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Lower–Early Middle Devonian Calmoniid Trilobites from Mato Grosso, Brazil, and Related Species from Paraná

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ABSTRACT

Calmoniidae from Emsian or Eifelian strata of the Chapada Group at Chapada dos Guimarães, Mato Grosso, Brazil, include *Calmonia* cf. *C. signifer* Clarke, *Calmonia*? *triacantha* n. sp., and *Paracalmonia* sp. A collection from the Chapada Group at Paranatinga includes *Calmonia*? *triacantha* n. sp. and *Metacryphaeus australis* (Clarke). Affinities are with assemblages from the Ponta Grossa Formation (Emsian-Eifelian), Paraná. *Bainella* is represented in the Ponta Grossa Formation by *B. pontagrossensis* (Popp, 1989) n. comb., with closest relatives in Bolivia and South Africa. *Paranacaste* Popp, 1989 (allegedly Acastinae) is a synonym of *Bainella* Rennie.

INTRODUCTION

Devonian trilobites from Brazil have received much less systematic study than those from Andean South America (e.g., Wolfart, 1968; Eldredge and Braniša, 1980) and other regions of the Malvinokaffric Realm (Cooper, 1982; Edgecombe, 1991a). Even Clarke's (1913) monograph, which included trilobites from the Ponta Grossa Formation, Paraná, has not received complete modern revision. Devonian Trilobita from the Paraná Basin have recently been considered by Carvalho et al. (1987), who described species from the

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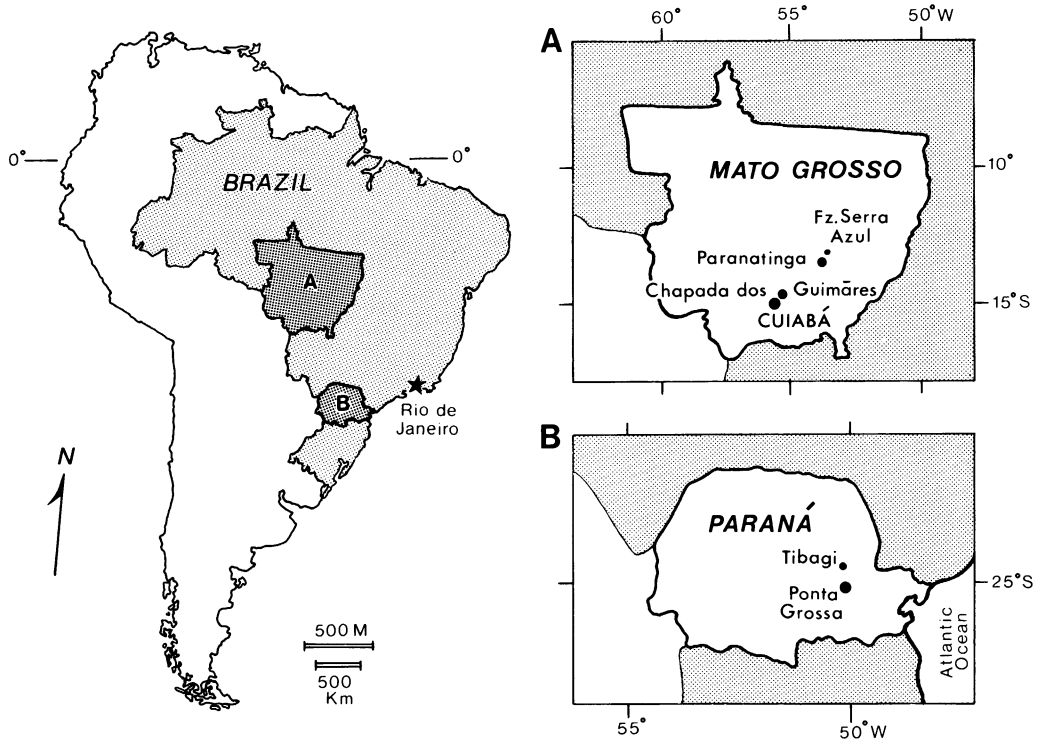


Fig. 1. Map of Brazil, showing location of States of Mato Grosso (inset A) and Paraná (inset B). Insets show locations of trilobite localities at Paranatinga, Chapada dos Guimarães, Tibagi, and Ponta Grossa.

states of Goiás and Mato Grosso do Sul. They are also the subject of a paper by Popp (1989), which presents partial results of a more extensive treatment in an unpublished dissertation (Popp, 1985).

Devonian Calmoniidae from the northern part of the Paraná Basin (Alto Garças Subbasin; Melo, 1988) and from the southeastern corner of the Parecis Basin (Siqueira, 1989) in the state of Mato Grosso are investigated in the present report. These assemblages are from the Chapada Group at Chapada dos Guimarães (Paraná Basin) and Paranatinga (Parecis Basin) (fig. 1). This is the first time that Devonian fossils are described from the Parecis Basin, whose eastern portion was formerly part of the northern Paraná Basin prior to tectonic separation in post-Devonian time (Melo, 1988). In the Paranatinga area (Morro Vermelho locality at Serra Azul Farm), calmoniids are associated with the brachiopods *Australocoelia* and *Notiochonetes,* suggesting an Emsian or Eifelian age (J. H. G. de Melo, personal commun.). Trilobites are preserved as molds, usually partly articulated, in pink-brown siltstone and mudstone.

Calmoniid affinities in these faunas are clearly with taxa known from the Ponta Grossa Formation (Emsian–early Eifelian), Paraná and Rincón de Alonso and Arroyo del Cordobes, Uruguay. Biogeographic evidence includes widespread species occurring in both Ponta Grossa and Chapada strata [*Metacryphaeus australis* (Clarke)], species only doubtfully differentiated between the two subbasins (*Calmonia* cf. *C. signifer* Clarke), and genera otherwise known only from the Ponta Grossa Formation (*Paracalmonia* sp.). In addition to documenting the Mato Grosso faunas, we present new information on calmoniid diversity in the Ponta Grossa Formation, confirming the occurrence of the genus *Bainella,* widespread in the Malvinokaffric Realm.

Figured specimens are housed in the following institutions: Department of Invertebrates, American Museum of Natural History (AMNH), New York; Departamento

Nacional de Produção Mineral (DNPM), Rio de Janeiro; Museu de Paleontologia, PETROBRÁS (CENPES), Rio de Janeiro; and, Departamento de Geologia, Universidade Federal do Mato Grosso (MP), Cuiabá.

Morphological terminology used herein is generally as outlined by Harrington et al. (1959) and Eldredge and Braniša (1980). Glabellar lobes and furrows are described with the prefix L or S respectively, and numbered 0–4 from rear (occipital) to front.

ACKNOWLEDGMENTS

The authors are indebted to PETROBRÁS (Petróleo Brasileiro S/A) for the loan of the Paranatinga specimens housed at its research center. J. H. G. de Melo provided information on the stratigraphic context, and made useful revisions of the manuscript. R. Quadros loaned specimens from Chapada dos Guimarães housed at Universidade Federal do Mato Grosso, and D. R. B. Campos arranged loans from Departamento Nacional de Produção Mineral. We thank A. R. Ormiston, M. R. Cooper, and N. Eldredge for comments on the manuscript. S. Klofak and A. Modell (Department of Invertebrates, American Museum of Natural History) assisted us with specimen preparation and photography, respectively. Figure 1 was prepared by L. Meeker. The senior author's research was supported in part by an American Museum of Natural History collections study grant.

SYSTEMATIC PALEONTOLOGY

FAMILY CALMONIIDAE DELO, 1935

GENUS *CALMONIA* CLARKE, 1913

TYPE SPECIES: *Calmonia signifer* Clarke, 1913.

Calmonia cf. *C. signifer* Clarke, 1913
Figure 2B, 2F

MATERIAL: Internal mold of pygidium with articulated posterior thoracic segment, MP 198, Chapada Group (Emsian or Eifelian), Chapada dos Guimarães, Mato Grosso.

DISCUSSION: This specimen is illustrated (fig. 2B, F) in lieu of a full description. It resembles *Calmonia signifer* Clarke and Bolivian *Calmonia* sp. of Edgecombe (1991a) in the presence of 6 slender marginal spines, 11 axial rings, and a stout-based terminal spine. It appears unlikely that this pygidium is associated with the co-occurring cephalothorax assigned to *Paracalmonia* sp. (fig. 2H), since the tip of the rearmost thoracic segment forms only a short point. In *Paracalmonia* sp. [and *P.* cf. *cuspidata* (Clarke, 1913)], the thoracic pleural tips on rearward segments are extended as prominent, posteriorly deflected spines.

Calmonia*? *triacantha, new species
Figure 3

?*Phacops brasiliensis* Clarke. Ammon, 1893: fig. 1a–c.

DIAGNOSIS: *Calmonia*? of large size; cephalon strongly arched (tr.), glabella raised well above eye; eye short (exsag.) (Large Eye Index 0.20–0.22), elevated on steep genae; pygidial pleurae bearing three or four pairs of bluntly triangular marginal spines.

TYPES: Holotype CENPES 690-I, external mold of cephalon (fig. 3A, B), Chapada Group (Emsian or Eifelian), Paranatinga area, Mato Grosso. Paratypes CENPES 691-I–696-I, from type locality; MP 199, from Chapada Group, Chapada dos Guimarães, Mato Grosso. All type material except paratype MP 199 collected by J. H. G. de Melo, 1990.

ETYMOLOGY: Compounding *tri,* three, and *acantho,* spine (Greek), in reference to the apparent number of pygidial pleural spines.

DESCRIPTION: Cephalic anterolateral margin straight. Cranidial anterior border short abaxially, extended anteromedially as short, triangular process; preglabellar furrow shallow (sag., exsag.). Anterior branch of facial suture weakly inflected adaxially, transecting anterolateral corner of frontal glabellar lobe in broad curve. Glabellar length (sag.) subequal to width across frontal lobe. Axial furrow lightly incised, very shallow between eye and L3, straight, weakly diverging forward; glabellar width across L1 80 percent of width across frontal lobe; axial furrow rather sharply inflected anterolaterally between S3 and cephalic border. Frontal lobe 60 percent length of glabella, rhomboid in outline, anterolateral margin nearly straight; strong, even arching (tr.); posterior median impression

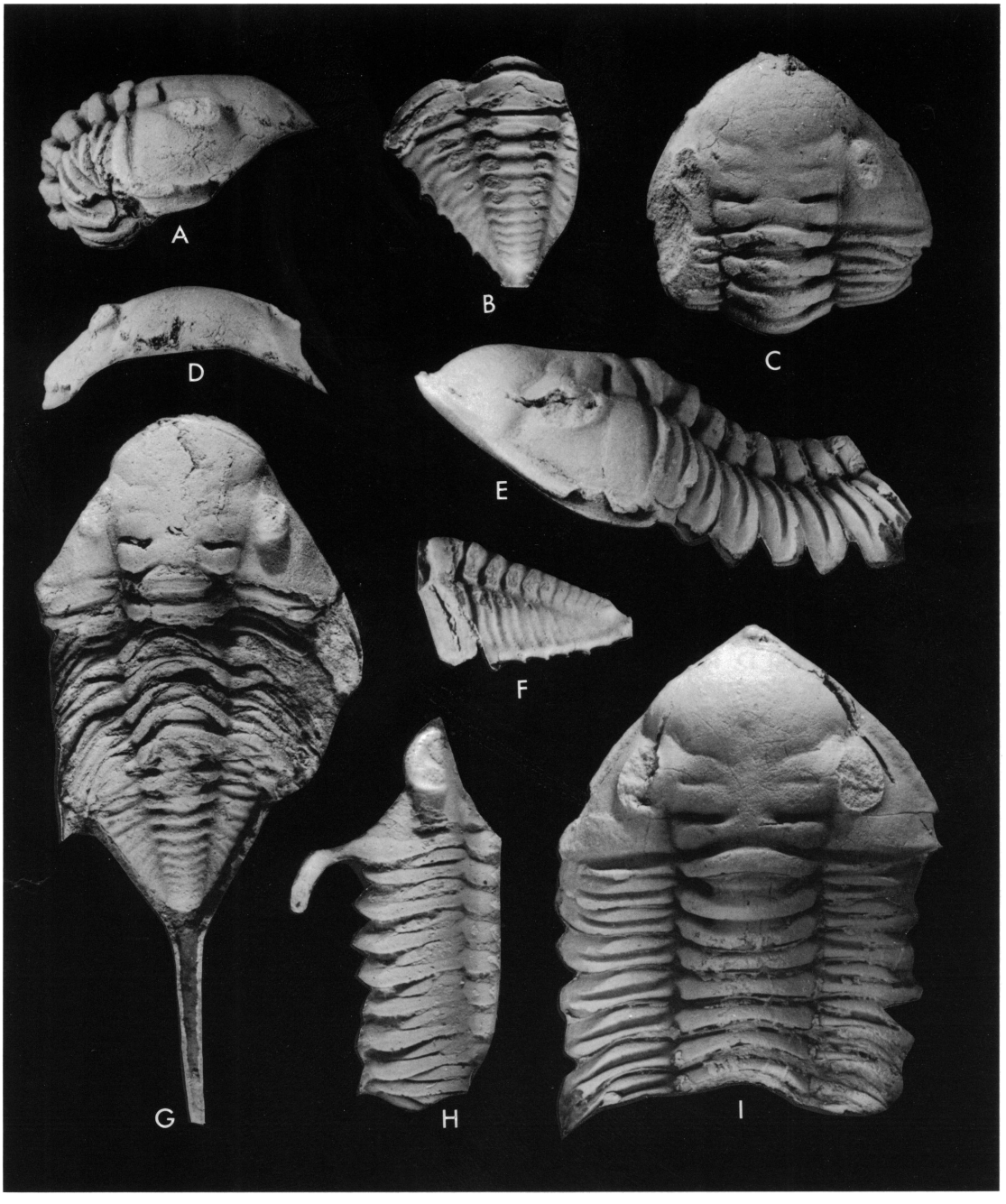


Fig. 2. *Calmonia* and *Paracalmonia* spp. **A, C, D.** *Calmonia* cf. *terrarocenai* Mendez-Alzola, 1934. Cantera Bossolo, Blanquilla, Duranzo Department, Uruguay. Lateral, dorsal cephalic, and anterior views of cephalon and partial thorax, internal mold, AMNH 44177, ×2. **B, F.** *Calmonia* cf. *C. signifer* Clarke, 1913. Chapada Group, Chapada dos Guimarães, Mato Grosso, Brazil. Dorsal and lateral views of pygidium and rearmost thoracic segment, internal mold, MP 198, ×3.5. **E, I.** *Calmonia signifer* Clarke, 1913. Ponta Grossa Formation, Ponta Grossa, Paraná, Brazil. Lateral and dorsal views of cephalon and partial thorax, internal mold, DNPM 3710, ×2. **G.** *Paracalmonia* cf. *cuspidata* (Clarke, 1913). Ponta Grossa Formation, Ponta Grossa, Paraná, Brazil. External view of exoskeleton, internal mold, DNPM 3708, ×2. **H.** *Paracalmonia* sp. Chapada Group, Chapada dos Guimarães, Mato Grosso, Brazil. Dorsal view of partial cephalothorax, latex cast from external mold, MP 200, ×3.

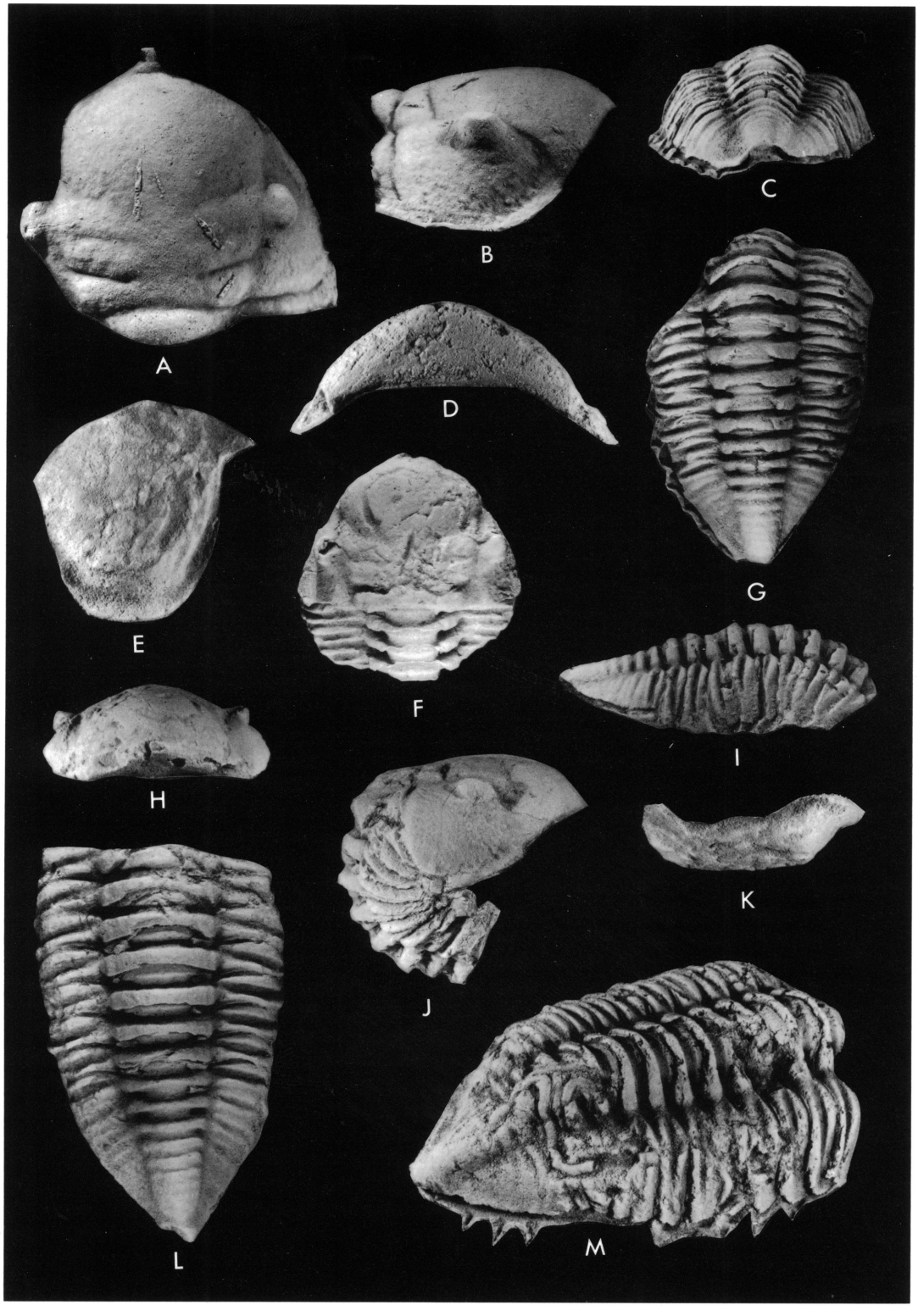
obscure. Glabella faintly convex (sag.) between S0 and anterior third of frontal lobe, moderately sloping anteromedially. L2–L3 gently convex (tr.), lateral lobes flattened; L1 moderately, evenly arched (tr.). S3 shallow, consisting of proximal branches diverging at 130°, distal branch sharply flexed forward to axial furrow. S2 shallow, not confluent with axial furrow, approximately straight, moderately inclined abaxially. S1 developed as moderately deep, straight or faintly crescentic apodemal groove, parallel to S2 or more steeply inclined abaxially, shallowing distally but wholly confluent with axial furrow. L1 shortest behind expanded proximal end of S1, lengthening exsagittally, slightly longer (exsag.) than L2. S0 short, shallow (sag.), incised as narrow, transverse apodemes distally. L0 weakly arched forward medially and adjacent to axial furrow, sagittal length about 20 percent of width (tr.), slightly narrower (tr.) than L1, gently convex (sag.), raised to plane of posterior glabellar region, with semicircular transverse arching, lacking occipital spine. Large Eye Index 0.20–0.22; anterior edge of eye adjacent to axial furrow, opposite anterior third length (exsag.) of L3; posterior edge of eye opposite anterodistal corner of L2. Palpebral lobe gently inflated; palpebral furrow very shallow. Posterior branch of facial suture with nearly straight/gently sinuous, transverse course (in dorsal orientation) between ϵ and lateral border furrow. Librigena flat or faintly convex, steeply declined outward beneath eye; librigena and extraocular fixigena scrobiculate, with coarse, shallow pits. Lateral border furrow very shallow; lateral border moderately wide, less steeply declined than librigenal field. Posterior border furrow short (exsag.), moderately impressed, with gentle anterolateral inflection. Posterior border short proximally, lengthening and gently flexed forward distally; genal angle apparently with small point. Cephalic doublure flattened, inclined forward at about 45°, lengthening medially, bounded by low ridge; hypostomal suture gently, evenly convex forward. Cephalic anterior border flattened, almost vertically inclined exsagittally, weakly projecting in front of cranidial border (in dorsal orientation), narrowing medially to thin strip.

Length (sag.) of hypostome about 75 percent width across anterior wings. Middle body rounded in outline, gently arched (tr.), of faint convexity (sag.) for most of length, rather steeply sloping down on posterior lobe; margins of anterior lobe weakly defined. Middle furrow shallow; maculae positioned distinctly adaxial to lateral margin of middle body, anterior to midlength. Lateral border very narrow behind anterior wing, gently widening backward. Posterior border furrow shallow. Posterior border uniformly short (sag., exsag.), almost 10 percent length of hypostome, lacking marginal spines.

Thorax of 11 segments, gently narrowing backward. Axial ring 36–38 percent width of thorax, short sagittally, length about 15 percent of width, faintly convex (sag.), posterior margin transverse, anterior margin flexed forward distally against deep, teardrop-shaped apodemes; ring of moderate, even convexity (tr.), raised above articulating half-ring; ring furrows long, rather shallow. Inner part of pleura gently declined abaxially, outer part moderately turned down; posterior pleurae rather strongly declined across most of width. Pleural furrow rather broad, well incised, with approximately straight, diagonal course, gently flexed forward across articulating facet, effaced on distal part of facet. Anterior band longest near midwidth (tr.) of pleura, gently convex (exsag.), of equal height to posterior band at pleural midwidth, depressing abaxially. Pleurae terminate as blunt points.

Pygidium triangular, length 60–65 percent of width (excluding posteromedian spine). Axis about 35 percent of pygidial width, raised well above pleurae, of moderate convexity (tr.) anteriorly, strongly arched and elevated posteriorly. Ten complete axial rings, crests of rings in nearly flat (sag.) plane; anterior three ring furrows long, moderately impressed, incised distally as short, transverse apodemes; succeeding rings low, with shallow, transverse ring furrows. Axial terminus bluntly rounded. Anterior pleurae gently convex (tr.); posterior unfurrowed region flattened, with moderate slope. Three or four distinct pleural furrows, anterior two well incised; interpleural furrows shallow. Base of posteromedian spine stout. Doublure narrow, gently convex.

DISCUSSION: Several characters ally this species with the genus *Calmonia* Clarke, 1913,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known from Paraná, Uruguay, and Bolivia (see Edgecombe, 1991a). Similarities include the pointed cephalic anteromedian margin, form and spacing of the lateral glabellar furrows, the genal angle recurved forward distally (evidently with no more than a tiny spine), and the pygidium with marginal spines and a posteromedian spine. The strong cephalic arching of *Calmonia*? *triacantha* n. sp. exceeds that of *C. signifer* Clarke from the Ponta Grossa Formation (fig. 2E, I), but more closely approaches specimens of *Calmonia* from Blanquilla, Uruguay (fig. 2A, C, D). Specific assignment of the Uruguayan form awaits revision of the apparently oversplit species erected by Mendez-Alzola (1938); it appears referable to *Calmonia terrarocenai* Mendez-Alzola, 1934 (probably a senior synonym of *C. cordobesa* Mendez-Alzola, 1938, and *C. signifer* var. *brevicaudata* Mendez-Alzola, 1938). Likewise, eye size of the Uruguayan species (Large Eye Index 0.32) is slightly closer to *C.*? *triacantha* n. sp. than is that of *C. signifer* (L.E.I. 0.34–0.40).

The hypostome of this species (fig. 3E, K) displays apomorphic characters shared with other genera of the "*Calmonia* group" of Eldredge and Ormiston (1979) (Edgecombe, 1991a: fig. 3). With *Pennaia* Clarke and *Oosthuizenella* Cooper, the middle body is short and rounded; *Deltacephalaspis* Eldredge and Braniša groups with these taxa in having the maculae displaced adaxially. All genera of the "*Calmonia* group" have short, aspinose posterior borders.

The generic assignment of *Calmonia*? *triacantha* n. sp. is in question because of the condition of the pygidial margin. Species of *Calmonia* s.s. have six slender marginal spines and a posteromedian spine; variation in form and number of marginal spines has been used in diagnosing genera within the group (e.g., *Oosthuizenella* Cooper, 1982, having only four marginal spines and a posteromedian spine). None of the available material of *C.*? *triacantha* n. sp. has a well-preserved pygidial margin. However, at least three (fig. 3M), or apparently four (fig. 3G) marginal spines are preserved in some specimens, with the third positioned closer to the posteromedian spine than is the third (of six) spines in *Calmonia signifer*. The posterolateral margin appears to be smooth between this third or fourth spine pair and the posteromedian spine in *C.*? *triacantha* (length of the posteromedian spine is undetermined). Presence of three or four marginal spines corresponds to only three or four defined pleural furrows (versus six pleural furrows observed on external molds of six-spined *C. signifer*). In the number of pygidial pleural spines, the species thus appears closer to *Oosthuizenella*. However, the Brazilian species is more comparable to *Calmonia* in its pointed cephalic anteromedian process (compare figs. 2I, 3A), subangular cephalic doublure, and straight S2. We are reluctant to erect a new monotypic genus for *C.*? *triacantha* n. sp. solely to weight number of pygidial spines. Although possession of exactly six spines appears to be a valid synapomorphy of *Calmonia* s.s., this feature is variable in other taxa of the "*Calmonia* group" (e.g., *Pennaia*).

Some characters of *Calmonia*? *triacantha* n. sp. are suggestive of *Bainella* Rennie, 1930. Shared derived features include a strong degree of cephalic arching, small eye raised on tall genae, and the scrobiculate texture of the gena (fig. 3B). Many species of *Bainella* also have a pygidial posteromedian spine, and some possess marginal denticles. The Mato Grosso species obviously lacks certain apo-

←

Fig. 3. *Calmonia*? *triacantha* n. sp. Chapada Group, all specimens from Paranatinga area, Mato Grosso, Brazil except F, H, from Chapada dos Guimarães, Mato Grosso. All internal molds except A, B, latex cast from external mold; figures C–M depict paratypes. **A, B.** Dorsal and lateral views of holotype cephalon, CENPES 690-I, ×1.5. **C, G, I.** Posterior, dorsal, and lateral views of thoracopygidium showing pleural spines on external mold, CENPES 691-I, ×1. **D.** Ventral view of cephalon, CENPES 692-I, ×2. **E, K.** Ventral and lateral views of hypostome, CENPES 693-I, ×2. **F, H.** Dorsal and anterior views of cephalon and partial thorax, MP 199, ×1. **J.** Lateral view of cephalon and partial thorax, CENPES 694-I, ×1. **L.** Dorsal view of thoracopygidium, CENPES 695-I, ×1.5. **M.** Oblique posterolateral view of thoracopygidium, CENPES 696-I, ×1.5.

morphies which group species of *Bainella* (e.g., eye distinctly removed from axial furrow with an ocular ridge; occipital and thoracic sagittal spines). However, it suggests a possible phylogenetic connection between generalized taxa of the "*Calmonia* group" and the rather autapomorphic genus *Bainella.*

Phacops (*Cryphaeus*) *ceres* Schwarz, 1906, from the Bokkeveld Group of South Africa is another comparable species. Cooper (1982) has revised this species as *Kozlowskiaspis* Braniša and Vaněk, although this assignment is questionable (i.e., some diagnostic features are lacking). *Kozlowskiaspis*? *ceres* resembles *C.*? *triacantha* n. sp. in its small eyes positioned adjacent to the axial furrow, and straight cephalic anterolateral margin. Similarities in glabellar form (including transection of the frontal lobe by the facial suture) reflect, in large part, the general plan of the "*Calmonia* group," and thus are symplesiomorphic.

GENUS *METACRYPHAEUS* REED, 1907

TYPE SPECIES: *Phacops caffer* Salter, 1856.

Metacryphaeus australis (Clarke, 1913)
Figure 4

Cryphaeus australis Clarke, 1913: 108, pl. 3, figs. 7–14; pl. 4, figs. 1–5.
Hadrorachus australis (Clarke). Delo, 1935: 415, fig. 34, 35.
Metacryphaeus australis (Clarke). Struve, 1959: 486, fig. 383: 3a, b. Lieberman et al., 1991: fig. 1.7, 1.10, 1.14.
Metacryphaeus cf. *M. australis* (Clarke). Carvalho et al., 1987: 548, pl. 1, fig. 1.

MATERIAL: Two external molds of cephala, CENPES 697-I, 699-I; external mold of thorax; internal mold of pygidium, 698-I, Chapada Group (Emsian or Eifelian), Paranatinga area, Mato Grosso.

DISCUSSION: The species-level taxonomy of *Metacryphaeus australis* and its closest relatives [*M. tuberculatus* (Kozlowski, 1923); *M. caffer* (Salter, 1856)] is complicated by considerable intraspecific variation but subtle distinction between species (see Lieberman et al., 1991). Specimens from the Chapada Group at Paranatinga correspond in all respects with *M. australis* from the Ponta Grossa Formation, Paraná, sharing such distinctive features as: rhomboid frontal glabellar lobe; relatively long (exsag.) L3; S2 apodemes distinctly isolated from the axial furrow; relatively large eyes (Large Eye Index 0.38), with the anterior edge abutting the axial furrow; and cuticle prosopon of coarse, dense granules. Morphology of the pygidial pleural tips, extended as angular spines (fig. 4B, D), also distinguishes *M. australis* (related species have blunt, often lobate pleural tips). This species is thus widespread in the Paraná Basin.

GENUS *PARACALMONIA* STRUVE, 1959

TYPE SPECIES: *Proboloides cuspidatus* Clarke, 1913.

Paracalmonia sp.
Figure 2H

MATERIAL: External mold of partial cephalon and anterior nine thoracic segments, MP 200, Chapada Group (Emsian or Eifelian), Chapada dos Guimarães, Mato Grosso.

DESCRIPTION: Cephalic axial furrow straight between S0 and opposite anterior edge of eye, weakly diverging forward, shallow, narrow. L1 long (exsag.). Eye adjacent to axial furrow, posterior edge opposite S1; visual surface relatively tall, at least 7 lenses in some dorsoventral files. Cephalic posterior border furrow narrow, moderately incised adjacent to axial furrow, approximately transverse, shallowing abaxially. Posterior border gently lengthening abaxially, flexed forward to base of genal spine; genal spine long, slender, gently curved, projecting posterolaterally, extending strongly distal to thoracic pleural tips.

Outer part of thoracic pleural rib flattened (tr.), moderately turned down anteriorly, becoming more steeply declined in rearward segments. Pleural furrow sharply incised, with approximately straight, diagonal course across rib, distinct across much of articulating facet. Anterior and posterior bands flattened (exsag.), of equal height on inner part of pleura. Anterior five pleural terminae bluntly rounded, segments 5–7 (and presumably 8–11) bearing sharp, slender spines projecting backward. Articulating facet and distal part of posterior band densely covered with granules.

DISCUSSION: The divergent fixigenal spine

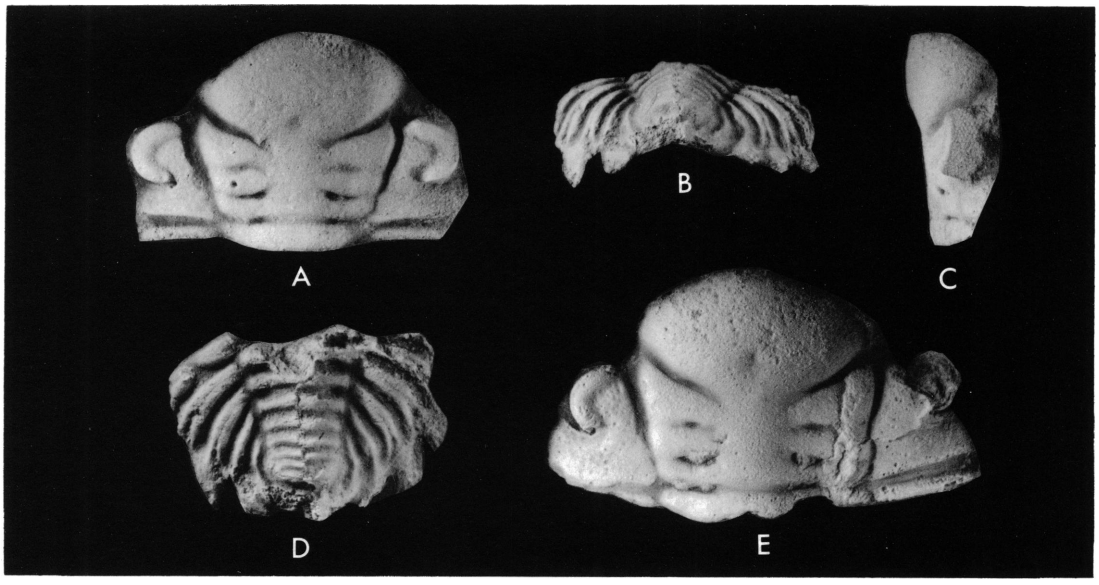

Fig. 4. *Metacryphaeus australis* (Clarke, 1913). Chapada Group, Paranatinga area, Mato Grosso, Brazil. **A, C.** Dorsal and lateral views of partial cephalon, latex cast from external mold, CENPES 697-I. **B, D.** Posterior and dorsal views of pygidium, internal mold, CENPES 698-I. **E.** Dorsal view of partial cephalon, latex cast from external mold, CENPES 699-I. All ×1.5.

and spinose tips of rearward thoracic pleurae are distinctive features shared with *Paracalmonia cuspidata* (Clarke). Other characters consistent with assignment of the Chapada dos Guimarães specimen to *Paracalmonia* include: long (exsag.) L1; weakly divergent cephalic axial furrow; weak palpebral furrow; and eye set in close to the axial furrow. Specific assignment is complicated by incomplete knowledge of *Paracalmonia* from Paraná, including the type species. A specimen from the Ponta Grossa Formation that may represent *P. cuspidata* has a lengthy, curved genal spine (fig. 2G); Clarke's (1913) illustrations depict a short spine. Most similarities of the Mato Grosso specimen to *Paracalmonia* are shared with *Deltacephalaspis* Eldredge and Braniša, 1980, supporting the contention that these genera are sister taxa (Eldredge and Cracraft, 1980: fig. 6.15). However, characters listed by Eldredge and Braniša, 1980: 215) to distinguish between *Paracalmonia* and *Deltacephalaspis* (e.g., anterior median cephalic spine; course of anterior branch of facial suture; prolibrigenal spine) are not preserved for comparison in the Chapada dos Guimarães specimen. The genal spine's curvature, however, is shared with some Ponta Grossa *Paracalmonia* (versus the straight, divergent spine of *Deltacephalaspis*).

GENUS *BAINELLA* RENNIE, 1930

TYPE SPECIES: *Bainella bokkeveldensis* Rennie, 1930 [=*B. africana* (Salter, 1856)].

DISCUSSION: *Bainella* has been extensively discussed in several recent works on Calmoniidae. Eldredge and Braniša (1980) recognized two subgenera, *B.* (*Bainella*), and a new subgenus *B.* (*Belenops*). Several species from the South African Bokkeveld Group were revised by Cooper (1982), who chose not to recognize subgenera. Edgecombe (1991a) outlined a cladistic analysis of ingroup taxa, including a new species from the Falkland Islands.

With the concepts of *Bainella* used by these workers, it is evident that the alleged acastine *Paranacaste* Popp, 1989, is a junior synonym of *Bainella*. Specimens from the Ponta Grossa Formation, Paraná, described herein are regarded as conspecific with the type species of *Paranacaste, P. pontagrossensis* Popp, 1989, which is accordingly reassigned to *Bai-*

nella. The types of *B. pontagrossensis* (Popp) originate from the Jaguariaíva Member of the Ponta Grossa Formation. Discussion is restricted to the holotype cephalon (Popp, 1989: pl. 1, fig. 1); the associated pygidium (Popp, 1989: pl. 1, fig. 2) is doubtfully conspecific. Typical of Calmoniinae (i.e., unlike Acastinae s.s.) are small eyes, a weak palpebral furrow, S1 inclined abaxially, and L1 of subequal length (exsag.) to L2 (see Edgecombe, 1991b, for comments on Acastinae). Diagnostic of *Bainella,* the eyes are set relatively high on coarsely pitted genae, the lateral glabellar furrows are broad (tr.), and the thoracic axial rings are constricted sagittally. As in several species of *Bainella,* the glabella has a tuberculate prosopon. *Bainella pontagrossensis* shares apomorphic similarities with *B.* (*Belenops*) sensu Eldredge and Braniša, 1980, in particular. Features grouping it with *B. insolita* (Wolfart, 1968) (revised by Eldredge and Braniša, 1980) and *B. gamkaensis* Rennie, 1930 (revised by Cooper, 1982) include: sinuous S3; sinuous cephalic axial furrow (flexed inward opposite the distal end of S3); and a rounded cephalic anterior margin. These affinities imply an area of endemism including Bolivia (*B. insolita*), South Africa (*B. gamkaensis*), and the Paraná Basin (*B. pontagrossensis*). More detailed similarity with *B. insolita* is discussed below.

The pygidium referred to *Bainella pontagrossensis* by Popp (1989) differs from Acastinae s.s. in its obscure border furrow and relatively strong pleural and interpleural furrows. The rounded posteromedian margin is atypical for *Bainella,* but is comparably developed in *B. gamkaensis.*

Bainella pontagrossensis (Popp, 1989), new combination

Figure 5

Paranacaste pontagrossensis Popp, 1985: 103, pl. 6, fig. D (nomen nudum). Popp, 1989: 25, pl. 1, fig. 1.

DIAGNOSIS: *Bainella* with cephalic margin smoothly rounded, axial region not bulging anterior to genae; frontal glabellar lobe gently inflated (sag., tr.); S2–S3 moderately impressed; anterior edge of eye adjacent to axial furrow; extraocular gena broad (tr.); large "metagenal" process on cephalic posterior border; genal angle blunt.

MATERIAL: Internal mold of cephalon, DNPM 1708, Ponta Grossa Formation, Tibagi, Paraná. Counterpart molds of partial cephalon, DNPM 1612, from same locality.

DESCRIPTION: Cephalon broadly semicircular in outline, length 45–50 percent of width; lateral margin indistinctly shouldered. Preglabellar furrow shallow (sag.). Anterior branch of facial suture nearly straight, gently inflected adaxially, entirely distal to frontal glabellar lobe. Axial furrow narrow, straight and gently diverging forward between S0–S2, curved outward against L3. Glabella slightly wider across anterior corner of L3 than frontal lobe, slightly shorter than width of frontal lobe, raised well above eye. Frontal lobe broadly elliptical in outline, anterior margin rounded. Glabella faintly convex (sag.) between S0 and posterior third of frontal lobe; frontal lobe gently convex (sag.), moderately declined forward; posterior median impression shallow. Numerous small, rather subdued tubercles scattered on frontal lobe, a few tubercles on L3–L2 lateral lobes. S3 sinuous, with distinct proximal and distal moieties, distal moiety sharply flexed forward near axial furrow. L3–L2 gently convex (tr.). S2 straight, gently inclined anterolaterally, shallowing adjacent to, and not confluent with, axial furrow. S1 approximately straight for most of length, moderately inclined anterolaterally, deeply incised, wholly confluent with axial furrow, proximal end may be weakly bifurcate. L1 short at proximal end of S1, lengthening abaxially, subequal in length (exsag.) to L2. S0 short, moderately deep, anterior margin gently arched forward medially. Large Eye Index about 0.34. Palpebral furrow shallow; visual surface low. Posterior branch of facial suture nearly straight between ϵ and lateral border furrow, sharply flexed backward across lateral border. Librigena flattened or faintly convex, moderately declined outward; librigena and extraocular fixigena scrobiculate, with pervasive coarse, shallow pits. Lateral border furrow broad, shallow: border moderately wide, convex, gently turned down. Posterior border furrow short (sag., exsag.), moderately deep, flexed forward distally, distinctly continuous with lateral border furrow. Rounded "metagenal"

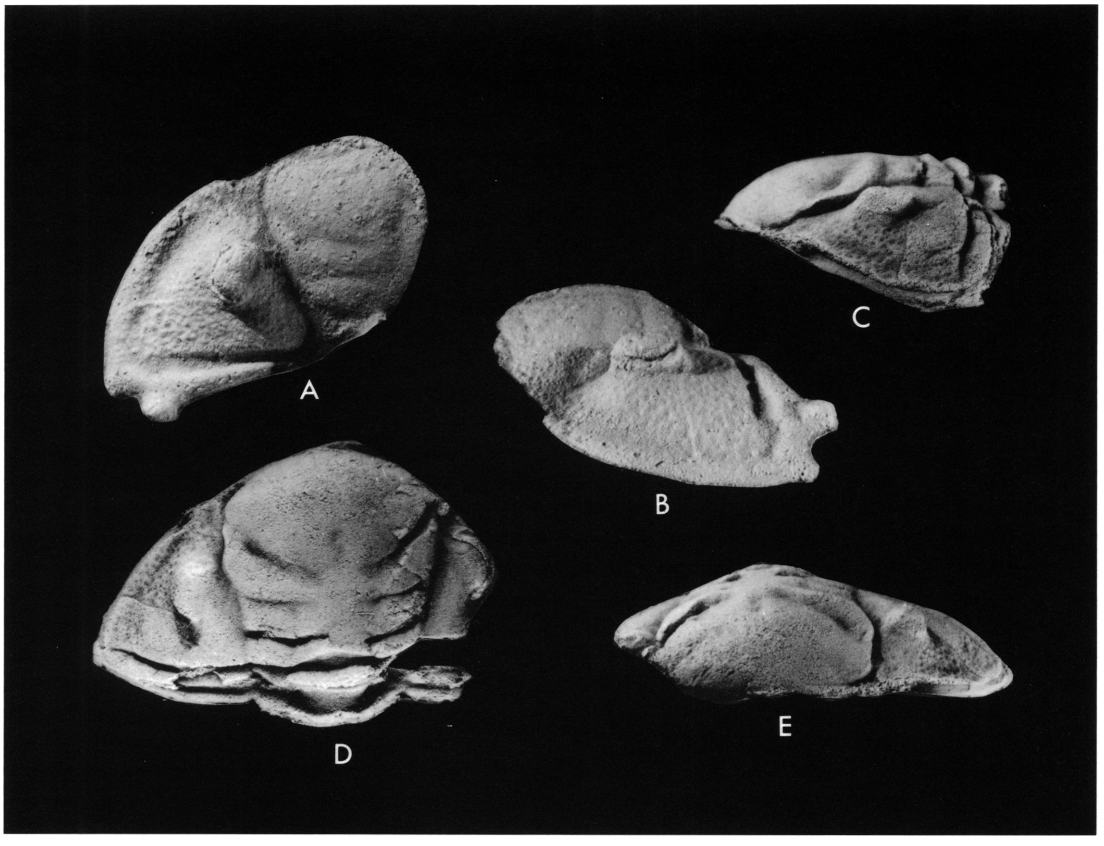

Fig. 5. *Bainella pontagrossensis* (Popp, 1989). Ponta Grossa Formation, Tibagi, Paraná, Brazil. **A, B.** Slightly lateral of dorsal and lateral views of partial cephalon, latex cast from external mold, DNPM 1612, ×2.5. **C-E.** Lateral, dorsal, and anterior views of partial cephalon and first thoracic segment, internal mold, DNPM 1708, ×2.

process extending from cephalic posterior border, situated well inward of genal angle.

Thoracic axial ring constricted medially, moderately convex (tr.). Ring furrow long, shallow sagittally. Pleural rib gently convex (tr.). Pleural furrow narrow, moderately deep.

DISCUSSION: The species description above has also considered the holotype, an internal mold of a small cephalon (Popp, 1989: pl. 1, fig. 1), from the Ponta Grossa Formation at Jaguariaíva, Paraná. Specimens figured here, from the Tibagi "Sandstone," are evidently of Eifelian age (Melo, 1988: fig. 3).

As noted above, *Bainella pontagrossensis* (Popp) is regarded as most closely related to *B. insolita* (Wolfart) and *B. gamkaensis* Rennie. It is distinguished from *B. insolita* by its broader (tr.) genae, and failure of the cephalic axis to overhang the genae anteromedially. Incision of S2 and S3 is variable in Bolivian samples, but they are consistently shallower than in *B. pontagrossensis.* The occipital ring is incompletely preserved in the most complete specimen of *B. pontagrossensis* (fig. 5C), but it does not appear to rise above the plane of L1 (sag.) as in other species of *Bainella. Bainella gamkaensis* is more readily distinguished from the Brazilian species by its distally positioned eyes, strongly expanded frontal lobe, and lack of glabellar tubercles. Although tuberculation is indistinct on weathered internal molds of *B. pontagrossensis,* it is pronounced on the external mold (fig. 5A). The lesser degree of cephalic arching and weaker inflation of the frontal glabellar lobe in *Bainella pontagrossensis,* when compared with the Bolivian and South African taxa, are probably at least in part due to tec-

tonic flattening. The prominent "metagenal" process of *B. pontagrossensis* corresponds to a swelling on the cephalic posterior border of *B. insolita* (Eldredge and Braniša, 1980: fig. 6C, 7B, C). This structure is preserved only on an external mold (fig. 5A, B); it does not appear to be a preservational artefact, since the distinctive prosopon of the surrounding border is continued onto this swelling, and its position conforms topologically to an expansion of the border in *B. insolita.* The abaxial displacement of this evidently homologous "metagenal" process is a distinctive shared character, suggesting that *B. insolita* is the closest relative of *B. pontagrossensis.*

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