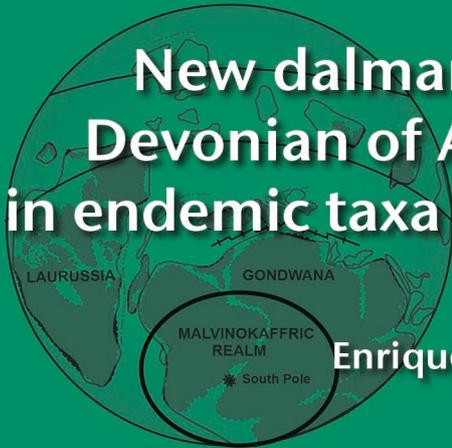




New dalmanitid trilobite taxa from the Lower Devonian of Argentina: comments on spinosity in endemic taxa from southern high paleolatitudes



Enrique A. RANDOLFE, Juan José RUSTÁN & Arnaud BIGNON



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ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

New dalmanitid trilobite taxa from the Lower Devonian of Argentina: comments on spinosity in endemic taxa from southern high paleolatitudes

Enrique A. RANDOLFE

Centro de Investigaciones en Ciencias de la Tierra: Consejo Nacional de Investigaciones Científicas y Técnicas-Universidad Nacional de Córdoba, Avenida Vélez Sarsfield 1611, Córdoba (X5016GCA) (Argentina)
enrique.randolfe@gmail.com (corresponding author)

Juan José RUSTÁN

Centro de Investigaciones en Ciencias de la Tierra: Consejo Nacional de Investigaciones Científicas y Técnicas-Universidad Nacional de Córdoba, Avenida Vélez Sarsfield 1611, Córdoba (X5016GCA) (Argentina)
and Universidad Nacional de La Rioja, Avenida Luis M. de la Fuente S/N, Ciudad Universitaria de la Ciencia y de la Técnica, La Rioja (F5300) (Argentina)
juanjorustan@gmail.com

Arnaud BIGNON

Centro de Investigaciones en Ciencias de la Tierra: Consejo Nacional de Investigaciones Científicas y Técnicas-Universidad Nacional de Córdoba, Avenida Vélez Sarsfield 1611, Córdoba (X5016GCA) (Argentina)
arnaudbignon@yahoo.fr

Submitted on 4 May 2020 | Accepted on 3 August 2020 | Published on 12 January 2022

[urn:lsid:zoobank.org:pub:1A719E89-49DC-4818-9821-BA8B97D2B654](https://doi.org/10.5852/cr-palevol2022v21a2)

Randolfe E. A., Rustán J. J. & Bignon A. 2022. — New dalmanitid trilobite taxa from the Lower Devonian of Argentina: comments on spinosity in endemic taxa from southern high paleolatitudes. *Comptes Rendus Palevol* 21 (2): 17-38. <https://doi.org/10.5852/cr-palevol2022v21a2>

ABSTRACT

Three new Lower Devonian dalmanitid trilobite taxa are recognized from the Talacasto Formation in the Precordillera Basin, Argentina, which includes two monospecific genera (*Ivanites leonorae* n. gen., n. sp. and *Aguaditaspis mediaspina* n. gen., n. sp.), and one additional new genus and species left in open nomenclature. These taxa combine characters of the subfamilies Dalmanitinae Vogdes, 1890 and Synphoriinae Delo, 1935, challenging their taxonomic distinction. Forty percent of the dalmanitids from high paleolatitudinal basins from southwestern Gondwana (Malvinokaffric) exhibit non-homologous dorsal spinosity. *Aguaditaspis mediaspina* n. gen., n. sp. shares similar spines with *Trypaulites calypso* (Hall, 1861). The unnamed new genus resembles the spinosity of endemic Malvinokaffric dalmanitids, like *Dalmanitoides* Delo, 1935 and *Fenestraspis* Braniša & Vaněk, 1973. Considered defensive, the recorded spinosity along with putative sublethal-attack marks, suggest higher predation pressure than previously thought at high paleolatitudes. This evidence is in accordance with some hypothesis on rising predation pressure in the mid-Paleozoic marine ecosystems.

KEY WORDS

Dalmanitidae,
Devonian,
Malvinokaffric,
predation,
spines,
trilobite,
new genera,
new species.

RÉSUMÉ

Nouveaux taxons de trilobites dalmanitidés du Dévonien inférieur d'Argentine : discussion sur les épines des taxons endémiques de hautes paléolatitudes australes.

Trois nouveaux taxons de trilobites dalmanitidés provenant de la formation Talacasto, du Dévonien inférieur, sont identifiés dans le bassin de la Précordillère, en Argentine. Deux nouveaux genres monospécifiques sont décrits (*Ivanites leonora* n. gen., n. sp. et *Aguaditaspis mediaspina* n. gen., n. sp.). Un spécimen additionnel, correspondant probablement à un nouveau genre et espèce, est laissé en nomenclature ouverte. Ces taxons présentent la combinaison de caractères diagnostiquant les sous-familles Dalmanitinae Vogdes, 1890 et Synphoriinae Delo, 1935, remettant en cause leur distinction taxonomique. Quarante pour cent des dalmanitidés de hautes paléolatitudes des bassins sud-ouest du Gondwana (Malvinokaffrik) montrent des épines dorsales non homologues. *Aguaditaspis mediaspina* n. gen., n. sp. partage des épines avec *Trypaulites calypso* (Hall, 1861). Le genre laissé en nomenclature ouverte a des épines proches de celles des dalmanitidés endémiques du Domaine Malvinokaffric, tels que *Dalmanitoides* Delo, 1935 et *Fenestraspis* Braniša & Vaněk, 1973. Les épines, considérées comme défensives, associées à l'enregistrement de marques probables d'attaques sublétales, suggèrent une contrainte de prédation plus importante sous les hautes paléolatitudes qu'on ne le supposait précédemment. Ces données soutiennent l'hypothèse d'une augmentation de la prédation dans les écosystèmes du Paléozoïque moyen.

MOTS CLÉS
Dalmanitidae,
Dévonien,
Malvinokaffric,
prédation,
épines,
trilobite,
genres nouveaux,
espèces nouvelles.

INTRODUCTION

The dalmanitid trilobites, abundant worldwide and diverse in the Silurian-Devonian, attracted comparatively little attention in basins of southwestern Gondwana. In spite of this, Eldredge & Ormiston (1979) had considered an important diversification of this family in these basins (basins of the Malvinokaffric Realm). At that time most of the information derived from a number of main works (e.g. Clarke 1890; Kozłowski 1923; Swartz 1925; Wolfart 1968) which assigned species to classic genera like *Dalmanites* Barrande, 1852 or *Odontochile* Hawle & Corda, 1847. Several new genera, endemic in this area, were subsequently erected by Braniša & Vaněk (1973). In recent years, those genera were revised with focus on morphological characters rare for dalmanitids (Edgecombe 1993; Carvalho & Fonseca 2007; Holloway & Carvalho 2009, 2010; Rustán & Vaccari 2012). These characters include robust dorsal spines (*Dalmanitoides* Delo, 1935; and *Fenestraspis* Braniša & Vaněk, 1973), a distinctly inflated frontal lobe (*Francovia* Braniša & Vaněk, 1973), bifid caudal spines (*Chacomurus* Braniša & Vaněk, 1973) and intersegmental fenestrae (*Fenestraspis*). With these previous works, it became clear that Malvinokaffric dalmanitids are important for diversification studies because of those distinctive characters.

In this contribution, we report new dalmanitids from the Precordillera Basin, Argentina, which is the main source of well-known Devonian trilobite records from Argentina (Rustán *et al.* 2011a). Three new genera are recognized, two formally erected and one left in open nomenclature, including some specimens only preliminarily reported in previous contributions (Rustán 2011, 2016).

Accounting for a diversification of the family, some of these new dalmanitid taxa reported herein exhibit clear dorsal spines, an unusual character for the family, documented only in a few

Devonian taxa. Hence, we perform a preliminary analysis of spinosity in dalmanitid trilobites of southern Gondwana. The evolutionary/ecological meaning of these spines, generally considered as defensive structures in trilobites (Clarkson & Ahlberg 2002; Pates & Bicknell 2019), is taken as an indirect proxy of predation pressure, together with other additional clues such as signs of failed attacks.

Various data suggest a latitudinal gradient of predation in marine ecosystems with higher predation pressure at lower paleolatitudes (Dudley & Vermeij 1978; Leighton 1999; Harper & Peck 2016), hence demonstrating the significance of our new evidence from high paleolatitudes during the Devonian.

GEOLOGICAL SETTING

The sampled unit is the Lower Devonian Talacasto Formation (Padula *et al.* 1967), mainly exposed in the Central Precordillera in the San Juan Province, Argentina (Fig. 1B), although isolated outcrops are also known from the northernmost extension of the Precordillera, in the Sierra de las Minitas (Fig. 1A), La Rioja Province, Argentina (Rustán *et al.* 2011a). This formation is composed of a marine succession of intensely bioturbated greenish-gray mudstones with intercalated sandstones. It begins with Lochkovian dark, fine-grained, muddy levels, passing upwards into Pragian and Emsian sandy levels. In the type locality at Quebrada de Talacasto, in San Juan Province, the formation reaches around 300 m in thickness, but a maximum of more than 1000 m is recorded in the north at the Loma de los Piojos section, near Jáchal city (Fig. 2).

The Talacasto Formation represents a muddy shelf depositional system developed during a highstand (Astini 1991). The unit covers the (mainly) upper Silurian shelf succession of the Los Espejos Formation (Cuerda 1965) and is overlain by

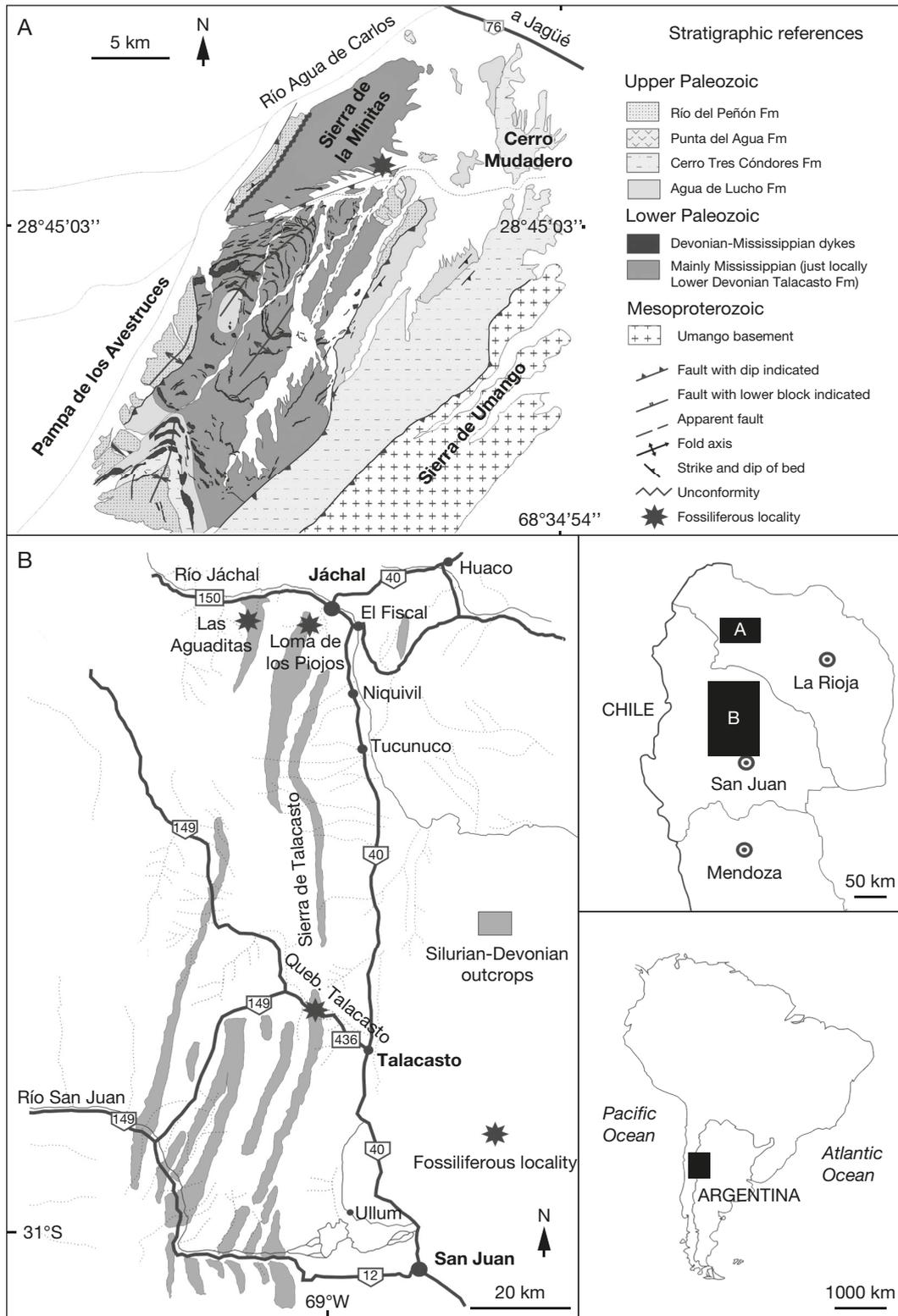


FIG. 1. — Locations of Lower Devonian fossil localities (black stars) in the Precordillera Basin, Argentina: **A**, detail of the outcrops at Sierra de las Minitas, La Rioja Province; **B**, detail of the outcrops in San Juan Province. Modified from Cichowski & Rustán (2017).

a turbiditic system of the Lower to probably Middle Devonian Punta Negra Formation (Braccini 1949; Bustos & Astini 1997; García Muro *et al.* 2018). The Talacasto Formation is the source of most Devonian macrofossils from Argentina,

including brachiopods, trilobites, bivalves, gastropods, cephalopods, echinoderms, corals, tentaculitids, ostracods, hyoliths, conulariids, and scarce plant remains of uncertain assignation (Rustán & Balseiro 2016).

Based on brachiopod and palynological information (Benedetto *et al.* 1992; Herrera 1993; Racheboeuf & Herrera 1994; Herrera & Bustos 2001; García Muro *et al.* 2017, 2018), the Talacasto Formation spans from the Lochkovian to the Pragian, with Emsian ages recently discussed (García Muro *et al.* 2018). Except for a few localities, the base of the Devonian is usually missing due to a discontinuity with the Los Espejos Formation (Benedetto *et al.* 1992; Carrera *et al.* 2013; García Muro *et al.* 2017).

FOSSILIFEROUS LOCALITIES

Quebrada de las Aguaditas, Sierra de los Blanquitos, approximately 12 km southwest of Jáchal city (Fig. 1B). The fossiliferous interval, about 100 m in thickness, corresponds to the Lochkovian-Pragian dark lower muddy stratigraphic interval of the Talacasto Formation. Fossils were collected in the proximity of GPS waypoint $30^{\circ}18'22.95''\text{S}$, $68^{\circ}50'12.15''\text{W}$, preserved in dark grey to black nodules (the same that contain the phacopid *Echidnops taphomimus* Rustán & Balseiro, 2016).

Loma de los Piojos, a classical section located about 8 km, southwest of Jáchal city (García Muro *et al.* 2018). Only one specimen originates from this locality, preserved inside a nodule from the Lochkovian-Pragian greenish lower muddy interval at GPS waypoint $30^{\circ}17'45.6''\text{S}$, $68^{\circ}46'27.8''\text{W}$.

Quebrada de Talacasto, the type section of the Talacasto Formation. It is located over the provincial road route 436, about 60 km to the northwest of San Juan city. The cephalon from this locality is preserved in grey-bluish fine-grained sandstones, from the middle-upper part of the unit. Palynological data of this locality suggests a Pragian age (García Muro *et al.* 2018).

Sierra de las Minitas is a mountain region located to the west of Jagüé town, at north-west of the Province La Rioja, Argentina (Fig. 1A). The geology of this locality is complex, because stratigraphy of several folding and faulting stages. A portion of the Lochkovian-Pragian lower muddy interval of the Talacasto Formation locally crops out here, which is equivalent to that of the Quebrada de las Aguaditas on the basis of lithology and fauna (Rustán *et al.* 2011a; Rustán & Balseiro 2016). Specimens were collected in proximity of the GPS waypoints $28^{\circ}42'50''\text{S}$, $68^{\circ}39'29''\text{W}$ and $28^{\circ}42'43.8''\text{S}$, $68^{\circ}39'40.9''\text{W}$.

MATERIAL AND METHODS

Material is housed at the Centro de Investigaciones en Ciencias de la Tierra (CONICET-Universidad Nacional de Córdoba), numbered with the prefix CEGH-UNC; and the Museo de Paleontología of the Universidad Nacional de Córdoba, numbered with the prefix CORD-PZ, both in Córdoba city. Specimens from Sierra de las Minitas are housed in the collection of Museo de Ciencias Antropológicas y Naturales of the Universidad Nacional de La Rioja, La Rioja, numbered with the prefix PULR.

Specimens were prepared using pneumatic vibro-tools (micro jacks) and needles under binocular microscope. Fossils were covered with black Chinese ink. In the case of external molds, rubber casts were obtained and colored in black. Fossils and rubber casts were coated with ammonium

chloride sublimated prior to photography. Specimens were photographed using a digital camera Canon Power Shot S50 mounted on a binocular loupe Leica MZ75.

ABBREVIATIONS

Technical terms are abbreviated as traditional in trilobite descriptions:

exsag.	exsagittal/exsagittally;
sag.	sagittal/sagittally;
tr.	transversal/transversely.

SYSTEMATIC PALEONTOLOGY

REMARKS

In the description of the pygidial terminal piece, we counted any furrow that indicates segmentation, including those barely impressed (see discussions in Campbell 1977). Open nomenclature follows criteria by Bengtson (1988). Morphological structure denomination follows Whittington & Kelly (1997).

Order PHACOPIDA Salter, 1864
Suborder PHACOPINA Struve *in* Moore, 1959
Superfamily DALMANITOIDEA Vogdes, 1890

Family DALMANITIDAE Vogdes, 1890

REMARKS

Subfamilies of Dalmanitidae have long been discussed. For Silurian and Devonian taxa, the most widely accepted groups include Dalmanitinae Vogdes, 1890 and Synphoriinae Delo, 1935. In particular, Synphoriinae was considered either a distinct family (Delo 1935; Lespérance 1975), or a subfamily closely related to Dalmanitinae (Lespérance & Bourque 1971; Holloway 1981; Edgecombe 1993; Holloway & Carvalho 2009). Currently, the proposals of subfamilies by Holloway (1981) along with characters proposed by Campbell (1977) are the most frequently used for classification. Dalmanitinae is defined mainly by apodems of S1 equidistant between those of SO and S2; a cephalic epiborder furrow; large exsag. eyes extending close to the posterior border furrow; a well-developed pygidial border; a pygidium with 12 or more axial rings; and anterior pleural bands sloping steeply posteriorly and posterior ones sloping more gently anteriorly on the pygidial pleural furrows which are asymmetrical in cross section. On the other hand, Synphoriinae is mainly supported by the exsagittal distance between S1 and S2 apodems 1.5 times longer than between S1 and SO apodems; S2 reduced tr. tending to be subcircular; shorter exsag. eyes; pygidium without a well-defined border; pygidial pleural bands of equal length exsag. with a symmetrical pleural furrow in cross section; and apodemal pits of inter-ring furrows without contacting axial furrows on the pygidium. However, some taxonomic issues remain unsolved, so that several genera cannot be clearly assigned to a subfamily based on their current definitions (Edgecombe 1991; Rustán & Vaccari 2012). For example, a number of characters is demonstrably variable within a single genus, such as the spacing between apodems of the glabellar furrows in *Lygdozoon* Holloway, 1981,

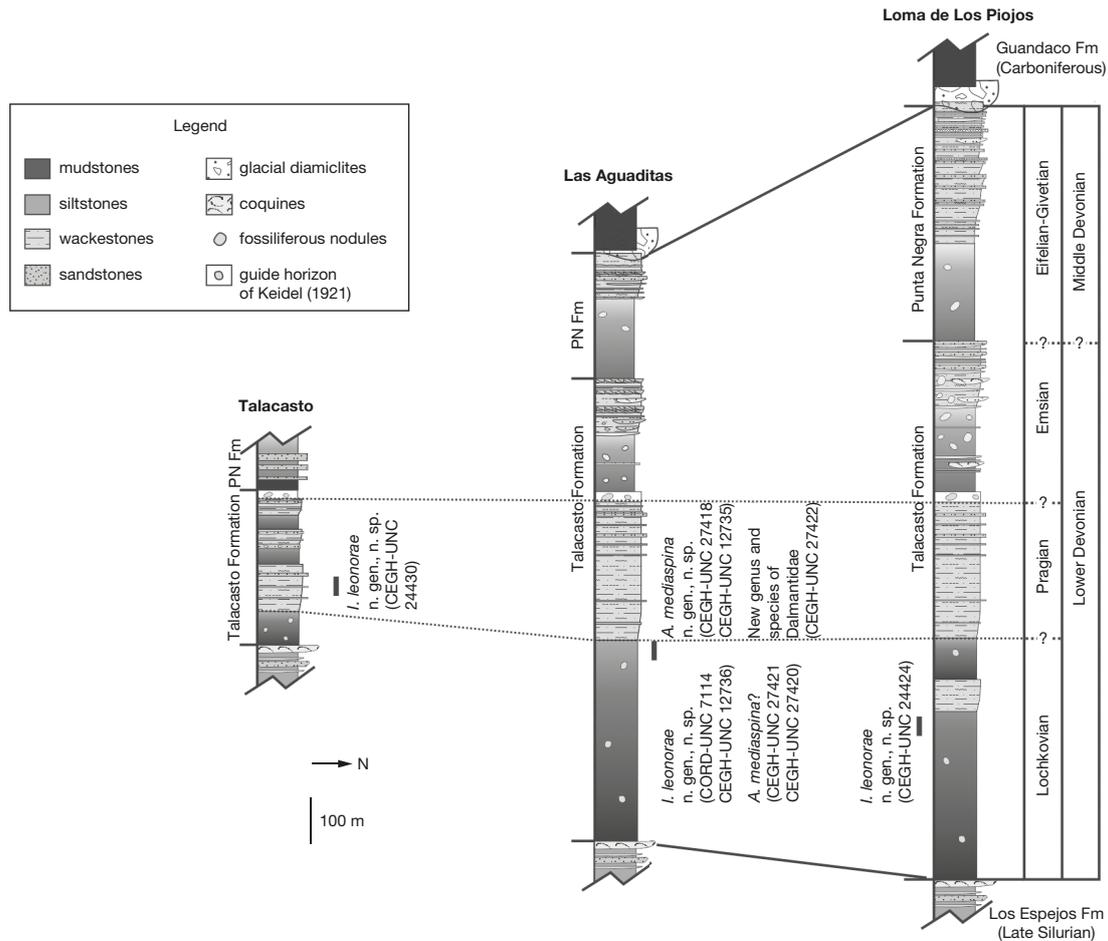


FIG. 2. — Stratigraphic sections of the Talacasto Formation, showing its diachronic top and dalmanitid occurrences. Modified from Cichowski & Rustán (2017).

from the Silurian of the United States. Additionally, the diagnosis of Synphoriinae does not consider the absence of a cephalic epiborder furrow or the number of pygidial axial rings (Holloway 1981), in order to classify taxa as *Lygdozoon*. In spite of this, such characters are still usually considered diagnostic of Dalmanitinae. In our case, we recognize a combination of character states of more than one subfamily in some new taxa proposed herein. Consequently, pending a complete phylogenetic analysis of Dalmanitidae in order to clarify their taxonomy, in the present contribution we do not propose subfamilial assignments for these new taxa. In discussions, for matter of ease, we refer to Dalmanitinae and Synphoriinae taking into account considerations given by Holloway (1981).

Ivanites n. gen.
(Figs 3; 4)

[urn:lsid:zoobank.org:act:05E3FE79-071D-4804-8373-F32E8FD7C6F6](https://doi.org/10.5281/zenodo.6811111)

TYPE AND ONLY SPECIES. — *Ivanites leonorae* n. sp.

TYPE LOCALITY. — Quebrada de Talacasto, San Juan Province, Argentina.

ETYMOLOGY. — Belonging to Ivan, for Ivan Grunewald, EAR's cousin.

OCCURRENCE. — Lochkovian-Pragian, lower part of the Talacasto Formation, Quebrada de las Aguaditas, Quebrada de Talacasto and Loma de los Piojos sections, San Juan Province, Argentina.

DIAGNOSIS. — Dalmanitid with a smooth, widely subparabolic, cephalic margin. Very narrow sag. and exsag. anterior border, with a shallow epiborder furrow. Absence of preglabellar field. Glabella piriform-shaped, nearly flat in the mid-posterior portion; with frontal lobe slightly inflated and less convex sagittally in lateral view, nearly oval to sub-rhombic and evenly convex anteriorly in dorsal view. S1-S2 nearly straight and transversal, without contacting the axial furrows, with the adaxial portion apodemal and incised. Apodems of S1 slightly convex forward, located nearly at the same exsagittal distance to SO and apodems of S2. Eye maximum length exsag. nearly 40% of maximum cranidium length sag. Ocular surface anteriorly taller, with approximately 45 vertical rows of no more than 16 lenses each. Pygidium without ornamentation, broadly subtriangular with 18-20 axial rings and 14 pleurae. Five to six anteriormost pleurae sinuous (more convex forward at level of fulcrum), then tending to be evenly curved backward. Anterior and posterior pygidial pleural bands of equal length exsag. Pygidial pleural furrows incised and symmetrical in cross-section exsag. Pygidial interpleural furrows incised, approximately parallel to pleural furrows. Pygidial border and distal part of pleurae steeply inclined downward. Post axial region ridge-like dorsally, as a stout mucro in posterior view.

REMARKS

The material used to define *Ivanites* was doubtfully assigned to *Kasachstania* Maksimova, 1972 by Rustán (2016). *Ivanites* differs from *Kasachstania*, based on our recent emendation of its diagnosis (Randolfe *et al.* 2020), in having shorter exsag. eyes, S1 and S2 without contacting axial furrows, subtriangular pygidium (not heart-shaped), higher number of axial rings and pleurae, pleural bands and furrows parallel and more sinuous, pleural bands of equal width exsag., and pleural furrows symmetrical in cross-section.

Ivanites challenges the current classification of subfamilies because it possesses diagnostic characters of both Dalmanitinae and Synphoriinae. The lack of well-developed cephalic and pygidial borders, the location of eyes and the width of pygidial pleural bands resemble the synphoriinines but the spacing between glabellar apodems, the number of pygidial segments and the presence of an epiborder furrow are characteristic of dalmanitines. This particular combination of characters supports *Ivanites* as a new genus and encourages a taxonomic revision of dalmanitid subfamilies.

Ivanites leonorae n. gen., n. sp.
(Figs 3; 4)

[urn:lsid:zoobank.org:act:4E9AE8A7-77D6-4E5D-B465-D4FB4EC303ED](https://doi.org/10.1111/zoo.12736)

Kasachstania? sp. Rustán, 2016: 137; fig. 6.

TYPE MATERIAL. — **Holotype.** One enrolled specimen CORD-PZ 7114; Fig. 3B, E, H, K, M-N; and Fig. 4A, D, E, G, from Quebrada de las Aguaditas (Lochkovian-Pragian).

Paratypes. Two cephalae: CEGH-UNC 12736, from Quebrada de las Aguaditas (Lochkovian-Pragian); Fig. 3C, F, I, L, O-Q; and CEGH-UNC 24430 (assigned with doubt), from Quebrada de Talacasto (Pragian); Fig. 3A, D, G, J; and one pygidium: CEGH-UNC 24424, from Loma de los Piojos (Lochkovian-Pragian); Fig. 4B, C, F, H.

TYPE LOCALITY. — Quebrada de Talacasto, San Juan Province, Argentina.

ETYMOLOGY. — This taxon is dedicated to Irene Leonor Grunewald, EAR's mother.

OCCURRENCE. — As for the genus.

DIAGNOSIS. — As for the genus (monospecific).

DESCRIPTION

Whole dorsal surface of carapace lacking ornamentation.

Cephalon widely parabolic in dorsal view. Cranium with length/width index approximately 0.55, with a minimum of convexity in the anterolateral sides. Very short sag. and exsag. preglabellar area, less than 0.1% of total cranial length sag. Shallow epiborder furrow running close to margin, narrowest in the anterior portion.

Glabella expanding tr. rather evenly forward, maximum width tr. located in the middle part of the frontal lobe, nearly equivalent to 0.6 of maximum cephalic width tr.

Glabella piriform-shaped, with axial furrows nearly straight and weakly divergent forward (approx. 16°) in the posterior part up to the junction with S3, then strongly divergent (approx. 34°) up to the cephalic border, shallowest adjacent to the anterior part of the eye and deepest adjacent to S1. Shallow and delicately incised preglabellar furrow. Preglabellar field not developed.

SO nearly straight, barely sinuous laterally, very narrow sag., exsag. and shallow (Fig. 3H). S1 nearly straight, narrow sag., exsag., shallowing laterally to fade without contacting axial furrows, incised, becoming deeper, apodemal, adaxially. Apodems slightly convex forward, located nearly at the same exsagittal distance to SO and apodems of S2. S2 nearly straight, shorter tr. than S1, shallowing and fading laterally without contacting axial furrows, apodemal adaxially. S3 anterolaterally oriented, narrowest exsag. adaxially then broadening anterolaterally, effaced adjacent to anterior part of the eye in the contact with axial furrows. LO insufficiently appreciable. L1 short exsag., subrectangular, scarcely inflated and corresponding to 10% of glabellar total length sag. L2 slightly larger sag. than L1, subrectangular and barely more inflated near the axial furrows. L3 larger exsag. than L2, rapidly expanded anterolaterally, slightly inflated near the axial furrows.

Glabellar frontal lobe dorsally oval to sub-rhombic, from slightly convex in posterior part to gently convex and sloping forwards anteriorly in lateral view, weakly inflated and convex dorsally with a slightly depressed median dorsal area subtly elongated exsag.; posteromedial impression subtly expressed.

Eye kidney-shaped in dorsal view, with posterior edge opposite of S1 and anterior edge opposite to contact between axial furrows and S3. Eye maximum length exsag. about 40% of cranium total length sag., and maximum width tr. about 15% of cephalon total width tr., ocular surface taller in anterior part, gently convex and subvertical in general, more vertically oriented in the posterior part (Fig. 3E). Lenses regularly ordered in 45 vertical rows with a maximum of 16 lenses, with smaller ones in lower position. Lens formula, according the most complete eye from CORD-PZ 7114, is (from anterior): 2? 7? 9? 9 11 12 13 13 14 14? 15 15? 15 16 15 15 15 15 15 15 15 15 14 14 13 12 12 12 11 11 10 10 9 9 8 8 8 7 6 6 6 6? 5? 4? 2? (Fig. 3M).

Palpebral furrow moderately deep and strongly convex exsag., deeper anteriorly, narrower tr. and shallower backward.

Shallow and broad exsag. subocular ridge. Anterior branch of facial suture running subparallel to axial furrows, then circumscribing the glabellar frontal lobe. Posterior branch of facial suture running with a strong convexity anterolaterally from the posterior part of the eye, turning backwards and reaching lateral margin a little behind of the half exsag. of eye. Palpebral area elevated in comparison with remaining fixigenal field, slightly convex dorsally in posterior view. Postocular area moderately inclined laterally and slightly convex. Posterior border furrow in appearance deep and narrow exsag. Librigenal field narrow tr., depressed and steeply sloped downwards. Lateral border furrow broader tr. and deeper on librigenal field than on fixigenal field. Anterior border furrow indistinguishable of preglabellar furrow. Genal spine (from specimen CEGH-UNC 24430, Fig. 3G), slightly shorter than the cranium total length sag., as wide as 10% of cephalon maximum width tr. Posterior border

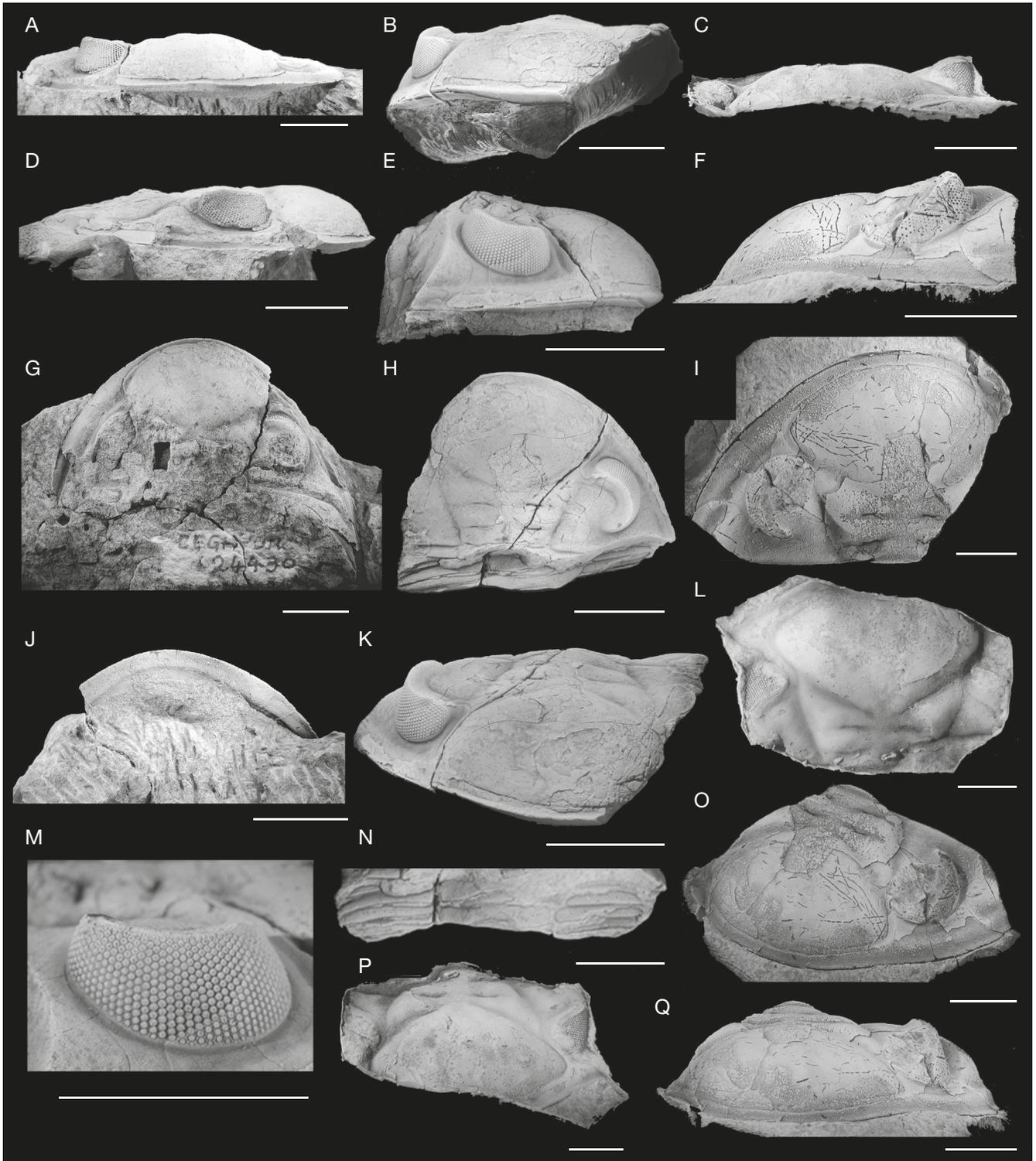


FIG. 3. — *Ivanites leonorae* n. gen., n. sp., cephalons from the Lochkovian-Pragian of Talacasto Formation, Precordillera Argentina: **A, D, G, J**, CEGH-UNC 24430, internal mold of cephalon assigned with doubt, from Quebrada de Talacasto: **A**, frontal view; **D**, lateral view; **G**, dorsal view; **J**, ventral view; **B, E, H, K, M, N**, CORD-PZ 7114, holotype, enrolled specimen, from Quebrada de las Aguaditas: **B**, frontal view; **E**, lateral view; **H**, dorsal view; **K**, dorsofrontal view; **M**, eye; **N**, dorsal view of thoracic segments; **C, F, I, L, O-Q**, CEGH-UNC 12736, cephalon from Quebrada de las Aguaditas: **F**, internal mould lateral view; **I**, idem dorsal view; **O**, idem dorsolateral view; **Q**, idem dorsofrontal view; **C**, latex mould, frontal view; **L**, idem dorsal view; **P**, idem dorsofrontal view. Scale bars: 1.0 cm.

furrow continued into the base of the genal spine. Anterior cephalic doublure (according specimen CEGH-UNC 24430, Fig. 3J), with length sag. about 15% of total cranidium length

sag., nearly flat to barely concave with a very shallow furrow near margin. More depressed internal area about 50% of total doublure length sag., posteriorly located.

Hypostome unknown.

Thorax scarcely known (Fig. 3N). Axis with 37% of thorax total width tr. across the most anterior segments. Median part sag. of axial rings convex anteriorly and concave posteriorly in dorsal view, lateral sides slightly convex. Axial rings more convex medially in transversal view.

Pygidium broadly subtriangular in dorsal view, with length/width index approximately 0.8. Axial furrows nearly straight to barely convex laterally, very narrow tr. and moderately deep, diverging from sagittal plane about 6–7°. Pygidial axis narrow, approximately 25% of the maximum pygidial width tr., with a maximum of dorsal convexity tr. medially and just a barely concave profile in lateral view, with 18–20 well-defined axial rings plus a terminal piece. First pygidial eight axial rings gently elevated dorsally in the posterior part, in lateral view, then becoming nearly flat and effaced backward. Nearly first seven axial rings with convex to sub-rectangular lateral sides in dorsal view, posterior ones nearly sub-rectangular. Inter-ring furrows narrow sag., deepest laterally, effaced medially sag. Inter-ring furrows effaced sagittally in the posterior part of the axis, defining a median band of even width tr. Pleural field with 14 pleurae, narrow exsag. and deep pleural furrows, gradually less impressed backward and more posteriorly directed. Antermost pleurae (particularly the first seven) sinuous (slightly convex backward near axial furrow, then strongly convex forward toward fulcrum) bending backwards at fulcrum. Posteriormost pleurae becoming progressively straighter and backwardly oriented, trending to be parallel to the axis. Interpleural furrows well-impressed, incised, and symmetrical in cross-section exsag. Pleural bands and furrows progressively fading distally to efface next to pygidial margin, leaving an insinuated pygidial border. Pygidial border and distal part of pleurae steeply inclined downward. Stout caudal mucro slightly downward directed with acute dorsal convexity, tip not adequately preserved.

REMARKS

Ivanites leonorae n. gen., n. sp. resembles “*Kasachstania*” *gerardo*i Edgecombe & Ramsköld, 1994, a species with current uncertain generic assignment (Randolfe *et al.* 2020), from the upper Silurian of Bolivia and Lower Devonian of Argentina. *Ivanites leonorae* n. gen., n. sp. differs in having smaller exsag. eyes, anteriorly evenly rounded glabellar frontal lobe in dorsal view (not acute), a less rounded pygidium, much narrower exsag. pygidial pleural furrows, distal part of pleural bands without elevations and depressions, delicately convex pygidial border instead of being wide tr. and concave, and distal part more depressed toward the mucro.

The cephalon CEGH-UNC 24430 (Fig. 3A, D, G, J) is assigned with doubt to *I. leonorae* n. gen., n. sp. Differences with other cephalons of *I. leonorae* n. gen., n. sp. include a lower profile in lateral view, margin nearly straight in lateral and frontal view, lower eyes in appearance with less rows of lenses and frontal lobe not so convex and steeply inclined forward anteriorly. This specimen originated from sandy layers (Pragian of the Quebrada de Talacasto section), in contrast with remaining specimens of *I. leonorae* n. gen.,

n. sp. coming from nodules from the pelitic lowermost part of the Talacasto Formation (Lochkovian to Pragian from Quebrada de las Aguaditas and Loma de los Piojos sections), and thus some morphological differences might be, taphonomic, due to a slight dorso-ventral compression. This specimen is the only one preserving a genal spine and consequently its characters were not included in the diagnosis. Such genal spines, exhibiting the posterior border furrow continued in a longitudinal genal furrow, were considered typical of Dalmanitinae (Campbell 1977).

Aguaditaspis n. gen. (Figs 5; 6)

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TYPE SPECIES. — *Aguaditaspis mediaspina* n. sp.

TYPE LOCALITY. — Quebrada de Talacasto, San Juan Province, Argentina.

ETYMOLOGY. — From Quebrada de las Aguaditas, the type locality in San Juan Province to the southwest of Jáchal city (Argentina), and the Greek end meaning shield, as usual in trilobites.

OCCURRENCE. — Lochkovian-Pragian, lower muddy part of the Talacasto Formation, Quebrada de las Aguaditas, San Juan Province and Sierra de las Minitas, La Rioja Province, Argentina.

DIAGNOSIS. — Dalmanitid with strongly impressed glabellar furrows, nearly contacting axial furrows. S1 and S2, posterolaterally directed, with short tr. and deep apodems adaxially, with convex projections of glabellar lobes protruding them from behind. S1 slightly concave forward. S2 nearly straight. L1 elongated tr., L2 subrectangular and L3 subtriangular (broadest abaxially and acute adaxially). Tall palpebral area with very shallow and broad exsag. palpebral furrow anteriorly. Eye socle furrow deep and broader exsag. Robust subocular ridge. Anterior branch of facial suture cuts subocular ridge, dividing space between subocular ridge and eye socle furrow in a librigenal and a cranial portion. Wide tr., exsag. postocular area. Lateral border furrow broad tr. anteriorly, fading posteriorly without contacting posterior border furrow. Very shallow epiborder furrow. Deep and wide exsag. posterior border furrow. Pygidium subtriangular with 18–24 axial rings, most anterior ones usually bearing postero-sagittal spines dorsally or inflations variably developed. Well-defined pygidial pleurae, anterior ones evenly wide exsag., five posterior ones progressively straighter, broader tr. and effaced distally. Pygidial interpleural furrows weakly impressed. Pleural furrows broad and deep, with anterior slope steeper than posterior one, posteriormost five somewhat sinuous and variably in width and depth each.

REMARKS

This genus is based on a new combination of characters and some derived characters. Particularly distribution, orientation, width and depth of cephalic furrows are unique. A convex projection of cephalic lobes forward into the glabellar apodems, as reported in detail on the S2 of *Dalmanitoides*, from the Lower Devonian of Southwestern Gondwanan basins (Rustán & Vaccari 2012), is a character often overlooked in dalmanitid descriptions. In *Aguaditaspis* n. gen., a similar

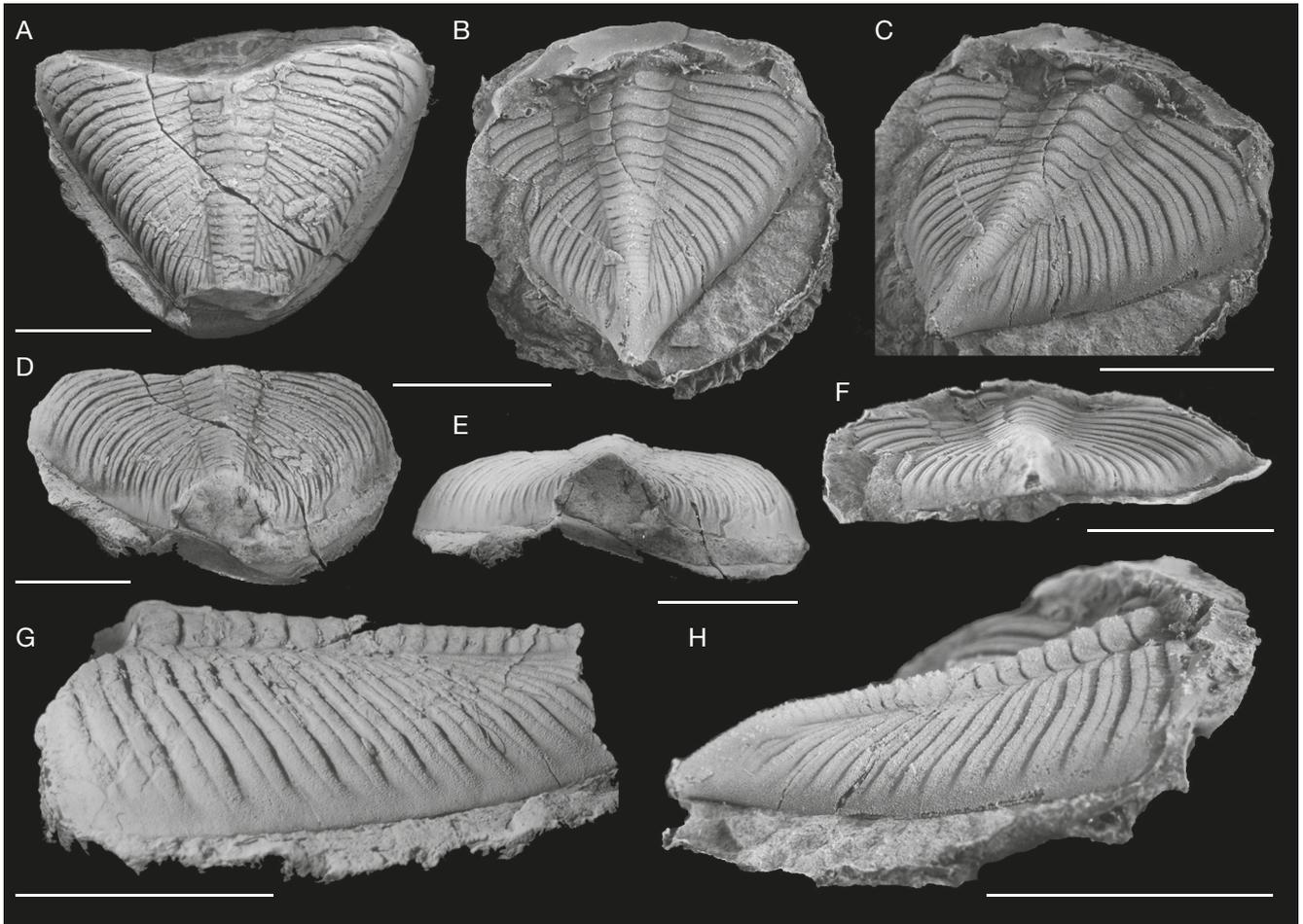


FIG. 4. — *Ivanites leonorae* n. gen., n. sp., pygidia from the Lochkovian-Pragian of Talacasto Formation, Precordillera Argentina: **A, D, E, G**, CORD-PZ 7114, holotype, enrolled specimen from Quebrada de las Aguaditas: **A**, dorsal view; **D**, dorsoposterior view; **E**, posterior view; **G**, lateral view; **B, C, F, H**, CEGH-UNC 24424, pygidium from Loma de los Piojos, latex mould: **B**, dorsal view; **C**, dorsolateral view; **F**, posterior view; **H**, lateral view. Scale bars: 1.0 cm.

convex projection is particularly clear on S1. However, the only known cephalon is an internal mold (CEGH-UNC 27418, Fig. 5A, B), so that some features of these external characters might be slightly different than described herein. A subocular ridge is a character also overlooked in many dalmanitid descriptions. However, in *Aguaditaspis* n. gen. the facial suture cuts this robust subocular ridge, in a particular and rare case (Fig. 5A). Median spines or inflations variably developed in several pygidial axial rings is a character extremely unusual in dalmanitids. This derived character may also include single median spines on thoracic axial rings or even in the occipital ring, but the available material is insufficiently preserved to assess this (Fig. 5E, F, L). The area corresponding to the five posteriormost pleurae in the pygidium is distinctive in terms of its expression, orientation, course, width and depth of furrows. The furrows are not strictly sinuous but somewhat irregular, even in internal molds (Fig. 5E, F, M, N).

Aguaditaspis n. gen. shares characters of both subfamilies, Synphoriinae and Dalmanitinae (Holloway 1981), challenging their taxonomic recognition. Particularly, a cephalic epiborder furrow, a pygidium with more than twelve axial rings

and a steeply inclined anterior slope of pleural furrows, are related to Dalmanitinae. In turn, a weakly defined cephalic and pygidial border, and the sagittal distance between S1 and S2 apodems 1.5 times than distance between S1 and SO apodems, belong to Synphoriinae diagnosis. The shape of the hypostome of *Aguaditaspis* n. gen. is similar to some synphoriinines as *Lygdozoon*, but having a very shallower maculae.

Aguaditaspis mediaspina n. gen., n. sp.
(Figs 5; 6)

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TYPE MATERIAL. — **Holotype**. 1 enrolled specimen CEGH-UNC 27418; Fig. 5A-D, G, from Quebrada de las Aguaditas (Lochkovian-Pragian).

Paratypes. 4 pygidia: CEGH-UNC 27419, from Quebrada de las Aguaditas (Lochkovian-Pragian); Fig. 5E, F, H, I, K, L; CEGH-UNC 12735, from Quebrada de las Aguaditas (Lochkovian-Pragian); Fig. 5N, Q; PULR-I 006, from Sierra de las Minitas (Lochkovian-Pragian); Fig. 5J, M, P; PULR 132, from Sierra de las Minitas (Lochkovian-Pragian); Fig. 5O.

TYPE LOCALITY. — Quebrada de Talacasto, San Juan Province, Argentina.

ETYMOLOGY. — From Latin. Refers the presence of one dorsal median spine in some pygidial axial rings.

OCCURRENCE. — As for the genus.

DIAGNOSIS. — As for the genus (monospecific).

DESCRIPTION

Cephalon approximately subparabolic in dorsal view. Shallow epiborder furrow running close to the margin.

Glabella expanding tr. rather evenly forward in dorsal view, maximum width tr. located in frontal lobe, equivalent to half of maximum cephalic width tr. Posterior part of glabella sloping slightly forward up to S3, in lateral view. Glabellar frontal lobe incompletely known but with a barely depressed or gently convex medial dorsal area in the posterior part, in lateral view.

Glabellar axial furrows, nearly straight and weakly divergent (approx. 16°) forward up to junction with S3, where describe a local outward convexity, and then slightly more divergent (approx. 25°), shallowest adjacent to the anterior part of the eye and deepest adjacent to S1. SO slightly convex anteriorly in medial part where is shallowest, and concave forward laterally becoming apodemal. S1 nearly posterolaterally directed, broader exsag. abaxially, shallowest at junction with axial furrows, more adaxially with a short tr. apodemal pit with a little convex intrusion of the L1. S2 nearly straight and barely posterolaterally directed, shallowest at junction with axial furrows, apodemal adaxially with a little convex intrusion of the L2. S3 anterolaterally directed, effaced sagittally, narrow adaxially then broadening and deepening anterolaterally nearly at junction with axial furrows. LO not well-preserved but long sag.; exsag., longer sagittally, slightly convex anteromedially, lateral sides nearly concave forward in dorsal view. L1 short exsag., subrectangular to elongated, laterally acuminate, scarcely inflated, higher than L2 in lateral view. L2 approximately twice longer (sag.; exsag) than L1, subrectangular, inflated. L3 subtriangular, expanded anterolaterally, barely longer exsag. than L1 abaxially, inflated, protruding slightly anterolaterally.

Eye kidney-shaped in dorsal view, with posterior edge opposite to posterior part of L2 and anterior edge opposite to contact between axial furrows and S3. Eye maximum width tr. about 10% of cephalon total width tr., ocular surface taller in anterior part, gently convex and steeply inclined in general, more vertical in posterior part. Complete lens formula unknown. Lenses regularly ordered in approximately 48 vertical rows with not more than 4-18 lenses each.

Palpebral furrow shallow and slightly convex laterally, broader tr. anteriorly.

Anterior branch of facial suture running subparallel to and near external sides of axial furrows from the anterior part of eye, cuts subocular ridge (Fig. 5A), then circumscribing exteriorly the anterolateral corner of the glabellar frontal lobe. Posterior branch of facial running anterolaterally from behind the eye along the posterior part of the eye socle furrow, then strongly and evenly convex forward across the lateral border furrow opposite to S2, and turning backwards to the margin

across the border opposite to L2. Subocular ridge robust and extended anteriorly almost reaching axial furrows. Eye socle furrow shallow, broadest tr. anteriorly. Palpebral area elevated, slightly convex dorsally in posterior view. Postocular area moderately inclined towards lateral border, gently convex in lateral view. Posterior border furrow wide exsag. and deep, shallowest and narrower exsag. adaxially. Librigenal very narrow tr., steeply sloped downward to lateral border furrow.

Anterior cephalic doublure ventrally convex (Fig. 5B).

Hypostome big (of about 28 mm sagittal length), with a shield-like shape resembling an inverted bell, slightly wider than longer (length/width index, 0.9), convex ventrally; with anterior margin evenly convex forward; conspicuous anterior wings, lateral side concave anteriorly and evenly convex posteriorly, posterior margin incompletely known but convex with at least one posterolateral denticle. Separation between anterior border and middle body without any furrow. Middle body more elevated medially than anterior border, convex in lateral view. Middle furrow and macula only slightly expressed. Lateral border furrow shallow and narrow. Posterior border furrow broader sag. and deeper than lateral border furrow. Posterior body not completely known, subtriangular in ventral view and lower than middle body in lateral view (Fig. 5C).

Thorax known from a few incomplete segments (Fig. 5A, D-F, L). Axis about 25-30% of thoracic width tr. Axial furrows well-impressed. Axial rings subrectangular in dorsal view, strongly convex medially in transversal view; with a discrete dorsal inflation in the anterolateral corner (Fig. 5D). Pleural tips unknown, pleural furrows deep, broad exsag., and asymmetrical in cross section, the anterior slope more steeply inclined, shallowest and narrowest at junction with axial furrows. Anterior pleural band narrower exsag. than posterior pleural band. Short and stout dorsal spine posteromedially located in at least some posterior thoracic segments (Fig. 5E, F, L).

Subtriangular pygidium, with length/width index of nearly 1.0, based on an estimated total length sag. Axial furrows nearly straight, narrow tr. and shallow, with a low divergence from the sagittal line (about 6°). Pygidial axis approximately 30% maximum pygidial width tr., measured at the first axial ring. As much as 18-20 well-defined pygidial axial rings plus a terminal piece. First six pygidial axial rings slightly convex forward anteriorly and concave backward posteriorly, adaxially, in dorsal view; with lateral sides somewhat broader and barely inflated; posteriormost ones more subrectangular in dorsal view. Each axial ring gently inclined forward dorsally and more convex and higher posteriorly in lateral view, with a short posteromedial spine or inflation variably developed typically in anteriormost 12 axial rings. Inter-ring furrows narrow (sag., exsag) but well-impressed, becoming apodemal abaxially. Apodemal pits without contacting axial furrows. Pleural field with at least 13 pleurae gently inclined forward in lateral view, bearing broad exsag. and deep pleural furrows. Anteriormost pleurae (particularly the first five) somewhat sinuous (slightly convex backward near axial furrow, then strongly bending backward at fulcrum). Posteriormost pleurae progressively becoming nearly straight and backwardly oriented, trending to be parallel to the axis, straighter and more

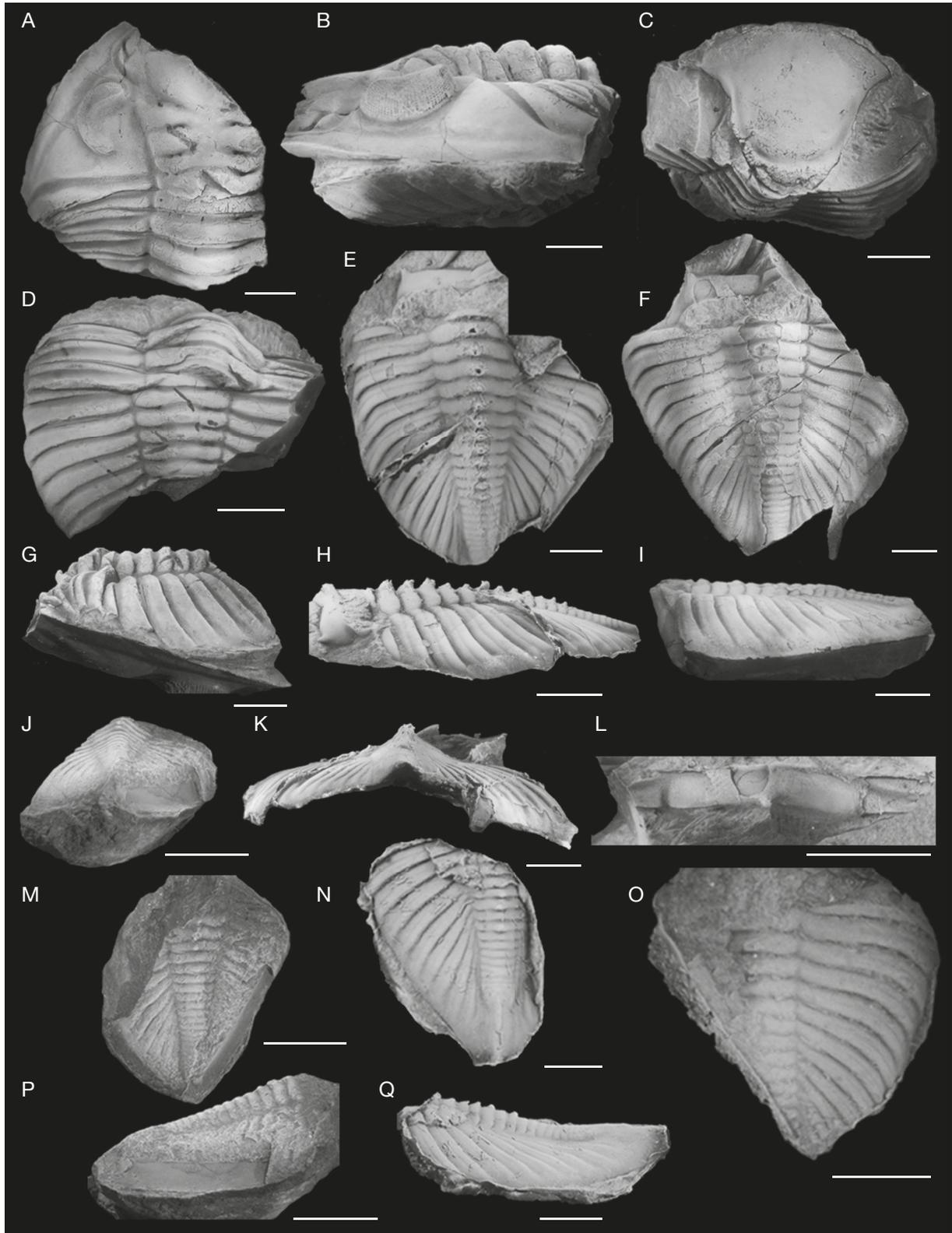


FIG. 5. — *Aguatitaspis mediaspina* n. gen., n. sp., from the Lochkovian-Pragian of Talacasto Formation, Precordillera Argentina: **A–D, G**, CEGH-UNC 27418, holotype, internal mould of enrolled specimen, from Quebrada de las Aguaditas: **A**, dorsal view of cephalon and some thoracic segments; **B**, lateral view of cephalon; **C**, dorsal view of hypostome; **D**, dorsal view of pygidium; **G**, lateral view of pygidium; **E, F, H, I, K, L**, CEGH-UNC 27419, pygidium from Quebrada de las Aguaditas: **F**, internal mould dorsal view; **I**, idem lateral view; **L**, idem detail of thoracic segment; **E**, latex mould dorsal view; **H**, idem lateral view; **K**, idem posterior view; **J, M, P**, PULR-I 006, internal mould of pygidium from Sierra de las Minitas: **J**, posterior view; **M**, dorsal view; **P**, lateral view; **N, Q**, latex mould of pygidium CEGH-UNC 12735 from Quebrada de las Aguaditas: **N**, dorsal view; **Q**, lateral view; **O**, latex mould of pygidium PULR 132 from Sierra de las Minitas, dorsal view. Scale bars: 1.0 cm.

posterolaterally directed. Interpleural furrows shallow, sinuous as pleural bands, barely impressed in internal molds. Anterior pleural bands broader exsag. and extended more distally than posterior band. Anterior pleural bands broader exsag. near pygidial margin. Pleural furrows asymmetrical with anterior slope steeper than posterior one. Pleural bands and furrows become progressively faint distally to efface next to pygidial margin, leaving an insinuated pygidial border. Short pygidial doublure, slightly convex ventrally (Fig. 5J, M, P). Postaxial region wide tr. and elongated, with a gently dorsal postaxial keel-like ridge (Fig. 5N), but unknown in the very rear part from the available material, in appearance, tapering in wide-based and stout mucro or spine.

REMARKS

Pygidial interpleural furrows of *Aguaditaspis mediaspina* n. gen., n. sp. are extremely shallow in external molds (Fig. 5E), and barely impressed in internal molds (Fig. 5D, F). Thus, the apparent absence of interpleural furrows is a doubtful character to use when external information of the carapace is not available.

The distribution pattern of dorsal median spinosity on axial rings of the pygidium, and the expression of the spines, varies among specimens. We interpret it as intraspecific variability, as was recognized in other dalmanitids (Rustán & Vaccari 2012) such as *Dalmanitoides drevermanni* (Delo, 1935).

External morphology of the thoracic axial rings of *A. mediaspina* n. gen., n. sp. is known from a single segment derived from the specimen CEGH-UNC 27419 (Fig. 5E, F, L), which exhibits a dorsal postero-sagittal spine. However, as spines expression seems to be variable, we did not include spines of thoracic axial rings as a diagnostic character.

Aguaditaspis mediaspina?

MATERIAL. — Two incomplete pygidia from Quebrada de las Aguaditas (CEGH-UNC 27421; Fig. 6A, B, D, E, I, J; and CEGH-UNC 27420; Fig. 6C, F-H).

OCCURRENCE. — Lochkovian-Pragian, Talacasto Formation, Quebrada de las Aguaditas, San Juan, Precordillera Argentina, Argentina.

DESCRIPTION

Because of their tentative assignment, description of these specimens is herein focused on characters differing from others *A. mediaspina* n. gen., n. sp.

Axial furrows broad tr., moderately deep, with a weak divergence from sagittal line (7°). Axis with at least 24 axial rings. Axial terminus poorly defined. Anterior 13 rings strongly defined, lateral sides convex in dorsal view. Anterior side of first 13 rings convex and posterior side slightly concave. First four axial rings bearing dorsal posteromedial nodes. Pleural field with 15 pleurae, bearing pleural furrows, gradually less impressed backward and more posteriorly directed. Anterior-most pleural furrows (particularly the first six) slightly convex adaxially, interpleural furrows nearly straight. Interpleural furrows slightly impressed in first six pleurae, then even less impressed, and symmetrical in cross-section. Posterior pleural

bands narrower exsag. and more vaulted than anterior pleural bands. Pygidial caudal border with a little sag. and relatively broad tr. spine with a rounded base ventrally directed. Regular granular ornamentation in posterior region of axial rings and anterior pleural bands, also present in surface of terminal piece but less densely distributed.

REMARKS

A number of pygidia assigned herein with doubt to *A. mediaspina* n. gen., n. sp., co-occur in the same layers of the Quebrada de las Aguaditas type locality, and are very similar to those of *A. mediaspina* n. gen., n. sp. They share some diagnostic characters: a steeply inclined anterior slope of pleural furrows; ornamentation posteromedially located on some axial rings, similar sinuosity of pleural bands and furrows and an elongated and stout post-axial region. Differences include, in these specimens, wider pleural bands exsag., interpleural furrows better impressed, higher number of axial rings, an extremely subdued post-axial ridge, and ornamentation of axial rings compound of medial nodes or subtle inflations instead of spines. Furthermore, the number of axial rings is remarkably high for most dalmanitids (more than 20 is extremely rare) and the anterior slope of pleural furrows is typically much steeper than the posterior slope. However, the general pygidial morphology is consistent, and no similar taxa are known outside from the fossiliferous interval of the Quebrada de las Aguaditas. Hence, we interpret that differences among specimens might be due to intraspecific variability and refer putatively the specimens to *A. mediaspina* n. gen., n. sp.

A caudal spine, relatively short, stout, subtriangular in cross-section and ventrally directed distally is a unique character within dalmanitids. However, this character cannot be appreciated in *A. mediaspina* n. gen., n. sp., which caudal part is unknown in type specimens. Thus, the downturned caudal spine could not be used to solve the taxonomic proposal, nor was included in the diagnosis.

New genus and species of Dalmanitidae
(Fig. 7)

MATERIAL. — One incomplete pygidium from Quebrada de las Aguaditas CEGH-UNC 27422; Fig. 7.

OCCURRENCE. — Lochkovian-Pragian, Talacasto Formation, Quebrada de las Aguaditas, San Juan Province, Argentina.

DESCRIPTION

Pygidium subtriangular in dorsal view, with length/width index approximately 1.1. Axial furrows nearly straight, narrow tr., moderately deep, with a weak divergence from sagittal line (about 7°) along the first 15 axial rings, and then nearly parallel to the sagittal line, after a subdued constriction of the axis. Axis with 24 axial rings plus a terminal piece, slightly concave in lateral view. First axial ring approximately 30% of the maximum pygidial width tr. Axial rings narrow sag., exsag. almost rectangular with slightly convex lateral sides in dorsal view. First 14 axial rings bearing typically two strong

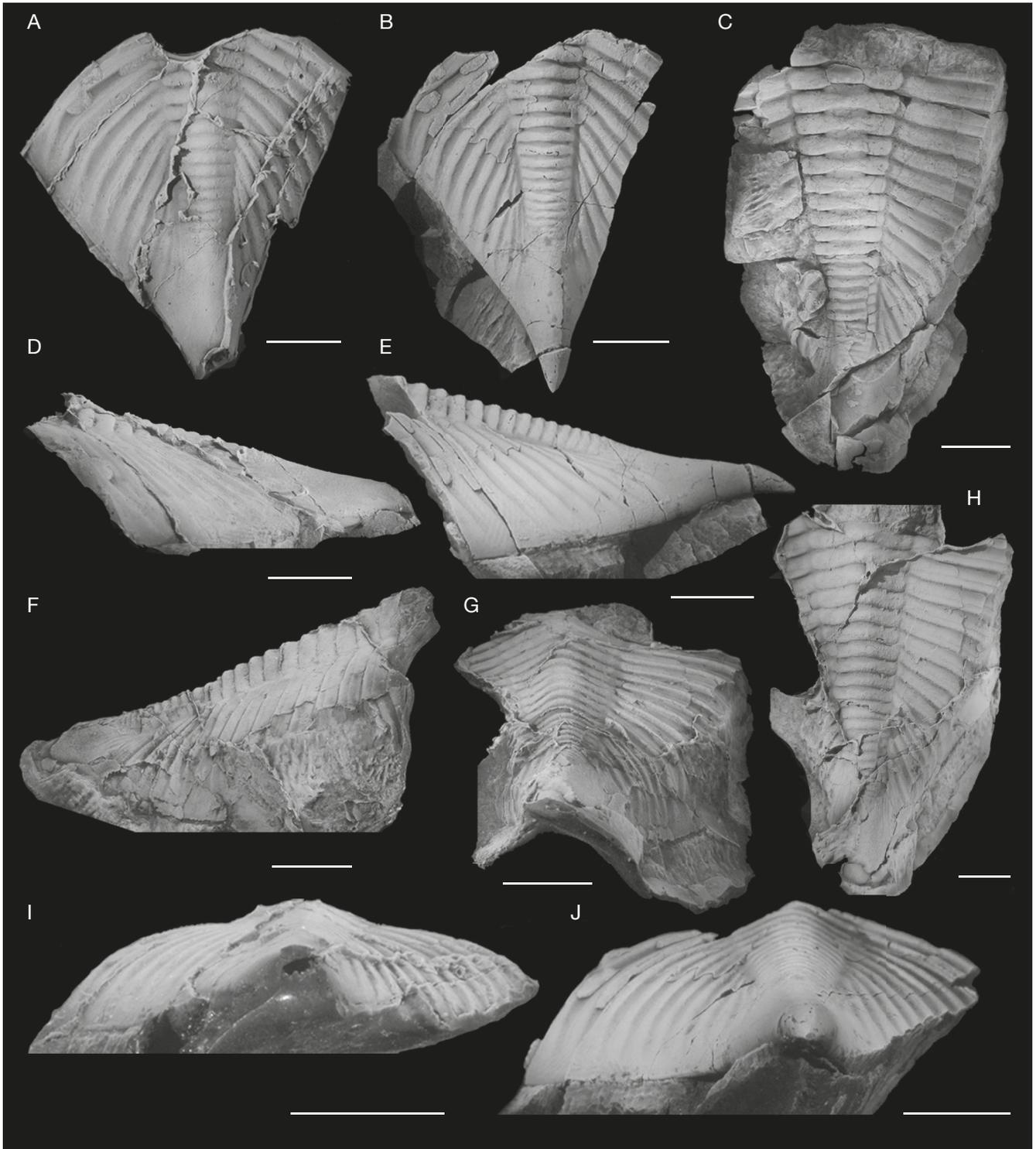


FIG. 6. — *Aguaditaspis mediaspina?*, pygidia from the Lochkovian-Pragian of Quebrada de las Aguaditas, Talacasto Formation, Precordillera Argentina: **A, B, D, E, I, J**, CEGH-UNC 27421: **A**, latex mould dorsal view; **B**, internal mould dorsal view; **D**, latex mould lateral view; **E**, internal mould lateral view; **I**, latex mould posterior view; **J**, internal mould posterior view; **C, F-H**, CEGH-UNC 27420: **C**, internal mould dorsal view; **F**, latex mould lateral view; **G**, idem dorsoposterior view; **H**, idem dorsal view. Scale bars: 1.0 cm.

adaxial dorsal small spines or spine-like tubercles, variably developed and arranged in two longitudinal rows (each on different sides of the sagittal plane), and usually two or more additional much smaller spines either laterally (in rings 1 to 5) or between them (in rings 1-2?; 5-11). Inter-ring furrows

well-impressed, apodemal abaxially. Apodemal pits without contacting axial furrows. Pleural field with 16 pleurae, bearing broad exsag. and deep pleural furrows, gradually less impressed backward and more posterolaterally directed. Anteriormost pleurae (particularly the first nine) nearly straight to slightly

concave forward in the pleural field adaxially from fulcrum, slightly convex backward toward the fulcrum, then bending strongly backward abaxially at fulcrum, distinguishable up to near the margin. Posteriormost pleurae progressively becoming nearly straight and backwardly oriented, trending to be parallel to the axis. Interpleural furrows well-impressed but incised and shallow. Anterior pleural bands convex dorsally in cross-section, higher, slightly broader exsag., and extending more distally than the posterior bands, becoming broadest exsag. near fulcrum. Anterior band of first six pleurae bearing typically 3–4 spine-like small tubercles irregularly and asymmetrically distributed. Posterior pleural band of the first two pleurae with little spines abaxially near fulcrum. Pleural bands and furrows becoming progressively faint distally to efface next to the pygidial margin, leaving a barely defined pygidial border. Caudal region elongated backward, with no ornamentation. Pygidial terminus continued in a gently upturned caudal spine of unknown total length. Regular granular ornamentation.

REMARKS

The new genus and species of Dalmanitidae combines diagnostic characters of Dalmanitinae, such as asymmetrical width exsag. of pygidial pleural bands, with characters of Synphoriinae as a poorly defined pygidial border and apodemal pits of pygidial axis without contacting axial furrows.

Ornamentation appears to be similar to that of *Roncellia* Lespérance & Bourque, 1971, from the Lower Devonian of Canada; *Fenestraspis*, from the Lower Devonian of Bolivia; and especially *Dalmanitoides*. These genera share a very narrow tr. pygidial border, and spines/tubercles on several axial rings, usually paired and trending to define longitudinal rows. However, specimens of *Dalmanitoides* and *Roncellia* differ from our specimen by spines developed on the posterior pleural bands, instead of being located on the anterior ones. In turn, the broad bases of spines in *Dalmanitoides* protrude into the following anterior pleural band, which contrasts with the delicate spine bases of the new genus and species of Dalmanitidae. Our specimen could be differentiated from *Dalmanitoides* and *Roncellia* from its narrower tr. pygidium, a higher number of axial rings and pleurae, a straighter lateral margin, and absence of dorsal ornamentation on the last axial rings. *Fenestraspis*, in contrast, is clearly different by its unique intersegmental fenestrae and nearly straight pleurae. Hence, similarities in the ornamentation pattern among these genera are most probably due to evolutionary convergence, although this must be tested in a phylogenetic analysis.

The combination of the spines distribution pattern, the high number of axial rings and the sharp subtriangular shape with weakly convex lateral margins, is unique for a dalmanitid and suggest that this specimen corresponds to a new genus. We leave it in open nomenclature due to the scarcity of material.

It is worth mentioning an irregularity in the last three pleurae on the left side specimen (Fig. 7I). These pleurae appear to be fused adaxially, suggesting a malformation or a post-damage regeneration. It is closely similar to interpretations of post predation-marks (Šnajdr 1981). These abnormalities are

explained as evidence of regeneration after failed predation, in which the margin regenerates first while successive moults change the pre-damage distribution of pleural furrows and bands. The typical result of this process would be a pygidial margin without any damage but pleural furrows and bands irregularly distributed, as in our case. However, it is very difficult to objectively distinguish post-damage regeneration from some teratological conditions (Owen 1985). Bicknell *et al.* (2019) proposed to reject a teratological origin for distinctive shapes of marginal embayments, marks of cicatrization and/or single spine injuries. Nevertheless, none of these characteristics have been seen in our specimen. In a study about abnormalities and spinosity in Cambrian trilobites, a correlation was found between development of spines and abundance of abnormalities (Pates & Bicknell 2019). The conclusion of that publication was that in such cases abnormalities would correspond to post-predation marks. In either case, this is the first abnormality of this kind registered in post-Ordovician dalmanitids.

On the other hand, this specimen exhibits two little circular marks also located in the left pleural field, which look like sessile epibiont attachment structures (Fig. 7H). We interpret that these structures were probably post mortem and not related to predation.

DISCUSSION

THE DALMANITID TRILOBITES IN THE CONTEXT OF THE MALVINOKAFFRIC REALM

Trilobite faunas from the Early Devonian of Southwestern Gondwana were characterized as noticeably endemic already since their first reports (Clarke 1913; Richter & Richter 1942), which allowed to recognize a major Early-Middle Devonian paleobiogeographical region of cold waters in high paleolatitudes (Dowding & Ebach 2018). This region, known as the Malvinokaffric Realm, embraced relatively isolated tectonic basins and was considered a natural laboratory for analyzing evolutionary and paleobiogeographical patterns and processes in trilobites (Lieberman *et al.* 1991; Lieberman 1993). The earliest hypothesis to explain the extraordinary morphological disparity in Malvinokaffric trilobites proposed regional diversifications from previous Silurian cosmopolitan stocks (Eldredge & Ormiston 1979). The bulk of studies focused on the calmoniids, an extremely diversified family occurring in the late Silurian-Middle Devonian, virtually endemic from Malvinokaffric basins (Eldredge & Braniša 1980; Abe & Lieberman 2009, 2012). However, other families include some wide-distributed representatives as is the case of phacopiids (Holloway & Rustán 2012; Rustán & Balseiro 2016). Dalmanitids in particular, were considered remarkably diversified and endemic of the Malvinokaffric basins, similarly to calmoniids (Eldredge & Ormiston 1979). Thus, *Kasachstania*, previously reported from the upper Silurian-Middle Devonian of Kazakhstan, United States, Bolivia and Argentina was recently excluded from the Malvinokaffric Realm and interpreted as restricted

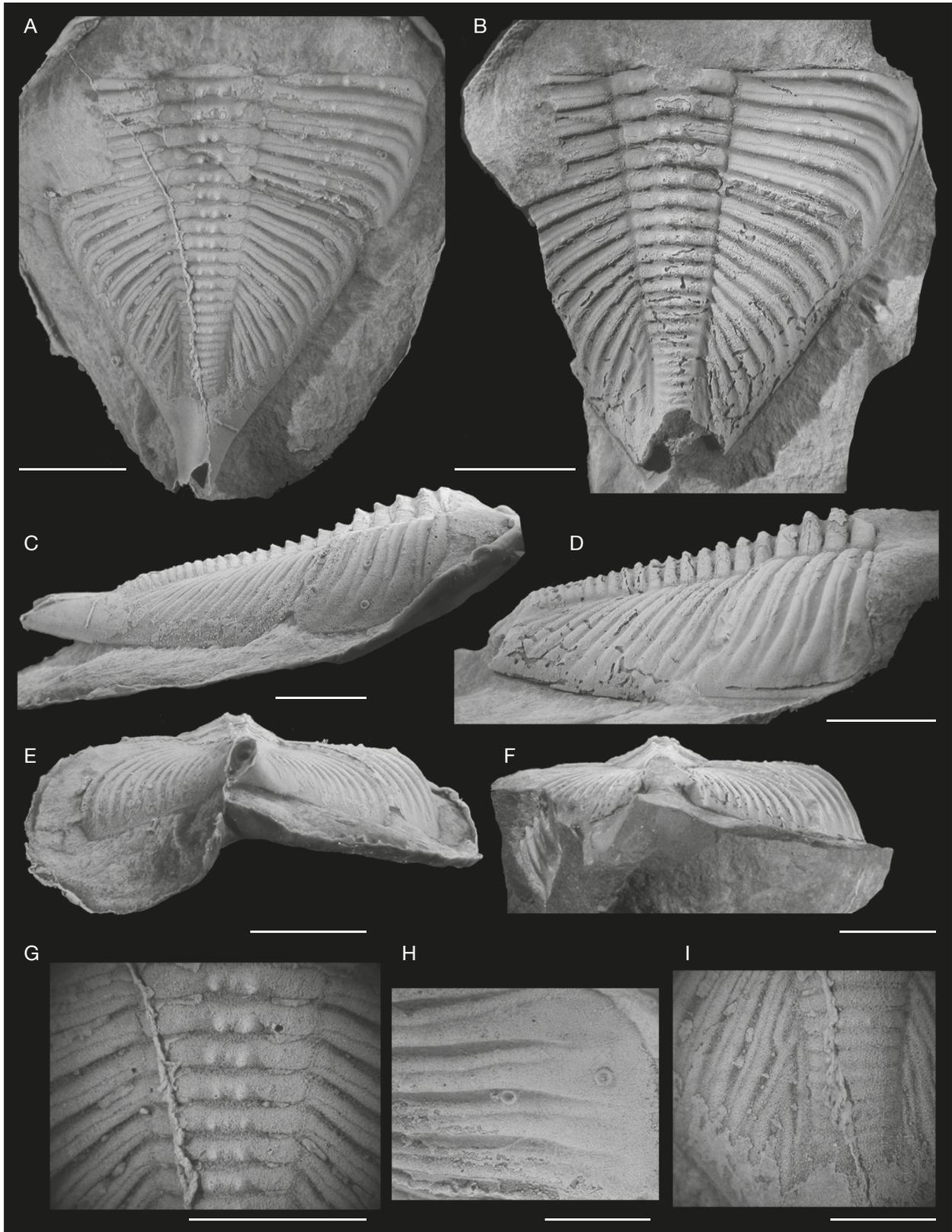


FIG. 7. — New genus and species of Dalmanitidae, pygidium from the Lochkovian-Pragian of Quebrada de las Aguaditas, Talacasto Formation, Precordillera Argentina. CEGH-UNC 27422: **A**, latex mould dorsal view; **B**, internal mould dorsal view; **C**, latex mould lateral view; **D**, internal mode lateral view; **E**, latex mould posterior view; **F**, internal mould posterior view; **G**, latex mould detail of axis; **H**, idem detail of circular marks on left pleural field; **I**, idem detail of abnormality in left pleural field. Scale bars: A-G, 1.0 cm; H, I, 0.5 cm.

TABLE 1. — List of dalmanitid trilobites recorded from the Devonian of southwestern Gondwana (Malvinokaffric Realm), indicating dorsal spinosity.

Dalmanitid taxa	Age	Units with records	Geographic occurrence	Dorsal spinosity	References	Pattern of spines
<i>Amazonaspis maecurua</i> (Clarke, 1890)	Eifelian	Maecurú Formation	Brazil	No	Carvalho & da Fonseca 2007	Absent. Thorax unknown
<i>Chacomurus confragosus</i> (Braniša & Vaněk, 1973)	Lochkovian-Emsian	Lower Belén Formation, Chacoma	Bolivia	No	Braniša & Vaněk 1973; Holloway & carvalho 2010	Thorax unknown. Pygidium only with marginal spines
<i>Dalmanites patacamayensis</i> Kozłowski, 1923	Early Devonian	Sica-Sica Formation	Bolivia	No	Kozłowski 1923	Absent
<i>Dalmanitoides accola</i> (Clarke, 1913)	Early Devonian	Ponta grossa Formation	Brazil	Yes	Rustán & Vaccari 2012	One spine on occipital ring. In pairs on some pygidial axial rings. Irregularly distributed on posterior pleural bands.
<i>Dalmanitoides boehmi</i> (Knod, 1908)	Pragian-Emsian	Tarabuco and Talacasto Formation	Bolivia and Argentina	Yes	Rustán & Vaccari 2012	Two to four spines on thoracic posterior pleural bands
<i>Dalmanitoides drevermanni</i> (Thomas, 1906)	Pragian-Emsian	Talacasto Formation	Argentina	Yes	Rustán & Vaccari 2012	One medial spine and two lateral on occipital ring. Little ones on posterior cephalic border. Four on thoracic axial rings, symmetrically located. In pairs on pygidial axial rings. Irregularly distributed on posterior pleural bands
<i>Dalmanitoides scutata</i> (Braniša & Vaněk, 1973)	Early Devonian	Gamoneda Formation, Gamoneda-Curuyo	Bolivia	Yes	Edgecombe 1993; Rustán & Vaccari 2012	Spines in pairs on thoracic axial rings
<i>Fenestraspis amauta</i> Braniša & Vaněk, 1973	Pragian-Emsian	Lower Belén Formation, Chacoma	Bolivia	Yes	Holloway & Carvalho 2009	Spines in pairs on axial parts of L1-L3. One medial and two lateral ones on occipital ring. Some on base of genal spines. In pairs on thoracic axial rings. In pairs on pygidial axial rings, and isolated ones on distal part (and in some cases also medial) of posterior pleural bands
<i>Francovichia branisi</i> (Wolfart, 1968)	Early Devonian	Lower Belén Formation, Limabamba	Bolivia	No	Braniša & Vaněk 1973	Absent. Thorax unknown
<i>Francovichia clarkei</i> (Ulrich, 1893)	Emsian-Eifelian	Icla Formation and Gydo Formation	Bolivia and South Africa	No	Cooper 1982	Absent
“ <i>Kasachstania</i> ” <i>gerardoi</i> Edgecombe & Ramsköld, 1994	Ludlow-Lochkovian	Los Espejos Formation and Catavi Formation	Argentina and Bolivia	No	Edgecombe & Ramsköld 1994	Absent
<i>Ivanites leonorae</i> n. gen, n. sp.	Lochkovian-Pragian	Talacasto Formation	Argentina	No	This current work	Absent
<i>Aguaditaspis mediaspina</i> n. gen, n. sp.	Lochkovian-Pragian	Talacasto Formation	Argentina	Yes	This current work	One spine on at least one thoracic axial ring. One on anteriormost pygidial axial rings
New genus and species of Dalmanitidae	Lochkovian-Pragian	Talacasto Formation	Argentina	Yes	This current work	Cephalon and thorax unknown. Spines in pairs on axial rings (except posterior ones). Small ones between or lateral to these pairs on axial rings. Irregularly distributed on anterior pleural bands. Small ones on anteriormost posterior pleural bands

to the Devonian of central Kazakhstan (Randolfe *et al.* 2020). The excluded specimens from other locations were either assigned to other unrelated genera or pointed out for pending further taxonomic revision (Randolfe *et al.* 2020).

Table 1 summarizes the dalmanitid trilobites recorded in basins of the Malvinokaffric Realm, excluding some poorly known records which should be considered *nomina dubia*.

Of the total taxa reliably recognized, 9 genera (90% of the total), and 13 species (more than 90% of the total) are endemic of the Malvinokaffric Realm. Only *Dalmanites* seems to be a widely distributed taxon, but some referred specimens, mainly from Bolivia, were never revised after their original assignment (Kozłowski 1923) and deserve a thorough revision. Other putative *Dalmanites*, from the

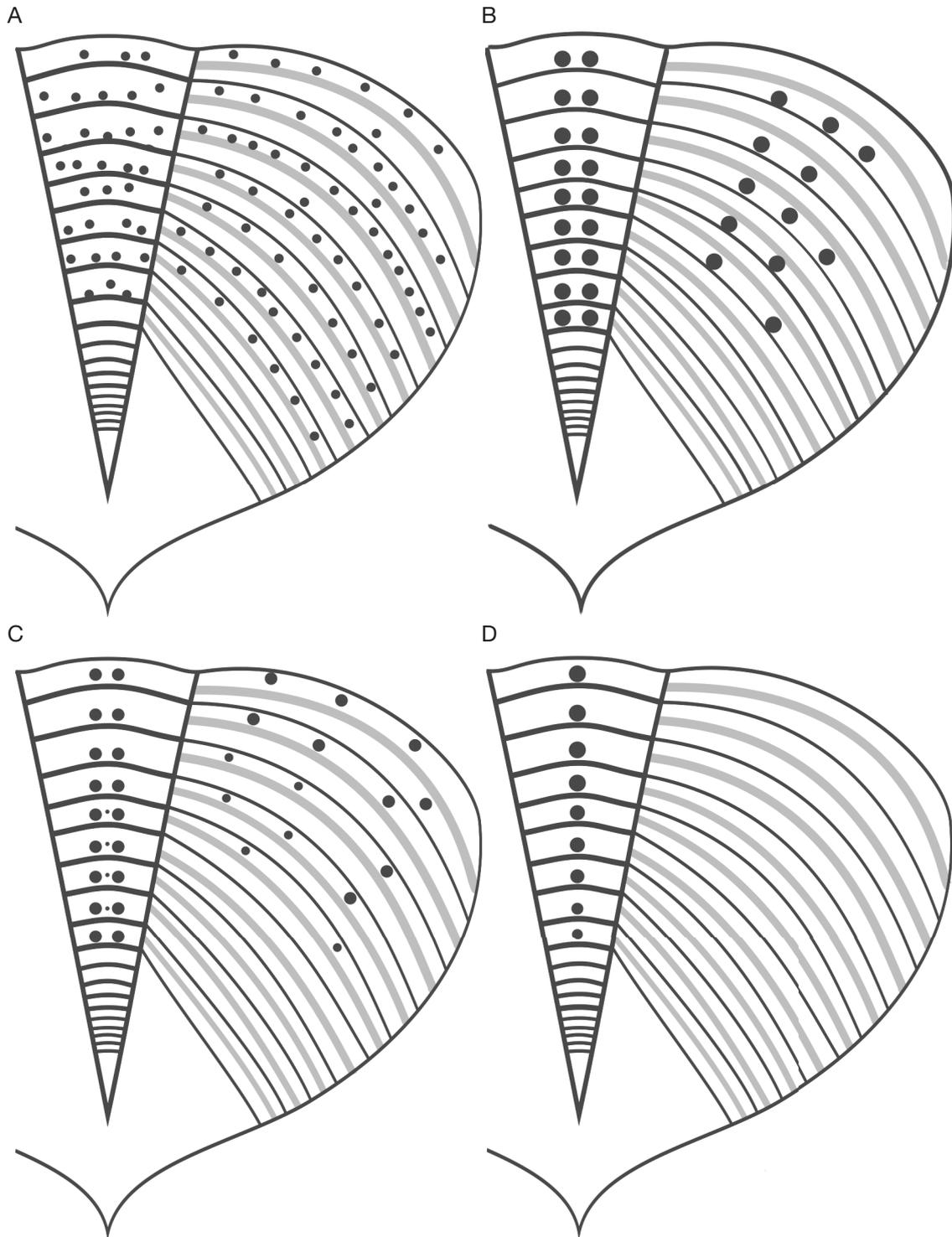


FIG. 8. — Schematic drawings of main dorsal spine patterns (only the location of base of spines is shown) among dalmanitids: **A**, pattern of *Zlichovaspis (Zlichovaspis) spinifera spinifera* (Barrande, 1852) from the Lower Devonian of the Prague Basin; **B**, pattern of *Dalmanitoides drevermanni* (Delo, 1935) from the Lower Devonian of Southern Gondwana; **C**, pattern of a new genus and species of Dalmanitidae from the Lower Devonian of Southern Gondwana; **D**, pattern of *Trypaulites calypso* (Hall, 1861) from the Devonian of the United States. Spines are not necessarily distributed in perfect longitudinal rows.

Middle Devonian of the Maecurú Formation, Brazil, were originally described by Clarke (1890). They were considered as indeterminate taxa with calmonioid affinities by Eldredge & Ormiston (1979) and are not included in the table. *Dalmanites? infractus* Clarke, 1890, on the other hand, was erected

based on scarce material that is considered lost (Ponciano 2011), and consequently, is also excluded for the table.

The new dalmanitid genera reported herein include *Ivanites* n. gen., *Aguaditaspis* n. gen. and a new genus of Dalmanitidae, all restricted to the Lower Devonian (Lochkovian-Pragian)

from the Precordillera Basin, Argentina. These taxa contribute to the idea of endemism and diversification of this family in Malvinokaffric basins.

THE SPINOSITY IN DEVONIAN DALMANITID TRILOBITES AS EVIDENCE OF PREDATION PRESSURE

Two of the new taxa described herein (*Aguaditaspis* n. gen. and the new genus of Dalmanitidae) exhibit dorsal spinosity, a very rare character among dalmanitids.

Table 1 indicates the presence of dorsally projected spinosity in the dalmanitids recorded in Malvinokaffric basins. As many as four genera (40% of the total genera) and seven species (50% of total species) exhibit a clear dorsal spinosity in this paleobiogeographic region.

Spines in invertebrate prey-groups are usually interpreted as passive (morphologic) defenses (Vermeij 2002; Mikolajewski & Rolff 2004; Willman 2007; Ito *et al.* 2016). Their evolutionary dynamics are linked to the ecological context of an increase of predation pressure or predator evolutionary bursts (Leighton 2003; Johansson & Mikolajewski 2008; Nagel-Myers *et al.* 2009).

For trilobites, dorsally projected spines have been proposed for different functions including their use as a sensory apparatus or to fight in intraspecific contests for access to mates (Kneil & Fortey 2005). More commonly, dorsal spines have been proposed for defensive functions, as protection of the blind spots against predators (Brett & Walker 2002), to dissuade them (Clarkson & Ahlberg 2002) or for attachment of algae that help camouflage (Schraut 2000). Spinosity patterns composed of robust dorsal spines densely distributed are well-recorded in trilobites from low paleolatitudes during the middle Paleozoic, as is the case in the Asteropyginae, Aulacopleuridae, Odontopleuridae and Scutelluidae (Chatterton *et al.* 2006; Feist & Chatterton 2015). In the case of dalmanitids, an Ordovician-Devonian cosmopolitan group characterized by a conservative *bauplan*, dorsal spinosity is a very unusual character only documented in the Devonian.

This dorsal spinosity is organized in some main distinct patterns (Fig. 8). For example, spines are common in some species of *Zlichovaspis* Pýbil & Vaněk, 1971, a widely distributed genus, but absent in the basins of southern Gondwana. These spines are narrow-based and irregularly distributed on the pygidial axis and pleurae, commonly more abundant on anterior pleural bands. On axial rings, spines have a stochastic distribution, with three to five on each ring (Fig. 8A). Size, morphology and abundance of these spines are considered diagnostic at the specific level. Some species, like *Z. (Z.) tuberculata* (Hawle & Corda, 1847), have spines defining three to five irregular longitudinal rows along the axis (Budil *et al.* 2009). Distribution of thoracic spines is irregular, not necessarily similar to that of the pygidium of the same specimen. The cephalon exhibits thorn-like tubercles densely distributed on glabella and palpebral lobes, occipital ring and genal area. Some species assigned to *Odontochile* Hawle & Corda, 1847, such as *O. phacoptyx* (Hall & Clarke, 1888), share a similar distribution of spines or spiny tubercles, although their spines are usually dorsally shorter than that of *Zlichovaspis*.

Dalmanitoides, *Fenestraspis*, from southern Gondwana, and *Roncellia perceensis* (Clarke, 1905) from Laurussia, bear robust dorsal paired spines or tubercles on several pygidial axial rings and irregularly distributed ones on posterior pleural bands (Fig. 8B). This pattern is similar to the new genus and species of Dalmanitidae reported herein. Nevertheless, this taxon has spines on anterior rather than posterior pleural bands (Fig. 8C). We considered this pattern as not homologous with the one of *Dalmanitoides* and *Fenestraspis*. In addition, some little spines are insinuated on the first posterior pleural bands of the new genus and species of Dalmanitidae and two or more additional much smaller are placed laterally on axial rings or between the pair of major spines.

In some *Dalmanitoides* species and probably in *Fenestraspis* the thoracic pattern of spines is similar to pygidial ornamentation, with additional dorsal spines more abaxially placed on axial rings. In both genera the presence of cephalic pairs of spines on L1-L3, one medial spine in the occipital ring and additional spines on the cephalic posterior border are common.

On the other hand, *Aguaditaspis mediaspina* n. gen., n. sp. bears only a medial dorsal spine on pygidial axial rings, while pleural bands are free of spines (Fig. 8D). This is a rare pattern similar to *Trypaulites calypso* (Hall, 1861) from the Lower Devonian of North America. *Aguaditaspis* n. gen. has at least one thoracic axial ring, probably the posterior one, with a medial spine (Fig. 5E, F, L).

Another pattern is observed in *Erbenochile* Alberti, 1981, from the upper Emsian-Eifelian of Morocco and Algeria, a genus considered related to Dalmanitids (Bignon & Crônier 2014). Robust pointed spines are located medially on each axial ring and little spines (6-8) are distributed on each thoracic, and the anteriormost pygidial posterior pleural bands. Some little dorsal tubercles are also present on axial rings, more distally than medial spine, particularly prominent in *E. issoumourensis* Chatterton & Gibb, 2010. One robust medial spine is also located in the occipital ring and additional spines on the posterior cephalic border of this genus.

We do not support a common phylogenetic origin for all these different spine patterns since morphological differences indicate that all the involved taxa do not conform to a monophyletic group. Given this, each pattern of dorsally projected spines should be interpreted as parallel evolutionary acquisitions (analogies) of dalmanitids during the Devonian.

The Devonian is an important period for the fossil record of predation. A number of works suggests a general rising of new and more abundant predators during this period. Their ecological/evolutionary impact has been characterized as the mid Paleozoic Marine Revolution (Signor & Brett 1984; Brett & Walker 2002) and is particularly clear among Devonian nektonic carnivorous like cephalopods and fishes (Klug *et al.* 2010). The defensive evolutionary response in preys, mainly represented by spinosity, has been treated in several works focusing on brachiopods, bivalves and crinoids from the Silurian to the Carboniferous (Leighton 2003; Baumiller & Gahn 2004; Nagel-Myers *et al.* 2009). None of the studies were centered on how this process affected trilobites, apart from these being considered a main prey-group during the

Paleozoic. Robust spines of Middle Paleozoic trilobites have been interpreted as defensive structures tangentially in publications focused on taxonomic discussions and assignments (e.g. Chatterton & Gibb 2010; Feist & Chatterton 2015).

A latitudinal gradient of predation pressure has been recognized, estimated to be lower at high paleolatitudes (Dudley & Vermeij 1978; Leighton 1999; Harper & Peck 2016). A common explanation is that the warmer temperatures in tropics led to a greater importance of biotic interactions including predation, as a result of a sustainable abundance of potential preys (Schemske *et al.* 2009). The presence of a latitudinal gradient of predation pressure is supported by studies that highlight lower predation at high latitudes (Sanford *et al.* 2003) and more diverse predation-prey interactions and evidences of failed predation at lower latitudes (Kelley & Hansen 2007). In Devonian strophomenid brachiopods this hypothesis is supported by the latitudinal variation of ornamentation, decreasing at higher paleolatitudes (Leighton 1999). A latitudinal gradient of predation-prey interactions in accordance with this was also recognized for extant brachiopods using frequencies of samples with repaired damage (Harper & Peck 2016). A more complex analysis at a less global scale recognized a latitudinal gradient in extant bivalves from the United States (Alexander & Dietl 2001). This work used different indexes for measuring predation intensity, centered on drilling. Those include size of the valves, frequency of incomplete drilling and variety of predation marks. In such a scenario of a recognized latitudinal predation pressure gradient, the presence of so much spinose taxa in the Malvinokaffric Realm (high paleolatitudes) is relevant.

Furthermore, in addition to evidences from dalmanitids, spinosity is also a remarkable feature of other Devonian trilobites from southern Gondwana. Many calmoniids are highly spinose, contributing to their high morphological disparity (Abe & Lieberman 2009). Spines are also present in other trilobite families, like the homalonotids *Burmeisterella braziliensis* de Carvalho, 2005 and *Burmeisteria herschelii* (Murchison, 1839). Moreover, the phacopids, a group as morphologically conservative as dalmanitids, include spinose representatives like *Echidnops taphomimus* Rustán & Balseiro, 2016. This taxon is otherwise particularly interesting because performed the habit of infaunal molting, a unique behavior, interpreted as an active defense to avoid predators by molting under the sediment (Rustán *et al.* 2011b). This taxon co-occurs in the very same layers than the newly reported dalmanitids of the Talacasto Formation herein.

However, evidence of predators in Malvinokaffric basins is poor. Fishes (*sensu lato*), for example, are only known from very scarce records in Bolivia, South Africa, Malvinas/Falkland Islands and Brazil (Janvier & Suarez-Riglos 1986; Anderson *et al.* 1999; Maisey *et al.* 2002; Janvier & Maisey 2010). To explain such scarcity, Janvier & Maisey (2010) suggested a preservational bias. In Argentina, just mentions of remains were reported (Frenguelli 1951; Janvier & Suarez-Riglos 1986; Rustán & Balseiro 2016). Cephalopods, in turn, once interpreted as nearly absent from the Malvinokaffric Realm (Boucot & Racheboeuf 1993; Bosetti *et al.* 2010),

are nowadays been reported from the Talacasto Formation (Cichowolski & Rustán 2017, 2020).

In this hypothesis of rising predation-prey interactions, it is worth to mention the abnormality on last three pleurae of the left side of specimen CEGH-UNC 27422 (Dalmanitidae, new genus and species, Fig. 7I), postulated as a possible post-predation mark. Additional evidences from the same unit studied herein, has recently been reported from a pygidial axial ring of a specimen of *Burmeisteria notica* (Clarke, 1913), considered as a post-predation mark (Rustán *et al.* 2020).

The record of Devonian spines in trilobite families usually devoid of them, like the dalmanitids and phacopiids along with putative records of attacks, would support a more intense predation-prey interaction than previously thought in Malvinokaffric basins. Although indirect, these evidences account for a clear evolutionary/ecological impact of predation over preys, even in paleolatitudes where predation should be less observable according the latitudinal gradient. Our evidence is consistent with the major event of increasing predation pressure in all marine Devonian ecosystems, predicted by the hypothesis of the mid Paleozoic Marine Revolution.

Acknowledgements

R. Haude and I. Tapia help in paleontological surveys in Precordillera Argentina. We would also like to thank Eng. Roal Zárate from Compañía Minera del Pacífico (El Refugio limestone quarry near Jáchal), for allowing us to access Loma de los Piojos locality. This work benefited from the helpful improvement of the English and constructive review of the manuscript made by M. Ebach and A. van Viersen, and the associate editor, Annalisa Ferretti. We thank the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the Universidad Nacional de Córdoba for providing the support and facilities used in this investigation. This is a contribution to PUE 2016-CONICET-CICTERRA. Financial support was provided by University of La Rioja (projects PIC) and the Agencia Nacional de Promoción Científica y Tecnológica (ANPyT-FONCYT) project BID PICT-2017-3095 granted to J. J. Rustán.

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Submitted on 4 May 2020;
accepted on 3 August 2020;
published on 12 January 2022.