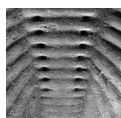


Trilobites and inarticulate brachiopods from the Devonian Floresta Formation of Colombia: a review

PIERRE MORZADEC, MICHAL MERGL, CARLOS VILLARROEL, PHILIPPE JANVIER & PATRICK R. RACHEBOEUF



The study of Devonian Colombian trilobites and inarticulate brachiopods allows to recognize two biostratigraphic levels within the Floresta Formation. The first level, in the lower part of the formation, is late Emsian in age, and yields 14 distinct trilobite taxa, including *Colombianaspis carvalhoae* gen. et sp. nov. The second one, in the upper part of the formation, is assigned to the Givetian based on the co-occurrence of the genera *Dipleura* and *Greenops*; this is the first record of a Givetian age for the upper part of the Floresta Formation. The inarticulate brachiopods collected from the uppermost part of the formation suggest a Givetian age. Inarticulate brachiopods as well as the trilobites show close affinities with the North Eastern Americas Realm, but they also suggest European affinities. The late Emsian occurrence of calmoniids from Colombia is indicative of restricted faunal exchanges with the Malvinokaffric Realm. • Key words: trilobites, inarticulate brachiopods, Devonian, Colombia, biostratigraphy, palaeobiogeography.

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In northwestern South America, Devonian strata outcrop around some of the Precambrian massifs in the northern part of the Cordillera Oriental of Colombia, namely the Quetame, Floresta and Santander massifs, and in the Serranía de Perijá, but also in the Cordillera de Mérida in Venezuela.

In Colombia, the Devonian sequence is over 1,500 m thick. From a lithological point of view, the succession is the same in all the known localities, and represents a sedimentary cycle overlying the Precambrian metasediments and metamorphites. It is covered by Carboniferous and/or Cretaceous. The Devonian succession begins with a conglomeratic level with decreasing graded-bedding, corresponding to the beginning of the Devonian marine transgression, up to 420 m thick; it is referred to as the El Tibet Formation in the Floresta area, and Gutiérrez Formation in the Quetame area. The basal lithologic unit is overlain by a 600 m thick monotonous succession of silts and silstones;

this level is highly fossiliferous (brachiopods, bryozans, crinoids, trilobites, ostracodes, corals, molluscs, vertebrates) and is referred to as the Floresta Formation in the eponymous area, or the Portachuelo Formation around Quetame.

The upper part of this succession is over 550 m thick and consists of an alternating sequence of pinkish to greenish, sandy, silty, and argillaceous levels yielding plant fragments, vertebrate remains, molluscs and ostracodes. In the Floresta area this unit, which corresponds to a regressive event, is referred to as the Cucho Formation, whereas it is known as the Pipiral Formation in the Quetame area (Villarroel in preparation). In other areas, such as the Serranía de Perijá (Forero 1970), and the Santander Massif (Boinet *et al.* 1986), the fossiliferous Devonian strata have not yet been named. As a whole, the litho- and biofacies strongly suggest that the sediments have been

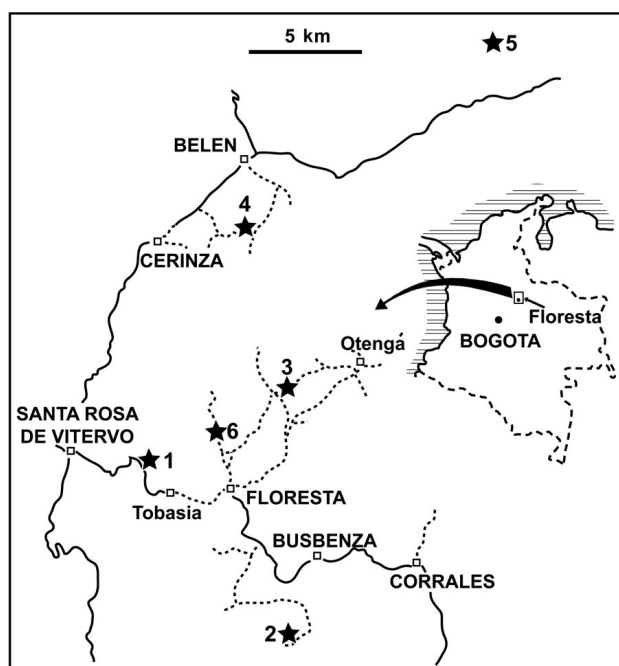


Figure 1. Geographic location of the fossiliferous localities and sections of the Floresta Fm. which provided the specimens. 1 – Quebrada Monticelo (N-NW of Tobasia), 2 – Quebrada Las Pilas (S-SW of Busbanza), 3 – W-SW of Otengá, 4 – Morro Cabezon (E-NE of Cerinza), 5 – Rio Pargua, 6 – N-NW of Floresta (2 km south of Las Cruces).

deposited in a shallow, epicontinental sea, opened towards the north (Barrett 1988) during the Emsian-Frasnian time interval.

Since the mid twentieth century, the Floresta Massif, which is located 125 km NE of Bogotá in the Boyacá department (Fig. 1), is a key area for the study of the Colombian Devonian fauna and flora of Colombia. Abundant and diverse plants, invertebrates and vertebrates have been described (e.g., Caster 1939, Berry *et al.* 2000, Janvier & Villarroel 2000). However, although fossils are abundant and widely distributed in the succession, their preservation is often poor, except in some localities.

Specimens described and illustrated in this paper are deposited in the collection of the Muséum d'Histoire Naturelle de Nantes, France under numbers MHNN.P.082701 to 082772, 082785 (trilobites), and MHNN.P.082773 to 082784, 082786 to 082798 (inarticulate brachiopods). They were collected by three of the co-authors. C. Villarroel collected the trilobites from the lower level of the Floresta Formation, whereas P. Janvier & P.R. Racheboeuf collected the specimens from the upper levels of this formation. Trilobite specimens are decalcified and variably distorted by tectonics. Only few specimens are available for each taxon and exoskeletons are most often disarticulated. Consequently, reliable identification was impossible for some forms which have been left in open nomenclature.

Stratigraphy (P. Morzadec)

Two distinct stratigraphic levels have been identified in the Floresta Formation, both are characterized by their markedly different lithofacies and faunal contents.

In the Quebrada Monticelo section (Fig. 2A), the lower part of the Floresta Formation consists of alternating shales and silts with numerous levels of coquinas yielding an abundant and diverse fauna that comprises bryozoans, tabulate corals, brachiopods, crinoids, trilobites and ostracods. Trilobites have been collected from beds 8 to 11, *i.e.* in a 3 meters thick interval (Fig. 2A). Three isolated fossiliferous localities, namely Morro Cabezon (E-NE of Cerinza, Fig. 1-4), W-SW of Otengá (Fig. 1-3), and the Rio Pargua section (Figs 1-5, 3) belong to the same time interval.

In the Las Pilas section (Figs 1-2, 2) trilobites were collected from the upper part of the Floresta Formation, in small sandy lenses intercalated in silts (bed 1, Fig. 2B), below the concretion level which yields the inarticulate brachiopod fauna; trilobite remains are disarticulated, and represented by small forms associated with rare brachiopods, crinoids and tentaculitids. The inarticulate brachiopods have only been collected from the upper part of the Las Pilas section, about 50 m above the trilobites level (bed 3, Fig. 2B) in siliceous concretions intercalated within grey to black silts. They are associated with undeterminable bivalve molluscs. This brachiopod fauna is indicative of a Givetian age.

The lower level provided us with 14 trilobite species preserved either in the silty layers, or in the decalcified coquinas that have yielded abundant bryozoans and brachiopods. Among the 14 species, *Cordania gasepiu* is known from the Grande Grève Limestones, Upper Gaspé Limestone in Québec (Lespérance & Sheehan 1988, p. 1441). *Anchiopsis armatus* occurs in the Schoharie Grit (late Emsian, *serotinus* Zone) of the Schoharie area, New York State. Lespérance & Bourque (1971, p. 204) recorded the species from the Grande Grève Formation in Québec. The genus *Coronura* is recorded from the Emsian–Eifelian of North America (Holloway & Carvalho 2010, p. 73). According to Lespérance (1975, p. 122), *Coronura lessepsensis* from the Grande Grève Formation (*Etymothyris* Zone, Emsian of Gaspé) is only known from its pygidium. Clarke (1901) described *Synphoria stemmata* from the Oriskany Formation of the Becraft Mountain, New York, whereas Lespérance & Bourque (1971, p. 196) mentioned the species in the Oriskany Formation in Virginia and in the Bois Blanc Formation of Michigan (late Emsian, *serotinus* Zone). According to Eldredge (1973) *Viaphacops cristata sensu lato* is mainly known from the Grande Grève Formation (Emsian of Québec), and the Esopus and Schoharie formations (late Emsian of the New York area). The species *Belenopyge contusa*, as well as the genus *Mannopyge*, both occur in the

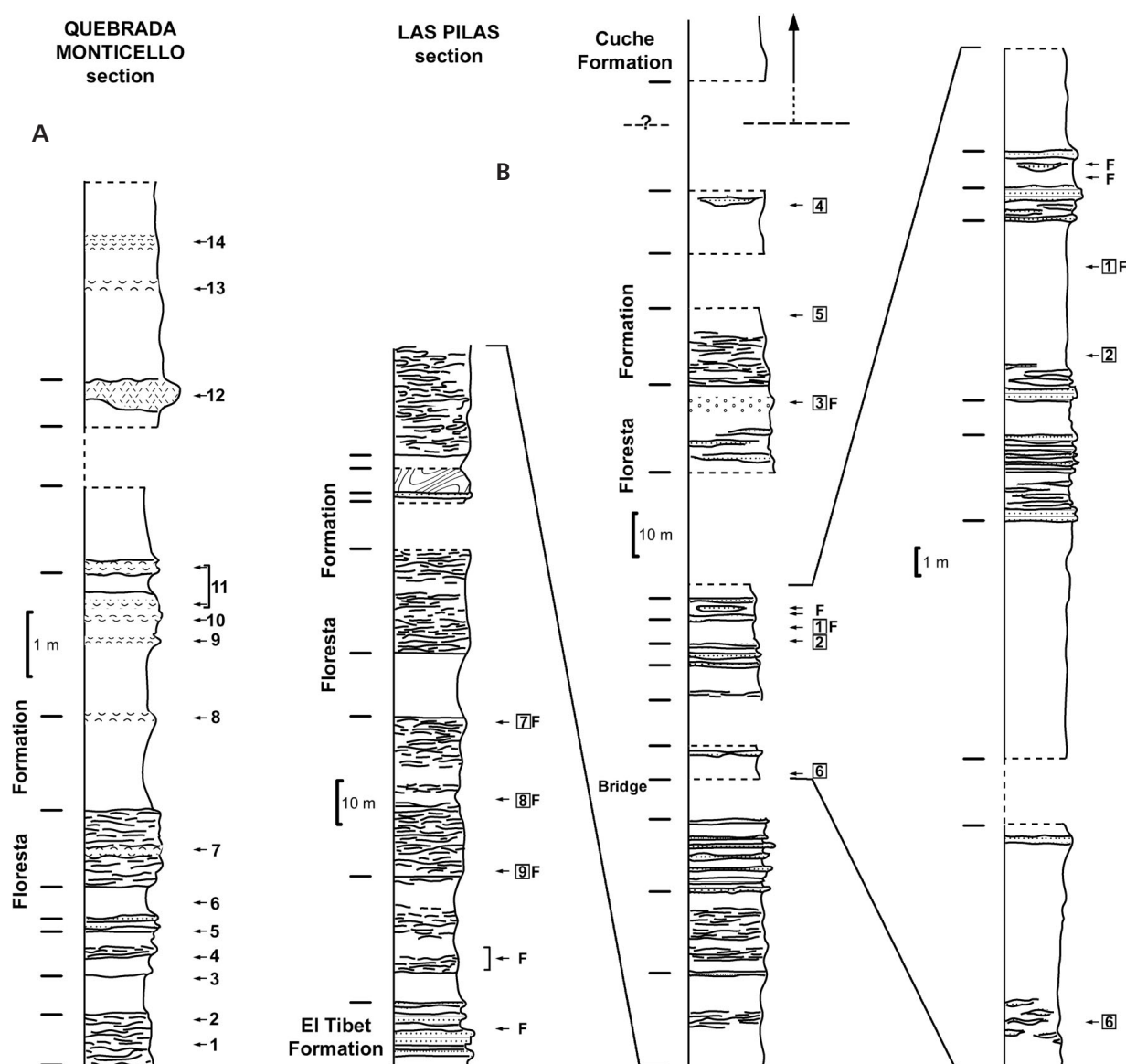


Figure 2. Lithostratigraphic columns of the Quebrada Monticello (A) and Quebrada Las Pilas (B) sections with localisation of the fossiliferous sampled levels.

Formosa member of the Amherstburg Formation of Ontario, which is assigned to the late Emsian *serotinus* Zone (Ludvigsen 1987). Consequently, and by comparison to the occurrences from Gaspé, Ontario, and the New York area, these fossiliferous levels of the Floresta Formation are likely to be late Emsian in age (*serotinus* Zone).

The sandy level that is intercalated within the silts, at the base of the upper half of the Las Pilas section (Fig. 2B, level 1) is mainly composed of thin sandstone beds and fossiliferous sandstone lenses which yield *Dipleura* cf. *dekayi* and *Greenops* cf. *grabaui* (see systematic section). The genus *Dipleura* and the species *D. dekayi* occur in the Givetian of North America, Michigan, Ontario, and the Appalachian range. The genus *Greenops* is also recorded

from the same area where it is restricted to the Givetian of the Appalachian Basin, whilst the species *G. grabaui* is restricted to the Hamilton Group (Lieberman & Kloc 1997, p. 96). Although two Colombian forms are still in open nomenclature, they allow to assign a Givetian age to the sandy trilobite level of the Las Pilas section.

Palaeobiogeography (P. Morzadec)

The occurrence of two distinct trilobite associations in the Floresta Formation is important with regard to the evolution of American palaeogeography during the Devonian.

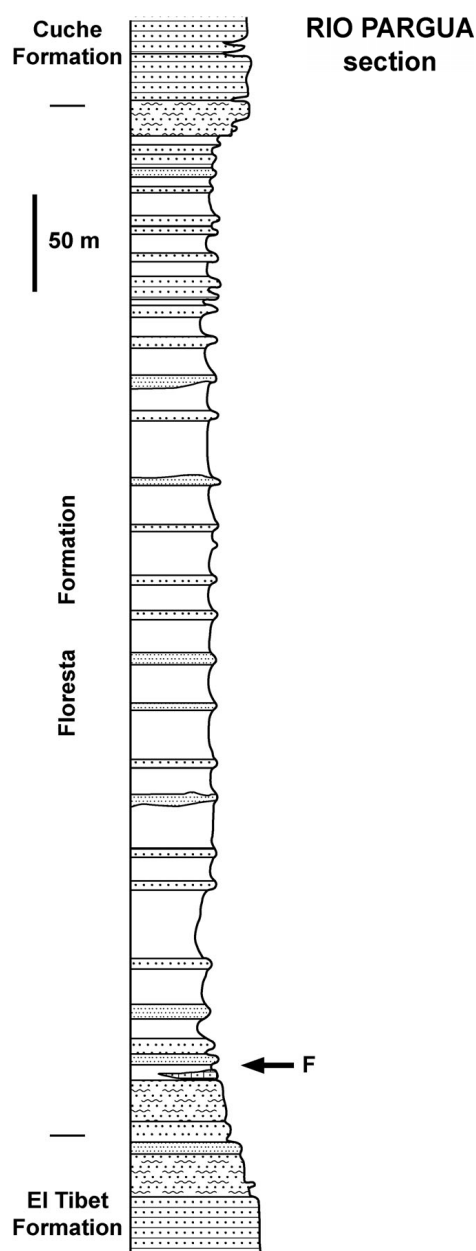


Figure 3. Lithostratigraphic column of the Rio Pargua section with the position of the trilobite level.

The lower trilobite association is typical for the North Eastern Americas Realm. These forms are mainly known from the Appalachian Basin to the Gaspé region of Canada where they have been described in the Emsian Upper Gaspé Limestone (Lespérance & Sheehan 1988). The genus *Cordania* Clarke, 1892 (Adrain & Kloc 1997, p. 709), *Viaphacops cristata* (Eldredge 1973, p. 314), *Anchiopsis armata* and *Synphoria stemmata* (Lespérance & Bourque 1971), as well as the genus *Coronura*, are typical early Devonian faunal components of the Appalachian Basin.

The trilobite fauna of the upper level is markedly less diverse. None of the taxa which occur in the lower level are

present, and the fauna includes representatives of the genera *Dipleura* (Homalonotinae), and *Greenops* (Asteroptyginae). However, this fauna exhibits the same North American affinities.

These two trilobite associations imply extensive faunal exchanges between the North Eastern Americas Realm (NEAR), and Colombia. Obviously, the faunal exchanges were better marked during the Emsian than in Givetian times, as suggested by the higher faunal diversity. The different lithologies of the sequences, carbonaceous deposits in the Appalachian Basin, and silty (and locally sandy) deposits in Colombia, may have influenced the geographic distribution of taxa. The small-sized Givetian specimens from Colombia may reflect this environmental factor.

The strong similarities between the faunas of the Floresta Formation and that of North America reflect the conclusions drawn by Morales (1965, p. 73), mainly from the brachiopod faunas. Close affinities with the Middle Devonian of Venezuela have also been established, based on the occurrence of the genera *Viaphacops* and *Greenops* (Carvalho & Moody 2000). Colombia and Venezuela were most probably very close to each other geographically, and had strong faunal relationships with the NEAR (Cooper 1982, p. 164).

Most importantly, only few genera, and none of the species listed from Colombia, are known to occur in the South American Malvinokaffric Realm, especially in Bolivia where a rich and diverse trilobite fauna has been described (Kozłowski 1923; Wolfart 1968; Eldredge & Branisa 1980; Holloway & Carvalho 2009, 2010). On the contrary, none of the Malvinokaffric species were found in Colombia. These observations agree with Eldredge & Ormiston's (1979, p. 148) who studied some faunal components from the Floresta Formation.

Only the genera *Dipleura*, *Viaphacops*, *Belenopyge*, and *Kettneraspis* and some rare calmonids are common to both domains. The homalonotid genus *Dipleura* has a large geographic distribution, since it occurs also in Africa and Europe, is therefore not unique to any of these biogeographic domains. The same applies to the genera *Viaphacops*, *Belenopyge* and *Kettneraspis* which show a relatively cosmopolitan distribution (Ramsköld & Chatterton 1991, p. 357; Thomas & Holloway 1988, p. 225).

The trilobite faunas suggest that a palaeobiogeographic barrier existed between the North-Eastern Americas Realm, including Venezuela and Colombia, and the Malvinokaffric Realm during the Devonian, as previously presented by, e.g., Barrett (1988), Barrett & Isaacson (1988), Johnson (1970), and Ormiston (1972). However, faunal exchanges were possible between these two domains, as suggested by Carvalho & Fonseca (2007, p. 10), and Colombia may have been on the dispersion route between these domains (Holloway & Carvalho 2010, p. 74).

In the Late Emsian of Colombia, the occurrence of a form close to the genus *Tarijactinoides*, a calmonioid known from the Late Lochkovian-Early Pragian *Scaphocoelia* Zone of Bolivia and from the Talacasto Formation of Argentina (Vaccari *et al.* 1994), strongly suggests such biogeographic relations. These are further supported by the occurrence of the calmonioid *Colombianaspis carvalhoae* gen. et sp. nov. in Colombia, the family Calmoniidae being known from Bolivia, Argentina, Brazil, South Africa. Similarly, the subfamily Synphoriinae, which is typical for the Early and Middle Devonian of the NEAR, has representatives both in Colombia and Bolivia (Holloway & Carvalho 2010). It is worth noting here that none of these species is hitherto known from the Devonian of Europe and North Africa. Only cosmopolitan genera such as *Dipleura*, *Greenops*, *Belenopyge* and *Kettneraspis* occur in these distinct biogeographic domains but they are represented by different species.

Systematic palaeontology

Inarticulate brachiopods (M. Mergl)

A small sample of lingulate brachiopods has been collected in the upper part of the Las Pilas section, in the uppermost part of the Floresta Formation, about 30 m below the boundary with the overlying Cuche Formation. The lingulate brachiopods co-occur with rare bivalve molluscs without any articulate brachiopod. Apart from the dominant brachiopod genus, three lingulid brachiopods have been recorded, but only two of them are identified at the generic level, namely *Schizobolus* and *Barroisella*; the remaining species (*Tarutiglossa*?) is more restricted quantitatively and qualitatively (preservation). This assemblage indicates a moderate diversity of the lingulate brachiopod fauna.

Records of the Devonian lingulids in South America are rather scarce. Kayser (1897) described *Lingula* (*Dignomia*) *subalveata* from Argentina, which he compared with *L. alveata* (Hall, 1863). In a more comprehensive paper Clarke (1913) reported five lingulids from the Devonian of the Parana Basin of Brazil. Some have been subsequently referred to *Dignomia* Hall, 1871 by Copper (1977). Boucot *et al.* (2001) noted the presence of *Lingula* sp. cf. *Lingula lepta* Clarke, 1913 from the Parecis Basin of Brazil. Recent papers (Bosetti 1989; Bosetti & Quadros 1996; Bosetti *et al.* 2011; Zabini *et al.* 2007, 2010) deal mostly with variation of shell morphology, taphonomy and taphofacies of lingulid brachiopods of the Paraná Basin of Brazil; the lingulids observed here more likely belong to *Dignomia* (Zabini *et al.* 2007).

Abbreviations. – Wsh – shell width; Lsh – shell length.

Class Lingulata Goryansky & Popov, 1985

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1828

Family Lingulidae Menke, 1828

Genus *Barroisella* Hall & Clarke, 1892

Type species. – *Barroisella campbelli* Cooper, 1942; Upper Devonian, Indiana, U.S.A.

Barroisella sp.

Figure 4A–E

Material. – Two ventral valves (internal and external moulds; MHNN.P.082773–082774); one incomplete dorsal valve (MHNN.P.082775), and an external mould of a small dorsal valve (MHNN.P.082776).

Description. – The shell is thin-walled, biconvex, with the largest specimen 12 mm long. The ventral valve is elongate, widest at the anterior third and having an evenly rounded anterior margin and an acute posterior margin. The apical angle is ca 80°. Lsh/Wsh ratio is 1.5. The valve is weakly convex at the mid-valve, having a more vaulted transverse profile near the apex. The ventral valve interior shows a weakly impressed rhomboidal visceral area extending to the mid-valve. Propareas are unknown. A pair of weakly diverging ridges is distinct at mid-valve. The dorsal valve is poorly documented and is characterized by an elongate-oval outline with a rounded posterior margin. The shell exterior has a distinct ornamentation of broad regular growth bands with superimposed concentric wavy lines. These lines are rather uniform in a size, ca 50 µm wide, numbering 10–12 per 1 mm anteromedially. Their size and density decreases laterally, depending on the width of the growth bands. Therefore, the lines are finer and more densely packed in the posterolateral shell sectors than in the median part of the shell.

Remarks. – A pair of prominent divergent ridges in the ventral interior and fine raised wavy concentric fila characterizes the shells of *Barroisella* sp. These long ridges on the ventral visceral area that run parallel to the pedicle nerve impressions are well documented in other species of *Barroisella* Hall & Clarke, 1892. However, details of the ventral interarea are unknown because beaks have been broken off in both available specimens before fossilisation. *Barroisella* is described from the late Middle and early Upper Devonian of the eastern United States (Hall & Clarke 1892, Cooper & Dutro 1982) and from the Frasnian and Famennian of Poland (Baliński 1979, 1995).

Our specimens are most similar to the specimens of *Barroisella campbelli* Cooper, 1942 illustrated by Holmer

& Popov (2000). However, the type specimens have anterior lateral muscles scars clearly impressed, whereas the Colombian specimens have faint impressions of almost all muscle scars. The Famennian specimens referred to *B. campbeli* by Baliński (1995) have a more elongately elliptical shell outline and may represent a separate species. Paired pedicle nerve supporting ridges on the visceral area are also developed in *Langella* Méndes, 1961, from the Carboniferous of eastern South America (Méndes 1961), and in *Argentiella* Archbold *et al.*, 2005, from the early Permian of Argentina (Archbold *et al.* 2005). Unfortunately, there are not sufficient data on the external microornament of these genera to elucidate their phylogenetic relationships.

Barroisella, *Langella*, and *Argentiella* and also the present specimens have a similar outline with evenly rounded anterior margin and maximum width anterior to the mid-valve. Although the taxonomic significance of the outline is restricted, these outlines probably indicate a seminafaunal rather than deeply infaunal mode of life that is characteristic of parallel-sided burrowing lingulids, *i.e.* *Lingula* Bruguière, 1797, *Glottidia* Dall, 1870, *Semilingula* Popov in Egorov & Popov, 1990 and *Dignomia* Hall, 1871.

***Tarutiglossa* Havlíček, 1984**

Type species. – *Tarutiglossa platyfabia* Havlíček, 1984; Famennian, Libya.

***Tarutiglossa?* sp.**

Figure 4F–I

Material. – Two external moulds of the dorsal valve (MHNN.P.082777–082778), and one internal mould of the dorsal valve (MHNN.P.082779).

Description. – The shell is subrectangular, 12 mm long, with well-rounded posterior margin, almost subparallel lateral margins and a weakly curved to almost straight anterior margin. Lsh/Wsh ratio is 1.3. The valve is posteriorly subcarinate in transverse profile, anteriorly becoming evenly and weakly convex. Maximum height (1.5 mm) is placed posteromedially. Posterolateral parts of the shell are clearly depressed. The apex is supramarginal, raised above the posterior margin by a low, steeply anacline slope. The dorsal pseudointerarea is very short, undivided. The dorsal valve interior has a well-defined visceral platform, extending over 30% of the valve length and occupying some 40% of the valve width. Large central scars are posterolaterally associated with less distinct muscle scars. A reverse V-shaped umbonal muscle scar is placed at the bottom of the umbonal chamber. The

shell ornamentation consists of subdued regular growth fila. Flanks bear oblique asymmetrical terrace lines, with a frequency of 70 µm apart. These lines are more regular anteriorly, with steeper slopes facing anteromedially. Triangular median shell sector almost smooth, always lacking the terrace lines.

Remarks. – The restricted material prevents generic identification. The absence of any plate in the dorsal pseudointerarea and the smooth exterior are consistent with the attribution of shells to the Lingulidae Menke, 1828. The present specimens show similarity with *Tarutiglossa* Havlíček, 1984 from the Famennian of Libya, but this genus lacks any traces of the terrace lines. The allocation of *Tarutiglossa* to the Pseudolingulidae Holmer, 1991 is uncertain; the genus probably belongs to true lingulids. The post-Devonian true lingulids (*Lingula* Bruguière, 1797, *Lingularia* Biernat & Emig, 1993, *Semilingula* Popov, in Egorov & Popov, 1990) have a large, anteriorly extended dorsal visceral area that is comparatively shorter in the Colombian material.

Superfamily Discinoidea Gray, 1840

Family Trematidae Schuchert, 1893

Genus *Schizobolus* Ulrich, 1886

Type species. – *Lingula concentrica* (Vanuxem, 1842); Middle Devonian, Tennessee, USA.

***Schizobolus pilasiensis* sp. nov.**

Figure 5A–N

Holotype. – Dorsal valve figured in Fig. 5A, J, K, M, MHNN.P.082780.

Paratype. – Ventral valve figured in Fig. 5D, E, I, MHNN.P.082783.

Etymology. – After the Las Pilas section, type locality.

Type locality. – Upper part of the Floresta Formation in the Las Pilas section.

Type horizon. – Givetian, Floresta Formation, upper part.

Material. – Eight dorsal and ten ventral valves (MHNN.P.082780–082784, 082786–082798) and several fragments, all preserved as undeformed internal and external moulds in siliceous concretions.

Diagnosis. – *Schizobolus* with subtriangular outline and concentric rugellate ornamentation.

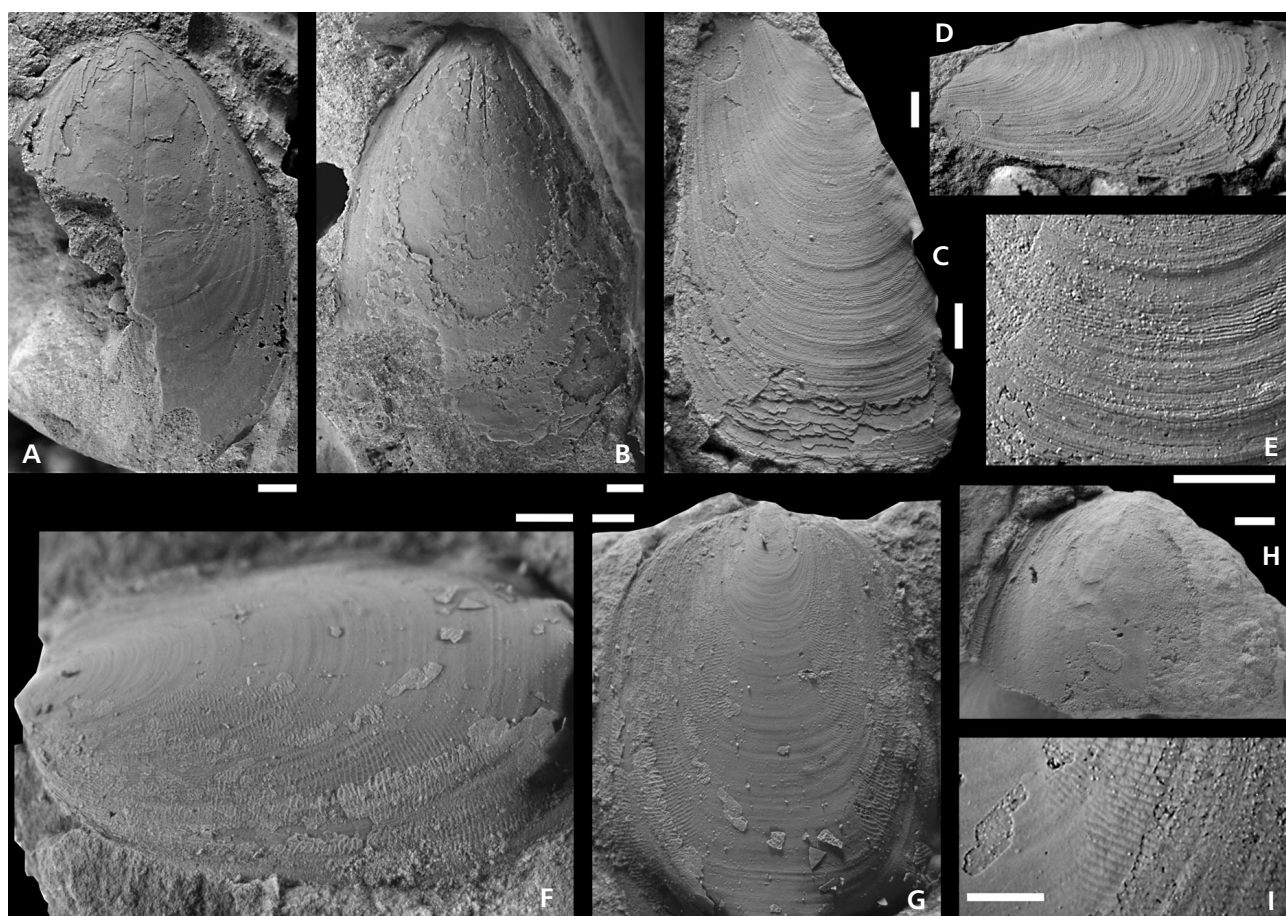


Figure 4. A–E – *Barroisella* sp. Upper part of the Floresta Formation, Las Pilas section, Givetian. • A, C–E – internal mould of the ventral valve (A), latex casts of exterior showing ornament (C), shell convexity (D) and microornament (E), MHNN.P.082773. • B – internal mould of the ventral valve, MHNN.P.082774. • F–I – *Tarutiglossa?* sp. Upper part of the Floresta Formation of Las Pilas section, Givetian. • F, G, I – dorsal valve, latex cast of external mould in oblique (F) and dorsal (G) views, and detail of terrace lines (I), MHNN.P.082777; H – dorsal valve, internal mould with muscle scars, MHNN.P.082778. Bar equals 1 mm.

Description. – The shell is thin-walled, subtriangular to subpentagonal in outline, rectimarginate, 7.2 mm long for the largest specimen. The dorsal valve is widest anterior to the midvalve, with Lsh/Wsh 0.97 to 1.02 ($n = 4$). The apex is submarginal. The anterior margin and posterolateral margins are weakly curved. A narrow median part of the posterior margin is almost straight. Lateral margins are most curved anterolaterally. The valve is moderately convex in lateral profile with maximum convexity at the mid-valve. The anterior slope is gently convex and flattened. The posterior slope is steep and slightly concave in an axial profile. The transverse profile is moderately convex having depressed median part. The visceral area is weakly impressed. Two pairs of small muscle scars posterolaterally flank the visceral area. Central muscle scars are oblique, large, extending to almost mid-valve. The vascular system is unknown.

The ventral valve has similar outline and convexity as

the dorsal valve except for a more depressed median sector of the valve. The pedicle notch is small, triangular, with posterior end closed by a small pseudointerarea. Propareas are flat, steeply procline, separated by a narrow and deeply concave pedicle groove. The surface of the pseudointerarea is covered by prominent growth lines. The shell ornamentation consists of almost regularly spaced concentric rugellae separated by much broader and flat concentric bands. The rugellae are thin, lamellose, slightly tilted forwards and having height 50 μm high maximum. The rugellae are 0.2 to 0.4 mm apart. Some shells possess only 15 rugellae, but most have 20 to 25 rugellae. Interspaces are broad, flat, covered by a few fine concentric growth fila, about 50 μm apart. Microornament unknown due to the poor preservation.

Discussion. – The new species differs from *Schizobolus concentricus* (Vanuxem, 1842) from the Middle Devonian

of Poor Valley, Tennessee, USA by a subtriangular shell outline having more convergent posterolateral margins than the type species. The ornament of the new species consists of evenly spaced rugellae, which are not well developed in *S. concentricus*. Insufficiency of data on shell morphology of the type species prevents a more accurate comparison. On the other hand, the similar shell size, the posteriorly located dorsal apex, the weak shell convexity and the narrowly triangular pedicle notch with a distinct pseudointerarea, which is in the type specimens (Baliński & Holmer 1999) accentuated by postmortem deformation, indicate the affinity of both species. The Famennian species *S. polonicus* Baliński & Holmer, 1999 differs by a smaller listrium and a finer external ornament.

Clarke (1913) reported and illustrated *Schizobolus truncatus* (Hall, 1863) (= *S. concentricus*) from the Upper Devonian black shales of Ereré, Parana. The illustrated specimens (Clarke 1913, pl. 25, figs 3, 4) also have a distinct rugellate ornament and may belong *S. pilasi*. *Schizobolus truncatus* has also been reported from Uruguay (Méndez-Alzola 1938), but both the description and illustrations are poor; illustrated specimen show only general morphology of a discinoid shell.

Conclusions

Although the collection is limited and the preservation bad, the lingulates from the upper part of the Floresta Formation clearly indicate affinity to the contemporaneous Givetian fauna of the Eastern America Realm and Europe. The presence of *Schizobolus* in the Floresta Formation in Colombia supports the similarity of the Colombian fauna with that of the North Eastern America Realm (NEAR, Boucot 1975). The genus is known from the Middle Devonian of USA and Poland (Baliński & Holmer 1999). With the single exception of Clarke's report (1913), the genus *Schizobolus* is generally unknown among the lingulate fauna from the South American basins, and its report from the Paraná Basin of Uruguay by Méndez-Alzola (1938) is questionable. Specimens of *Schizobolus* from Colombia are undeformed and show better preserved shell morphology, in particular the nature of the ventral pseudointerarea, than the type specimens of the genus (Baliński & Holmer 1999, fig. 2). *Barroisella* is known from the Upper Devonian and Lower Carboniferous of North America (New York, New Mexico), Poland, and the Czech Republic (unpublished).

Shell outline and development of distinct pedicle nerve supporting ridges in the ventral valve interior argue for the phylogenetic affinity of *Barroisella* with *Langella* and *Argentiella*. The latter are known from South America in Carboniferous and Permian beds.

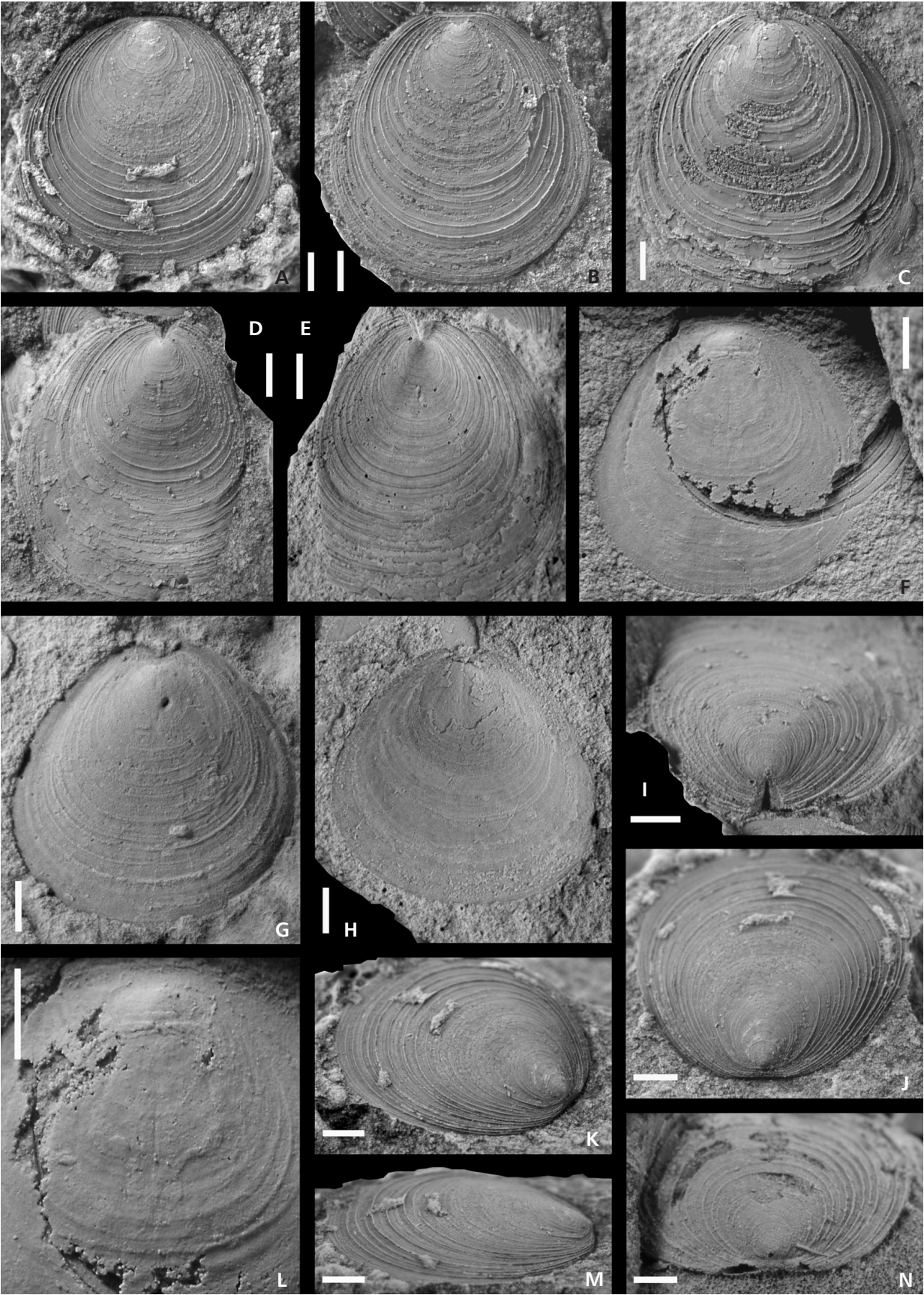
Trilobites (P. Morzadec)

The Devonian of the Floresta area of Colombia (NE of Bogotá, Fig. 1) have inspired several articles dealing mainly with its faunal contents and stratigraphy; see e.g., Caster (1939), Morales (1965), Forero (1970), and Barrett (1988). Unfortunately, the trilobite fauna was never thoroughly investigated in any of these publications, and descriptions as well as illustrations are of poor use; most identifications are often vague, erroneous, or left in open nomenclature.

Caster (1939, pp. 181–182, pl. 14) described and figured four trilobite species from the Floresta Formation namely: *Phacops* cf. *salteri* Kozłowski, ?*Dalmanites* cf. *patacamayaënsis* Kozłowski, ?*Cyphaspis* sp., and ?*Homalonotus* sp. Morales (1965, pp. 89–90, pl. 8) described and/or illustrated five trilobites: *Odontopleura callicera* (Hall & Clarke), *Phacops salteri* Kozłowski, *Cryphaeus* sp., *Proetus* sp., and *Dalmanites* sp., associated with a rich brachiopod fauna. Forero (1970, pl. 1) illustrated *Dalmanites* sp. and *Phacops salteri* Kozłowski from the Alto el Cielo locality, in the Serranía de Perijá, north of Floresta. Eldredge & Ormiston (1979, p. 148) listed *Phacops* (*Viaphacops*) sp., *Dechenella boteroi*, as well as undetermined odontopleurid and homalonotid. In his synthesis about the Devonian of Colombia, Barrett (1988, p. 710) only mentions the occurrence of “phacopid trilobites”.

The aim of this contribution is not to provide a detailed morphological study of the trilobites from the Floresta Formation, but rather establish their age by comparing them with other well-documented trilobite faunas, and define possible palaeobiogeographic relationships between Colombia and other American domains during the Devonian. One of the main difficulties was the lack of recent studies on North American Devonian species. A brief description of the sixteen identified trilobite species (Figs 6–12) allows comparison with already well known

Figure 5. *Schizobolus pilasiensis* sp. nov. Upper part of the Floresta Formation, Las Pilas section, Givetian. • A, J, K, M – holotype, dorsal valve, MHNN.P.082780; latex cast of external mould in dorsal (A), posterodorsal (J), oblique (K) and lateral (M) views. • B – dorsal valve, latex cast of exterior, MHNN.P.082781. • C – dorsal valve, latex cast of exterior, MHNN.P.082782. • D, E, I – paratype, ventral valve, MHNN.P.082783, latex cast of exterior (D), external mould (E) and posteroventral view (I). • F, L – dorsal valve internal mould with external mould of opposite valve (F) and detail of dorsal visceral area (L), MHNN.P.082784. • G – ventral valve, internal mould, MHNN.P.082786. • H – ventral valve, internal mould, MHNN.P.082776. • N – dorsal valve, latex cast of exterior, MHNN.P.082778. Bar equals 1 mm.



taxa, and provides further morphological data on some of them.

Family Homalonotidae Chapman, 1890
Subfamily Homalonotinae Chapman, 1890

Genus *Dipleura* Green, 1832

Type species. – *Dipleura dekayi* Green, 1832.

Dipleura cf. *dekayi* Green, 1832

Figure 6D, E

Material and locality. – Two small cranidia, (MHNN.P.082701, 082702), and an incomplete pygidium (MHNN.P.082703). First level of the upper half of the Floresta Formation, Quebrada Las Pilas section.

Description. – The two available cranidia are small-sized, 5 mm and 10 mm long respectively. The glabella is weakly convex, both longitudinally and transversally, and well defined anteriorly. The preglabellar border is flat and short. Axial furrows are subparallel, and weakly curved at the eyes, where the glabella narrows. These furrows exhibit two small anterolateral depressions. The occipital furrow is narrow, delimiting a flat occipital ring not higher than the high relief of the glabella. The anterior branches of the facial suture converge anteriorly. The palpebral lobes are located at mid-length of the glabella. On the smallest specimen, the glabella is shorter, markedly more convex, and the S1 furrows are weakly impressed. Similar ontogenetic morphological variations have already been described in *Dipleura lanvoiensis* Morzadec, 1969 from the Givetian of the Armorican massif, a species which is close to *Dipleura dekayi* Green, from the Hamilton Group of New York.

Discussion. – The paucity of the material collected does not allow identification at the species level. However the characters exhibited are very close to those of the North American species *Dipleura dekayi* which is common in the Givetian from Michigan (Stumm 1953) and Ontario where specimens are larger. Related species of *Dipleura dekayi* are known from the middle Devonian of Bolivia (Wolfart

1968), South Africa, Guinea Bissau, as well as in the Armorican Massif, W France (Morzadec 1983, p. 117).

Family Proetidae Hawle & Corda, 1847
Subfamily Dechenellinae Přibyl, 1946

Genus *Dechenella* Kayser, 1880

Type species. – *Phillipsia verneuili* Barrande, 1852.

Dechenella boteroi Caster & Richter, 1950

Figure 6A, B

1939 ?*Dalmanites* cf. *patacamayaënsis* Kosłowski. – Caster, p. 181, pl. 14, figs 3–6.

1950 *Dechenella* (*Basidechenella*?) *boteroi* Caster & Richter n. sp. in Richter R. & E., p. 161.

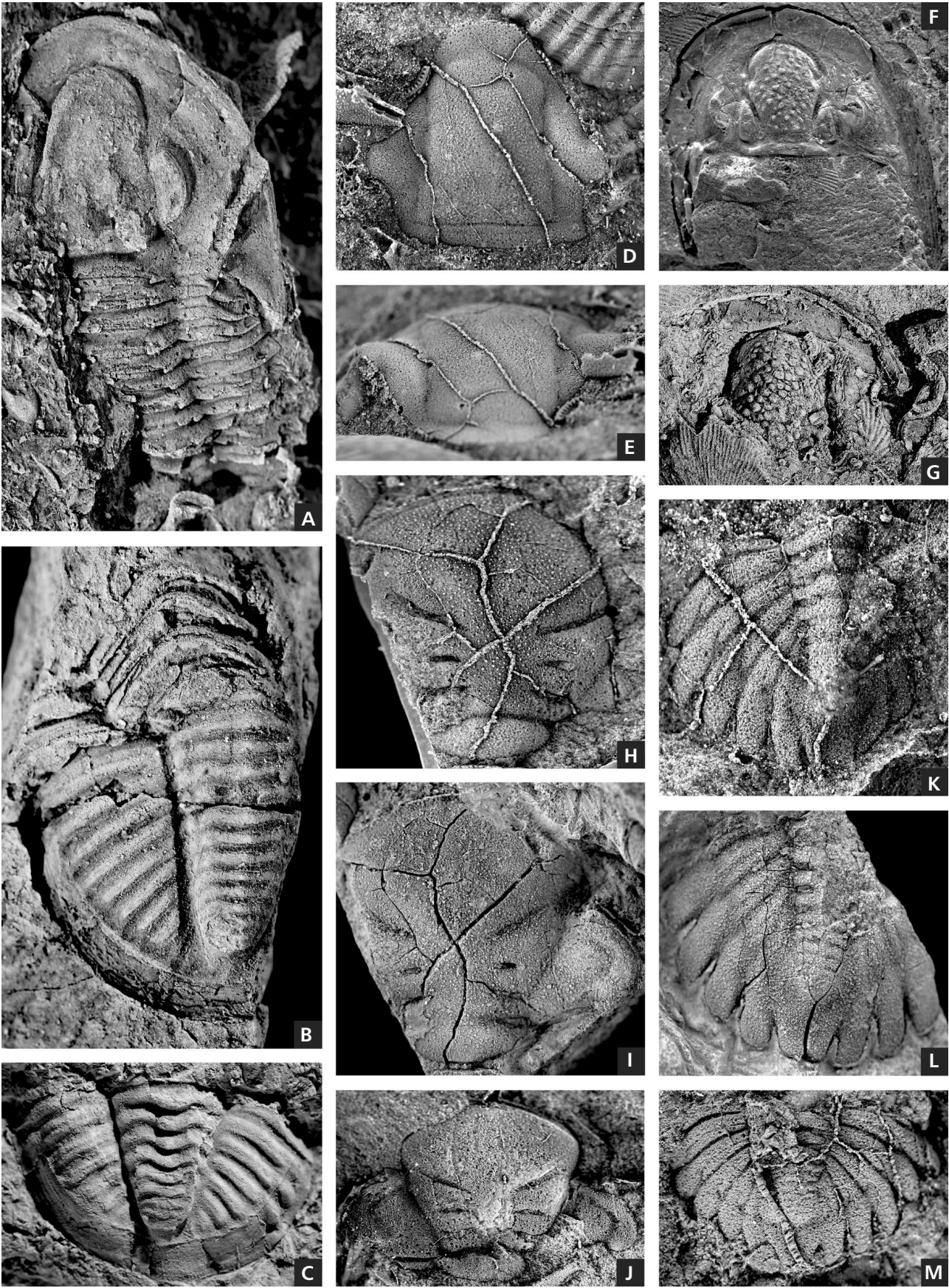
1979 *Dechenella boteroi* Caster & Richter. – Eldredge & Ormiston, p. 164.

Material and locality. – One cephalo-thorax (MHNN.P.082704), one pygidium with thoracic segments (MHNN.P.082705), one internal mould of pygidium (MHNN.P.082706). Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – The single available cephalon is unfortunately strongly distorted. Cephalic border equals one-fifth as long as the cephalon. It exhibits a well developed rim and extends backwards with short and flat genal spines. Axial furrows are sub-parallel. Eye half as long as the glabella. Nine thoracic segments are preserved, they are flat with axial rings as wide as the pleurae. The pygidium is slightly wider than long; its axis includes 12 narrow rings, wider than the pleural lobes, and bearing a median tubercle. Pleural lobes with 9 pairs of narrow ribs separated by wide pleural furrows. Interpleural furrow narrow and shallow. The doublure of the pygidium is wide.

Discussion. – The pygidium outline and the number of pleural ribs are similar to the material described by R. Richter (1950, p. 162), as well as *Dechenella boteroi* figured by Caster (1939, pl. 14, figs 3–6); the species was described from the Floresta Formation of the Oriental Cordillera of

Figure 6. A–C, F, G – lower part of the Floresta Formation, Quebrada Monticelo section, late Emsian. D, E, H, F, K, I, L, M – upper part of the Floresta Formation, Las Pilas section, Givetian. • A, B – *Dechenella boteroi* Caster & Richter. • A – cephalo-thorax, latex cast, dorsal view, × 10, MHNN.P.082704. • B – thorax and pygidium, internal mould, dorsal view, × 4.5, MHNN.P.082705. • D, E – *Dipleura* cf. *dekayi* Green. Cranidium, latex cast. • D – dorsal view, E – anterior view, × 4, MHNN.P.082701. • F, G – *Cordania gasepiu* Clarke. Cephalon, dorsal view, F – internal mould, G – latex cast, × 2, MHNN.P.082709. • H–M – *Greenops* cf. *grabaui* Lieberman & Kloc. • H, I – cranidium, dorsal view, H – latex cast; I – internal mould, × 5, MHNN.P.082740. • J – cranidium, latex cast, dorsal view, × 3, MHNN.P.082736. • K – pygidium, latex cast, dorsal view, × 10, MHNN.P.082743. • L – pygidium, internal mould, dorsal view, × 5, MHNN.P.082741. • M – pygidium, latex cast, dorsal view, × 6, MHNN.P.082744. • C – *Mannopyge* sp. Pygidium, internal mould, dorsal view, × 4, MHNN.P.082708.



Colombia. The cephalon was hitherto unknown and, although distorted by tectonic, the new material adds to the knowledge of the species. The assignment of this species to the genus *Dechenella*, rather than to the genus *Dalmanites*, had already been suggested by Caster (1939, p. 181). The type-specimen (external mould of pygidium) of the species was reviewed and carefully described by Eldredge & Ormiston (1979, p. 164).

Subfamily Warburgellinae Owens, 1973

Genus *Mannopyge* Ludvigsen, 1987

Type species. – *Dechenella* (*Dechenella*) *halli* Stumm, 1953.

Mannopyge sp.

Figure 6C

Material and locality. – One internal mould of a pygidium (MHNN.P.082708). Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – Pygidium semicircular in outline. Prominent longitudinal axis with 8 rings curved posteriorly, each possessing a median tubercle. Pleural lobes are convex and composed of 7 pleural ribs; their anterior part bears a tubercle in their distal part, whilst the posterior ones are short and do not reach the border of the pygidium. The doublure is wide.

Discussion. – The single internal mould of a pygidium possesses the diagnostic features of the genus *Mannopyge*. This genus is characterized by the development of tubercles on the distal end of the anterior half of the pleural ribs has to be noticed (see Ludvigsen 1987, p. 681, fig. 7). The genus is known from the upper part of the Lower Devonian of the New York state, and from the Amherstburg Formation of southern Ontario (Ludvigsen 1987).

Family Brachymetopidae Prantl & Přibyl, 1951

Genus *Cordania* Clarke, 1892

Type species. – *Phaethonides cyclurus* Hall & Clarke, 1888.

Cordania gasepiou Clarke, 1907

Figure 6F, G

1907 *Cordania gasepiou* nov.; Clarke, p. 172.

1960 *Cordania gasepiu* Clarke. – Whittington, p. 413, pl. 52, figs 1, 2.

1988 *Cordania gasepiu* Clarke. – Lespérance & Sheehan, p. 1440.

Material and locality. – One cephalon, external and internal moulds (MHNN.P.082709). Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – Cephalon semi-circular in outline, and 12 mm long without genal spines. The cephalic border is 2.5 mm wide and strongly concave. It exposes a very thin concentric rim located at 0.5 mm from the glabellar frontal lobe. The prominent glabella is ornamented by stout tubercles, the size and the density of which increase posteriorly. The glabellar lobes L1 are twice as long as wide and bear small tubercles. The S1 are deep and well exposed anteriorly on the internal mould. The eyes are less prominent than the glabella and are located at the anterior part of the lateral glabellar lobes. Genal spines are long and wide. The doublure exhibits thin concentric rims.

Discussion. – The illustration published by Whittington (1960, pl. 52, figs 1, 2) allows comparison with the Clarke's type specimen from Québec. The shape of the cephalic border, and the ornament of strong glabellar tubercles are identical on the Colombian specimen and on the specimen from the Grande Grève Limestone of Québec. Lespérance & Sheehan (1988, p. 1441) mentioned *Cordania gasepiu* from the Upper Gaspé Limestone of Québec.

Family Phacopidae Hawle & Corda, 1847

Subfamily Phacopinae Hawle & Corda, 1847

Genus *Viaphacops* Maksimova, 1972

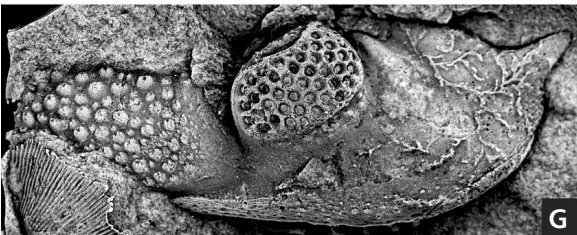
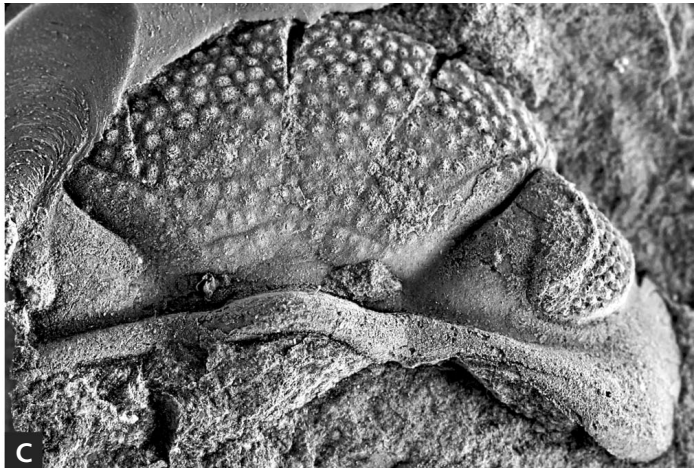
Type species. – *Phacops pipa* Hall & Clarke, 1888.

Viaphacops cristata (Hall, 1861)

Figure 7A–H

?1965 *Cryphaeus* sp.; Morales, p. 109, pl. 8, fig. 6.

Figure 7. Lower part of the Floresta Formation, Quebrada Monticelo section, late Emsian. *Viaphacops cristata* (Hall). • A – cephalo-thorax, internal mould, dorsal view, × 2, MHNN.P.082714. • B – cephalo-thorax, latex cast, dorsal view, × 2, MHNN.P.082713. • C – cephalon, latex cast, dorsal view, × 6, MHNN.P.082748. • D, E – cephalon, internal mould, dorsal (× 2) and lateral views (× 1.5), MHNN.P.082711. • F – complete exoskeleton, internal mould, lateral view, × 2, MHNN.P.082710. • G – cephalon, latex cast, antero-lateral view, × 2, MHNN.P.082712. • H – pygidium, latex cast, dorsal view, × 6, MHNN.P.082715.



Synonymy. – Stumm (1954), Eldredge (1973), Campbell (1977), Lespérance (1991), and Ramsköld & Werdelin (1991).

Material and locality. – One complete exoskeleton (MHNN.P.082710), one cephalon (MHNN.P.082711), one half of a cephalon (MHNN.P.082712), one cephalon and thorax (MHNN.P.082713), one cephalon and thorax, internal mould (MHNN.P.082714), one cephalon (MHNN.P.082748), one pygidium (MHNN.P.082715). Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – Large-sized cephalon with a moderately convex glabella bearing typical stout flattened tubercles. The variability in size and morphology of the glabellar tubercles is to observe. For example between the cephalons Fig. 7A–D with big flattened tubercles and Fig. 7B, C with smaller and sharp tubercles. The occipital ring is smooth, and the intermediate ring is restricted to two lateral tubercles. On three visual surfaces lenses number 14 dorsoventral files, with a maximum of 4 to 5 lenses per files. Each posterolateral angle bears a stout, dorsally curved, genal spine. No complete thorax is available. Each of the four anterior axial rings bears a median spine; rings 5 to 7 exhibit no more than a small tubercle, and rings 8 and 9 bear a spine. The pygidium axis is composed of nine rings, of which the two anterior ones bear a median tubercle. The seven pairs of pleural ribs do not reach the border. Interpleural furrows are developed on the four anterior ribs only. The anterior pleural bands are wider and more prominent than the posterior ones.

Discussion. – The stout tuberculate ornament of the glabella, combined with the development of genal spines and of spines on the thoracic axial rings are diagnostic of the species *Viaphacops cristata*, which includes several subspecies (see Eldredge 1973). According to this author, *Viaphacops cristata cristata* (Hall, 1861) is restricted to the Schoharie Formation of the New York state. *Viaphacops cristata* s.l. occurs in the Grande Grève Formation, Emsian of Québec, and in the Esopus and Schoharie formations, late Emsian, in the New York area, Ontario, Michigan, Indiana and Alabama (Eldredge 1973, p. 314).

***Viaphacops* sp.**

Figure 8F, G

Material and locality. – One complete exoskeleton, MHNN.P.082716, one carapace, external mould,

MHNN.P.082707; three cephalons, MHNN.P.082717, 082718, 082719. Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – The glabella is flat, ornamented by stout tubercles. The anterior rim is bounded by a well marked furrow in front of the glabella. The visual surface possesses 13 to 14 dorsoventral files, with a maximum of 6 lenses by file. Genal angles are rounded, without apparent genal spines.

Discussion. – This form differs from *V. cristata* by the lack of genal spines, by a smaller visual area, and by the finer ornament of the glabella.

Family Dalmanitidae Vogdes, 1890

Sub-family Synphoriinae Delo, 1935

Genus *Anchiopsis* Delo, 1935

Type species. – *Calymene anchiops* Green, 1832.

***Anchiopsis armata* (Hall, 1861)**

Figure 8A–D

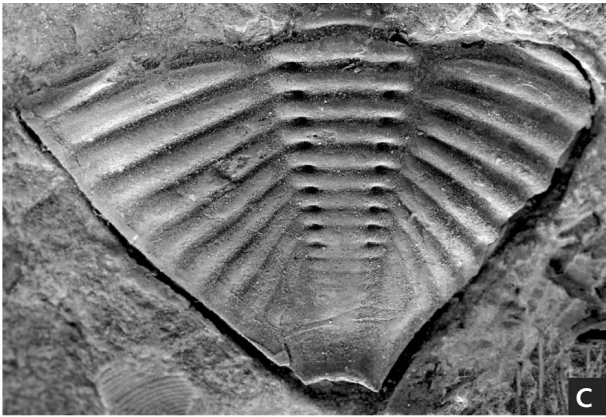
1861 *Dalmania anchiops* var. *armata*; Hall, p. 56.

1940 *Anchiopsis anchiops* var. *armatus* (Hall, 1861). – Delo, p. 84, pl. 10, figs 6, 7.

Material and locality. – Two incomplete cephalons, MHNN.P.082720, 082721, two internal moulds of pygidia, MHNN.P.082722, 082723. Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – The cephalon is large and ogival in outline, with genal angles elongated backward, but lacking genal spines. The occipital ring bears a stout spine, widened at the base. The anterior glabellar lobe flattens anteriorly. The central part of the glabella is depressed, unlike the L2 and L3 lobes. Axial furrows are shallow. The S1 furrows are short, and converge towards their adaxial extremities. The S2 are restricted to deep depressions connected to the axial furrows by very weak furrows. The L3 are more prominent than the L2, and the frontal lobes. Eyes are small, and situated with anterior edge opposite the S1 and posterior edge opposite the base of S3. The whole surface of the cephalon is smooth. The pygidium is triangular in outline. The rachis

Figure 8. Lower part of the Floresta Formation, Quebrada Monticelo section, late Emsian. • A–E – *Anchiopsis armata* (Hall). • A, B – cephalon, dorsal view; A – latex cast; B – internal mould, $\times 1.5$, MHNN.P.082720. • D, E – cephalon, dorsal view; D – internal mould, $\times 1.5$; E – latex cast, $\times 2$, MHNN.P.082721. • C – pygidium, internal mould, dorsal view, $\times 2$, MHNN.P.082723. • F, G – *Viaphacops* sp. Enrolled exoskeleton, antero-lateral view; F – internal mould; G – latex cast, $\times 3$, MHNN.P.082716.



bears 13 rings, and is one-third as wide as the pygidium. The pleural lobes show 9 segments, and interpleural furrows are indistinct. The pygidium ends in a spine which is wide proximally.

Discussion. – Specimens from the Floresta Formation show a strong occipital spine, rounded genal angles, and a stout pygidial spine which allow their assignment to the species *Anchiopsis armata* (Hall). Lespérance & Bourque (1971, p. 203) synonymized *A. anchiops* et *A. armata* despite the differences in the occipital and genal spines. *A. armata* is known from the late Emsian Schoharie grit, Schoharie area of New York. *A. anchiops* occurs in the same area, and in the Grande Grève Formation of Gaspé (Lespérance & Bourque 1971, p. 204).

Genus *Synphoria* Clarke, 1900

Type species. – *Dalmanites* (*Synphoria*) *stemma* Clarke, 1900.

Synphoria stemmata (Clarke, 1900)

Figure 9A–C

- 1900 *Dalmanites* (*Synphoria*) *stemma* sp. nov., Clarke, p. 15, pl. 1, figs 6–16, pl. 2, figs 1, 2.
- 1940 *Synphoria stemmata* Clarke, 1900. – Delo, p. 68, pl. 7, figs 1–3.
- 1971 *Synphoria stemmata stemmata* (Clarke, 1900). – Lespérance & Bourque, p. 194, pl. 26, fig. 4–7, 10–12.
- 1994 *Synphoria stemmata* Clarke. – Linsley, pl. 306, figs 1–13.

Material and locality. – External and internal moulds of five pygidia (MHNN.P.082724–082728). Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – The pygidium is flattened, semicircular in outline, and lacking a posterior median spine and ornament. The axis is one-fourth as wide as the pygidium. Thirteen axial rings bear a median tubercle, they are separated in the median part of the axis by shallow furrows becoming deeper laterally. The eight pleural ribs are bounded by deep pleural furrows, as wide as the half-ribs. Interpleural furrows of the six anterior ribs are narrow, and well developed

on the two thirds of the pygidial length. The anterior pleural bands do not reach the border of the pygidium, the posterior ones thicken and bend progressively backward before reaching the border. The rachis extends up to the pygidial border as a weak rim. The width of the pygidial doublure is one-fourth as wide as the pleural lobes.

Discussion. – The morphology of the Colombian pygidia compares closely with that of specimens illustrated by Clarke (1900, pl. 1), and reproduced by Linsley (1994, pl. 306, mainly fig. 9). The shape of the pleural ribs, as well as the rounded posterior border, agree with the intraspecific morphological variation of the species. Clarke (1901) described *Synphoria stemmata* from the Oriskany Formation of Becraft Mountain, New York. Lespérance & Bourque (1971, p. 196) mentioned the species in the Oriskany Formation from Virginia, and the Bois Blanc Formation, late Emsian of Michigan.

Genus *Coronura* Hall & Clarke, 1888

Type species. – *Asaphus aspectans* Conrad, 1841.

Coronura cf. lessepsensis Lespérance, 1975

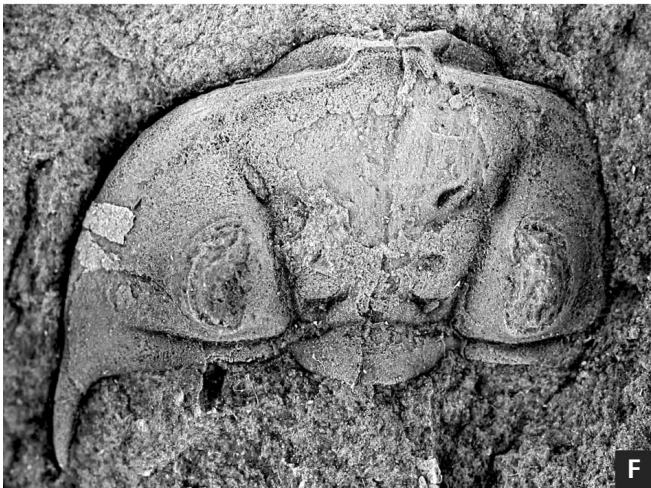
Figure 9D, E

- cf. 1975 *Coronura lessepsensis* n. sp., Lespérance, p. 122, pl. 4, fig. 6; pl. 5, fig. 1; pl. 7, fig. 1, text-fig. 6B.

Material and locality. – One complete exoskeleton, MHNN.P.082729. Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – The cephalon is semicircular in outline with long, flat genal spines, one-third as long as the cephalon. The cephalic border is wide and flat, undulating, with 4 nodes along its anterior margin. The glabella is limited by deep axial furrows. Furrows S1 are short and deep, S2 are restricted to a depression connected to the axial furrows by a weak furrow, whilst S3 are deep. The eyes are large, situated with anterior edge opposite S1 and posterior edge opposite S3. Visual surfaces are composed of very numerous small lenses. The occipital ring bears a median tubercle, and several large granules. The glabella and the genae are ornamented with numerous strong tubercles. The thoracic segments are also tuberculate. The axis of the pygidium

Figure 9. Lower part of the Floresta Formation, Quebrada Monticelo section, late Emsian. • A–C – *Synphoria stemmata* (Clarke); A – pygidium, internal mould, dorsal view, $\times 1.5$, MHNN.P.082724; B – pygidium, latex cast, dorsal view, $\times 4$, MHNN.P.082725; C – pygidium, internal mould, dorsal view, $\times 2$, MHNN.P.082726. • D, E – *Coronura cf. lessepsensis* Lespérance. Incomplete specimen. • D – cephalon, internal mould, dorsal view; E – exoskeleton, latex cast, dorsal view, $\times 2$, MHNN.P.082729. • F, G – *Colombianaspis* gen. nov. *carvalhoae* sp. nov. Cephalon, latex cast; F – dorsal view, G – lateral view, $\times 7$, MHNN.P.082752.



includes 16 rings, each bearing a stout median tubercle and two pairs of lateral tubercles. Sixteen pairs of narrow pleural ribs, with numerous small tubercles, are separated by deep pleural furrows. Interpleural furrows are not visible on the specimen. The axis ends in a median posterior rim. The pygidial border exhibits a median posterior indentation.

Discussion. – The morphological characters of the pygidium of the single available specimen, among which the indented posterior border, and its dense tuberculate ornamentation, strongly suggest that the Colombian specimen belongs to the genus *Coronura* (Stumm 1954, Holloway & Carvalho 2010, p. 73). This form is close to the species *lessepsensis* Lespérance based on the lack of pygidial spines and the number of pleural ribs. The genus *Coronura* occurs during the Emsian and the Eifelian of North America. According to Lespérance (1975, p. 122), *Coronura lessepsensis* is known only by its pygidium from the Grande Grève Formation (*Etymothyris* Zone) in Emsian of Gaspé.

Synphoriinae indet.

Figure 11D–G

Material and locality. – One incomplete cranium, MHNN.P.082730; three incomplete pygidia, MHNN.P.082731–082733; one internal mould of a pygidium, MHNN.P.082734. Lower part of the Floresta Formation, Rio Pargua section (Fig. 3).

Description. – The incomplete cranium does not allow a complete description, however, the glabella appears relatively flattened with a large anterior lobe ornamented with large tubercles. The S2 furrows are limited to two deep adaxial depressions and the S3 are well developed. The L1 are reduced. The pygidia are large and relatively flattened. The axis, one-fourth of the pygidium width, is limited by weakly divergent dorsal furrows. It is composed of 18 rings. The pleural lobes are composed of 12 pairs of pleural ribs, each bearing 3 tubercles. These tubercles are stouter on the third pair where the lateral ones develop as a stout spine. Along the axis, the second, third, seventh, eighth, twelve, thirteenth and seventeenth rings bear a median spine, whilst others are smooth. The interpleural furrows of the first three pairs of pleural ribs are weakly developed. The posterior end of the pygidium is not preserved.

Discussion. – The glabellar and pygidial segmentation suggest that this form belongs to the Subfamily Synphoriinae. The morphological characters of the pygidia are in agreement with those described by Hall & Clarke (1888, p. 31) for *Dalmanites phacoptyx* Hall & Clarke, 1888: the same number of pygidial pleural ribs, axial rings with or without median spine in alternance, presence of irregularly distributed spines or stout tubercles on the anterior pleural band. They also possess like *Dalmanites perceensis* Clarke, 1905, an ornament of alternating median spines and tubercles on the pleural lobes as well as on the axis. Since generic assignment of the species *phacoptyx* and *perceensis* has not yet been established, the original generic assignments are provisionally used. *Dalmanites phacoptyx* is known from the Upper Helderberg Limestones of Ontario. Delo (1940, p. 60) mentioned the species from the Lower Onondagan (Decewville) in Ontario and from the Oriskany Formation of the Becraft Mountain of New York. *Dalmanites perceensis* is known from the Murailles Limestones of the Percé area in Québec.

Family Acastidae Delo, 1935

Sub-family Asteropyginae Delo, 1935

Genus *Greenops* Delo, 1935

Type species. – *Cryphaeus boothi* Green, 1837.

***Greenops* cf. *grabaui* Lieberman & Kloc, 1997**

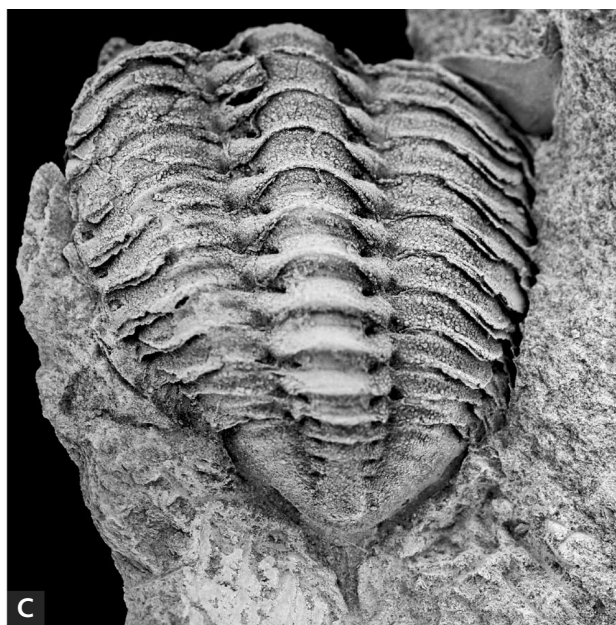
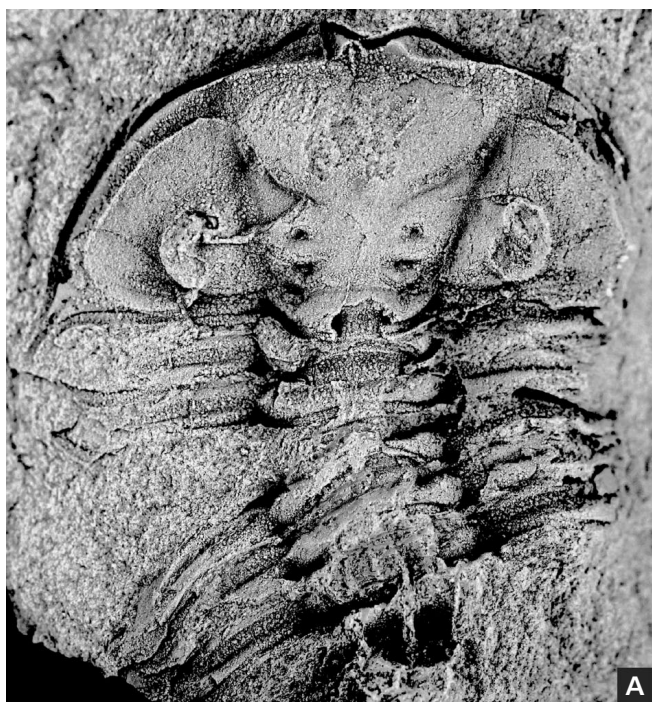
Figure 6H–M

cf. 1997 *Greenops grabaui* n. sp., Lieberman & Kloc, p. 93.

Material and locality. – Two internal moulds of a cranium, MHNN.P.082735, MHNN.P.082739; three external moulds of crania, MHNN.P.082736–082738; one cranium, external and internal moulds, MHNN.P.082740; two pygidia, internal moulds, MHNN.P.082741–082742; five external moulds, MHNN.P.082743–082747; one incomplete librigena, MHNN.P.082749. Upper part of the Floresta Formation, Quebrada Las Pilas section.

Description. – The collected material is small-sized; cranium 5.5 to 10 mm long and pygidium 5 to 7 mm. The glabella is as wide as long, and weakly arched, but relatively more convex in small specimens. The glabellar furrows

Figure 10. Lower part of the Floresta Formation, Quebrada Monticelo section, late Emsian. • A–G – *Colombianaspis* gen. nov. *carvalhoae* sp. nov. • A, B – cephalo-thorax, MHNN.P.082759; A – internal mould; B – latex cast, $\times 6$. • C, D – holotype, MHNN.P.082750. Complete exoskeleton, internal mould; C – thorax and pygidium, dorsal view, $\times 5$; D – cephalon, anterior view, $\times 8$. • E – cephalon, MHNN.P.082758; internal mould, dorsal view, $\times 7$. • F, G – cephalon, MHNN.P.082761, latex cast: F – dorsal view; G – lateral view, $\times 5$.



S2 appear as deep depressions separated from the axial furrows. The eyes are relatively long, extending from S1 to the extremity of S3, and they dorsally extend beyond the glabella. The anterior branches of the facial suture are weakly separated from the glabellar frontal lobe. The occipital ring is elevated above the glabella and bears a small median tubercle. The glabellar surface is granulose. Any fragments of the thorax are preserved. The pygidium is composed of 11 axial rings lacking median tubercle. The five pairs of pleural ribs have narrow but deep interpleural furrows. The posterior pleural bands are short and the anterior ones extend as lateral spines. Anterior and posterior pleural bands share the same relief. The five pairs of marginal spines are short, wide, rounded at their distal end, with narrow interspaces. The posteromedian spine is wide, rectangular in outline and shorter than the fifth spines.

Discussion. – The morphology of the cephalon, the segmentation of the glabella and the pygidium, and the presence of 11 axial rings on the pygidium, suggest that the specimens can be assigned to the genus *Greenops* Delo. The genus is well documented from the Givetian of North America. The small size of the material and its preservation make any specific identification uncertain. Nevertheless, according to Lieberman & Kloc (1997), the Colombian material can be tentatively assigned to *Greenops grabaui* Lieberman & Kloc from the Appalachian Givetian Hamilton Group.

Family Calmoniidae Delo, 1935

Genus *Colombianaspis* gen. nov.

Type species. – *Colombianaspis carvalhoae* gen. et sp. nov.

Etymology. – From Colombia, the country where the material was collected, and *aspis*: spine.

Diagnosis. – Small trilobite with the anterior part of the cephalon bearing a short angular extension bounded laterally by two small flat areas, eyes long and located posteriorly, visual surfaces narrow with a maximum of 4 lenses in each dorso-ventral file; genal spines short and weakly curved; occipital ring smooth; glabellar segmentation of calmonioid type; L1 narrow; L2 and L3 fused in their abaxial

part; pygidium small, convex, with 5 axial rings and 5 pairs of pleural ribs, ending in a long median spine; no lateral spines.

Discussion. – The glabellar segmentation of the new genus is diagnostic for the family Calmoniidae. Although it shares affinities with some species of the genus *Metacryphaeus*, it strongly differs in its pygidium. The pygidium, characterized by few rings, a smooth border, and a well developed terminal spine, show some similarity with the genus *Bainella* Rennie (Cooper 1982). The new genus *Colombianaspis* is hitherto monospecific. It show some convergences with the cephalon mentioned and figured as *Centauropyge* sp. (see discussion below) in the Indian Coves Formation of the Upper Gaspé Limestone, Emsian of Gaspé, by Lespérance & Sheehan (1988).

Colombianaspis carvalhoae sp. nov.

Figures 9F, G, 10A–G

aff. 1988 *Centauropyge* n. sp. – Lespérance & Sheehan, pl. 3, fig. 1.

Holotype. – Complete exoskeleton MHNN.P.082750, figured Fig. 10C–D.

Etymology. – In acknowledgement of Maria da Gloria Pires de Carvalho for her help.

Type horizon. – Lower part of the Floresta Formation, late Emsian.

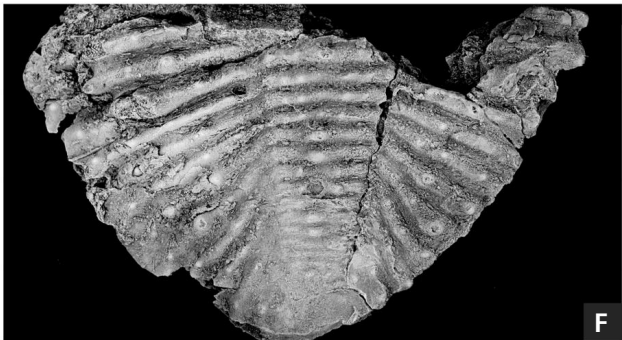
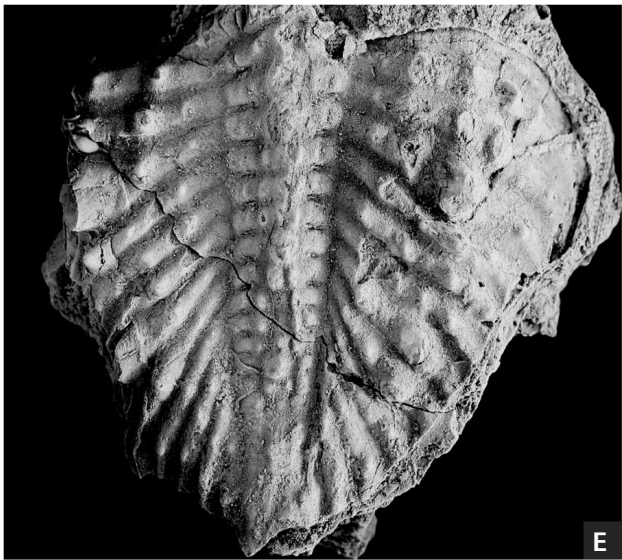
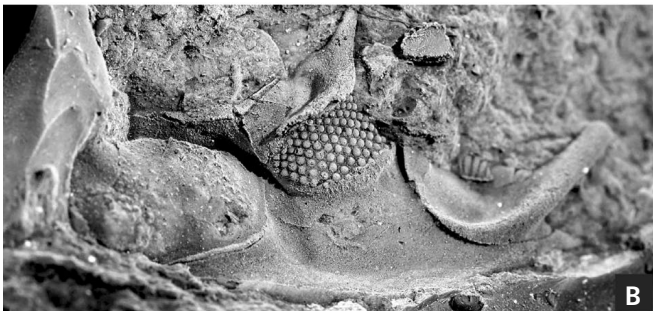
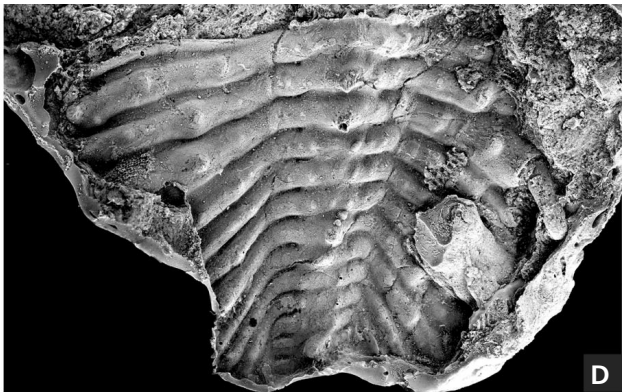
Type locality. – Quebrada Monticelo section, Colombia.

Material and locality. – Three complete exoskeletons, internal moulds, MHNN.P.082750–082751, MHNN.P.082757; 1 cephalon, internal mould, MHNN.P.082752; 1 cranidium, MHNN.P.082753; 3 cephalons, MHNN.P.082754–082756; one cephalon, MHNN.P.082758; two cephalo-thorax, MHNN.P.082759–082760; one cephalon, MHNN.P.082761. Lower part of the Floresta Formation, Quebrada Monticelo section.

Diagnosis. – As for the genus.

Description. – The cephalon is twice as wide as long and

Figure 11. Lower part of the Floresta Formation, late Emsian. A–C – Quebrada Monticelo section; D–G – Rio Pargua section. • A, B – cf. *Tarijactinoides* sp. nov. Complete exoskeleton, latex cast, MHNN.P.082762: A – dorsal view; B – antero-lateral view of the cephalon, × 4. • C – Calmoniidae indet. Cranidium, internal mould, dorsal view, × 2.5, MHNN.P.082763. • D–G – Synphoriinae indet. • D – pygidium, latex cast, dorsal view, × 1.5, MHNN.P.082731. • E – pygidium, internal mould, dorsal view, × 1, MHNN.P.082732. • F – pygidium, internal mould, dorsal view, × 1, MHNN.P.082733. • G – cranidium, internal mould, dorsal view, × 1, MHNN.P.082730.



is 5.5 to 7.5 mm long. Its anterior margin extends in a short angular extension. On each side of the extension, the cephalic border exhibits a typical small area, flat and subvertical (see Fig. 9F, G). The anterior branches of the proparian suture show an angular line, following the outline of the extension. The frontal lobe of the glabella is flat and smooth. The furrows S2 appear as deep depressions separated from the dorsal furrows. The lobes L2 and L3 are prominent, but L3 is more prominent than L2. Eyes one-third as long as the cephalon, elevated above the glabella and located posteriorly. The visual surfaces are small, with 17 dorso-ventral files, each with a maximum of 4 lenses. The occipital ring is smooth. Genal spines one-third as long as the cephalon; they are curved inwards and subcircular in cross section. The thorax is composed of 11 segments; axial rings one-third as wide as the thorax. The pygidium is small, almost rounded in outline, and markedly convex transversally; it exhibits 5 axial rings, and 5 pairs of pleural ribs. The border is narrow and extends posteriorly in a flat, long median spine, long about half of the length of the axis (see Fig. 10C). No marginal spines.

Discussion. – The cephalon from the Floresta Formation have some similarity with the Acastavinae figured by Lespérance & Sheehan (1988, pl. 3, fig. 1) from Gaspé, and assigned by the authors to the genus *Centauropyge* Haas, 1968 from the late Emsian of Turkey. Nevertheless the Canadian cephalon, single specimen, an internal mould, differs markedly by the contour, the glabellar furrows and the genal spines from the cephalon of the Turkish *Centauropyge*. However, the segmentation of the cephalon of the Colombian material and also the morphology of the pygidium with its posterior median spine, are distinct in the Turkish, Canadian and Colombian forms. Lespérance & Sheehan reported *Centauropyge* n. sp. from the Upper Gaspé Limestone, Indian Cove Formation (Emsian) of Gaspé.

Genus *Tarijactinoides* Suarez Soruco, 1971

Type species. – *Tarijactinoides jarcasensis* Suarez Soruco, 1971.

1980 *Tarijactinoides* Suarez Soruco, 1971. – Eldredge & Branisa, p. 277.

cf. *Tarijactinoides* sp. nov.

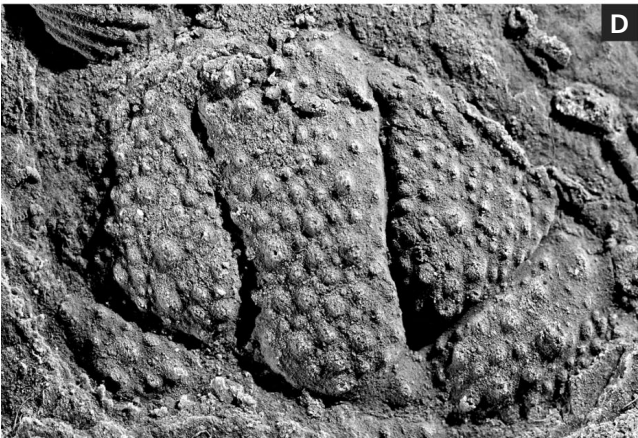
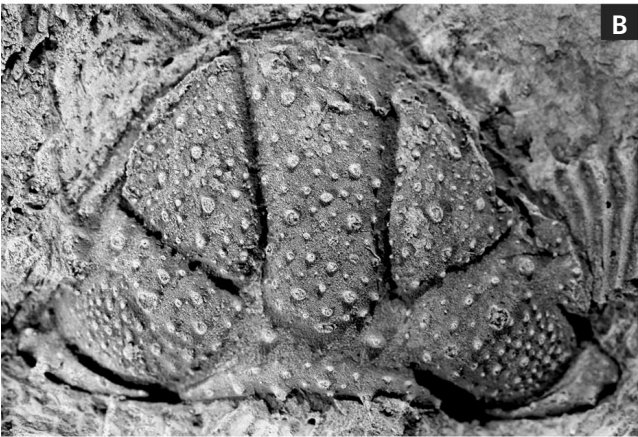
Figure 11A, B

Material and locality. – One incomplete exoskeleton, internal and external moulds, MHNN.P.082762. Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – The incomplete cephalon shows a markedly convex glabellar frontal lobe with a median spine. The glabellar segmentation is not preserved. The eyes are large, with at least 25 dorso-ventral files, each bearing a maximum of 8 lenses. The posterior margin of the palpebral lobes shows a relatively long and erected spine. The occipital ring bears a median spine. The anterior branch of the cephalic suture is accentuated by a thin rim. The posterior border of the cephalon bears a stout metafixigenal spine. The base of a genal spine is preserved. The thorax is composed of 11 segments, curved posteriorly, each axial ring bearing a thin median spine. The pleurae are ornamented with a mediolateral spine inserted on the posterior margin of each pleural rib which laterally ends in a flat, relatively short, and posteriorly bent pleural spine. The pygidium is small and triangular in outline; its axis is composed of 8 rings with a median tubercle. Pleural lobes are relatively flat; two weakly distinct pleural ribs bear an erected spine inserted where the ribs bend ventrally. The second pleural ribs are parallel to the axis. The third pair of pleural ribs is almost undistinguishable, and there are no furrows on the pleural lobes. The border of the pygidium is complete, and ends in a short, triangular median spine.

Discussion. – The Colombian specimen referred herein to cf. *Tarijactinoides* sp. nov. shares some characters (Eldredge & Branisa 1980, p. 277) with the Bolivian genus *Tarijactinoides* Suarez Soruco, 1971. Like *Tarijactinoides* it exhibits a spine on the frontal glabellar lobe, a metafixigenal spine, spinose thoracic segments, and a small pygidium. The main differences lie in the size of the eye and in the number of pygidial ribs. The unique incomplete specimen does not allow the erection of a new genus, nor a new species. However cf. *Tarijactinoides* sp. nov. differs from the two hitherto known species, namely *T. jarcasensis* Suarez Soruco and *T. tikanensis* Eldredge & Branisa, from the late Lochkovian–early Pragian *Scaphocoelia* Zone of Bolivia, by a lower number of pleural ribs on the pygidium (3 pairs instead of 7) among others (Vaccari *et al.* 1994).

Figure 12. Lower part of the Floresta Formation, late Emsian. A, B, D – Quebrada Monticelo section; C – section W-SW of Otenga; E–G – Morro Cabezon E-NE of Cerinza. • A–D – *Belenopyge contusa* (Hall & Clarke). • A – cranium, latex cast, dorsal view, × 4, MHNN.P.082765. • B, D – cranium, dorsal view; B – internal mould; D – latex cast, × 3, MHNN.P.082766. • C – pygidium, internal mould, dorsal view, × 3.5, MHNN.P.082767. • E–G – *Kettneraspis callicera* (Hall & Clarke). • E, F – cephalo-thorax, dorsal view; E – latex cast; F – internal mould, × 3, MHNN.P.082769. • G – distorted thorax and pygidium, latex cast, dorsal view, × 4, MHNN.P.082770.



Calmoniidae indet.
Figure 11C

Material and locality. – Two cranidia, internal moulds, MHNN.P.082763–082764. Lower part of the Floresta Formation, Quebrada Monticelo section.

Description. – The frontal lobe of the glabella is narrower than L3, conferring the glabella a “barrel-like” outline. L1 very narrow, S1 curved, S2 connected with the axial furrows and deeper in their proximal part; S3 markedly oblique. The anterior branches of the suture separated from the anterior lobe. The preglabellar furrow is well developed. Eyes with anterior edge opposite middle of L2 and posterior edge opposite middle of L3.

Discussion. – The glabellar shape and segmentation, the location and relative size of the palpebral lobes, only allow to place these specimens within the family Calmoniidae.

Family Lichidae Hawle & Corda, 1847
Subfamily Trochurinae Phleger, 1936

Genus *Belenopyge* Peck & Vaneck, 1991

Type species. – *Lichas balliviani* Kozłowski, 1923.

Belenopyge contusa (Hall & Clarke, 1888)
Figure 12A–D

Synonymy. – See Ludvigsen (1987, p. 687, figs 11, 12a–h).

Material and localities. – One cranidium, MHNN.P.082765; two cranidia, MHNN.P.082766, 082768, thorax and pygidium, MHNN.P.082785, lower part of the Floresta Formation, Quebrada Monticelo section. one pygidium, internal mould, MHNN.P. 082767, lower part of the Floresta Formation, W–SW of Otenga.

Description. – The cephalon is twice as wide as long and surrounded by a narrow cephalic border. The central part of the glabella is subrectangular in outline, bounded by weakly divergent furrows and characterized by numerous spinose tubercles. The lateral glabellar lobes are triangular, and bounded by deep furrows. The occipital ring bears numerous tubercles among which three are better developed. The eyes are small, and widely separated from the glabella. The thorax is relatively flat. The thoracic pleurae bear 5 tubercles. The pygidial axis is prominent, laterally bounded by deep furrows, and wider than the pleural lobes. A unique axial ring is visible on the axis that ends in a median posterior rib. Each pleural lobe possesses three ribs. The pygidial border is characterized by three pairs of short, flat-

tened, and posteriorly bent marginal spines. The whole pygidium bears numerous spinose tubercles.

Discussion. – The generic name *Belenopyge* Peck & Vaneck, 1991 is considered as synonym of *Lobopyge* Přibyl & Erben, 1952 by Ebach & Ah Yong 2001. Özdikmen (2009) considers *Lobopyge* as invalid and substitute the name *Belenopyge* for *Lobopyge*. The genus *Belenopyge* has a wide geographic distribution. It is represented by numerous species in the Emsian and the Eifelian of Europe (Czech Republic, Germany, France), as well as from Morocco and Australia (Ebach & Ah Yong 2001). It has also been described from North America, the New York area and Ontario, and from South America where the subfamily is represented by *Belenopyge balliviani* (Kozłowski, 1923). The Colombian specimens share all the characters of *Belenopyge contusa*: shape of the glabella, anteriorly reduced cephalic border, shape and length of pygidial spines, granulose ornament of both the glabella and pygidium. *Belenopyge contusa* is known to occur in the Onondaga Limestones of the New York area, and in the Formosa member of the Amherstburg Formation (late Emsian, *serotinus* Zone) of SW Ontario (Ludvigsen 1987).

Family Odontopleuridae Burmeister, 1843
Sub-family Odontopleurinae Burmeister, 1843

Genus *Kettneraspis* Prantl & Přibyl, 1949

Type species. – *Acidaspis pigra* Barrande, 1872.

Kettneraspis callicera (Hall & Clarke, 1888)
Figure 12E–G

1888 *Acidaspis callicera* n. sp.; Hall & Clarke, p. 69, pl. XVIIb, figs 1–13.

?1965 *Odontopleura callicera* (Hall & Clarke). – Morales, p. 89, pl. VIII, figs 3, 4.

2002 *Kettneraspis callicera* (Hall & Clarke). – Whiteley, Kloc & Brett, pl. 34.

Material and locality. – One complete exoskeleton, MHNN.P.082770; one cephalo-thorax, MHNN.P.082769; one thorax and pygidium, MHNN.P.082771; one cranidium internal and external moulds, MHNN.P.082772. Lower part of the Floresta Formation, Morro Cabezon, E-NE of Cerinza.

Description. – The cephalon is 7 mm long. The librigenae bear 12 spines along their lateral margin, the length of which increases backward, and 6 erected spinose tubercles. The anterior margin of the cranidium bears 10 short spines. The occipital ring possesses 3 pairs of tubercles, and a short

median spine. The central part of the glabella widens anteriorly, and is ornamented by very stout tubercles. The lateral ridges bear 4 tubercles. Lateral lobes, as well as the eyes, show some stout tubercles. The thoracic axis, very large, exhibits 4 spinose tubercles on each ring. Each of the pleurae of the 9 thoracic segments is ornamented by 2 spinose tubercles, and extends as flattened and curved pleural spines, the length of which decreases posteriorly. The length of the pleural spines of the 4th thoracic segment reaches the extremity of the pygidium. The pygidium possesses two tubercular axial rings, and two pleural ribs. The anterior pleural rib bears 2 tubercles, whereas the posterior one has one tubercle only. The pygidial margin bears four pairs of marginal spines; the third marginal spines are twice as long as the fourth ones.

Discussion. – The Colombian specimens are assigned to the genus *Kettneraspis* Prantl & Přibyl, 1949 based on the presence of two median posterior spines on the pygidium (Ramsköld & Chatterton 1991). The present specimens are very close to *Kettneraspis callicera* from the Schoharie Grit and the Onondaga Formation of the New York area described by Whiteley et al. (2002) in the ornament of the cephalon and the length of the posterior spines. Hall & Clarke (1888) described *K. callicera* from the limestones of the upper part of the Helderberg Formation in Ontario. Ramsköld & Chatterton (1991, p. 359, fig. 8) illustrated pygidia of *Kettneraspis aracana* (Steinmann, 1912) from the Lochkovian Cordillera Real Formation of Bolivia which are very close to the Colombian specimens, although the ornament of the cephalon is different.

Conclusions

This studied material show the diversity of the trilobites and inarticulate faunas from the Devonian Floresta Formation from Colombia. Sixteen species of trilobites and three species of inarticulate brachiopods are described with a new species in each group: *Colombianaspis carvalhoae* gen. et sp. nov. and *Schizobolus pilasiensis* sp. nov. The trilobite and inarticulate faunas permit to point out the presence of two biostratigraphic levels within the Floresta Formation. On the evidence of the trilobites an age range of Late Emsian (*serotinus* Zone) is assigned to the lower part of the Floresta Formation. Trilobites and inarticulate brachiopods allow to assign a Givetian age to the upper part of this formation.

The faunas show a great similarity with North American forms and implicate unrestricted faunal exchanges between NEAR and Colombia. However certain trilobites show some affinity to South American forms and restricted faunal exchanges were possible with the Malvinokaffric Realm.

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References

- ADRAIN, J.M. & KLOCK, G.J. 1997. Lower Devonian Aulacopleuroidean Trilobites from Oklahoma. *Journal of Paleontology* 71, 703–712.
- ARCHBOLD, N.W., CISTERNA, G.A. & STERREN, A.F. 2005. Lingulida (Brachiopoda) from the early Permian of Argentina. *Proceedings of the Royal Society of Victoria* 117, 307–317.
- BALINSKI, A. 1995. Brachiopods and conodont biostratigraphy of the Famennian from the Debnik anticline, southern Poland. *Palaeontologia Polonica* 54, 1–88.
- BALINSKI, A. 1979. Brachiopods and conodonts from the Frasnian of the Debnik anticline, southern Poland. *Palaeontologia Polonica* 39, 129–136.
- BALINSKI, A. & HOLMER, L.E. 1999. The Late Devonian trematid lingulate brachiopod *Schizobolus* from Poland. *Acta Palaeontologica Polonica* 44, 335–346.
- BARRANDE, J. 1852. *Système silurien du centre de la Bohême. 1ère partie. Recherches paléontologiques, I, Trilobites*. 935 pp. Privately published, Prague & Paris.
- BARRANDE, J. 1872. *Système silurien du centre de la Bohême. 1ère partie. Recherches paléontologiques, VI, Acéphales*. 342 pp. Privately published, Prague & Paris.
- BARRETT, S.F. 1988. The Devonian System in Colombia, 705–717. In McMILLAN, N.J., EMBRY, A.F. & GLASS, D.J. (eds) *Devonian of the World, Second International Symposium on the Devonian System Calgary, Canadian Society of Petroleum Geologists Calgary, vol. 1*.
- BARRETT, S.F. & ISAACSON, P.E. 1988. Devonian paleogeography of South America, 655–667. In McMILLAN, N.J., EMBRY, A.F. & GLASS, D.J. (eds) *Devonian of the World, Second International Symposium on the Devonian System Calgary, Canadian Society of Petroleum Geologists Calgary, vol. 1*.
- BERRY, C.M., MOREL, E., MOJICA, J. & VILLARROEL, C. 2000. Devonian plants from Colombia, with discussion of their geological and paleogeographical context. *Geological Magazine* 137, 257–268. DOI 10.1017/S0016756800003964
- BIERNAT, G. & EMIG, C. 1993. Anatomical distinctions of Mesozoic lingulide brachiopods. *Acta Palaeontologica Polonica* 38, 1–20.

- BOSETTI, E.P. 1989. Revisão sistemática dos Lingulida (Brachiopoda; Inarticulata) da Formação Ponta Grossa (Devoniano) Estado do Paraná, Brasil. *Anais do Congresso Brasileiro de Paleontologia* 11, 73–89.
- BOSETTI, E.P., GRAHN, Y., HORODYSKI, R.S., MAULLER, P.M., BREUER, P. & ZABINI, C. 2011. An earliest Givetian “Lilliput Effect” in the Paraná Basin and the collapse of the Malvinokaffric shelly fauna. *Paläontologische Zeitschrift* 85, 49–65. DOI 10.1007/s12542-010-0075-8
- BOSETTI, E.P. & QUADROS, R. 1996. Contribuição ao estudo dos Lingulida (Brachiopoda: Inarticulata) da Formação Ponta Grossa, Devoniano, Bacia do Paraná, Município de Chapada dos Guimarães, Mato Grosso, Brasil. *Anais do Simpósio Sul-americano do Siluro Devoniano*, 357–361.
- BOUCOT, A.J. 1975. *Evolution and extinction rate controls*. 427 pp. Elsevier, Amsterdam.
- BOUCOT, A.J. & RACHEBOEUF, P.R. 1994. Biogeographic summary of the Malvinokaffric Realm, silurian and devonian Fossils, 13–14, 71–75. In SUAREZ SORUCO, R. (ed.) *Fossiles y Facies de Bolivia*, YPFB.
- BOUCOT, A.J., ROWELL, A.J., RACHEBOEUF, P.R., PEREIRA, E., GONÇALVES DE MELO, J.H. & PEIXOTO DE SIQUEIRA, L. 2001. Position of the Malvinokaffric Realm’s northern boundary (Early Devonian) based on newly discovered brachiopods from the Parecis Basin (Brazil). *Journal of the Czech Geological Society* 46, 109–120.
- BRUGUIÈRE, J.G. 1797. *Vers, Coquilles, Mollusques et Polypiers. Tableau encyclopédique et méthodique des trois règnes de la nature*, vol. 2, pl. 96–314. Agasse, Paris.
- BURMEISTER, H. 1843. *Die Organisation der Trilobiten aus ihren lebenden Verwandten entwickelt; nebst einer systematischen bersicht aller seither beschriebenen Arten*. 147 pp. Reimer, Berlin. DOI 10.5962/bhl.title.9086
- CAMPBELL, K.S.W. 1977. Trilobites of the Haragan, Bois d’Arc and Frisco Formations (Early Devonian), Arbuckle Mountains Region, Oklahoma. *Oklahoma Geological Survey* 123, 1–227.
- CARVALHO, M.G.P. DE & FONSECA, V.M.M. DA 2007. The trilobite “*Dalmanites*” *maecurua* Clarke, 1890 (Middle Devonian, Amazon Basin, Brazil) and the new genus *Amazonaspis* (Synphoriidae). *American Museum, Novitates* 3591, 1–14. DOI 10.1206/0003-0082(2007)3591[1:TTDMCM]2.0.CO;2
- CARVALHO, M.G.P. DE & MOODY, J. 2000. A Middle Devonian Trilobite Assemblage from Venezuela. *American Museum, Novitates* 3292, 1–15. DOI 10.1206/0003-0082(2000)292<0001:AMDTAF>2.0.CO;2
- CASTER, K.E. 1939. A Devonian fauna from Colombia. *Bulletin of American Paleontology* 24(83), 1–218.
- CHAPMAN, E.J. 1890. Some remarks on trilobites as influenced by stratigraphical relations, with outline of a new grouping of these forms. *Transactions of the Royal Society of Canada* 7, 113–120.
- CLARKE, J.M. 1892. On *Cordania*, a proposed new genus of trilobites. *45th Annual Report of New York State Museum* 1891, 440–443.
- CLARKE, J.M. 1900. Oriskany fauna of Becraft Mountain. *New York State Museum, Memoir* 3, 1–128.
- CLARKE, J.M. 1905. Percé: a brief sketch of its geology. *Report of the State Paleontologist 1905. New York State Museum* 80, 134–172.
- CLARKE, J.M. 1907. Some new Devonian fossils. *New York State Museum, Geology* 12(107), 153–291.
- CLARKE, J.M. 1908–1909. Early Devonian history of New York and eastern North America. *New York State Museum, Memoir* 9(1), 1–366 pp.; (2), 1–250 pp.
- CLARKE, J.M. 1913. Fósseis Devonianos do Paraná. *Monographias do Serviço Geológico e Mineralógico do Brasil* 1, 1–353.
- CONRAD, T.A. 1841. On the paleontology of the State of New York. *Reports of the New York State Geological Survey* 39–40, 48–49.
- COOPER, G.A. 1942. New genera of North American brachiopods. *Journal of the Washington Academy of Sciences* 32, 228–235.
- COOPER, G.A. & DUTRO, J.T. 1982. Devonian brachiopods of New Mexico. *Bulletins of American Paleontology* 82 and 83, 1–315, 1–215.
- 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.
- COPPER, P. 1977. Paleolatitudes in the Devonian of Brazil and the Frasnian-Famennian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 21, 165–207. DOI 10.1016/0031-0182(77)90020-7
- DALL, W.H. 1870. A revision of the Terebratulidae and Lingulidae. *American Journal of Conchology* 6, 88–168.
- DELO, D.M. 1935. A revision of the Phacopid trilobites. *Journal of Paleontology* 9, 402–420.
- DELO, D.M. 1940. Phacopid trilobites of North America. *Geological Society of America, Special Papers* 29, 1–135. DOI 10.1130/SPE29-p1
- EBACH, M.C. & AHYONG, S.T. 2001. Phylogeny of the Trilobite subgenus *Acanthopyge* (*Lobopyge*). *Cladistics* 17, 1–10. DOI 10.1111/j.1096-0031.2001.tb00107.x
- EGOROV, A.N. & POPOV, L.E. 1990. Novyi rod lingulid in niznepermiskikh otlozhenii Sibirskoi platformy. *Palaeontologicheskii zhurnal* 1990(4), 111–115.
- ELDRIDGE, N. 1973. Systematics of lower and lower middle Devonian species of the trilobite *Phacops* Emmerich in North America. *Bulletin of the American Museum of Natural History* 151, 285–338.
- ELDRIDGE, N. & BRANISA, L. 1980. Calmonioid trilobites of the Lower Devonian *Scaphocoelia* Zone of Bolivia, with remarks on related species. *Bulletin of the American Museum of Natural History* 165, 181–289.
- ELDRIDGE, N. & ORMISTON, A.R. 1979. Biogeography of Silurian and Devonian trilobites of the Malvinokaffric Realm, 147–167. In GRAY, J. & BOUCOT, A.J. (eds) *Historical biogeography, plate tectonics, and the changing environment*. Oregon State University Press.
- FIGUEIRAS, A. 1991. Fauna eodevónica del Uruguay. *Revista Técnica de YPFB* 12, 57–64.
- FORERO, A.S. 1970. Estratigrafía del Precretácico en el Flanco Occidental de la Serranía de Perijá. *Geología Colombiana* 7, 1–77.
- GORYANSKY, V.Y. & POPOV, L.E. 1985. Morphology, systematic position and origin of the inarticulate brachiopods with calcareous shells. *Paleontologicheskii zhurnal* 1985(3), 3–14. [in Russian]

- GRAY, J.E. 1840. *Synopsis of the contents of the British Museum, 42th edition*. 370 pp. British Museum, London.
- GREEN, J.M. 1832. Synopsis of the trilobites of North America. *American Journal of Geology and Natural History* 1(12), 558–560.
- HAAS, W. 1968. Trilobiten aus dem Silur und Devon von Bithynien (NW Türkei). *Palaeontographica A* 130, 60–207.
- HALL, J. 1861. Descriptions of new species of fossils from the Upper Helderberg, Hamilton and Chemung Groups. *Advance Sheets of the Fifteenth Annual Report, New York State Cabinet of Natural History*, 1–83.
- HALL, J. 1863. Description of a new species of Brachiopoda, from the Upper Helderberg, Hamilton and Chemung Groups. *New York State Cabinet of Natural History, 16th Annual Report*, Albany, 19–37.
- HALL, J. 1871. Descriptions of new species of fossils, from the investigations of the Survey. *Geological Survey of Wisconsin, Report of the Superintendent, January 1, 1861*, 9–52.
- HALL, J. & CLARKE, J.M. 1888. Descriptions of the trilobites and other crustacea of the Oriskany, Upper Helderberg, Hamilton, Portage, Chemung and Catskill Groups. *Geological Survey of the State of New York, Palaeontology* 7, 1–152.
- HALL, J. & CLARKE, J.M. 1892. An introduction to the study of the genera of Palaeozoic Brachiopoda. *New York Geological Survey, part 1*, 1–367.
- HALL, J. & CORDA, A.J.C. 1847. Prodrum einer monographie der böhmischen Trilobiten. *Abhandlungen Königlischen böhmischen Gesellschaft der Wissenschaften* 5, 1–176.
- HAVLICEK, V. 1984. Diagnoses of new brachiopod genera and species. Part 1, 57–59. In PARIZEK, A., KLEIN, L. & RÖHLICH, P. (eds) *Explanatory booklet, Geological Map of Libya, 1/250 000 (NG 33-1), Sheet Idri*. Industrial Research Centre, Tripoli, Libya.
- HOLLOWAY, D.J. 1981. Silurian Dalmanitacean trilobites from North America, and the subfamilies Dalmanitinae and Synphoriinae. *Palaeontology* 24, 695–731.
- HOLLOWAY, D.J. & CARVALHO, M.G.P. DE 2009. The extraordinary trilobite *Fenestraspis* (Dalmanitidae, Synphoriinae) from the Lower Devonian of Bolivia. *Palaeontology* 52, 933–949. DOI 10.1111/j.1475-4983.2009.00878.x
- HOLLOWAY, D.J. & CARVALHO, M.G.P. DE 2010. The trilobite *Chacomurus* (Dalmanitidae Synphoriinae) from the Lower Devonian of Bolivia. *Memoirs of the Association of Australasian Palaeontologists* 39, 71–83.
- HOLMER, L.E. 1991. The systematic position of *Pseudolingula* Mickwitz and related brachiopods, 15–21. In MAC KINNON, D.I., LEE, D.E. & CAMPBELL, J.D. (eds) *Brachiopods through time*. Balkema, Rotterdam.
- HOLMER, L.E. & POPOV, L.E. 2000. Lingulata, 30–146. In WILLIAMS, A., BRUNTON, C.H.C., CARLSON S.J. et al. *Treatise on Invertebrate Paleontology, part H, Brachiopoda, Revised, Volume 2*. Geological Society of America & University of Kansas, Boulder & Lawrence.
- JANVIER, P. & VILLARROEL, C. 2000. Devonian Vertebrates from Colombia. *Palaeontology* 43, 729–763. DOI 10.1111/1475-4983.00147
- JELL, P.A. & ADRAIN, J.M. 2003. Available generic names for trilobites. *Memoirs of the Queensland Museum* 48, 331–553.
- JOHNSON, J.G. 1970. Taghanic onlap and the end of North American Devonian Provinciality. *Geological Society of America* 81, 2077–2106. DOI 10.1130/0016-7606(1970)81[2077:TOATEO]2.0.CO;2
- KAYSER, E. 1880. *Dechenella*, eine devonische Gruppe der Gattung *Phillipsia*. *Zeitschrift der Deutschen Geologischen Gesellschaft* 32, 703–707.
- KAYSER, E. 1897. Beiträge zur Kenntniss einiger paläozoischer Faunen Süd-Americas. *Zeitschrift der Deutschen Geologischen Gesellschaft* 49, 274–317.
- KOZŁOWSKI, R. 1923. La faune dévonienne de Bolivie. *Annales de Paléontologie* 12, 1–112.
- LANGE, F.W. 1943. Novos fósseis devonianos do Paraná. *Arquivos do Museu Paranaense* 3, 215–231.
- LESPÉRANCE, P.J. 1975. Stratigraphy and Paleontology of the Synphoriidae (Lower and Middle Devonian Dalmanitacean trilobites). *Journal of Paleontology* 49, 91–137.
- LESPÉRANCE, P.J. 1991. Vincular furrows in some early Silurian and Devonian Phacopidae (Trilobita), predominantly from North America. *Journal of Paleontology* 65, 276–294.
- LESPÉRANCE, P.J. & BOURQUE, P.A. 1971. The Synphoriinae: an evolutionary pattern of Lower and Middle Devonian trilobites. *Journal of Paleontology* 45, 182–208.
- LESPÉRANCE, P.J. & SHEEHAN, P.M. 1988. Faunal assemblages of the Upper Gaspé Limestones, Early Devonian of eastern Gaspé, Quebec. *Journal Canadien de Sciences de la Terre* 25, 1432–1449. DOI 10.1139/e88-137
- LIEBERMAN, B. & KLOC, G. 1997. Evolutionary and Biogeographic patterns in the Asteropyginae (Trilobita, Devonian) Delo, 1935. *Bulletin of the American Museum of Natural History* 232, 1–127.
- LINSLEY, D.M. 1994. Devonian Paleontology of New York containing the brachiopods, bivalves, rostroconchs, gastropods, tergomyans, ammonoids, trilobites, eurypterids and phyllocarids... based on the lithographs of J. Hall & J. Clarke. *Paleontological Research Institution Special Publication* 21, 1–472.
- LUDVIGSEN, R. 1979. Fossils of Ontario: The Trilobites. *Ontario Museum, Life Sciences, Miscellaneous Publications*, 1–96.
- LUDVIGSEN, R. 1987. Reef trilobites from the Formosa Limestone (Lower Devonian) of southern Ontario. *Canadian Journal of Earth Sciences* 24, 676–688. DOI 10.1139/e87-066
- MAKSIMOVA, Z.A. 1972. New Devonian trilobites of the Phacopoidea. *Paleontologicheskii zhurnal* 1, 88–94.
- MENDES, J.C. 1961. *Langella*, novo gênero de Lingulídeo da série Tubarão. *Boletim da Universidade do Paraná, Instituto de Geologia* 5, 1–8.
- MENDES-ALZOLA, R. 1934. Contribución al conocimiento de la Fauna Devónica de Rincón de Alonso. *Instituto de Geología y Perforaciones, Boletín* 21, 21–54.
- MENDEZ-ALZOLA, R. 1938. Fósiles Devónicos del Uruguay. *Instituto de Geología y Perforaciones, Boletín* 24, 1–115.
- MENDEZ-ALZOLA, R. & SPRECHMANN, P. 1971. Algunas orbiculoideas devonicas de la Precordillera de San Juan, Rep. Argentina. *Revista de la Asociación Geológica Argentina* 24, 517–525.
- MENKE, C.T. 1828. *Synopsis methodica molluscorum generum omnium et specierum earum quae in Museo Menkeano adservantur*. 91 pp. G. Uslar, Pyramonti.

- MORALES, P.A. 1965. A contribution of the knowledge of the Devonian Faunas of Colombia. Universidad Industrial de Santander (Colombia). *Boletín de Geología* 19, 51–109.
- MORZADEC, P. 1969. Le Dévonien de la rive nord de la rivière du Faou (Finistère). *Bulletin de la Société géologique et minéralogique de Bretagne*, 1–58.
- MORZADEC, P. 1983. Trilobites du Dévonien (Emsien-Famennien) de la rade de Brest (Massif armoricain). *Palaeontographica A* 181, 103–184.
- ORMISTON, A.R. 1972. Lower and Middle Devonian trilobite zoogeography. Northern North America. *Proceedings 24th International Geological Congress, section 7*, 594–604.
- OWENS, R.M. 1973. British Ordovician and Silurian Proetidae (Trilobita). *Monographs of the Palaeontographical Society* 535, 1–98.
- ÖZDIKMEH, H. 2009. Nomenclatural changes for twenty trilobites genera. *Munis Entomology & Zoology* 4(1), 155–171.
- PHLEGER, F.B. 1936. Lichadian trilobites. *Journal of Paleontology* 10, 593–615.
- PRANTL, F. & PRIBYL, A. 1949. A study of the Superfamily Odontopleuracea nov. superfam. (Trilobites). *Rozprawy Ústředního ústavu geologického ČSR* 12, 1–221.
- PRANTL, F. & PRIBYL, A. 1951. Revise čeledi Otariionidae R. & E. Richter z českého siluru a devonu (Trilobitae). *Sborník Ústředního ústavu geologického ČSR, Oddíl paleontologický* 17, 353–512.
- PRIBYL, A. 1946. O několika nových trilobitových rodech z českého siluru a devonu. *Příroda (Brno)* 38(5–6), 89–95.
- PRIBYL, A. & ERBEN, H.K. 1952. Über einige neue oder wenig bekannte Acanthopyginae (Tril.) des böhmischen und des deutschen Devons. *Paläontologische Zeitschrift* 26, 141–174. DOI 10.1007/BF03224495
- RAMSKÖLD, L. & CHATTERTON, B.D. 1991. Revision and subdivision of the polyphyletic “*Leonaspis*” (Trilobita). *Transactions of the Royal Society of Edinburgh, Earth Sciences* 82, 333–371. DOI 10.1017/S026359330000420X
- RAMSKÖLD, L. & WERDELIN, L. 1991. The phylogeny and evolution of some Phacopid Trilobites. *Cladistics* 7, 29–74. DOI 10.1111/j.1096-0031.1991.tb00021.x
- RICHTER, R. & RICHTER, E. 1950. Arten der Dechenellinae (Tril.). *Senckenbergiana lethaea* 31, 151–184.
- SCHUCHERT, C. 1893. Classification of the Brachiopoda. *American Geologist* 11, 141–167.
- STEINMANN, G. 1912. Beiträge zur Geologie und Paläontologie von Südamerika, 176–252. In STEINMANN, G. & HOECK, H. *Das Silur und Cambrium des Hochlandes von Bolivia und ihre Fauna. Neues Jahrbuch für Geologie und Paläontologie* 34.
- STUMM, E.C. 1953. Trilobites of the Devonian Traverse Group of Michigan. *Contributions from the Museum of Paleontology, University of Michigan, Ann Arbor* X (6), 101–157.
- STUMM, E.C. 1954. Lower Middle Devonian Phacopid Trilobites from Michigan, Southwestern Ontario, and the Ohio Valley. *Contributions from the Museum of Paleontology, University of Michigan, Ann Arbor* XI (11), 201–221.
- SUAREZ-SORUCO, R. 1971. *Tarijactinoides jaracasensis* n. gen. n. sp. del Devónico inferior. *Boletín del Servicio Geológico de Bolivia* 15, 53–56.
- THOMAS, A.T. & HOLLOWAY, D.J. 1988. Classification and phylogeny of the trilobite order Lichida. *Philosophical Transactions of the Royal Society of London, B – Biological Sciences* 321(1205), 179–262. DOI 10.1098/rstb.1988.0093
- ULRICH, E.O. 1886. Description of new Silurian and Devonian fossils. *American Paleontology, Contributions* 1, 3–35.
- VACCARI, N.E., WAISFELD, B.G. & EDGEcombe, G.D. 1994. Calmonioid trilobites of the Lower Devonian *Scaphocoelia* Zone in Argentine Precordillera. *Geobios* 27(5), 591–608. DOI 10.1016/S0016-6995(94)80257-2
- VANUXEM, L. 1842. *Geology of New York. Part 3, comprising the survey of the third geological district. Natural History of New York* (4, 3). 306 pp. D. Appleton & Co., New York.
- VOGDEN, A.W. 1890. A bibliography of Paleozoic Crustacea from 1698 to 1889 including a list of North American species and a systematic arrangement of genera. *United States Geological Survey, Bulletin* 63, 1–177.
- WAAGEN, W. 1885. Salt Range fossils, I. *Productus*-Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologica Indica, (series 13)* 4(5), 729–770.
- WHITELEY, T.R., KLOC, G. & BRETT, C.E. 2002. *Trilobites of New York: An Illustrated Guide*. 456 pp. Cornell University Press.
- WHITTINGTON, H.B. 1956. Type and other species of Odontopleuridae (Trilobita). *Journal of Paleontology* 30, 504–520.
- WHITTINGTON, H.B. 1960. *Cordania* and other trilobites from the Lower and Middle Devonian. *Journal of Paleontology* 34, 405–420.
- WOLFART, R. 1968. Die Trilobiten aus dem Devon Boliviens und ihre Bedeutung für Stratigraphie und Tiergeographie. *Geologisches Jahrbuch, Hannover* 74, 1–202.
- ZABINI, C., BOSETTI, E.P., HORODYSKI, R.S. & MARSUMURA, W.M.K. 2007. Lingulídeos: revisão dos conceitos morfo-anatômicos, fisiológicos, reprodutivos, paleo-ecológicos e a importância do grupo no Devoniano de região dos Campos Gerais do Paraná, Brasil. *Revista Terra Plural* 1, 123–141.
- ZABINI, C., BOSETTI, E.P. & HOLZ, M. 2010. Taphonomy and taphofacies analysis of lingulid brachiopods from Devonian sequences of the Paraná Basin, Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292, 44–56. DOI 10.1016/j.palaeo.2010.03.025