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Devonian Calmonioid Trilobites from the Parnaíba Basin, Piauí State, Brazil

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ABSTRACT

Two new species of calmonioid trilobites are described from the Middle Devonian of the Parnaíba Basin, Piauí State, northeastern Brazil. One of these occurs in the lower Pimenteiras Formation, and the other is found in the Passagem Member of the Cabeças Formation. The presence of the genus *Metacryphaeus* confirms faunal affinities with the Malvinokaffric Devonian fauna. Phylo-

genetic parsimony analysis is used to infer relationships within the previously unresolved "*Metacryphaeus tuberculatus* group," which is extended to include the form from the Cabeças Formation. The relationships of *Metacryphaeus* from the Pimenteiras Formation are less certain, but some morphologic similarities suggest that it is closely allied to *M. curvigera* Lieberman, 1993.

INTRODUCTION

The Devonian System is well represented in the Parnaíba Basin, which is situated in northeastern Brazil, and extends across the states of Ceará, Piauí, Maranhão, Pará, and Tocantins (fig. 1).

Lower to lower Middle Devonian [Emsian (?) and early Eifelian] sediments are repre-

sented by the Upper Serra Grande Group, i.e., Jaicós and Itaim Formations respectively, as indicated by new chitinozoan-based investigations (Grahn, 1992). The Middle Devonian is represented by the Pimenteiras and lower Cabeças formations (Melo, 1988). The upper Cabeças and Longá formations are Up-

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per Devonian and Lower Carboniferous (Famennian to Tournaisian; Quadros, 1982; Loboziak et al. 1992). Further details of the stratigraphy of the Parnaíba Basin are provided in Melo (1988: 676).

Although the deposits of this basin have been studied since the early 20th century (Small, 1914), its fossils are less well known than in other Devonian Brazilian areas and there is a paucity of information concerning its paleontology. There are only a few papers describing or illustrating fossil species, among them Krausel and Dolianiti (1957), Suárez-Riglos (1967), Castro (1968), Melo (1985), Caldas et al. (1987), and Fonseca and Melo (1987). Castro (1968) and Caldas et al. (1987) in particular presented systematic treatments of Devonian trilobites from the Parnaíba Basin.

The Malvinokaffric Realm (sensu Eldredge and Ormiston, 1979) is characterized by a highly endemic trilobite fauna known from austral localities. Members of the family Calmoniidae (Delo, 1935) represent three-quarters of the generic diversity (Eldredge and Ormiston, 1979). Recently published studies among these austral trilobites (Lieberman et al., 1991; Lieberman, 1993) recognized a complex phylogenetic pattern requiring the erection of new genera for some and the restriction of others to just a few species. The genus *Metacryphaeus* Reed, 1907, has proven particularly problematic; Lieberman (1993) retained nine species within this genus. The relationships of five of these species were completely resolved, but not those within the "*M. tuberculatus* (Kozłowski, 1923) species group" (comprising *M. tuberculatus*, *caffer*, *allardyceae*, and *australis*).

Two new species of calmonioid trilobites from the Middle Devonian of the Parnaíba Basin (Brazil) were referred to *Metacryphaeus* by Carvalho et al. (1994), but were not described; this paper presents comprehensive descriptions of this material. One of these taxa is known from only a few poorly preserved specimens, but its closest relations can be broadly determined. The other species is known from numerous specimens that provide sufficient data to suggest placement within the "*M. tuberculatus* group" of Lieberman (1993). We have appended a phylo-

genetic analysis of the taxa we believe belong in this group following the formal description of the new Brazilian material.

Metacryphaeus (in the restricted sense of Lieberman, 1993) is now known from the Parnaíba Basin of Brazil (Carvalho et al., 1994, and this paper), as well as from Devonian assemblages of Bolivia (Belén, Icla, and Sicasica formations; Wolfart, 1968; Falkland Islands (Fox Bay Formation; Edgecombe, 1991) and Paraná Basin (Ponta Grossa Formation and Chapada Group; Clarke, 1913; Castro, 1968; Carvalho et al., 1987). Alleged members of the "*M. tuberculatus* group" occur in all these areas. The only other previous record of *Metacryphaeus* in Brazil is *M. paituna* (Hartt and Rathbun, 1875), from the Ererê Formation, Amazon Basin. That form has been reassigned by Lieberman, 1993, to a new genus, *Eldredgeia*.

Morphological terminology follows that used in the Treatise on Invertebrate Paleontology, Part O (1959), and in Lieberman et al. (1991). Specimens figured herein are deposited in the Department of Geology, Section of Paleontology of University Federal do Rio de Janeiro, RJ, Brazil; Department of Invertebrates, American Museum of Natural History (AMNH), NY; Departamento Nacional de Produção Mineral (DNPM), Section of Paleontology, Rio de Janeiro, Brazil.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York.
DGM,DNPM	Divisão de Geologia Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil.
MCT	Museu Ciências da Terra, Setor de Paleontologia, DNPM, Rio de Janeiro, Brazil.
UCGM	University of Cincinnati, Geological Museum.
UFRJ	Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

SYSTEMATIC PALEONTOLOGY

FAMILY CALMONIIDAE DELO, 1935

SUBFAMILY CALMONIINAE DELO, 1935

Genus *Metacryphaeus* Reed, 1907

TYPE SPECIES: *Phacops caffer* Salter, 1856. [By subsequent designation of Rennie (1930); revised Cooper (1982)].

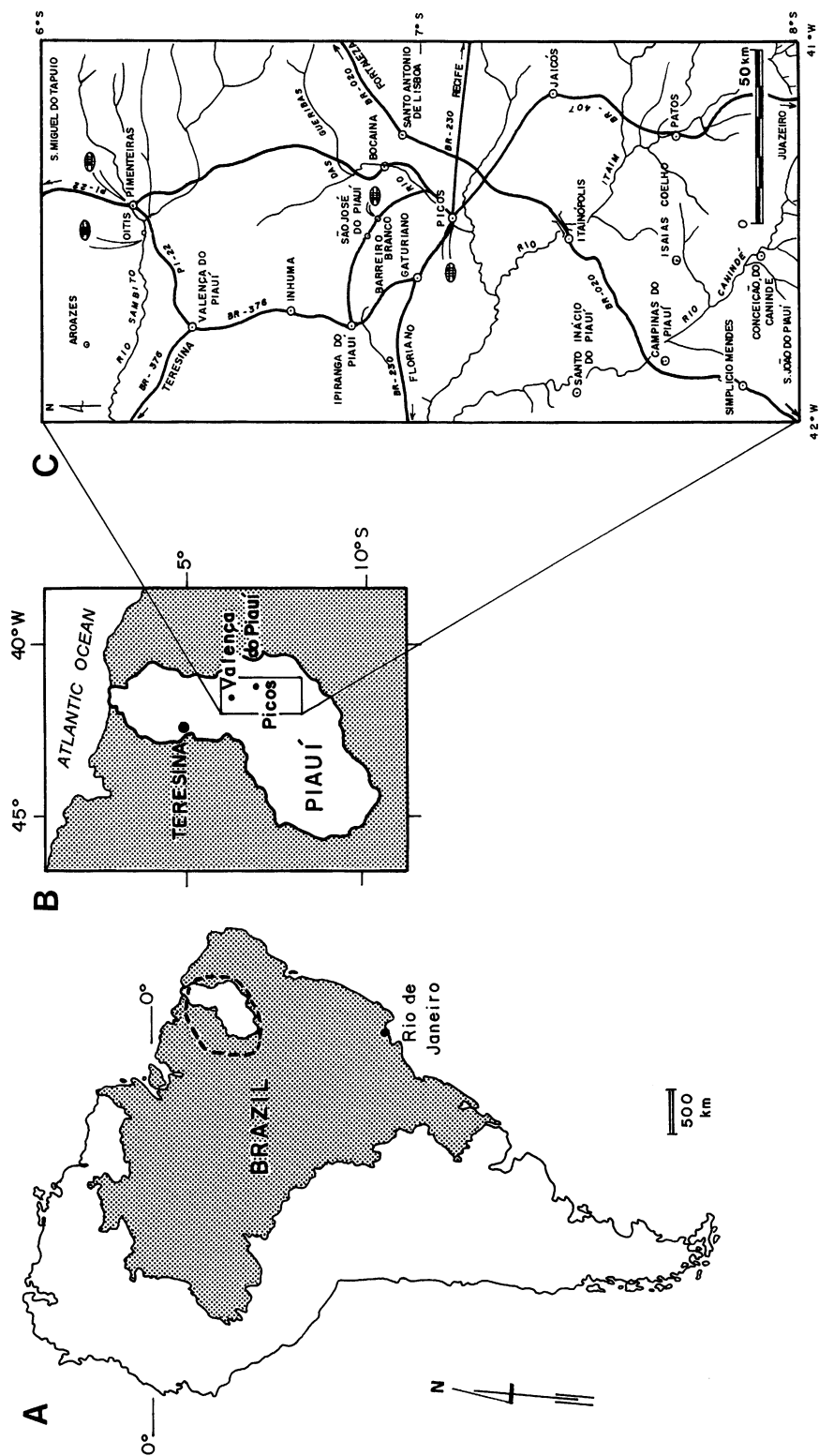


Fig. 1. Maps showing locations of Parnaíba Basin (dashed line); Piauí State; trilobite collecting sites in Piauí.

REMARKS: For a more complete discussion of *Metacryphaeus*, see Lieberman et al. (1991) and Lieberman (1993).

***Metacryphaeus kegeli*, new species**

Figure 2A–H

Asteropyge sp. Kegel, 1953.

Metacryphaeus sp. Melo, 1988: 681, pl. 25, figs. 9–15.

Metacryphaeus kegeli Carvalho et al., 1994: 119 (nomen nudum).

DIAGNOSIS: A *Metacryphaeus* with the frontal glabellar lobe steeply inclined anteromedially; cephalic anterior margin and frontal lobe of gentle even convexity; broad, deep cephalic axial furrows; small eyes well offset laterally from axial furrows; librigena steeply inclined.

ETYMOLOGY: In honor of Wilhelm Kegel, who made important geological studies on the Devonian of the Parnaíba Basin and who collected these specimens.

HOLOTYPE: DNPM N.6133-I, an internal mold of a cephalon, from the base of the Pimenteira Formation, nearly 11 km south of Pimenteira, Piauí State, Brazil.

PARATYPES: DNPM N.6131-I, an internal mold of a rolled up small specimen; 6132-I, an internal mold of a thorax and pygidium of a small specimen; 6134-I, an external mold of a small cephalon.

OCCURRENCE: Lower Pimenteira Formation; Eifelian (Fonseca and Melo, 1987), region of Pimenteira (sensu Kegel, 1953), Parnaíba Basin, Piauí State, Brazil.

DESCRIPTION: Cephalon moderately convex (tr.), with length (sag.) 50% of width. Axial region projects beyond arc of genae. Glabella is truncated anteriorly, with broad, deep axial furrows, weakly diverging to the anterior margin. Width (tr.) of occipital ring is 80% of width of frontal lobe. Cephalic anterior border is obscured medially. In dorsal view, its anterior margin is smoothly rounded, formed by frontal glabellar lobe medially. Frontal glabellar lobe is depressed beneath L1–L2 (sag.); L1–L3 are nearly flat (sag.) and gently declined forward. Posteromedian part of the frontal lobe is weakly convex (sag.). Frontal lobe is 60% of length (sag.) of glabella. Posterior median impression (PMI) is well developed and circular. Poste-

rior branch of facial suture has a weakly sinuous anterolateral course between ϵ and the lateral border furrow, and is sharply flexed backward across the lateral border. Anterior branch of facial suture circumscribes frontal lobe, crossing axial furrow at the cephalic anterolateral margin, and with a nearly straight posterodorsal course to γ . S3 are broad, deeply incised, straight, weakly divergent, and connect with the axial furrows; topographic separation between frontal lobe and posterior glabellar region is produced by a change in convexity. S2 are transverse, developed as apodemal grooves, shallowing distally, and weakly confluent with axial furrows. S1 are broad, crescent shaped, and become shallow adjacent to axial furrows. S0 is long (sag.), shallow, weakly arched forward medially, becoming deeper and narrower distally, connecting with the axial furrow. L2–L3 are flattened (tr.) medially; L3 lateral lobes are wedge shaped, weakly convex (tr.), and gently declined outward. L2 are convex anteriorly, concave posteriorly. L1 are crescent shaped, short (exsag.), depressed below L2 exsagittally, and moderately arched (tr.) medially. The occipital ring is uniformly long (sag.), and deflected backward (sag.). Large Eye Index (LEI) is 0.33; the visual surface has 23 dorsoventral lens files, with a maximum of six lenses per file. Interocular fixigena is elevated to height of palpebrum; librigenal field and extraocular fixigena have shallow pits. Palpebral furrow is narrow and moderately deep. Eyes are well offset laterally from axial furrow, nearly overhanging lateral border furrow in dorsal orientation, and eye ridge weakly connects with axial furrow. Cephalic lateral border furrow is shallow and broad. Cephalic posterior border furrow is deep, broad, with a gentle posterolateral inflection to behind outer (exsag.) edge of the eyes, then is flexed forward distally, where it is shallow but continuous with lateral border furrow. Posterior border is short (exsag.) adjacent to axial furrows, becoming longer abaxially, and genal margin is moderately convex.

DISCUSSION: Kegel (1953) noted differences between the samples here referred to *Metacryphaeus kegeli*, n. sp. (= *Asteropyge*, n. sp., of Kegel) and *Metacryphaeus australis* (Clarke, 1913), from the Ponta Grossa

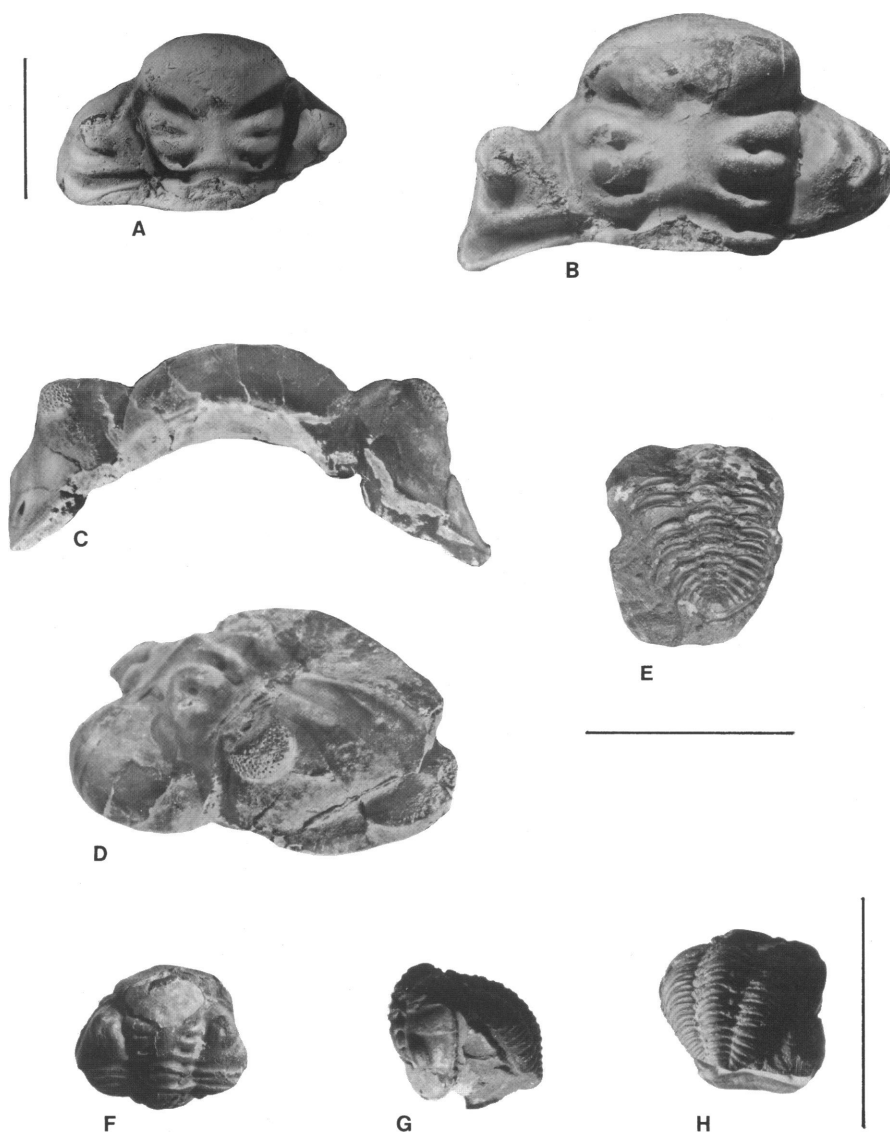


Fig. 2. *Metacryphaeus kegeli*, n. sp., Pimenteira Formation, Parnaíba Basin. A: Holotype DGM, DNPM 6133-I. Internal mold of cephalon, dorsal view. Scale bar = 10 mm. B–D: dorsal, frontal, and dorsolateral views of holotype. E: Paratype DGM, DNPM 6132-I, internal mold of thoracopygidium. Scale bar for B–E = 10 mm (below E). F–H: Paratype DGM, DNPM 6131-I, internal mold of small rolled-up specimen: (F) dorsal view of cephalon; (G) lateral view; and (H) dorsal-posterior view of thorax and pygidium. Scale bar for F–H = 10 mm (next to H).

Formation, Paraná Basin. *Metacryphaeus kegeli*, n. sp., has some distinctive derived characters shared with *M. curvigena* Lieberman, 1993, from the Icla Formation (Emsian) of Bolivia. These include the shape of the frontal glabellar lobe (broadened subrhomboid, slightly bulging anterior to the genal arc, steep anteromedially), and broad, well

incised axial furrows, with deeply impressed lateral glabellar furrows. *Metacryphaeus kegeli* nevertheless shows a more marked topographic break (sag.) between the frontal lobe and posterior glabellar region than *M. curvigena*. Another possible difference between these two species (the form of the genal angles) cannot be determined at present.

Genal spines are not preserved in specimens of *M. kegei*, although the holotype may have an eroded spine base.

***Metacryphaeus meloi*, new species**

Figure 3A–I

Metacryphaeus australis (Clarke). Castro, 1968: 485, plate III, figs. 2–5.

Metacryphaeus cf. *australis* (Clarke). Caldas et al., 1987: 539, phot. 01–03.

Metacryphaeus meloi Carvalho et al., 1994: 119 (nomen nudum).

DIAGNOSIS: Cephalon subtriangular, with short median frontal process; glabella densely covered with small, relatively subdued tubercles; genal angles bluntly pointed; eyes distinctly separated from axial furrows, moderately oblique (exsag.). Pygidial pleurae terminate as blunt spines; axial rings convex forward medially.

ETYMOLOGY: In honor of José Henrique Gonçalves de Melo, who has studied the Brazilian Devonian and has worked with the senior author in the Parnaíba Basin, where these specimens were collected.

HOLOTYPE: MCT N. 6 822-I, an internal mold of a cephalon, from the Cabeças Formation (Passagem Member), near the village of Oiti, a few kilometers from the junction of the road Valença do Piauí to Pimenteiras, Piauí State, Brazil.

PARATYPES: MCT N. 6 823-I, 6824-I, UFRJ N. 047-Tr, and 048-Tr, AMNH 45352 (Fossil Invertebrates Collection).

OCCURRENCE: Cabeças Formation (Passagem Member), type locality, also by road BR 316, km 305, near Picos, Piauí State, Brazil (see Caldas et al., 1987, fig. 1) and the village of Barreiro Branco (fig. 1C). The trilobites are preserved as disarticulated and mostly fragmentary molds in a fine- to medium-grained micaceous sandstone.

DESCRIPTION: Cephalic length (sag.) is about 55% of width across the genal angles. Anterior cephalic border is obsolete medially, becoming evenly lengthened abaxially. Anterior cranial border is short (exsag.) and visible in dorsal view. Angular antero-medial process is short (sag.). Cranial anterolateral margin is nearly straight. Preglabellar furrow is narrow, sharply impressed. Glabella is expanded anteriorly, with a length

(sag.) equal to width across frontal lobe. Frontal lobe is moderately convex (sag.) and raised above posterior glabellar region. Anterior branch of each facial suture has a straight course from γ to just outside antero-ventral corner of frontal lobe. Posterior branch of these sutures has a straight anterior inflection between ϵ and lateral border furrows, than is sharply flexed backward across lateral border; ϵ posterior to ω . Small tubercles are scattered on L0, the glabella, and interocular fixigenae. Frontal glabellar lobe is broadly ovate in outline, 60% length (sag.) of glabella. Axial furrows are narrow, straight, and moderately incised. Occipital ring (L0) is 60–70% width (tr.) of frontal lobe. Lateral glabellar furrows are well incised; S3 are faintly convex posteriorly; S2 are slightly shallower than S1, with very weak incision distally; S1 are deep adjacent to axial furrow, and crescent shaped. Median region of L1–L3 is flat (sag.) and inclined anteriorly. L3 lobes are wedge-shaped and expanded distally. L2 lobes are smaller than L3, and are rectangular; L2–L3 are gently arched (tr.). L1 lobes are almost transverse. Occipital furrow (S0) is moderately incised (sag.), longest medially, and impressed as transverse apodemes abaxially. Occipital ring (L0) is gently and evenly convex (sag.), moderately arched transversely, with constant length (sag., exsag.), and weakly curved forward distally. Posterior median impression (PMI) is obscure to moderately defined. Large Eye Index (LEI) is 0.29–0.34. Palpebral lobes are moderately oblique (exsag.), gently inflated, with their anterior margin distinctly separated from axial furrows. Number of dorsoventral lens files in visual surface is 26, with a maximum of 8 lenses per file. Extraocular fixigenae are strongly pitted, with postocular region gently sloping backward to border furrow. Librigenal fields are steeply declined outward, and faintly convex. Lateral border furrows are shallow, becoming deeper posteriorly. Posterior border furrow is transverse, deeper adjacent to axial furrows, broadening and shallowing distally, and distinctly continuous with lateral border furrows. Lateral cephalic borders are narrow anteriorly, broadening slightly posteriorly, and convex. Genal margins are gently and evenly convex laterally.

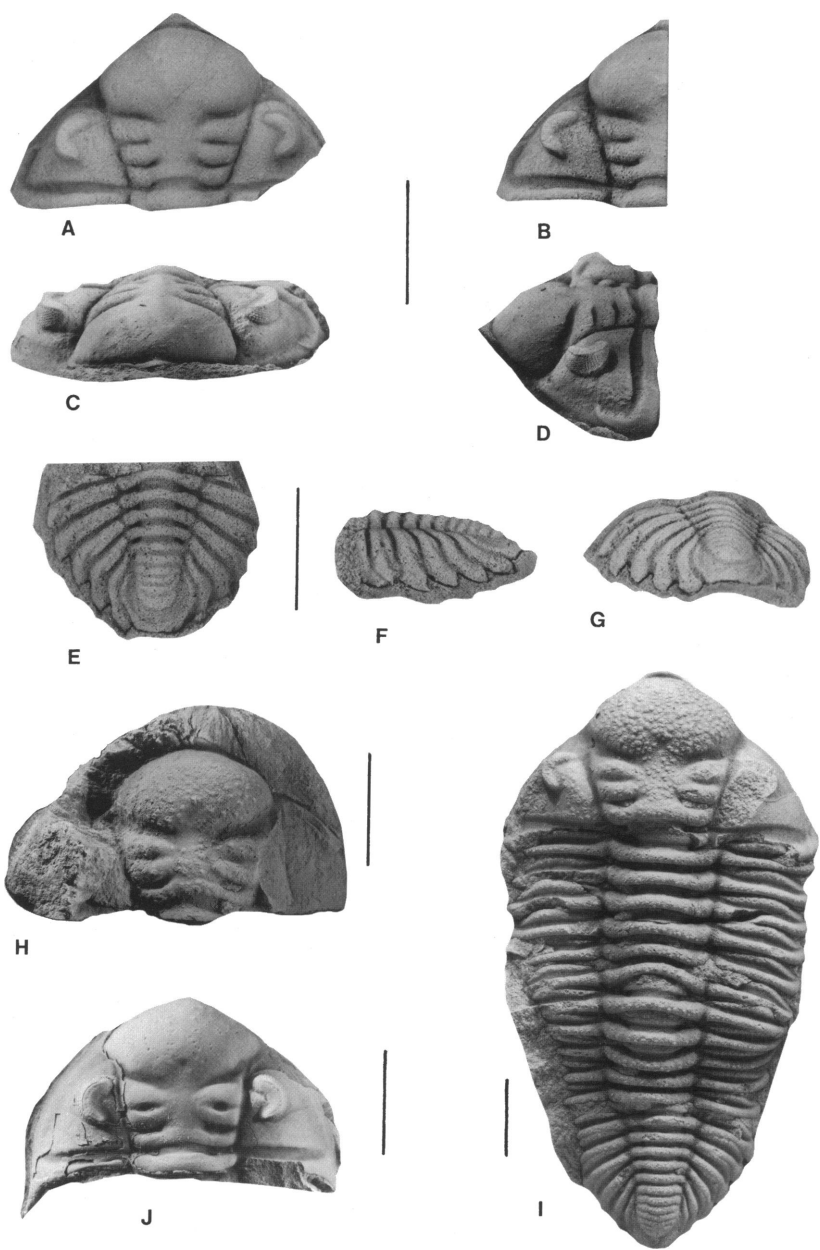


Fig. 3. *Metacryphaeus meloi*, n. sp., Cabeças Formation (Passagem Member). A: Holotype MCT 6822-I. Internal mold of cephalon, dorsal view. B: Detail of the holotype, showing the granulation on the cephalon. C, D: Frontal and dorsolateral views of holotype. Scale bar for A–D = 10 mm. E–G: Paratype MCT 6823-I, internal mold of pygidium: dorsal, lateral, and posterior views, respectively. Scale bar for E–G = 10 mm. H, I = *Metacryphaeus tuberculatus*. J: *Metacryphaeus rotundatus*. Scale bar for H–J = 10 mm.

Posterior border lengthens abaxially, and is gently flexed forward distally. Cephalic doubleure is weakly convex, longest medially, and narrowing abaxially, with a vincular furrow. Hypostomal suture is faintly convex forward.

Pygidium is triangular, with a length about 55% of width. Its axial furrows are shallow, weakly converging posteriorly, with a decreased angle of convergence behind fifth axial ring. Axis is moderately convex (tr.), about 35% of pygidium width anteriorly, and is composed of eight or nine rings plus an indistinctly segmented axial terminus, rounded posteromedially. First five rings of axis are well defined and slightly shortened sagittally, with anterior ring furrows deep and gently arched forward. Narrow (tr.) apodemes are slightly medial to axial furrows in four anteriormost ring furrows. First three pygidial lappets are gently curved posteriorly, but last two are more strongly flexed. Pleural furrows are almost straight, narrow, moderately deep, narrowing slightly adjacent to axial furrows. Interpleural furrows are shallow, with first three distinct. Pleural lappets have a straight or gently curved truncation, and they are pointed posteriorly. Postaxial region is short (sag.) and blunt, extending back to tips of fifth pair of pleural lappets.

DISCUSSION: All material referred to this species is from the Cabeças Formation, from a restricted stratigraphic and geographic range. Some of the observed variation can be accounted for by differences in preservation. For example, specimens preserved as internal molds in medium-grained sandstone lack evidence of exoskeletal tuberculation like that preserved on the holotype. Characters which vary continuously within the sample, such as depth of incision of the PMI and convexity (sag.) of the frontal lobe, are regarded as intraspecific variation.

Metacryphaeus meloi, n. sp., is referred to the "*Metacryphaeus tuberculatus* group" on the basis of exoskeletal tuberculation (albeit weak in *M. meloi*), triangular anteromedian cranial border extending beyond the glabella, rounded frontal glabellar lobe, and the anterior edge of the eye well separated from the axial furrows.

The weak posterior median impression

(PMI) in *Metacryphaeus meloi*, n. sp., is a distinctive difference separating it from other species of the "*Metacryphaeus tuberculatus* group." Other reports of this group in Brazil are *M. australis* (Clarke, 1913) from the Ponta Grossa Formation and Chapada Group, Paraná Basin (Carvalho and Edgecombe, 1991) and *M. tuberculatus* (Kozłowski, 1923), although the concretion with *M. tuberculatus* (illustrated here in fig. 3H) is lithologically different from the typical concretions that occur in the Pimenteira Formation, and its provenance is questionable.

Metacryphaeus meloi, n. sp., can be distinguished from *M. tuberculatus* (fig. 3H-I) by its less inflated frontal glabellar lobe, narrower cephalic axial furrows, and convex pygidial axial rings. In addition, in *M. tuberculatus* the lateral glabellar lobes are more strongly defined. Another potential difference is the Large Eye Index (LEI), which is 0.26–0.30 in *M. tuberculatus* and 0.29–0.34 in *M. meloi*, although these values weakly overlap. *Metacryphaeus tuberculatus* nevertheless shares several synapomorphies with *M. meloi*, n. sp., and we consider them to be closely related.

Metacryphaeus meloi, n. sp., differs from *M. australis* in the form of its anterior cephalic margin, which bears a distinct median process. In *M. meloi*, the anterior edges of the eyes are well-separated from the axial furrows, and their sculpture is more coarsely tuberculate. The 1p furrows (S1) are crescentic in *M. meloi* whereas they are almost straight in *M. australis*. The bluntly pointed genal angles, the pygidial axial rings that are convex anteriorly (sag.), and blunt pygidial pleural tips are other characters that distinguish *M. meloi* from *M. australis*.

Specimens from the Pimenteira Formation (Picos area) described by Castro (1968) as *Metacryphaeus australis* (Clarke) are closest to *M. meloi* from the Cabeças Formation. Indeed, our restudy of some of Castro's collection suggests that the Pimenteira form may be conspecific with our *M. meloi* material that is stratigraphically somewhat higher. An apparent difference is that cephalae from the Pimenteira Formation show a less pronounced cranial anteromedian process; the cranial anterolateral margin is convex out-

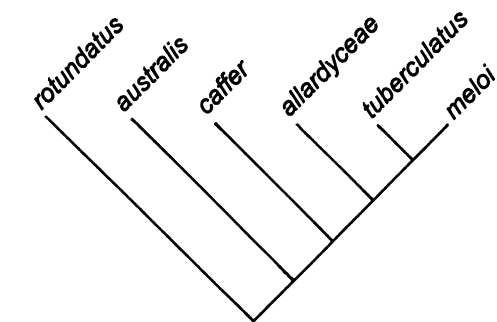


Fig. 4. Single most parsimonious tree; length 12 steps, consistency index 0.91, retention index 0.88, showing the phylogenetic relationships of the “*Metacryphaeus tuberculatus* group,” produced by analysis of the character data in table 2.

ward (vs. straight in Cabeças Formation specimens).

Species from South Africa, [like *M. caffer* (Salter, 1856)], and from the Falkland Islands [*M. allardyceae* (Clarke, 1913)] show significant differences from *M. meloi* including the placement of the eyes and more subdued exoskeletal tuberculation. Additionally, *M. caffer* differs from the new species in having spinose genal angles, a pygidium with transverse rings, and longer pygidial pleural lappets.

PHYLOGENETIC ANALYSIS

The Hennig86 program of Farris (1988) was used to perform a cladistic parsimony analysis on six species of the “*Metacryphaeus tuberculatus* group,” employing 11 characters (fig. 4; tables 1, 2). In this analysis, *M. rotundatus* (Kozłowski, 1923; see fig. 3J) is held to be exemplar for the sister taxon of the “*M. tuberculatus* group” of Lieberman (1993). Analysis with this outgroup coding produced a single most parsimonious tree of length 12 steps, with a consistency index of 0.85 and a retention index of 0.91. *Metacryphaeus meloi* and *M. tuberculatus* are resolved as sister taxa, and the most topologically derived members of the “*M. tuberculatus* group.” *Metacryphaeus allardyceae* and *M. caffer* are successive sister taxa to *M. meloi*, n. sp., plus *M. tuberculatus*, and *M. australis* is topologically basal.

Bolivian species and *M. tuberculatus*/*M. meloi* material of the Parnaíba Basin are

TABLE 1
Characters Used in Phylogenetic Parsimony Analysis, with Various Character States in Parentheses

(0) plesiomorphic state, (1) apomorphic state. See table 2 for taxon character matrix

- Character 0: Dorsoventral height of pygidium—(0) gradually decreases posteriorly; (1) sharply reduces posterior to the posteriormost apodemal ring.
- Character 1: Anterior margin of cephalon—(0) rounded point at the midline; (1) with triangular median process.
- Character 2: Frontal glabella lobe—(0) moderately inflated; (1) strongly inflated.
- Character 3: Anterior edge of eye—(0) adjacent to or in contact with axial furrow; (1) displaced from axial furrow.
- Character 4: Width of cephalic axial furrows—(0) narrow; (1) broad.
- Character 5: Shape of S1—(0) straight to slightly curved; (1) crescentic shape.
- Character 6: Cephalic tuberculation—(0) absent or weak; (1) coarse.
- Character 7: Genal angle—(0) spinose; (1) blunt.
- Character 8: Pygidial margin—(0) lappets ending in pointed spines; (1) lappets shorter and blunter spines.
- Character 9: Shape of anterior 3–4 pygidial rings—(0) with spatulate distal terminations; (1) without spatulate distal terminations.
- Character 10: Pygidial terminus—(0) short triangular spine; (1) blunt triangular point.

TABLE 2
Character State Distributions for Taxa Used in Phylogenetic Parsimony Analysis

Characters and alternative states are as listed in table 1

	0	1	2	3	4	5	6	7	8	9	10
<i>Metacryphaeus rotundatus</i>	0	0	0	0	0	0	0	0	0	0	0
<i>M. tuberculatus</i>	0	1	1	1	1	1	1	1	1	1	1
<i>M. caffer</i>	1	1	0	0	0	0	0	0	0	0	1
<i>M. allardyceae</i>	0	1	0	0	0	0	0	1	1	0	1
<i>M. australis</i>	0	0	0	0	0	0	0	0	0	1	1
<i>M. meloi</i>	0	1	0	1	0	1	0	1	1	1	1

more closely allied to taxa from the Falkland Islands and South Africa than to species from the Paraná Basin.

BIOGEOGRAPHY

Eldredge and Ormiston (1979) contended that the family Calmoniidae is exclusively Malvinokaffric. The presence of the calmoniid genus *Metacryphaeus* in the Parnaíba Basin is therefore biogeographically important. Discovery of this Malvinokaffric form in the Parnaíba Basin significantly extends the geographic range of the family.

The associated brachiopods of this basin probably represent a mixed fauna, with forms typical of the Old World and the eastern Americas (Copper, 1977; Fonseca and Melo, 1987; Melo, 1988). This mixture of endemic and more cosmopolitan taxa suggests that the Parnaíba Basin represents a biogeographic boundary area which contains faunal elements of the Old World, eastern American and Malvinokaffric biogeographic regions (Melo, 1988).

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