, J.L. & Vaccari, N.E. 1995. The early Paleozoic evolution of the Argentine Precordillera as a Laurentian rifted, drifted, and collided terrane: a geodynamic model. *Geological Society of America Bulletin*, **107**:253–273. *doi:10.1130/0016-7606(1995)107<0253:TEPEOT>2.3.CO;2*.

Astini, R.A.; Davila, F.M.; Gamundí, O.L.; Gómez, F.J.; Collo, G.; Ezpeleta, M.; Martina, F. & Ortiz, A. 2005. Cuencas de la región precordillerana. *In*: G.A. Chebli; J.S. Cortiñas; L.A. Spalletti; L. Legarreta & E. Vallejo (eds.) *Frontera exploratoria de la Argentina: Buenos Aires*, Instituto Argentino del Petróleo y Gas, p. 115–146.

Baldis, B.A. & Chebli, G. 1969. Estructura profunda del área central de la Precordillera sanjuanina. *In*: JORNADAS GEOLÓGICAS ARGENTINAS, 4, 1969. Actas, SBG, Buenos Aires, **1**:47–65.

Baldis, B.A. & Longobucco, M. 1977. Trilobites devónicos de la Precordillera noroccidental (Argentina). *Ameghiniana*, **14**:145–161.

Baldis, B.A. & Peralta, S.H. 1999. Silúrico y Devónico de la Precordillera de Cuyo y bloque de San Rafael. *In*: R. Caminos (ed.) *Geología Argentina*, Servicio Geológico Minero Argentino (SEGEMAR), p. 215–238.

Baldis, B.A.; Benedetto, L.; Blasco, G. & Martel, M.E. 1976. Trilobites silúrico-devónicos de la Sierra de Zapla (nordeste de Argentina). *Ameghiniana*, **13**:185–225.

Baldis, B.A.J. 1967. Some Devonian trilobites of the Argentine Precordillera. *In*: INTERNATIONAL SYMPOSIUM ON THE DEVONIAN SYSTEM, 1, 1967. *Papers*, Alberta Society of Petroleum Geologists, p. 789–796.

Baldis, B.A.J. 1970. *Estratigrafía del Devónico de la precordillera sanjuanina entre los paralelos 30 y 32*. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ph.D. Thesis, 168 p.

Baldis, B.A.J. 1975. Valoración de elementos faunísticos para una zonación y datación de edades en el Devónico inferior de la Precordillera Argentina. *In*: CONGRESO ARGENTINO DE PALEONTOLOGÍA Y BIOESTRATIGRAFÍA, 1, 1975. *Actas,* APA, p. 219–240.

Boedo, F.L.; Luján, S. P.; Ariza, J.P. & Vujovich, G.I. 2021. The mafic-ultramafic belt of the Argentine Precordillera: a geological synthesis. *Journal of South American Earth Sciences*, **110**:103354. *doi:10.1016/j.jsames.2021.103354*.

Boucot, A.J. & Racheboeuf, P.R. 1993. Biogeographic summary of the Malvinokaffric Realm Silurian and Devonian fossils. *Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos*, **13**:71–75.

Carbonaro, F.A.; Langer, M.C.; Nihei, S.S.; de Souza Ferreira, G. & Ghilardi, R.P. 2018. Inferring ancestral range reconstruction based on trilobite records: a study-case on *Metacryphaeus* (Phacopida, Calmoniidae). *Scientific Reports*, **8**:15179. *doi:10.1038/s41598-018-33517-5*.

Carbonaro, F.A.; Meira, F.V.E.; Leme, J.D.M.; Bosetti, E.P. & Ghilardi, R.P. 2016. *Metacryphaeus tuberculatus* and *Metacryphaeus australis* (Trilobita, Phacopida) from the Devonian of the Paraná Basin: taxonomy and paleobiogeography. *Ameghiniana*, **53**:552–564. *doi:10.5710/AMGH.23.06.2016.2966*.

Carvalho, M.D.G.P. & Oliveira Ponciano, L.C.M. 2015. The Devonian trilobites of Brazil: A summary. *Journal of South American Earth Sciences*, **64**:217–228. *doi:10.1016/j.jsames.2015.10.010*.

Clarke, J.M. 1913. Fósseis devonianos do Paraná. In: *Monografias do Serviço Geológico e Mineralógico do Brasil*, Rio de Janeiro, Serviço Geológico e Mineralógico do Brasil, p. 55–79; 326–332.

Colombo, F.; Limarino, C.O.; Spalletti, L.A.; Busquets, P.; Cardó, R.; Mendez-Bedia, I. & Heredia, N. 2014. Late Palaeozoic lithostratigraphy of the andean Precordillera revisited (San Juan province, Argentina). *Journal of Iberian Geology*, **40**:241–259. *doi:10.5209/rev_JIGE.2014.v40.n2.45311*.

Cooper, M.R. 1982. A revision of the Devonian (Emsian-Eifelian) Trilobita from the Bokkeveld Group of South Africa. *Annals of the South African Museum*, **89**:1–174.

d'Orbigny, A. 1842. *Voyage dans l'Amérique méridionale: (le Brésil, la république orientale de l'Uruguay, la République argentine, la Patagonie, la république du Chili, la république de Bolivia, la république du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832, et 1833*, Paris, P. Bertrand, vol. 3, Paléontologie, 188 p.

Dalenz Farjat, A.D.; Suárez Riglos, M.S.; Paulsen, O.L.; Soruco, R.S.; Leyton, M.A.P.; Ortiz, J.L. & Rios, G. 2024. Lower Devonian Diachronic *Scaphiocoelia* Biofacies in Western Gondwana. *Ameghiniana*, **61**:1–24. *doi:10.5710/AMGH.28.12.2023.3555*.

Edgecombe, G.D. 1993. Silurian acastacean trilobites of the Americas. *Journal of Paleontology*, **67**:535–548. *doi:10.1017/S0022336000024884*.

Edgecombe, G.D. 1994. Calmoniid trilobites from the Devonian Fox Bay Formation, Falkland Islands: systematics and biogeography. *Bulletin - New York State Museum*, **481**:55–68.

Edgecombe, G.D., & Fortey, R.A. 2000. Silurian trilobites from the El Carmen Formation, Bolivia. *Palaeobiodiversity and Palaeoenvironments*, **2**:329–355. *doi:10.1007/BF03043645*.

Edgecombe, G.D.; Waisfeld, B.G. & Vaccari, N.E. 1994. *Andinacaste* (Trilobita) from the earliest Devonian of Argentina. *Journal of Paleontology*, **68**:837–841. *doi:10.1017/S0022336000026275*.

Eldredge, N. & Ormiston, A.R. 1979. Biogeography of Silurian and Devonian trilobites of the Malvinokaffric Realm. *In*: J. Gray & A.J. Boucot (eds.) *Historical Biogeography, Plate Tectonics, and the Changing Environment*, Oregon State University Press, p. 147–167.

Eldredge, N. & Braniša, L. 1980. Calmoniid trilobites of the Lower Devonian *Scaphiocoelia* zone of Bolivia, with remarks on related species. *Bulletin of the American Museum of Natural History*, **165**:181–290.

Furque, G. & Cuerda, A.J. 1979. Precordillera de La Rioja, San Juan y Mendoza. *In*: J.C. Turner (ed.) *Geología Regional Argentina*, Academia Nacional de Ciencias, p. 455–522.

Gallastegui, G.; González Menéndez, L.; Rubio Ordóñez, Á.; Cuesta Fernández, A. & Gerdes, A. 2014. Origin and provenance of igneous clasts from late Palaeozoic conglomerate formations (Del Ratón and El Planchón) in the Andean Precordillera of San Juan, Argentina. *Journal of Iberian Geology*, **40**:261–282. *doi:10.5209/rev_JIGE.2014.v40.n2.45298*.

García Muro, V.J.; Rubinstein, C.V. & Rustán, J.J. 2017. Early Devonian organic-walled phytoplankton and miospores from the Precordillera Basin of San Juan, Argentina: biostratigraphic and paleobiogeographic implications. *Palynology*, **41**:138–157. *doi:10.1080/01916122.2017.1366191*.

García Muro, V.J.; Rubinstein, C.V.; Rustán, J.J. & Steemans, P. 2018. Palynomorphs from the Devonian Talacasto and Punta Negra formations, Argentinean Precordillera: new biostratigraphic approach. *Journal of South American Earth Sciences*, **86**:110–126. *doi:10.1016/j.jsames.2018.06.009*.

Grahn, Y.; Mauller, P.M.; Bergamaschi, S. & Bosetti, E.P. 2013. Palynology and sequence stratigraphy of three Devonian rock units in the Apucarana Sub-basin (Paraná Basin, south Brazil): additional data and correlation. *Review of Palaeobotany and Palynology*, **198**:27–44. *doi:10.1016/j.revpalbo.2011.10.006*.

Grahn, Y.; Mendlowicz Mauller, P.; Pereira, E. & Loboziak, S. 2010. Palynostratigraphy of the Chapada Group and its significance in the Devonian stratigraphy of the Paraná Basin, south Brazil. *Journal of South American Earth Sciences*, **29**:354–370. *doi:10.1016/j.jsames.2009.09.001*.

Guerstein, M.; Laya, H. & Pezutti, N. 1965. Bosquejo fotogeológico de la zona de "Las Juntas" (Dto. Calingasta, provincia de San Juan). *Acta Geológica Lilloana*, **7**:231–242.

Keller, M. 1999. Argentine Precordillera: sedimentary and plate tectonic history of a Laurentian crustal fragment in South America. *Geological Society of America*, **341**:131. *doi:10.1130/0-8137-2341-8.1*.

Kozlowski, R. 1923. Faune devonienne de Bolivie. *Annales de Paléontologie*, **12**:1–112.

Lake, P. 1904. The trilobites of the Bokkeveld Beds. *Annals of the South African Museum*, **4**:201–220.

Leanza, A.F. 1968. Acerca del descubrimiento de Ammonoideos Devónicos en la República Argentina. *Revista de la Asociación Geológica Argentina*, **23**:326–330.

Lieberman, B.S. 1993. Systematics and biogeography of the "*Metacryphaeus* group" Calmoniidae (Trilobita, Devonian), with comments on adaptive radiations and the geological history of the Malvinokaffric Realm. *Journal of Paleontology*, **67**:549–570. *doi:10.1017/S0022336000024902*.

Ortiz, A. & Zambrano, J.J. 1981. La provincia geológica Precordillera oriental. *In*: CONGRESO GEOLÓGICO ARGENTINO, 8, 1981. *Actas*, AGA, San Luis, **3**:59–74.

Padula, E.L.; Rolleri, E.O.; Mingramm, A.R.G.; Roque, P.C.; Flores, M.A. & Baldis, B.A. 1967. Devonian of Argentina. *In*: INTERNATIONAL SYMPOSIUM ON THE DEVONIAN SYSTEM, 1, 1967. *Papers*, Alberta Society of Petroleum Geologists, p. 165–199.

Penn-Clarke, C.R. & Harper, D.A. 2021. Early–Middle Devonian brachiopod provincialism and bioregionalization at high latitudes: a case study from southwestern Gondwana. *Geological Society of America Bulletin*, **133**:819–836. *doi:10.1130/B35670.1*.

Penn-Clarke, C.R. & Harper, D.A.T. 2023. The rise and fall of the Malvinoxhosan (Malvinokaffric) bioregion in South Africa: Evidence for Early-Middle Devonian biocrises at the South Pole. *Earth-Science Reviews*, **246**:104595. doi:10.1016/j.earscirev.2023.104595

Ramos, V.A.; Jordan, T.E.; Allmendinger, R.W.; Mpodozis, C.; Kay, S.M.; Cortés, J.M. & Palma, M. 1986. Paleozoic terranes of the central Argentine-Chilean Andes. *Tectonics*, **5**:855–880. *doi:10.1029/TC005i006p00855*.

Richter, R. & Richter, E. 1942. Die Trilobiten der Weismes-Schichten am Hohen Venn, mit Bemerkungen über die Malvinocaffrische Provinz. *Senckenbergiana*, **25**:156–279.

Rolan, J.D.; Arnol, J.A.; Uriz, N.J.; Cingolani, C.A.; Basei, M.A.S.; Abre, P.; Lugo, F.I. & Naipauer, M. 2023a. Análisis preliminar de la procedencia sedimentaria de la Formación Codo, Devónico de la Precordillera Occidental de San Juan. *In*: REUNIÓN ARGENTINA DE SEDIMENTOLOGÍA, 18, CONGRESO LATINOAMERICANO DE SEDIMENTOLOGÍA, 9,2023. *Actas*, Asociación Argentina de Sedimentología, p. 180.

Rolan, J.D.; Arnol, J.A.; Uriz, N.J.; Cingolani, C.A.; Basei, M.A.S.; Abre, P.; Lugo, F.I. & Naipauer, M. 2023b. Petrografía y Geocronología de la Formación del Ratón (Tournaisiano–Viseano Tardío?): evidencias de aportes de arco devónico-carbonífero en la Precordillera Occidental de San Juan. *In*: REUNIÓN ARGENTINA DE SEDIMENTOLOGÍA, 18, CONGRESO LATINOAMERICANO DE SEDIMENTOLOGÍA, 9, 2023. *Actas*, Asociación Argentina de Sedimentología, p. 181.

Rubinstein, C.V. & Toro, B.A. 2006. Aeronian (Llandovery, Lower Silurian) palynomorphs and graptolites from the Lipeón Formation, eastern Cordillera, north-west Argentina. *Geobios*, **39**:103–111. *doi:10.1016/j.geobios.2004.08.002*.

Rustán, J.J. 2016. Los trilobites devónicos de Precordillera Argentina: Sistemática, filogenia, bioestratigrafía y paleobiogeografía. Revista de la Facultad de Ciencias Exactas, *Físicas y Naturales*, **3**:133–143.

Rustán, J.J.; Vaccari, N.E. & Balseiro, D. 2015. Infaunal molting in Mid Paleozoic trilobites: new insights based on data from South America. *Strata*, **1**:124–125.

Rustán, J.J.; Vaccari, N.E. & Astini, R.A. 2011. Early Devonian trilobites from the Sierra de las Minitas, northernmost Precordillera (La Rioja Province), Argentina. *Ameghiniana*, **48**:226–241. *doi:10.5710/AMGH.v48i1(335)*.

Sessarego, H.L. 1988. *Estratigrafía de las secuencias epiclásticas devónicas a triásicas aflorantes al norte del río San Juan y al oeste de las Sierras del Tigre, provincia de San Juan*. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ph.D. Thesis, 330 p.

Sessarego, H.L.; Amos, A.J.; Teixeira, W.; Kawashita, K. & Remesal, M.A. 1990. Diques Eocarbónicos en la Precordillera Occidental, margen oeste de las Sierras del Tigre. Provincia de San Juan. *Revista de la Asociación Geológica Argentina*, **45**:98–106.

Troth, I.; Marshall, J.E.; Racey, A. & Becker, R.T. 2011. Devonian sea-level change in Bolivia: A high palaeolatitude biostratigraphical calibration of the global sea-level curve. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **304**:3–20. *doi:10.1016/j.palaeo.2010.10.008*.

Von Gossen, W. 1997. Early Paleozoic and Andean structural evolution in the Río Jáchal section of the Argentine Precordillera. *Journal of South American Earth Sciences*, **10**:361–388. *doi:10.1016/S0895-9811(97)00029-1*.

Waisfeld, B.G.; Edgecombe, G.D. & Vaccari, N.E. 1994. *Tormesiscus*, a new blind calmoniid trilobite from the Lower Devonian, Argentine Precordillera. *Geologica et Palaeontologica*, **28**:27–43. *doi:10.1016/S0016-6995(94)80257-2*.

Whittington, H.B. & Kelly, S.R.A. 1997. Morphological terms applied to Trilobita. *In*: R.L. Kaesler (ed.) *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1*, Geological Society of America and University of Kansas Press, vol. 1, p. 313–329.

Received: 17 June 2024. Accepted: 13 November 2024.

Associated editor: Sergio Martínez
Editor-in-chief: Matias do Nascimento Ritter