

SYSTEMATIC REVISION OF CALMONIIDAE (TRILOBITA, PHACOPIDA) OF THE PONTA GROSSA FORMATION (DEVONIAN), PARANÁ BASIN, APUCARANA SUB-BASIN, BRAZIL

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ABSTRACT – Previous taphonomic studies about the calmonioid trilobites of the Ponta Grossa Formation, Apucarana sub-basin, revealed that some species might correspond to artificial taxa, or taphotaxa, whose diagnostic characters are artifacts of the fossilization process. This article presents a systematic revision of the Calmoniidae, and a discussion about the influence of taphonomy in the preservation of the diagnostic characters of this group, which can be altered by the external factors that they are exposed to. The most current record comprised 17 species of calmonioids in the Ponta Grossa Formation; an inaccurate number because it included invalid species that were never duly published, as well as some taphotaxa. At least eight species of calmonioids can be considered as artificial: *Calmonia? gonzagana* Clarke, *C. signifer* var. *micrischia* Clarke, *Metacryphaeus granulata* Popp, *M. sedori* Popp, *Tibagya parana* Struve, *Paracalmonia pessula* Clarke, *P. salamunii* Popp *et al.*, and *P. mendesi* Popp *et al.*, and are herein synonymized with previously erected species. This revision highlights the importance of allying a taphonomic vision with the taxonomic studies in order to reach a more accurate depiction of the calmonioid diversity. Furthermore, the designation of new species should be based preferably on numerous, well-preserved specimens in order to avoid the erection of artificial taxa.

Key words: systematics, trilobite, Calmoniidae, Devonian, Ponta Grossa Formation, Paraná Basin.

RESUMO – Estudos tafonômicos anteriores sobre os trilobitas calmoniídeos da Formação Ponta Grossa, Sub-bacia Apucarana, revelaram que algumas espécies possam corresponder a táxons artificiais, ou tafotáxons, cujos caracteres diagnósticos são artefatos do processo de fossilização. Esse artigo apresenta uma revisão sistemática de Calmoniidae e uma discussão sobre a influência da tafonomia na preservação dos caracteres diagnósticos desse grupo, os quais podem ser alterados pelos fatores externos aos quais eles estiveram expostos. A mais recente contagem inclui 17 espécies de calmoniídeos na Formação Ponta Grossa; um número impreciso, pois incluiu espécies inválidas que nunca foram publicadas, bem como alguns tafotáxons. Pelo menos oito espécies podem ser consideradas como artificiais: *Calmonia? gonzagana* Clarke, *C. signifer* var. *micrischia* Clarke, *Metacryphaeus granulata* Popp, *M. sedori* Popp, *Tibagya parana* Struve, *Paracalmonia pessula* Clarke, *P. salamunii* Popp *et al.*, e *P. mendesi* Popp *et al.* foram aqui sinonimizadas com espécies anteriormente descritas. Essa revisão sistemática destaca a importância de aliar a visão tafonômica aos estudos taxonômicos a fim de alcançar uma representação mais precisa da diversidade de calmoniídeos. Além disso, a designação de novas espécies deve ser preferivelmente baseada na presença de vários espécimes bem preservados, a fim de evitar designação de táxons artificiais.

Palavras-chave: sistemática, trilobita, Calmoniidae, Devoniano, Formação Ponta Grossa, Bacia do Paraná.

INTRODUCTION

The marine macroinvertebrate fauna of the Devonian in Paraná, Ponta Grossa Formation is one of the most diverse faunas of the Paleozoic in Brazil. Systematic reviews of the invertebrates have dealt with Linguliformea (Bosetti, 1989a,b; Bosetti & Moro, 1989; Zabini, 2007, 2011; Zabini *et al.*, 2012) and Rhynchonelliformea brachiopods (Quadros, 1987; Cerri, 2013), Bivalvia (Kotzian, 1995, 2003), Gastropoda (Kotzian & Marchioro, 1997; Marchioro *et al.*, 1998), Tentaculida (Ciguel, 1989; Azevedo-Soares, 1999), Cnidaria, and Conularida (Leme, 2002; Leme *et al.*, 2004, 2008, 2010). In addition, the calmonioid trilobites are amongst the most

common and conspicuous groups of the fossil record in the Ponta Grossa Formation, Paraná Basin, Apucarana Sub-basin. Species are particularly abundant in pelitic facies generated within or below the storm wave base level (Clarke, 1913; Popp, 1985; Carvalho & Edgecombe, 1991; Popp *et al.*, 1996; Carvalho *et al.*, 1997; Soares *et al.*, 2008a; Leme *et al.*, 2010; Mori & Leme, 2012; Mori, 2013).

The studies with calmonioids in the Ponta Grossa Formation began with the classic monograph of Clarke (1913), who described not only trilobites, but also several other groups of marine invertebrates. After this, many other authors have contributed to the knowledge of this family (Clarke, 1890, 1913; Kozłowski, 1913, 1923; Struve, 1958; Copper, 1977;

Eldredge & Ormiston, 1979; Cooper, 1982; Carvalho & Edgecombe, 1991; Popp *et al.*, 1996; Ghilardi & Simões, 2007; Soares *et al.*, 2008a; Leme *et al.*, 2010; Mori & Leme, 2012; Mori, 2013).

Popp (1985) reviewed the calmoniids of the Ponta Grossa Formation in her monograph and designated six new species, five of which are considered invalid because they were never duly published. A few years later, Popp *et al.* (1996) revised the genus *Paracalmonia*, and erected three new species, whose current standings are discussed in this paper. Ghilardi & Simões (2007) presented a historical synthesis of the development of paleontological researches with trilobites in Brazil, and also compiled a general list of valid calmonioid species described in the Paraná Basin, which was later updated by Soares *et al.* (2008a), totaling 17 species. However, Soares *et al.* (2008b) stated that the calmonioid diversity in the Paraná Basin is potentially lower, because some of these species might be taphonomic species that were erected based on diagnostic characters, which were possibly altered via the fossilization process or by weathering (Holz & Schultz, 1998; Simões *et al.*, 2003, 2009; Soares *et al.*, 2008b).

More recently, Leme *et al.* (2010), Mori & Leme (2012) and Mori (2013) presented preliminary data from a systematic revision of Calmoniidae from the Ponta Grossa Formation. Such data revealed that it is possible to assert that at least five of the 17 described calmonioid species correspond to taphotaxa. However, these authors highlighted the fact that a more comprehensive study would be necessary to reach the best clarification of the taxonomic problems, as well as to accomplish a finely resolved systematic revision. Based on these observations, the current status of the calmonioid species can be questioned.

Hence, the main goal of the present contribution is to provide a systematic revision of the Calmoniidae from the Ponta Grossa Formation, Sub-basin Apucarana, involving a taphonomic analysis of the specimens studied.

GEOLOGICAL SETTING

The Ponta Grossa Formation is situated in the Paraná Basin, extending over more than one state of Brazil (Figure 1). The specimens analyzed in this work all come from the Apucarana Sub-basin, and they were collected in the Paraná State, specifically from the municipalities of Jaguaiaíva and Ponta Grossa, and also from the municipality of Tibagi to a lesser extent (Figure 1). The Jaguaiaíva county stratigraphic section is summarized in Figure 2. In this section, the Ponta Grossa Formation is up to 80 m thick and consists predominantly of shales and siltstones. Shallow marine, fine-grained sandstones bearing wavy structures and hummocky cross-stratification occur at the base of the unit (Petri, 1948; Lange & Petri, 1967; Melo, 1988), whereas the rest of the section is made up of fairly fossiliferous muddy shelf rocks, mainly light-grayish siltstones, strongly bioturbated, which are intercalated with massive, dark shales. These shales were deposited below storm wave base and represent the record of marine flooding surfaces (Bergamaschi, 1999). Stratigraphic

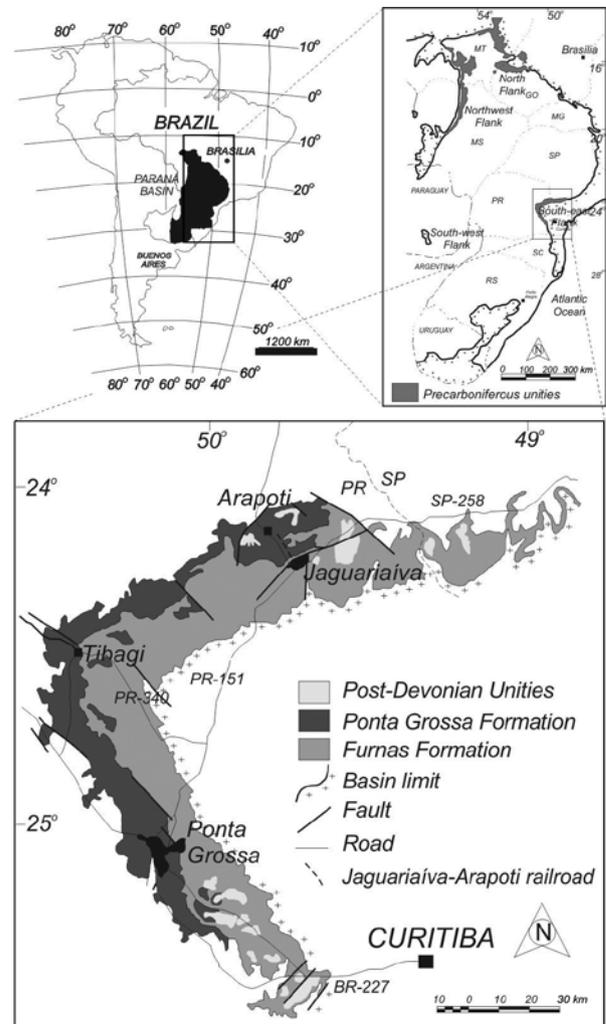


Figure 1. Map with locations of the studied geological sections, Ponta Grossa Formation, State of Paraná, Brazil.

intervals particularly suitable to Calmoniidae collecting are the railroad cuts at km 2.2, and km 6.0 (Figure 2). Pyritic, well-laminated, poorly fossiliferous dark shales enclose the Devonian sequence at the top of the Jaguaiaíva section (Petri, 1948; Lange & Petri, 1967; Melo, 1988; Bergamaschi, 1999; Bergamaschi & Pereira, 2001) (Figure 2). According to Bergamaschi (1999), these rocks record the transgressive maximum in the area and were deposited under dysaerobic bottom conditions, as indicated by the scarcity of burrowing fauna.

MATERIAL AND METHODS

The analysis of material entailed collections from several institutes, including Departamento Nacional de Produção Mineral (DNPM), Universidade Estadual de Ponta Grossa (UEPG), Universidade Estadual de São Paulo (UNESP), Universidade Federal do Paraná (UFPR), Universidade Federal do Rio de Janeiro (UFRJ), Universidade de Guarulhos (UnG) and Universidade de São Paulo (USP). The correspondence between the acronyms used to number each fossil and the institute from which they derive is as follows: fossils identified with **DGM** are from DNPM; **DZP** from

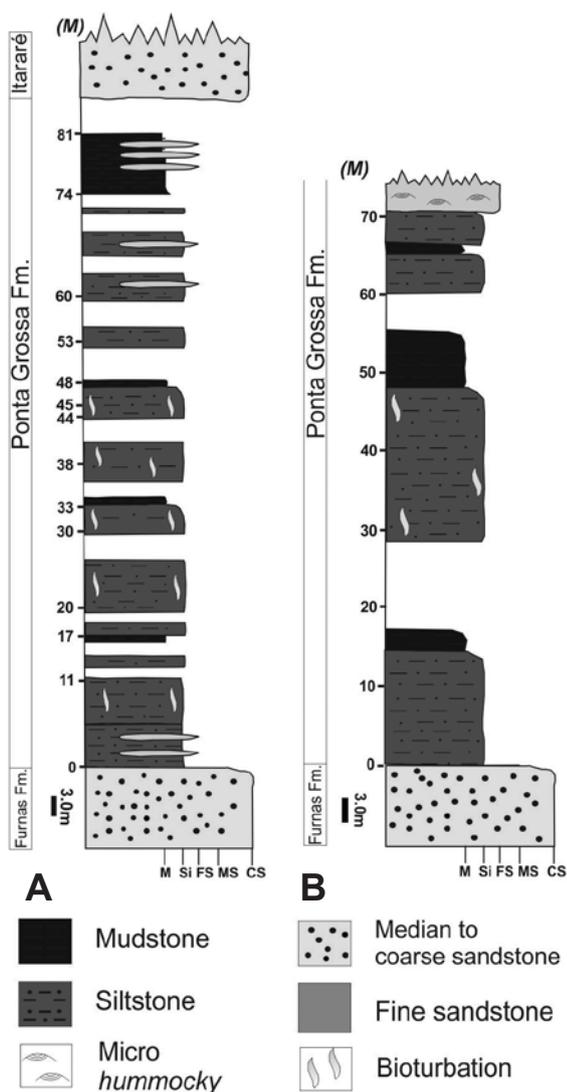


Figure 2. Columnar sections of the Ponta Grossa Formation. **A**, Columnar section at the Jaguariáiva-Arapoti railroad, Jaguariáiva County. **B**, Composed columnar section of the Ponta Grossa Formation. At the base, the rocks cropping-out along the PR-340 highway, Tibagi County. In the middle/upper portion of the section, the rocks of the Ponta Grossa Formation that are exposed along the road from Tibagi to Telémaco Borba. All columnar sections modified from Ghilardi (2004), Bosetti (2004) and Soares *et al.* (2008b).

UNESP; **CPUFPR** and **NR** from UFPR; **Tr** from UFRJ; **MN** from Museu Nacional (UFRJ); **UEPG** from UEPG; **TPg** from UnG; and **GP/1E** and **GP/1C** from USP.

In total, 838 trilobite fossils were examined with a stereomicroscope and microscope. In some cases, molds made of a mixture of latex and silicon were produced to highlight important features. The photographs were taken using a Zeiss stereomicroscope, model SV6, digital camera, and the Axiovision software. Most of the specimens used for pictures were fumigated with magnesium oxide.

The systematic description follows the morphological terms applied by Clarke (1913), Eldredge & Branisa (1980), Lieberman *et al.* (1991) and Lieberman (1993).

Terminology: **L0**, occipital lobe; **L1-L3**, glabellar lobes; **S0**, occipital furrow; **L1-L3**, glabellar furrows.

SYSTEMATIC PALEONTOLOGY

Family CALMONIIDAE Delo, 1935
Subfamily CALMONIINAE Delo, 1935

Calmonia Clarke, 1913

Type species. *Calmonia signifer* Clarke, 1913; original designation. Devonian, Brazil.

Calmonia signifer Clarke, 1913
(Figures 3A-F)

1913 *Calmonia signifer* Clarke, p. 121, pl. 6, figs. 1,3,4,5,7-12.

1913 *Calmonia ? gonzagana* Clarke, p. 131, pl. 7, fig. 1 (n. syn.)

1913 *Calmonia signifer* var. *micrischia* Clarke, p. 124, pl. 6, figs. 13-16 (n. syn.)

1985 *Calmonia paranaensis* Popp, p. 103, pl. 2, figs. A-E (*nom. nud.*)

Diagnosis. Genal angle angular; glabella pentagonal and inflated; lateral glabellar furrows obscure, except for S1, S1 and S3 confluent with axial furrows; thorax bearing pleural spines; pygidium with 5 pairs of ribs, and 6 pairs of lateral spines; short terminal spine.

Material. DGM 13 (lectotype), DGM 17, DGM 19, DGM 22, DGM 30, DGM 1576, DGM 1577, DGM 3709, DZP-18401, GP/1C423, GP/1E4790, NR 3106, NR3110, NR3133b, NR3181, NR3878, NR3956, NR6473, TPg1, TPg72. Type of sclerites: three complete exoskeletons, four cephalae, five thoraxes with pygidia, eight pygidia.

Occurrence. Municipalities of Jaguariáiva, Ponta Grossa and Tibagi, Ponta Grossa Formation, (Pragian/Eifelian).

Description. Exoskeleton oval in outline; cephalon short (sag.) and subtriangular, bearing a short frontal median process; eyes small, distant from the posterior border, and positioned very close to the glabella, Large Eye Index around 0.35, genal angles angular, with short genal spines; axial furrows slightly divergent forward and shallow, cephalic length measuring around 33% of total exoskeletal length. Glabella large, pentagonal in shape, usually inflated when compared with the cheeks, frontal lobe more inflated than lateral lobes, L0 moderately curved forward, especially in the middle, lateral glabellar lobes depressed and subequal in size, all in the same plane, L1 moderately curved; L2 and L3 slightly curved, L2 and L3 connected fused distally. S0 deep, curved forward medially; lateral glabellar furrows weakly developed, except for S1; S1 relatively deep, almost straight, reaching axial furrows; S2 shallow and straight, disconnected from axial furrows; S3 almost transverse, slightly bent in a curve, shallower than S1, confluent with axial furrows; glabella longer than wide (width across the frontal lobe about 85% of total glabellar length); glabellar width around 50% of cephalic width. Thoracic pleurae ending in spines, pleural spines directed slightly backwards; axis narrower and more elevated than pleurae, all the rings curved to the front, especially in the middle, axial furrows

shallow and parallel; inter-ring furrows wavy and deeper than axial furrows; pleural furrows deep and straight, becoming more transverse towards the end portion of the thorax; thoracic length around 44% of total exoskeletal length. 11 thoracic segments.

Pygidium triangular in outline with anterior margin almost convex and lateral margins almost straight diagonally; axial furrows slightly divergent forward in the anterior portion, but becoming straighter posteriorly; inter-ring furrows straight and shallow, interpleural furrows shallow and transverse, becoming shorter towards the posterior margin. Axis not elevated above pleural fields; axis with eight or nine rings; pleural fields bearing five pairs of ribs; pygidial margin with six pairs of spines, all directed backwards; posterior margin ending in a small terminal spine, pygidium wider than long (length about 60% of width, not including terminal spine); pygidial length occupying around 23% of total exoskeletal length.

Remarks. *Calmonia signifer* is by far the most abundant trilobite of the Ponta Grossa Formation. Aside from the common occurrences, it is also relatively easy to identify, even if the fossils are not completely articulated, mostly because of the distinctive characters on the cephalon and pygidium, such as the characteristic set of spines (Figures 3A-C, E). Clarke (1913) described and named one pygidium from Jaguariaiva as *Calmonia ? gonzagana*, and compared it with *C. signifer*, pointing out that the former differs only by having axial tubercles and lacking marginal spines. However, the revision of this pygidium did not reveal any tubercles, save for one small bump that does not appear to be a taxonomic character, but instead a taphonomic one (Figure 3D).

The problem with using only spines to separate species is that it is necessary to consider that such structures are liable to being broken and therefore lost. In fact, it is very rare to find a pygidium with a full set of 12 pleural spines plus the entire terminal spine preserved. The pygidium assigned to *C. ?gonzagana* (Figure 3D) shows broken lateral and posterior margins, which can explain the absence of the marginal and terminal spines. Hence, *C. ?gonzagana*, is regarded herein as a synonym of *C. signifer*.

Clarke (1913) also erected *Calmonia signifer* var. *micrischia* (Figure 3F), noting that it represents a transition between *Calmonia* and *Pennaia* because of the presence of four pairs of marginal spines and pleural ribs (one less pair than *Calmonia* and one more pair than *Pennaia*). However, the analysis of the specimen designated as *C. signifer* var. *micrischia* revealed that the anterior margin of the pygidium could be incomplete, and the lateral margins are not very well preserved, which means that the number of visible spines could be misleading. In this paper, this variation of *C. signifer* is no longer considered as valid, for the characters used to diagnose it could easily be explained by incomplete or poor preservation.

Kozlowskiaspis Branisa & Vanek, 1973

Type species. *Kozlowskiaspis superna* Branisa & Vanek, 1973; original designation. Devonian, Brazil.

Kozlowskiaspis subseciva Clarke, 1913
(Figures 3G-J)

1913 *Calmonia subseciva* Clarke, p. 126, pl. 7, figs. 2–10.

Diagnosis. Cephalon subtriangular in outline; genal angles rounded, without spines; frontal glabellar lobe inflated; S3 sinuous; anterior and lateral cephalic border distinct; pygidium with five pairs of ribs; pygidial marginal and terminal spines absent.

Material. DGM 25 (holotype), DGM 26, DGM 27, DGM 28, DGM 29, CPUFPR-80, 87Tr. Types of sclerites: two complete exoskeletons, one cephalon, two thoraxes with pygidia, two pygidia.

Occurrence. Municipalities of Jaguariaiva, Ponta Grossa and Tibagi, Ponta Grossa Formation, (Pragian/Eifelian).

Description. Exoskeleton oval in outline; cephalon proportionately short (sag.) and subtriangular, without frontal median process; eyes small, distant from the posterior cephalic border, positioned very close to the glabella; Large Eye Index around 0.33; genal angles rounded, without genal spines; axial furrows shallow, slightly divergent forward; cephalic length measuring around 28% of total exoskeletal length. Glabella large, pentagonal in shape, frontal lobe wide (tr.), more inflated than lateral lobes; L0 moderately curved forward, especially in the middle; lateral glabellar lobes depressed and subequal in size, all in the same plane; L1 moderately curved, L2 and L3 slightly curved, L2 and L3 fused distally. S0 deep, curved forward medially; lateral glabellar furrows weakly developed, with except for S1, S1 relatively deep, almost straight, disconnected in the middle, reaching axial furrows; S2 shallow and straight, without contact with axial furrows; S3 almost transverse, sinuous, deeper than S2 but shallower than S1, confluent with the axial furrow; glabella longer than wide (width across the frontal lobe about 83% of total glabellar length); glabellar width around 50% of cephalic width. Thoracic pleurae without pleural spines; axis narrower and more elevated than pleurae; all the rings curved to the front, especially in the middle; axial furrows shallow moderately deep and parallel, inter-ring furrows wavy and deeper than axial furrows, pleural furrows deeper and straight, becoming more transverse towards the terminal portion of the thorax; thorax wider than long anteriorly (length around 70% of width), but becoming longer than wide as it gets closer to the pygidium (width in the ultimate thoracic segment around 82% of length); thoracic length around 52% of total exoskeletal length. Eleven thoracic segments. Pygidium subtriangular in outline, anterior margin curved forward, lateral margins almost straight diagonally, axial furrows slightly divergent forward in the anterior portion, but becoming straighter towards the posterior margin; inter-ring furrows straight, distinct, axis in the same plane as the pleurae; axis with eight or nine rings; pleurae bearing five pairs of ribs, without marginal spines, posterior margin ends in acute extremity, terminal spine absent, pygidium wider than long (length about 57% of width, not including terminal spine); pygidial length measuring around 30% of total exoskeletal length.

Remarks. Initially described as *Calmonia subseciva* Clarke, 1913, this species was later transferred to the genus *Kozlowskiaspis* by Edgecombe (1994), due mostly to the presence of a wide, diamond-shaped frontal glabellar lobe and a broad arched cephalic outline (Figure 3H). As mentioned above, Soares *et al.* (2008b) observed problems in the systematics of calmoniids, stating that Clarke (1913) differentiated *Calmonia subseciva* from *Calmonia signifer* only because of the absence of a terminal spine in the pygidium, and raising questions about whether this difference could be merely a taphonomic artifact. However, the revision of the specimens described as *C. subseciva* revealed that there are enough characters to exclude them from the genus *Calmonia*, including those already highlighted by Edgecombe, 1994 (*i.e.* genal

angles rounded and wide diamond-shaped frontal glabellar lobe). Furthermore, the posterior border of the pygidium is entire (see Figures 3G, I-J) so there does not seem to be any indication of a terminal spine. Thus, this species remains valid.

Pennaia Clarke, 1913

Type species. *Pennaia pauliana* Clarke, 1913; original designation. Devonian, Brazil.

Pennaia pauliana Clarke, 1913
(Figures 4A-D)

1913 *Pennaia pauliana* Clarke, p. 129, pl. 5, figs. 18–25.

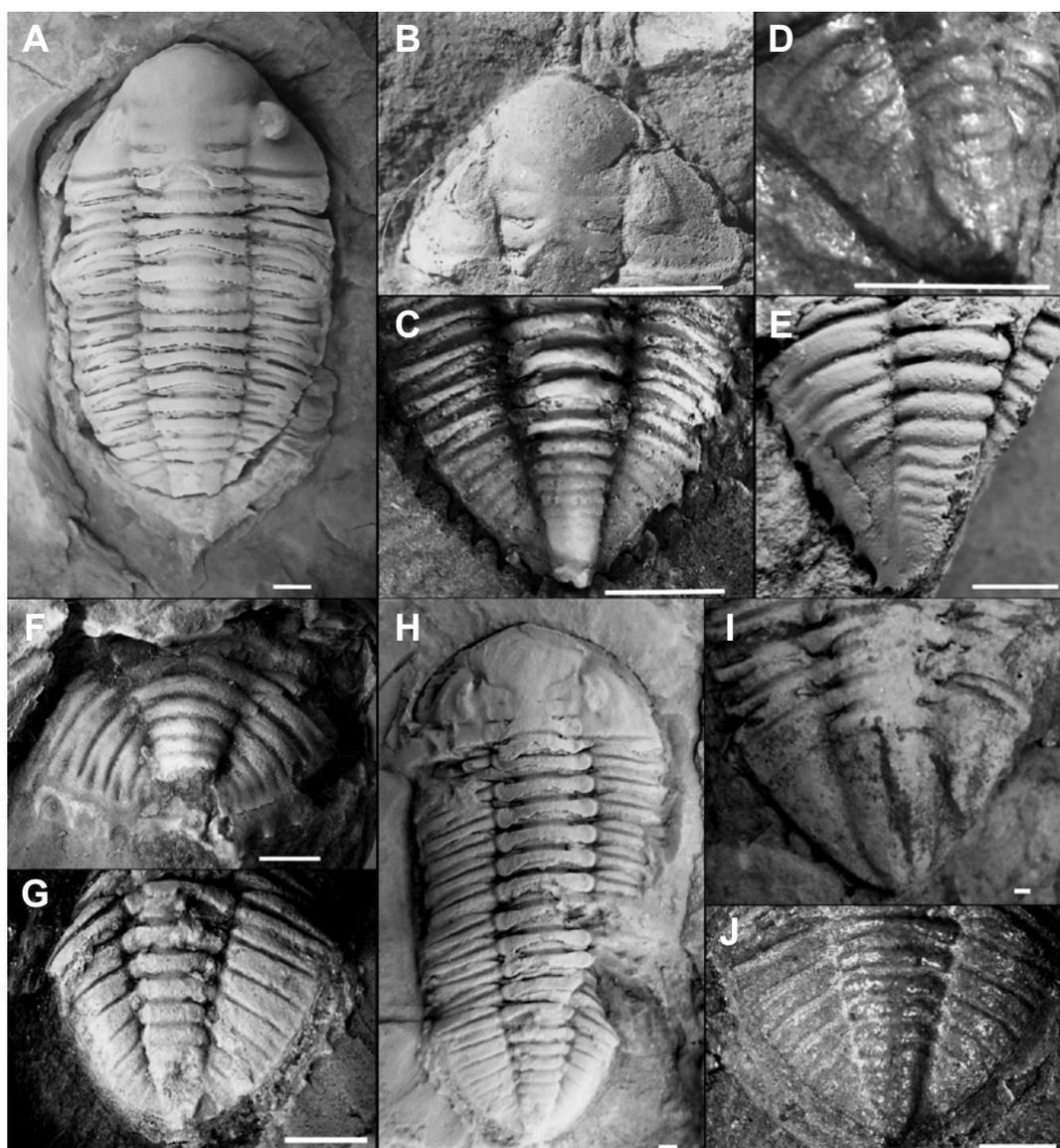


Figure 3. Internal molds of *Calmonia signifer*. **A**, DGM13; lectotype. **B**, NR3133B; cephalon with median frontal process. **C**, NR5906; pygidium and part of thorax, with pleural spines and terminal spine broken. **D**, DGM19; pygidium previously assigned to *C. ? gonzagana*, showing the supposed tuberculation on the pleural field. **E**, Tpg1; incomplete pygidium, with pleural spines. **F**, DGM22; pygidium previously assigned to *C. signifer* var. *micrischia*. Internal molds of *Kozlowskiaspis subseciva*. **G**, DGM25; pygidium of holotype. **H**, DGM25; entire exoskeleton of holotype. **I**, CPUFPR-80; thoracopygon. **J**, DGM28; pygidium. Scale bars = 5mm.

Diagnosis. Medial frontal spine or genal spines absent, S1 and S3 confluent with axial furrows, pleural terminations rounded, terminal spine absent.

Material. DGM 71 (lectotype), DGM 72, DGM 74, DGM 75, DZP-17461, GP/1E4791, NR3104, NR3130, TPg211. Types of sclerites: two complete exoskeletons, one cephalon, two thoraxes with pygidia, four pygidia.

Occurrence. Municipalities of Jaguariaíva, Ponta Grossa and Tibagi, Ponta Grossa Formation (Emsian).

Description. Exoskeleton oval in outline; cephalon proportionately short (sag.), triangular in outline; median frontal process and genal spines absent; eyes small, positioned very closely to the glabella, and very distant from the posterior cephalic border; Large Eye Index around 0.38; genal angles rounded; axial furrows divergent forward, especially around the front of the glabellar margin until L1, becoming progressively parallel; cephalic length measuring around 29% of the total exoskeletal length. Glabella large and pentagonal, frontal lobe more inflated than the lateral ones; L0 slightly convex and bent forwards in the middle, all lateral glabellar lobes depressed, with L3 being the longest and L1 the shortest, L1 moderately curved, L2 slightly curved, L3 triangular, L3 and L2 fused distally; S0 shallow and curved forward medially; lateral glabellar furrows with different sizes, with S3 being the longest, and S2 the shortest; S1 sinuous and shallow, reaching the axial furrows; S2 curved and shallow, disconnected from axial furrow; S3 transverse and the deepest, reaching the axial furrows; glabella longer than wide (width across the frontal lobe about 90% of length); glabellar width around 58% of cephalic width. Thorax ending in rounded extremities; axis very large, more inflated and wider than the pleurae; rings very thick, bending forward in the middle, axial furrows almost parallel; pleural furrows shallow; thoracic length around 55% of entire body length. Pygidium very short, semielliptical in outline; anterior margin strongly convex; axial furrows converging towards the posterior margin; inter-ring furrows shallow; interpleural furrows very shallow and transverse; axis a little more elevated than pleural fields; pleural fields bearing 3 lappets at the end of 3 ribs; all the lappets directed backwards; anterior margin convex; posterior margin between lappets is rounded, without a terminal spine; axis with 5 rings; pygidium much wider than long (length about 45% of width); pygidial length occupying around 16% of entire body length.

Remarks. *Pennaia pauliana* has been a well-established species since its conception by Clarke (1913) because of its unique pygidial characteristics. This taxon is very peculiar not only in showing a combination of three pleural ribs and three marginal spines, but also due to being the only calmonioid species in from the Ponta Grossa Formation to have a micropygidium (Figures 4B-D). Identification is usually straightforward when the pygidium is present. On the other hand, the cephalon is not so distinct, as it is basically similar to *Calmonia* but without cephalic spines (Figure 4A). Nonetheless, the revision showed that this species does not have any taxonomic problems.

1935 *Hadorrachus* Delo, p. 415.

1940 *Hadoracos* Delo, p. 9.

1942 *Asteropyge* Richter & Richter, p. 174.

Type species. *Phacops caffer* Salter, 1856; original designation. Devonian, South Africa.

Metacryphaeus australis Clarke, 1913

(Figures 4E-I)

1913 *Cryphaeus australis* Clarke, 108-114, pl. 3, figs. 7, 9, 11-14; pl. 4, figs. 3-5.

1925 *Dalmanites australis* Reed, 145, pl. 11, fig. 9.

1935 *Hadorrachus australis* Delo, p. 415, figs. 34-35.

1938 *Dalmanites australis* Méndez-Alzola, p. 9, pl. 75-76.

1942 *Asteropyge australis* Richter & Richter, p. 134.

1954 *Asteropyge australis* Lange, p. 48.

1985 *Metacryphaeus sadori* Popp, p. 87, pl. 5, figs. A-B (*nom. nud.*)

1985 *Metacryphaeus granulata* Popp, p. 92, pl. 5, figs. C-D (*nom. nud.*)

Diagnosis. Cephalon semicircular, without a median frontal process, genal angles subangular; S3 and S1 confluent with axial furrows; pygidial axis with eight to nine rings; pleural fields bearing five lappets with acute ends, all directed backwards; terminal spine absent.

Material. DGM 31 (lectotype), DGM 33, DGM 35, DGM 36, DGM 1581, DGM 1582, DGM 1991, GP/1C402, GP/1E7492, NR3099, NR3126, NR3130, NR3167, NR3202, NR5182, NR17821, TPg3b, TPg15, TPg29, 89Tr, UEPG17644. Types of sclerites: four complete exoskeletons, six cephalon, two cephalon with thorax, three thoraxes with pygidia, six pygidia.

Occurrence. Municipalities of Jaguariaíva, Ponta Grossa and Tibagi, Ponta Grossa Formation (Emsian–Givetian).

Description. Cephalon semicircular, highly vaulted, without a median frontal process; eyes small, very close to the glabella, and distant from the posterior border; Large Eye Index around 0.32; genal angles subangular; axial furrows deep and conspicuously divergent; cephalon surface smooth or with granulation; cephalic length corresponding to 26% of entire body length. Glabella large, pentagonal and inflated especially in the frontal lobe; frontal lobe oval, distinctly detached from rest of the glabella by S3; L0 sinuous, bending forward in the middle; lateral glabellar lobes with different sizes, with L3 the largest and L1 the smallest; L1 moderately curved; L2 slightly curved; L3 thick and triangular; L2 and L3 fused distally; S0 deep and convex; all lateral glabellar furrows visible and with distinct lengths, with S3 as the longest, and S2 as the shortest; S1 mostly straight and shallow, reaching the axial furrows; S2 also straight and shallow, disconnected from the axial furrows; S3 the deepest, transverse and confluent with the axial furrows; glabella a little longer than wide (width across the frontal lobe about 90% of length); glabellar width around 54% of cephalic width. Thorax ending in pleural lappets, all pointed outwards; axis more elevated and wider than the pleural fields; axial rings straight and thick; axial

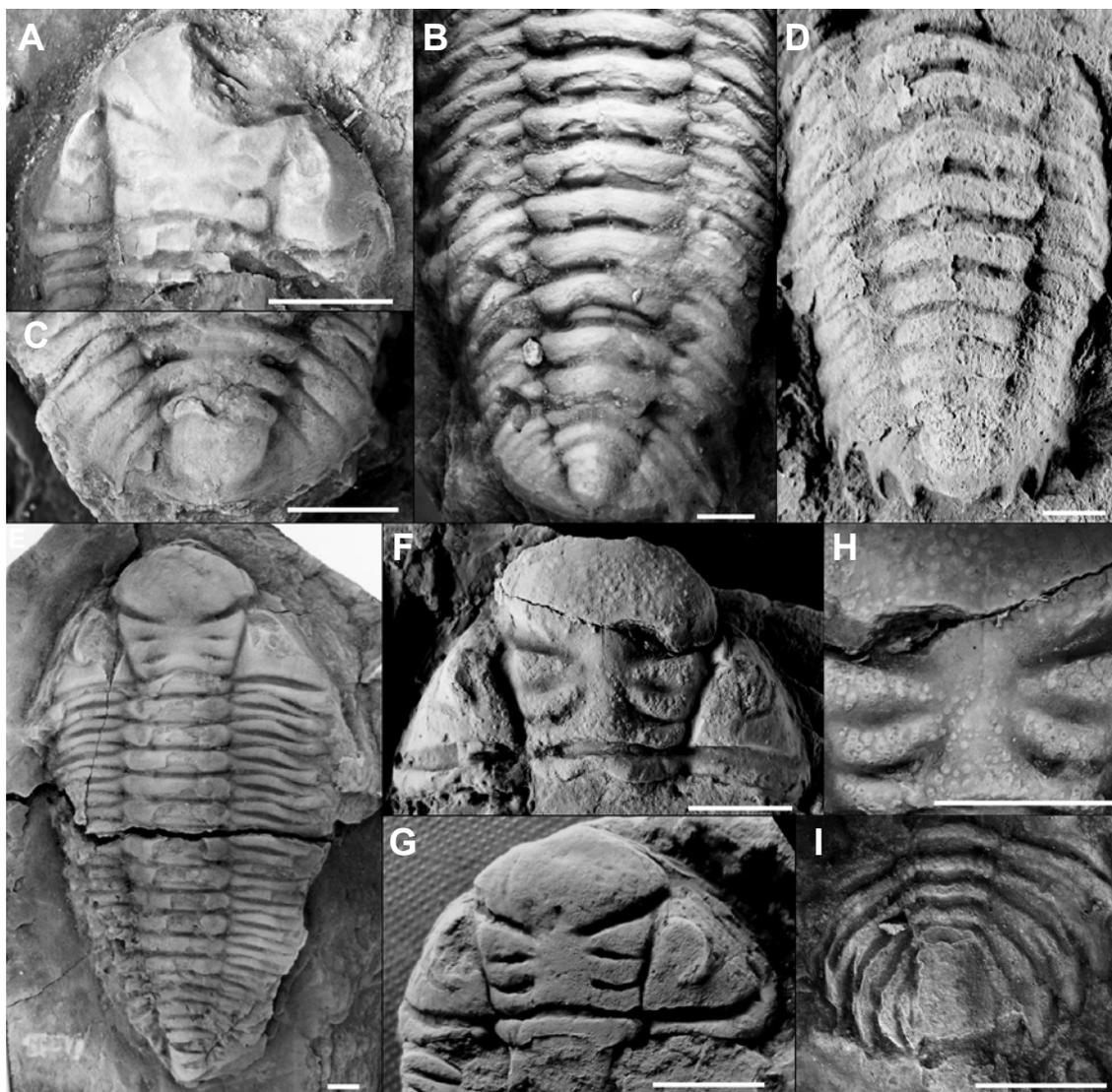


Figure 4. Internal molds of *Pennaia pauliana*. **A**, DGM71; broken cephalon. **B**, DGM74; pygidium of lectotype. **C**, DGM74, lectotype. **D**, GP/1E7491; latex mold of a thoracopygon, with the characteristic three pairs of spines. Internal molds of *Metacryphaeus australis*. **E**, DGM31, lectotype. **F**, NR3130; cephalon previously assigned to *M. granulata*, with the granulated surface. **G**, cephalon previously assigned to *M. sedori*. **H**, NR3130; glabellar granulation in detail. **I**, NR3167; pygidium, with the pleural lappets preserved. *Metacryphaeus rotundatus*. **G**, DGM69; pygidium of *Tibagya parana*. Scale bars = 5mm.

furrows straight, parallel; inter-ring furrows wavy and deeper than axial furrows; thoracic length around 53% of entire body length. Eleven thoracic segments. Pygidium semicircular and vaulted; anterior margin almost straight; lateral margins curved; inter-ring furrows moderately deep and convex; interpleural furrows shallow and transverse; axis in the same plane as pleural field, bearing eight or nine rings; pleural field with five ribs; lateral pygidium margin with five pleural lappets with acute ends, all directed backwards; axis ending before reaching posterior margin; terminal spine absent; pygidium wider than long (length about 57% of width); pygidial length around 21% of entire body length.

Remarks. *Metacryphaeus australis* is a very common trilobite species in the Ponta Grossa Formation. This species has undergone several name changes, mostly because the genus *Metacryphaeus* itself was the target of many discussions about its taxonomic standing (Reed, 1927; Rennie, 1930;

Delo, 1935; Richter & Richter, 1942; Struve, 1959; Wolfart, 1968; Lieberman *et al.*, 1991). Lieberman *et al.* (1991) and Lieberman (1993) made a comprehensive synthesis of the scope of *Metacryphaeus*. Popp (1985) erected *Metacryphaeus granulata* based on one cephalon showing distinct granulation, especially on the glabellar surface, which was the sole character considered to separate it from *M. australis* (Figures 4F, H). However, it was not an appropriate designation because there are specimens of *M. australis* with visible granulation on the exoskeletal surface, as already noticed by Lieberman *et al.* (1993). In the Ponta Grossa Formation, it is very common to find fossils with smooth surface, and the analysis of numerous exfoliated cephalata of *M. australis* revealed that some specimens show very faint evidences or a smaller amount of these granules, demonstrating that the granulation can be lost due to exfoliation by taphonomic processes (*e.g.* weathering). Therefore, although this species

remains as invalid (*nomen nudum*) because it was never duly published, it provides an example of another taxonomic character being influenced by taphonomy. Similarly, Popp (1985) proposed *Metacryphaeus sedori* (unpublished; *nomen nudum*) based on a very flattened and exfoliated cephalon, and stated that it differs from *M. australis* by having more rounded genal angles, a glabellar S2 furrow that is confluent with axial furrows, and a moderate cephalic arching (Figure 4G). However, the revision of this material did not corroborate such differences. The genal angles and cephalic arching do not differ essentially from those of *M. australis*. In addition, S2 does not reach the axial furrows since L2 and L3 are fused. In any case, the confluence of the lateral glabellar furrows with the axial furrows is a character that should be assessed with caution because most of the trilobites from the Ponta Grossa Formation are partially exfoliated and/or compressed and their furrows are often filled or erased.

Metacryphaeus parana Kozłowski, 1923
(Figures 5A-C)

1892 *Cryphaeus giganteus* Ulrich, pl.1, fig. 7.

1913 *Homalonotus parana* Clarke, p. 97, pl. 3, figs. 5-6 (n. syn.)

1923 *Cryphaeus australis* var. *rotundatus* Kozłowski, pl. 3, figs. 1 and 11.

1958 *Tibagya parana* Struve, p. 301-302 (n. syn.)

1965 *Metacryphaeus giganteus* Branisa, pl.13, figs. 8, 11 and 12.

2010 *Pennaia pauliana* Bosetti *et al.*, p. 58, fig. 6e.

Diagnosis. Frontal glabellar lobe rounded anteriorly; genal spine long and slender; pygidial axis bearing eight rings;

pygidial pleurae with five ribs, all ending in large, posteriorly curved lappets having rounded terminations; posterior margin of pygidium rounded, forming a terminal lappet that overlaps the last axial ring; terminal spine absent.

Material. DGM 69, DZP-18570a, DZP-18626, NR3108, NR3201. Types of sclerites: one cephalon, one thorax with pygidium, three pygidia.

Occurrence. Municipality of Jaguariaíva and Ponta Grossa, Ponta Grossa Formation (Pragian–Givetian). The specimens were collected in 48 m at the base of Jaguariaíva-Arapoti railroad section, Jaguariaíva County, and at 48 m and 8 m at the base of composed columnar section of the Ponta Grossa Formation, Tibagi County (Figure 2).

Description. Cephalon semicircular, heavily arched, without median frontal process; eyes small, very close to the glabella, and distant from the posterior border; Large Eye Index around 0.32; genal angles acute, ending in genal spines; axial furrows deep, highly divergent, almost straight diagonally. Glabella large, pentagonal and inflated especially around the frontal lobe area; frontal lobe oval, distinctly detached from the rest of the glabella by S3; L0 sinuous, pointing forward in the middle; lateral glabellar lobes with different sizes, with L3 being the largest, and L1 the smallest L1 moderately curved; L2 slightly curved; L3 thick and triangular; L2 and L3 fused distally; S0 deep and convex; all three lateral glabellar furrows visible; S3 the longest, and S2 and S1 subequal in length; S1 almost straight, slightly concave and shallow, confluent with axial furrows; S2 straight and shallow, disconnected from axial furrows; S3 the deepest and thickest, transverse and confluent with axial furrows; glabella a little longer than wide (width across the frontal lobe about 85% of the length); glabellar width around 48% of cephalic width. Pygidium semicircular and vaulted; anterior margin slightly curved forward; axial

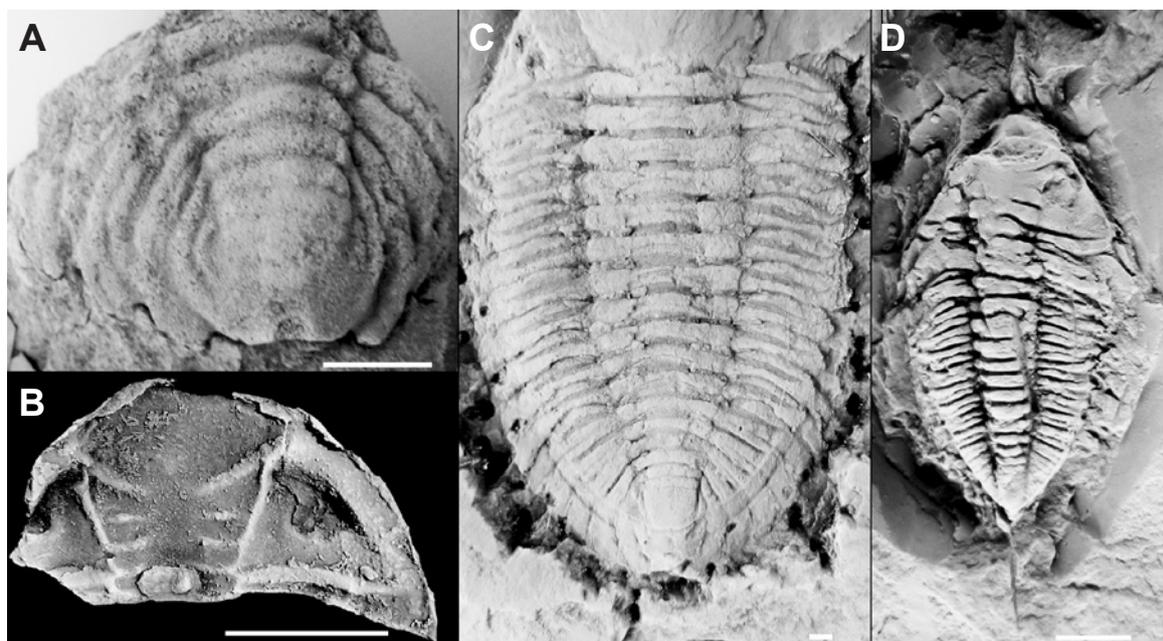


Figure 5. *Metacryphaeus parana*. **A**, DGM69; internal mold of pygidium previously assigned to *Tibagya parana*. **B**, DZP-18626; external mold of cephalon; photo taken by Soares *et al.*, 2008a. **C**, NR3108; internal mold of thoracopygon. *Paracalmonia cuspidata*. **D**, NR2265A; internal mold of exoskeleton. Scale bars = 5mm.

furrows divergent; inter-ring furrows curved; interpleural furrows shallow and transverse; axis more elevated than pleural field, bearing eight rings; pleural field with five ribs, all of which ending in large lappets, with rounded terminations; posterior margin of pygidium rounded, with a terminal lappet that overlaps the last axial ring; terminal spine absent.

Remarks. This species was initially considered a variation of *Cryphaeus australis* by Kozłowski (1923). Later on, Lieberman (1993) elevated *M. rotundatus* to species level, stating that *M. rotundatus* is the sister-group of *Metacryphaeus giganteus*, and not of *M. australis*, because of the long genal spine that they share. Struve (1958) erected the monospecific genus *Tibagya* based only on a pygidium that had been assigned to *Homalonotus parana* by Clarke (1913) (see also Thomas, 1977) (Figure 5A). This pygidium looked very similar to *Metacryphaeus australis*, but Struve (1958) erected the new genus based mostly on two characteristics: the pygidial pleural lappets, which are thicker than those of *M. australis*, and the presence of four pairs of pleural ribs and lappets, which differ from the typical five pairs of *Metacryphaeus*. However, a close study of the type specimen of *Tibagya parana* (DGM69) revealed that it is actually incomplete; because its anterior part is broken, certainty about how many pleural ribs and lappets really existed is not possible to achieve (Figure 5A). The presence of pleural lappets and a pygidial-rounded termination indicates that this pygidium belongs to *Metacryphaeus* and is conspecific with *M. rotundatus*. Thus, *M. parana* is regarded here as a senior synonym of *M. rotundatus*. *M. parana* was first described in the Devonian of the Paraná Basin by Soares *et al.* (2008a), utilizing characters such as the pigaxis extending in a termination that reaches the pleural lappets, rounded pleural lappets, long genal spine, and cephalic margin extended anteriorly (Figures 5B-C). Bosetti *et al.* (2010) interpreted one thorax and one pygidium as belonging to *Pennaia pauliana*. However, the analysis of the image (Bosetti *et al.*, 2010, fig. 6e) revealed that the specimen actually corresponds to *M. parana*, because of the pygidium, which bears five pairs of pleural ribs and lappets, as well as the characteristic terminal lappet of this species, and none of these characters are found in *Pennaia pauliana*. This new assignment adds another specimen to *M. parana*, which is relatively rare in the Ponta Grossa Formation. Additionally, the occurrence of *Metacryphaeus* in the Ponta Grossa Formation was interpreted as Emsian - Givetian (Melo, 1988). The presence of *M. parana* in the basal portion of the Ponta Grossa Formation (Soares *et al.*, 2008a) extends the distribution of the *Metacryphaeus* to Pragian- Givetian.

Paracalmonia Struve, 1958

1913 *Proboloides* Clarke, p. 135-139, Pl. 7, figs. 11–19.

Type species. *Proboloides cuspidatus* Clarke, 1913; original designation. Ponta Grossa Formation.

Paracalmonia cuspidata Clarke, 1913
(Figures 5D, 6A-F)

1913 *Proboloides cuspidatus* Clarke, p. 135-137, pl. 7, figs. 13-19.

1913 *Proboloides pessulus* Clarke, p. 138, pl. 7, figs. 11-12 (n. syn.)

1996 *Paracalmonia paranaensis* Popp *et al.*, p. 23, fig. 4A-D (n. syn.)

1996 *Paracalmonia mendesi* Popp *et al.*, p. 29, fig. 5D-F (n. syn.)

Diagnosis. Cephalon triangular with long median frontal spine, usually longer than cephalon, separated from glabella by facial sutures surrounding frontal lobe closely; S1 and S3 confluent with axial furrows; fixigenal and prolibrigenal spines short; thorax with pleurae ending in spines; pygidium triangular with five pairs of pleural spines directed outwards; long terminal spine present, considerably longer than the rest of the pygidium.

Material. DGM 77, DGM 78 (lectotype), DGM 79, DGM 83, DGM 84, DGM 85, DGM 1580, DGM 3708, DZP-18419, GP/1C404, CPUFPR31256, NR2265A, NR3131, NR3160, NR3161, NR3195, 5Tr, 34Tr. Types of sclerites: four complete exoskeletons, five cephalae, two thoraxes with pygidia, seven pygidia.

Occurrence. Municipalities of Jaguariaíva, Ponta Grossa and Tibagi, Ponta Grossa Formation (Emsian).

Description. Cephalon triangular; frontal margin bearing a very large frontal spine, usually longer than the cephalon; eyes small, very close to the glabella, distant from the posterior border of the cephalon; Large Eye Index around 0.34; genal angles angular, bearing two small fragile spines in each side of the cheeks: one fixigenal and one prolibrigenal, both pointing outwards; axial furrows slightly divergent; cephalic length measuring around 31% of entire body length. Glabella pentagonal, not inflated; frontal glabellar lobe medium-sized and not inflated; L0 a little thick and almost straight, bending forward in the middle; lateral glabellar lobes subequal; L1 moderately curved; L2 and L3 slightly curved; L2 and L3 fused distally; S0 shallow and curved medially; all lateral glabellar furrows fairly visible and in different sizes, with S3 being the longest, and S2 the shortest; S1 the deepest and straight, confluent with axial furrows; S2 straight, shallow and obscure, disconnected from axial furrows; S3 transverse, shallow and obscure, reaching the axial furrows; glabella longer than wide (width across the frontal lobe about 77% of length); glabellar width around 59% of cephalic width.

Thorax ending in very acute spines directed outwards; axis narrower and more inflated than the pleurae; thoracic rings curved to the front in the middle; axial furrows shallow, almost parallel; pleural furrows shallow and wavy; thoracic length corresponding around 45% of entire body length. Eleven thoracic segments. Pygidium triangular; anterior margin straight; axial furrows convergent; lateral margins transverse; inter-ring furrows deep and straight; interpleural furrows shallow and transverse; axis not inflated, bearing seven or eight rings; pleural field bearing five ribs, with five pleural spines in each side of the pygidium, all pointing outwards; terminal spine present and longer than the pygidium; pygidium

wider than long (length about 72% of width); pygidial length occupying 24% of entire body length.

Remarks. Clarke (1913) originally described this species as *Proboloides cuspidatus* based on the presence of a large frontal spine and prolibrigenal spines on each side of the cephalon. The name *Proboloides* was maintained until Struve (1958) substituted it for *Paracalmonia*, because the former is a homonym of *Proboloides* Della Valle, 1893 (Crustacea) and *Proboloides* Morley, 1903 (Hymenoptera). Clarke (1913) also erected *Proboloides pessulus*, renamed to *Paracalmonia pessula*, and based only on one specimen that had a median frontal process of different size. Unlike the frontal spine found in *P. cuspidata*, the frontal spine of *Paracalmonia pessula* has about the same length as the glabella, instead of being

longer than it is (Figure 6D). In addition, the pygidium of *P. pessula* seems to be a little rounder than that of *P. cuspidata*, and apparently lacks marginal spines (Figure 6F). However, the pygidial margin of *P. pessula* is not well-preserved (Figure 6F) and it is more than likely that the absence of spines is a taphonomic character. In fact, the only character that would separate both species would be the size of the frontal spine. In the Ponta Grossa Formation, it is very hard to find specimens with complete spines, especially when they are as long as in *Paracalmonia*. The analysis of the specimens of *Paracalmonia* show that there is no rule to the size of the frontal spine in the specimens that were classified as *P. cuspidata*. In some cephalons, the size of the spine is just a little longer than the cephalon, while other cephalons

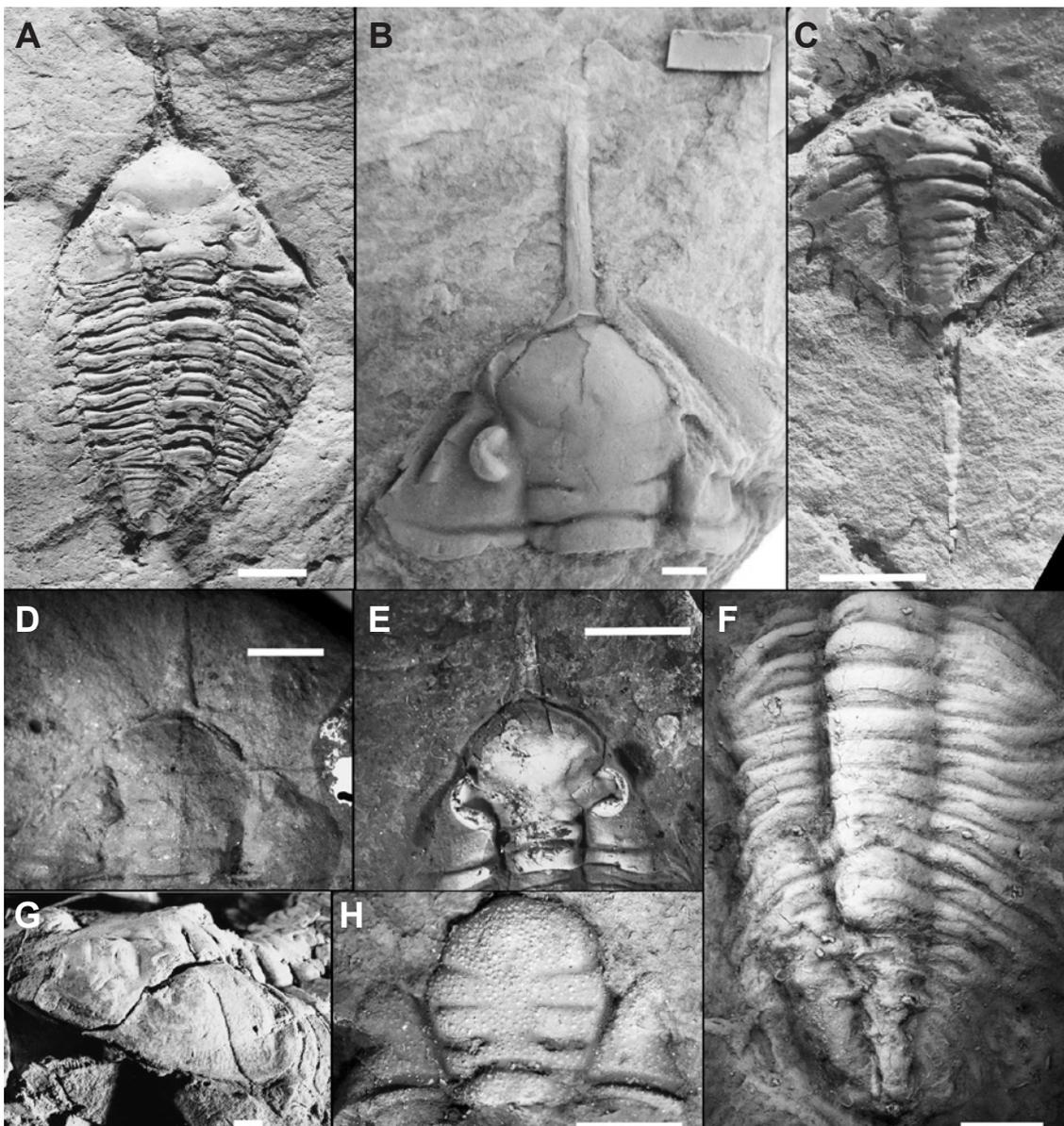


Figure 6. Internal molds of *Paracalmonia cuspidata*. **A**, CPUFPR-31256; exoskeleton previously assigned to *P. paranaensis*; photo taken by Popp *et al.*, 1996. **B**, DGM78; lectotype, displaying the very large frontal spine. **C**, NR3195; pygidium, with pleural and terminal spines preserved. **D**, DGM85; poorly preserved cephalon previously assigned to *P. pessula*. **E**, GP/1C404; latex mold of a cephalon, with smaller frontal spine. **F**, DGM85; poorly preserved thoracopygon previously assigned to *P. pessula*. **G**, NR3161, detail of the poorly preserved glabella of *P. salamunii*. Photo taken by Popp *et al.*, 1996. *Paranacaste pontagrossensis*. **H**, GP/1E7488; internal mold of glabella, showing distinct granulation. Scale bars = 5mm.

show frontal spines measuring double the cephalic length (Figures 5D, 6A-B, E). Thus, *P. cuspidata* and *P. pessula* are regarded herein as synonyms, and the size of the frontal spine is considered to be a variable character. Popp *et al.* (1996) revised the genus *Paracalmonia* and erected three new species based mostly on glabellar characters. However, Soares *et al.* (2008b) questioned the validity of one of them, *Paracalmonia paranaensis*. Although Popp *et al.* (1996) distinguished *P. paranaensis* from *P. cuspidata* by having more inflated frontal and L3 glabellar lobes, Soares *et al.* (2008b) noticed that the glabellar lobes of the type material of *P. paranaensis* are compressed (Figure 6A), suggesting that *P. paranaensis* and *P. cuspidata* are synonyms. Similarly, *Paracalmonia mendesi* by Popp *et al.* (1996) was erected on the basis of an inflated frontal glabellar lobe, which was compared with that of *P. paranaensis* (Popp *et al.*, 1996). Following Soares *et al.* (2008b), it is likely that the specimens of *P. mendesi* also represent well-preserved specimens of *P. cuspidata*. Carvalho & Edgecombe (1991) had regarded the holotype of *P. mendesi* as conspecific with *P. cuspidata*; a reassignment that is endorsed herein. The third species erected by Popp *et al.* (1996), *Paracalmonia salamunii*, seems to differ from *P. cuspidata* also by differences in the glabella, including a sinuous S3 and shallow axial furrows at level of L2 and L3 (Popp *et al.*, 1996). However, it is important to note that the holotype of *P. salamunii* is not well preserved, especially the glabella, which is compressed, fractured and exfoliated (Figure 6G). The glabellar lateral furrows and lobes are obscure and barely visible. Therefore, we cannot rule out the possibility that *P. salamunii* and *P. cuspidata* are synonyms.

Paranacaste Popp, 1989

Type species. *Paranacaste pontagrossensis* Popp, 1989; original designation. Ponta Grossa.

Paranacaste pontagrossensis Popp, 1989
(Figure 6H)

Diagnosis. Cephalic margin rounded medially; very large and inflated frontal glabellar lobe; granulation present on cephalon surface; genae bluntly angular; pygidium small and semicircular.

Material. GP/1E7488, DG-126Tr (holotype), DG - 127Tr. Types of sclerites: one cephalon, one cephalon with thorax, one thorax with pygidium.

Occurrence. Municipality of Jaguariaíva, Ponta Grossa Formation (Emsian).

Description. Glabella rounded and wide; glabellar surface with conspicuous granulation; frontal lobe highly inflated; L0 curved, bending slightly backwards in the middle; all lateral glabellar lobes distinct, with L3 being the largest, and L1 the smallest; L1 moderately curved; L2 and L3 inflated, slightly curved; S0 deep and convex; all lateral furrows visible, with S3 being the longest, and S2 and S1 being subequal in length; S1 deep and straight; S2 straight and shallow; S3 transverse and shallow; glabellar length and width subequal.

Remarks. *Paranacaste* was described as a monotypic genus by Popp (1989). Carvalho & Edgecombe (1991) considered this species to be congeneric with *Bainella*, therefore transferring it to *Bainella pontagrossensis*. However, Carvalho & Edgecombe (2006) found two specimens that matched the original description of *Paranacaste pontagrossensis* done by Popp (1989), and thus proposed the conservation of this taxon, based on the two new specimens. However, they proposed that the species specimen previously assigned by Carvalho & Edgecombe (1991) as *Bainella pontagrossensis* should be kept in the genus *Bainella*, and so it was then renamed as *Bainella paranaense* by Carvalho & Edgecombe (2006). A fragmentary cephalon from the municipality of Jaguariaíva is described herein (Figure 6H). The specimen shows the diagnostic characters of *Paranacaste pontagrossensis* Popp, 1989 such as a large, inflated and subcircular glabella, as well as a sculpture of raised granules. *Paranacaste* is reported from Jaguariaíva for the first time.

DISCUSSION

Lucas (2001) introduced the term “taphotaxon”, referring to taxa that were erected based on taphonomic characters (*i.e.* characters that resulted from taphonomic processes, be it biostratigraphic or diagenetic). Such term is deeply relevant to the scope of the systematic paleontology, considering that identifying characters altered during the fossilization process has been of one of the major concerns of paleontologists. In fact, there have been many studies in the Ponta Grossa Formation that analyzed groups under taphonomic vision, frequently leading to the invalidation of previously described species (Simões *et al.*, 2003; Rodrigues *et al.*, 2003; Leme *et al.*, 2004; Ghilardi, 2004; Soares *et al.*, 2008b; Simões *et al.*, 2009; Leme *et al.*, 2010; Mori & Leme, 2012; Mori, 2013).

Ghilardi (2004) studied the trilobites of the Ponta Grossa Formation with this taphonomic approach, focusing on the taphonomic alterations that may have caused a poor interpretation of systematics. The author observed several preservation issues in different positions of the stratigraphic sequence, concluding that the taphonomy of these groups were complex and should be considered in any study about them.

Soares *et al.* (2008a) showed that so far 17 calmonioid species were reported from the Ponta Grossa Formation. However, several of these species might correspond to taphotaxa, with artificial characters that resulted from external factors. This is particularly evident for specimens that were preserved in different lithotypes or taphofacies, and therefore were subjected to distinct fossilization processes. For instance, the degree of compression of the different rocks and the exfoliation of the fossils are the main factors that obliterate and affect diagnostic characters of calmonioids (Soares, 2007; Soares *et al.*, 2008b; Simões *et al.*, 2009).

Soares *et al.* (2008b) had previously presented some morphological characters that might be altered taphonomically, for example: the shape and inflation of glabellar lobes, the depth of the axial and glabellar furrows and the presence or absence of external ornamentation (*e.g.* spines/lappets).

In addition, here were observed that the shape and size of the axial and glabellar furrows, the confluence of the lateral glabellar furrows with the axial furrows, the size of the spines and the presence or absence of granulation or tuberculation throughout the exoskeleton are morphological characters that were modified by taphonomical process.

Calmoniidae is a family with great taxonomic similarity amongst the genera and species, which incurs the fact that the diagnostic characters are in many cases represented by small details. This causes several problems, since such details are malleable against the external factors to which the fossils and organisms are exposed. The results presented revealed that the diversity of calmoniids was overestimated beyond what Soares *et al.* (2008b) had already pointed out, with several other taphotaxa erected (see Table 1, for valid taxonomic species).

CONCLUSIONS

Based on the results presented in this paper, the following conclusions are obtained: (i) *Paracalmonia cuspidata* and *P. paranaensis* are considered as synonyms, as already suspected by Soares *et al.* (2008a); (ii) *Calmonia? gonzagana*, as well as *C. signifer* var. *micrischia*, are considered as synonyms of *C. signifer*, which makes this genus monospecific in the Ponta Grossa Formation; (iii) *Tibagya parana* is synonymized with *Metacryphaeus parana*, now considered a senior synonym of *M. rotundatus*; (iv) *Paracalmonia pessula* and *P. mendesi* are considered as synonyms of *P. cuspidata*; (v) *P. salamunii* is considered as a *nomen nudum*, as the holotype was poorly preserved; (vi) a new occurrence of *Paranacaste pontagrossensis* is documented; (vii) now it is possible to provide an updated list of the valid calmonioid species of the Ponta Grossa Formation, which stands with eight species: *Bainella paranaense* Carvalho & Edgecombe, 1991; *Calmonia signifer* Clarke, 1913; *Kozlowskiaspis subseciva* Clarke, 1913; *Paracalmonia cuspidata* Clarke, 1913; *Paranacaste pontagrossensis* Popp, 1989; *Pennaia pauliana* Clarke, 1913; *Metacryphaeus australis* Clarke, 1913; *Metacryphaeus parana* Kozlowski, 1923; (viii) the faunal diversity of calmonioid trilobites in the Ponta Grossa Formation is lower than what was previously thought; (ix) all these systematic results highlight the importance of adding a taphonomic view to the taxonomic study, in order to identify potential taphonomic characters that

might be used to create artificial taxa. They also stress the idea that the designation of new species must be based preferably on numerous and well-preserved specimens, as to allow the identification of taphonomic variations and their respective taxonomic consequences.

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Table 1. List of taxonomic valid species of Calmoniidae in the Ponta Grossa Formation, Paraná Basin, Apucarana Sub-basin, Brazil.

Species	Author
<i>Bainella paranaense</i>	Carvalho & Edgecombe, 1991
<i>Calmonia signifer</i>	Clarke, 1913
<i>Kozlowskiaspis subseciva</i>	(Clarke, 1913)
<i>Paracalmonia cuspidata</i>	(Clarke, 1913)
<i>Paranacaste pontagrossensis</i>	Popp, 1989
<i>Pennaia pauliana</i>	Clarke, 1913
<i>Metacryphaeus australis</i>	(Clarke, 1913)
<i>Metacryphaeus parana</i>	(Kozlowski, 1923)

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