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New Calmoniid Trilobites (Phacopina: Acastoidea) from the Devonian of Bolivia

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ABSTRACT

Four new taxa of Lower Devonian Calmoniidae from Bolivia are described: *Gemelloides delasernai*, n. gen. and sp., *Eldredgeia eocryphaeus*, n. sp., *Wolfartaspis liebermani*, n. sp., and *Granadocephalus hannibali*, n. gen. and sp. The new genus *Gemelloides* is sister taxon to *Vogesina* Wolfart, 1968. *Eldredgeia eocryphaeus*, from the *Scaphiocoelia* Assemblage Zone in La Paz and Tarija Departments, closes a stratigraphic gap/ghost lineage in the early history of the *Metacryphaeus* group. *Wolfartasapis liebermani* (Icla Formation, Kochis, central Bolivia) predates its only congener, *W. cornutus*. A novel combination of features within Calmoniidae characterizes *Granadocephalus hannibali*, from the Icla Formation in Cochabamba Department. This monotypic genus may have its closest relatives in the *Calmonia* group.

RESUMEN

Se describen cuatro nuevos taxa de la familia Calmoniidae del Devónico Boliviano: *Gemelloides delasernai*, n. gen. y sp., *Eldredgeia eocryphaeus*, n. sp., *Wolfartaspis liebermani*, n.sp., y *Granadocephalus hannibali*, n.gen. y sp. El nuevo género *Gemelloides* es el grupo hermano de *Vogesina* Wolfart 1968. *Eldredgeia eocryphaeus*, registrada para la fauna de la biozona *Scaphiocoelia* en los departamentos de La Paz y Tarija, cierra un

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gap estratigráfico/linaje duende en la historia temprana del grupo *Metacryphaeus*. También parte de este grupo, la especie *Wolfartaspis liebermani* (Formación Icla, Kochis, Departamento de Cochabamba) antecede a su único congénere, *W. cornutus*. Entre los Calmoniidae, *Granadocephalus hannibali* (Formación Icla del Departamento de Cochabamba) es caracterizada por una combinación de caracteres nueva para la familia. Este género monotípico podría presentar como taxa más cercanos miembros del grupo *Calmonia*.

INTRODUCTION

Calmoniid trilobites from the Devonian of Bolivia have a long history of study. Since the initial descriptive work by d'Orbigny (1842), numerous papers have documented a rich diversity in the Lower and Middle Devonian (e.g., Kozlowski, 1923; Braniša, 1965; Wolfart, 1968; Eldredge and Ormiston, 1979; Eldredge and Braniša, 1980; Lieberman et al., 1991; Lieberman, 1993). Most Bolivian calmoniids occur in three formations localized in distinct geographic areas (fig. 1): the Belén Formation (Belén-La Paz-Sicasica region of the West Bolivian Altiplano); the Icla Formation (Icla-Padilla region, Sierras Subandinas of central Bolivia), and the Gamoneda Formation (Tarija region, southern Bolivia). The basal portion of all three formations is considered to be time-equivalent, falling within the ''*Scaphiocoelia*-bearing beds'' (Isaacson, 1977) recognized as the *Scaphiocoelia* Assemblage Zone by Eldredge and Braniša (1980). Trilobites occur both within and above this level. The total stratigraphic range of Calmoniidae in Bolivia is Late Silurian (Přídolí) (Edgecombe and Fortey, 2000) to Middle Devonian (Givetian).

It is now well established that calmoniid trilobites are endemic to a Southern-hemisphere biogeographic region that Clarke (1913) first characterized as an ''austral fauna'', which he was able to distinguish from a ''meridional fauna''. Richter and Richter (1942) observed the endemic character of this fauna and coined the term ''Malvinokaffric Province'', which corresponds generally to the Malvinokaffric Realm of Eldredge and Ormiston (1979).

Smith and Edgecombe (1996) informally reported two new genera and four new species of Calmoniidae from Bolivia, but did not name or describe them. In this paper we present a systematic description of this material, which contributes to the taxonomic and stratigraphic record of Bolivian calmoniids. Morphological terminology follows that used in the *Treatise on Invertebrate Paleontology, Part O* (Whittington and Kelly, 1997) as well as the terminology of Eldredge and Braniša (1980). The term Large Eye Index was introduced by Wolfart (1968), calculated as the ratio between the exsagittal length of the eye and the sagittal length of the glabella excluding S0. The chronostratigraphic scheme for the Devonian of Bolivia is as summarized by Adrain and Edgecombe (1996: fig. 2), after Blieck et al. (1996). Specimens studied and figured here are deposited in the collections of American Museum of Natural History (AMNH), Division of Paleontology (Invertebrates), and Museo de História Natural de Cochabamba (MHNC), Bolivia.

SYSTEMATIC PALEONTOLOGY

FAMILY CALMONIIDAE DELO, 1935

GEMELLOIDES, NEW GENUS

DERIVATION OF NAME: Literally, ''like *Gemellus*'', in reference to the name *Dalmanites gemellus* Clarke, 1890; gemellus (Latin), a twin.

TYPE SPECIES: *Gemelloides delasernai*, n. gen. and sp.

REFERRED SPECIES: *Dalmanites gemellus* Clarke, 1890 (= ''*Vogesina*'' *gemellus* (Clarke) fide Lieberman et al., 1991) is provisionally assigned.

DIAGNOSIS: Cephalon twice wider than long, gently convex (tr. and sag.). All lateral glabellar furrows well incised; apodemal part of S1 abruptly shallowing, S1 faintly confluent with axial furrow; S2 effaced abaxially; S3 steeply inclined exsagittally. Pygidium triangular in outline, relatively wide, lacking marginal spines or lappets; pygidial axis comprises 11 rings (first 5 separated by groovelike impression of distal part of ring furrows, posterior rings progressively weak-

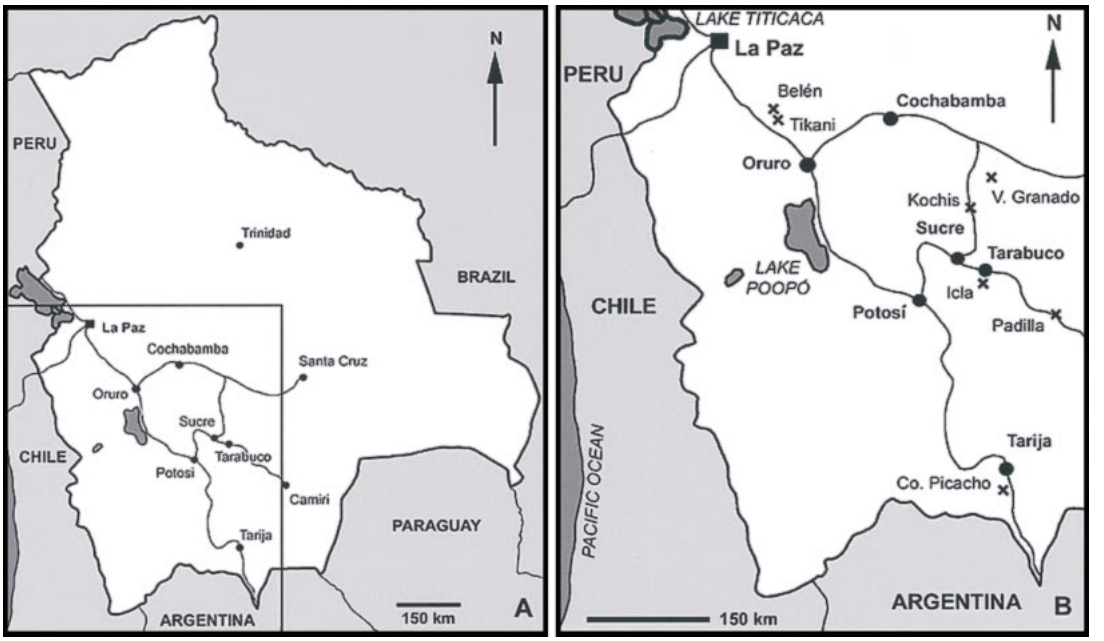


Fig. 1. **A,** map of Bolivia, showing location of inset (map B); **B,** locations of trilobite collection sites in this work (indicated by ×) relative to major cities and towns.

er); pleural field moderately convex (tr.), with at least six ribs.

Gemelloides delasernai, new species

Figure 2A, B

DERIVATION OF NAME: After Salvador de la Serna, field companion to L. Smith for many years, who helped to collect the material.

DIAGNOSIS: Lateral glabellar furrows S2 and S3 sharply defined; apodemal part of S1 wedge-shaped; sculpture consisting of small, strong pits widely distributed on cephalon, thorax, and pygidium, without coarse granules or tubercles.

TYPES: Holotype: MHNC 8130, external mold of almost complete specimen (fig. 2A, B), from the lower part of the Upper Member of the Belén Formation, layer of *Wolfartaspis cornutus* (Wolfart, 1968), late Emsian, Belén area, La Paz Department, Bolivia (latex cast AMNH 48073). Paratype: AMNH 48074, internal mold of part of thorax and external mold of frontal glabellar lobe, from type locality.

DESCRIPTION: The cephalon is wider than long, with length (sag.) of cranidium 7.2 mm and width (tr.) across posterior border approximately 16 mm. Axial furrows are very distinct, narrow, weakly divergent, slightly curved externally at L2. The widest point of the glabella (across L3) is approximately 7 mm, and its posterior width is 4.9 mm. The occipital furrow (S0) is deep, moderately wide, curving anteriorly (sag.). S1 is a deep, wedge-shaped groove, widest mesially, sharply narrowing and shallowing distally, faintly confluent with the axial furrow, posteromedian part positioned close to S0; S2 is longer and narrower than S1 (tr.), slightly convex forward, with weak posteromedial orientation, effaced well inward of axial furrow; S3 is straight, narrow, widest distally, strongly divergent toward the anterior glabellar margin (this margin is not preserved, and it is uncertain whether S3 reaches it); the strongly divergent arrangement of S3 gives rise to a pattern in which the glabellar furrows appear to radiate away from the center of the glabella. The glabellar furrows do not cross the median region of the glabella, which is not inflated. The glabellar lobes likewise lack independent inflation; L1 is narrow mesially, becoming wider near the axial furrow; L2 is wider than L1 and is trap-

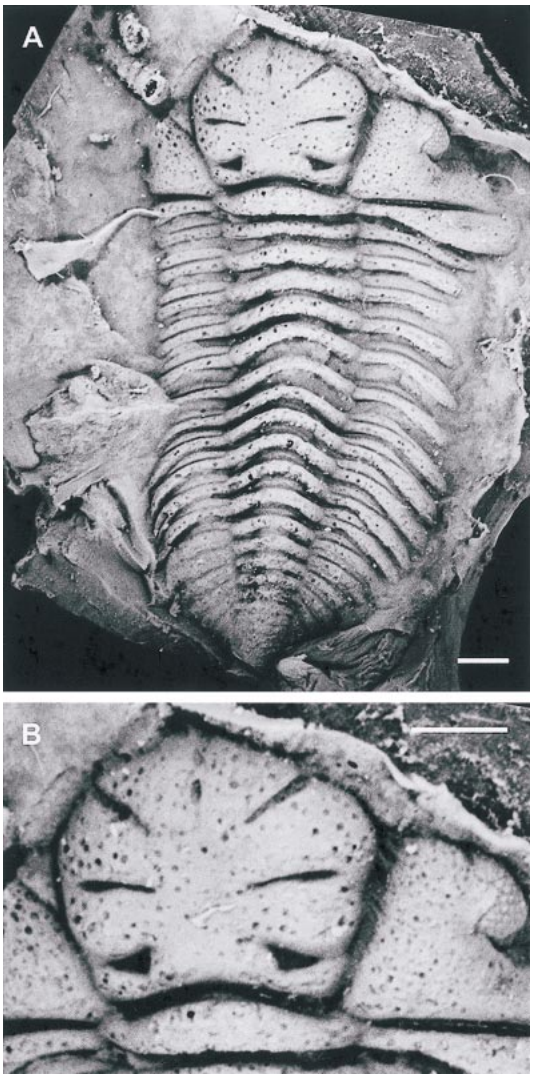


Fig. 2. *Gemelloides delasernai*, n. gen. and sp. Holotype MHNC 8130, Upper Member of Belén Formation, Belén, La Paz Department. **A,** dorsal view of nearly complete specimen, latex cast from external mold, scale 2 mm; **B,** detail of cephalon, scale 2 mm.

ezoidal, becoming wider laterally; L3 is also trapezoidal in outline and is larger than L2. The posterior median impression is a short (sag.), elongate pit on the frontal lobe, anterior to the tips of S3. The frontal lobe is not inflated or distinguished from the rest of the glabella. L0 is moderately arched (tr.), longest sagittally, distinctly wider than L1, with a width of 5.5 mm. The posterior border furrow is straight and moderately wide across most of its extent, gradually narrowing near the genal angle. The posterior border is very narrow adjacent to the axial furrow but is considerably wider (exsag.) abaxially, with an evenly convex posterior margin and a rounded genal angle. The palpebral lobe and surrounding area of the fixigena are somewhat swollen, sloping down laterally behind and around the eye. The palpebral lobe is narrow, bounded by a faint palpebral furrow. The cephalon (glabella, L0, fixigenal field, and posterior border) is ornamented with small, widely distributed pits, but lacks any granular or tuberculate sculpture.

The thorax comprises 11 segments, all weakly convex (tr.) with the axial region somewhat higher than the pleurae. Maximum axial width is about one- third that of the thorax. The first four axial rings are faintly convex forward sagittally; this convexity is gradually accentuated in more posterior rings. Axial furrows are shallow and narrow but well defined. Thoracic pleurae are transverse and horizontal proximally, becoming weakly flexed posteriorly in the distal portion; this flexure is also more accentuated posteriorly. Pleural furrows are deep, narrow, and run straight across the pleurae onto the articulating facets. The margin of the anterior pleural band is convex proximally; the posterior band is longer than the anterior (tr.) and is broader distally (exsag.).

The pygidium is moderately large (9.4 mm maximum width) and triangular in outline. The axis is only slightly higher than the pleural field, defined by shallow, narrow axial furrows, and includes 11 discernible rings. The first four rings are gently flexed anteriorly and are separated by broad ring furrows, which are deepest distally and impressed as transverse grooves; the following rings are progressively fainter. The axial terminus is indistinctly defined, but a postaxial field, if present, is short (sag.). The pleural field is gently arched (tr.) and comprises at least six ribs. The first three are gently curved posteriorly, but the remaining ribs are more distinctly flexed. Pleural furrows are narrow but more distinct than the interpleural furrows, which are only weakly developed. Little of the pygidial margin is visible, but its exposed part (at the ends of the anterior three ribs)

lacks marginal spines or lappets. The axial rings and pleurae of the thorax and pygidium are ornamented with small pits like those covering the cephalon.

DISCUSSION: The close similarity between *Gemelloides* and *Vogesina* Wolfart, 1968 indicates membership in the *Malvinella* group (sensu Lieberman et al., 1991), and the genus possesses more general apomorphies of that group, such as depression of the abaxial part of L1 beneath L2 (character 23 of Lieberman et al, 1991). *Vogesina* is united with *Palpebrops* Lieberman et al., 1991 by a convex (sag.) glabella (Lieberman et al., 1991, node 9, character 8), which is shared to a lesser degree by *Gemelloides*. None of the three characters supporting node 10 in their phylogeny (which pertain to the anterior part of the cephalon and the hypostome) can be determined in our material, but both characters supporting their node 11 (*Vogesina* s.l., characters 5, 11) are present (weakly divergent cephalic axial furrows and steep inclination of S3). The latter feature gives rise to a distinctive radial pattern of glabellar furrows which is also weakly evident in *Palpebrops*, and may thus represent a synapomorphy of *Vogesina*, *Gemelloides*, and perhaps *Palpebrops*.

Within *Vogesina* as recognized by Lieberman et al. (1991), *V. aspera* and *V. lacunafera* are separated from ''*Vogesina*''*gemellus* (= *Gemelloides gemellus* here) by 12 characters. Three of these cannot be observed in the specimens of *Gemelloides delasernai*, n. sp., but this taxon definitely lacks two other characters (8, 18; strongly convex glabella; elongate but nearly effaced S2 and S3) and shares seven apomorphies with *V. aspera* and *V. lacunafera* (12, 20, 27, 29, 32, 45, 48; S3 straight; absence of coarse spines on lateral glabellar lobe L2; L0 not elevated above posterior glabellar region; absence of spines on L0; palpebral furrow weak and palpebral rim low; absence of spines on thoracic axial rings and on pygidial axis). The well-developed lateral glabellar furrows in *Gemelloides delasernai*, n. sp. clearly distinguish this form from all *Vogesina* spp., which have S2 and S3 as shallow to indistinct, typically resembling thin pencil lines (Wolfart, 1968). This difference between *Gemelloides* and *Vogesina* is marked even on external molds of *Vogesina* of equivalent size to the holotype of *G. delasernai*. The glabella is considerably less convex (sag.) in *Gemelloides delasernai* than in *Vogesina* and is not significantly elevated above L0. The pygidium of *Gemelloides delasernai* resembles that of *Vogesina* in lacking marginal lappets, but has a relatively broader outline, with the distal part of the pleurae less steeply turned down than in *Vogesina*. Collectively, these findings suggest that *G. delasernai* is the sister taxon to *Vogesina* but can be differentiated as a distinct taxon on the basis of cephalic as well as pygidial characters.

''*Vogesina*'' *gemellus* (Clarke), from the Maecuru Formation in the Amazon Basin, is known only from an isolated, poorly preserved glabella (Lieberman et al., 1991: fig. 8.5, 8.6), and the state of only one of the apomorphic characters uniting *G. delasernai* with *V. aspera* and *V. lacunafera* (Lieberman et al., 1991) could be determined. ''*Vogesina*'' *gemellus* has a similar glabellar profile (sag.) and arrangement of lateral glabellar furrows to *G. delasernai*. We provisionally assign it to *Gemelloides* based on these characters, although the generic diagnosis emphasizes the better known *G. delasernai*. Specific distinction between *G. gemellus* and *G. delasernai* is made based on the wider glabellar furrows, more elongated longitudinal median groove on the glabella, and tuberculate sculpture of the former species.

Eldredgeia Lieberman, 1993

TYPE SPECIES: *Metacryphaeus venustus* Wolfart, 1968, from the Sicasica Formation (Givetian), La Paz Department, Bolivia. Also known from the Upper Member of the Belén Formation, La Paz Department (Lieberman, 1993).

Eldredgeia eocryphaea, new species

Figure 3A–L

DERIVATION OF NAME: ''Early Cryphaeus'', being geologically an early representative of the ''*Metacryphaeus* group''.

DIAGNOSIS: Species of *Eldredgeia* with the following unique character combination: frontal glabellar lobe gently inflated, with rounded profile sloping down to anterior cephalic margin; posterior median impression a

small pit when present. Eyes set above glabella; visual surface bearing at least 24 dorsoventral files with maximum of nine lenses per file. Genal angle blunt, lacking a spine. Hypostome with pronounced ovoidal maculae; posterior border only moderately long; two pairs of short marginal spines present posterolaterally.

TYPES: Holotype: MHNC 8129, internal mold of cephalon (fig. 3D–G) with hypostome in situ (fig. 3D), from the Lower Member of the Belén Formation, *Scaphiocoelia* Assemblage Zone, Tikani, Estación de Bombeo, Sicasica, La Paz Department. Paratypes: MHNC 12900, pygidium with partial thorax (fig. 3J–L) in same concretion as holotype and probably belonging to same individual; AMNH 47147, internal mold of cephalon and articulated thorax (fig. 3A–C), and AMNH 47146, internal mold of pygidium (fig. 3H, I), both from the Gamoneda Formation, Cerro Picacho, 17 km S of Tarija, Tarija Department. Other trilobites collected from the same stratigraphic interval at Cerro Picacho are *Tarijactinoides jarcasensis*, *Kozlowskiaspis* (*Romanops*) sp., and *Gamonedaspis scutata*, all indicative of the *Scaphiocoelia* Assemblage Zone.

DESCRIPTION: The cephalon is nearly twice as wide as long and is moderately convex (tr.), with a widely pointed and arched outline. Some details of the anteriormost part of the cephalon can be observed only in AMNH 47147 (fig. 3A–C), as this region is missing in the holotype. The anterior cephalic border is narrow and extends medially into a short median triangular frontal process. The frontal lobe is subrhomboidal, with a rounded anterior margin and a rounded profile (sag.) with independent convexity from the posterior glabellar region, sloping down to the anterior cephalic margin. A pitlike posterior median impression is present on the frontal lobe in the holotype (fig. 3G), well in front S3, but is indistinct in the paratype (fig. 3A, C). The auxiliary impression system is obscured by the granulation covering the frontal lobe. The axial furrow is slightly divergent from S0 to S1, but becomes more divergent from S1 anteriorly. All three pairs of lateral glabellar furrows are well developed and reach the axial furrow on the internal mold. S1 is broad, deep, and distinctly concave forward; S2 is straight, narrower (tr.), and shallower than both S1 and S3. S1 and S2 are gently directed forward medially, whereas S3 is more oblique, diverging anterolaterally. S0 is weakly curved forward medially, of even width (sag., exsag.), with a U-shaped section and deep apodemal pits distally. The lateral glabellar lobes are well defined and ornamented by coarse granules. L1 is narrow (exsag.) in comparison with L2 and L3 and can be traced across the glabella by faint impression of S1 medially. L2 is more or less rectangular in outline; L3 is more wedge-shaped. L0 has a uniform width (sag., exsag.) throughout; its posterior margin is approximately transverse. In profile, L0 lies in almost the same plane as the central part of the glabella. The lateral border furrow is wide but very faint, and it does not distinctly separate the lateral border from the genal field. The posterior border furrow is U-shaped in cross-section, deepest near the axial furrow, and becomes gradually wider before curving forward and shallowing distally. The posterior border is narrower (exsag.) than L0 proximally but becomes longer distally. Although the genal angles are not well preserved in either specimen, they are blunt and lack a spine (the cavity behind the external mold of the genal doublure in fig. 3A is not a genal spine). The palpebral lobe is swollen, gently inclined adaxially/posteriorly, and is ornamented by granules. The palpebral furrow is narrow but relatively sharply impressed along its length. In frontal view the free cheek is almost vertical and also has granular sculpture. The eye projects higher than the glabella, with its anterior margin located opposite the anterodistal corner of L3, adjacent to (but still separate from) the axial furrow. The posterior margin of the eye is positioned far from the axial furrow, opposite the posterolateral corner of L1 (exsag.). The visual surface is not well preserved in either specimen; the number of dorsoventral files cannot be determined in the holotype, but AMNH 47147 has 24 dorsoventral files on the visual surface. In that specimen no more than seven lenses are preserved per file, but the top of the eye is damaged and the uppermost lenses are missing. In the holotype as many as nine lenses are discernible in the longest files, as was probably the case in

AMNH 47147. The anterior section of the facial suture runs parallel to the axial furrow, and it reaches the anterolateral corner of the frontal lobe without cutting across it.

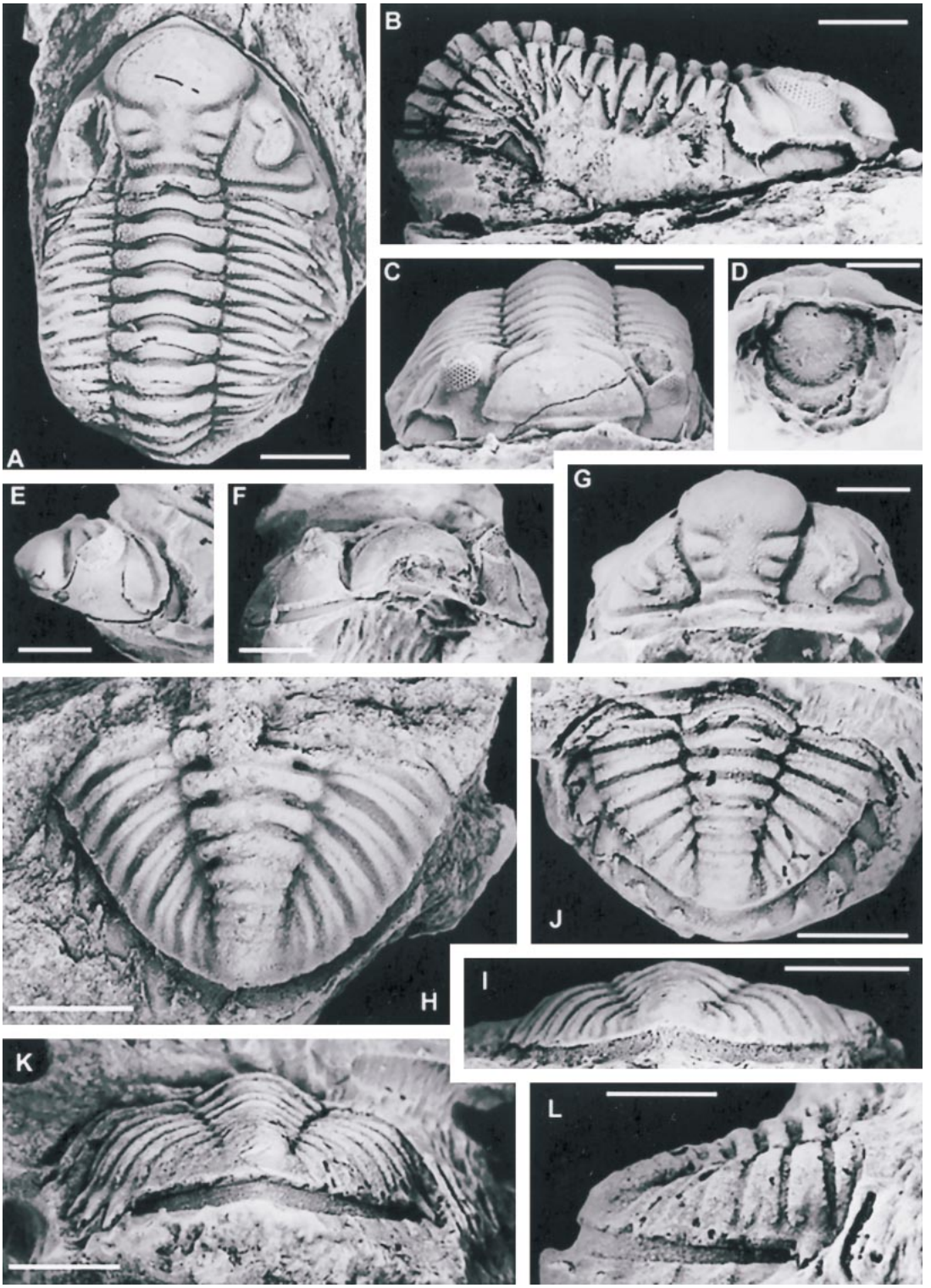
The hypostome is preserved in situ beneath the cephalon of the holotype, but has been pushed forward below the doublure and against the anterior part of the glabella. Thus, the anterior morphology of the hypostome (including its anterior margin, border, and wing) are hidden from view. The middle body is roughly circular and moderately convex (tr. and sag.). The maculae are very distinct, forming a pair of ovoid protuberances positioned abaxially, near to the junction of the middle furrow (which is faint) and the lateral border furrow (which is moderately deep); the border furrow maintains about equal depth posterolaterally and posteromedially. The lateral border is narrow, slightly convex, and runs subparallel posteriorly, and the posterior border is long (sag.) and slightly convex (sag.). The posterior margin is rounded, with at least one pair of small spines posterolaterally and traces of a second pair laterally. The posteromedian margin appears to be gently curved backward, and lacks a median spine.

The thorax, in lateral view, is moderately convex, with the axis raised above the pleurae, and is one-third of the thoracic width. The axial rings are spatulate, shortened (sag.) medially, with granular ornament concentrated distally. Apodemal pits are developed inward of the anterolateral edges of the rings. The articulating half ring is located below its corresponding axial ring. The proximal one-third of the pleural field is more or less horizontal and the remainder is gently flexed ventrolaterally. Each pleural furrow is deep and wide, extending straight diagonally across the proximal two-thirds of the pleura. The anterior band is narrowest proximally and longest (exsag.) at the fulcrum; conversely, the posterior band is longest (sag.) proximally and tapers to the fulcrum. The pleural furrow is effaced distally. The distal extremities of the pleurae are pointed. Granular sculpture is present across most of the width of the pleurae, but is more prominent proximal to the fulcrum.

The pygidium is broadly triangular in outline, wider than long (length approximately four-fifths of pygidial width, excluding marginal lappets). The axial furrow is moderately deep and narrow; the anterior part of the axis tapers strongly back as far as the sixth ring, but the remainder is almost parallel-sided and has a blunt termination that does not reach the posterior margin of the pygidium. The axis is composed of at least eight rings, of which the first six are well developed and the following two are weaker but distinct; a ninth ring is faintly defined in the poorly segmented terminal part of the axis. The first axial ring is markedly arched anteriorly and somewhat spatulate distally; the second, third, and fourth rings are likewise spatulate distally, but are less arched anteriorly. The first five axial rings are separated by broad, deep ring furrows with apodemes distally; behind this, ring furrows are shallow and transverse. The pleural field has six pairs of ribs defined by wide pleural furrows, separated by narrow and shallow interpleural furrows; the fourth interpleural furrow is the last discernible on the internal mold. The ribs gradually increase in obliquity from front to back, and the sixth is strongly oblique and positioned near to the axis. The anterior five pleurae terminate as spinelike lappets with a convex anterior margin and faintly concave posterior margin. The terminal lappet (known only from impressions) is wide but its shape and length cannot be established from the available material.

DISCUSSION: The new species *Eldredgeia eocryphaea* shares numerous detailed similarities with *E. venusta*, including a narrow anterior border to the cephalon, with a short median triangular frontal process; the anterior part of the frontal lobe is rounded; the eye is relatively long (exsag.); the thoracic and pygidial axial rings have similar shapes; the anterior five pygidial pleurae terminate as pointed spines; the posterior border of hypostome is relatively long (sag.); and coarse granular ornament is widely distributed over the cephalon, thorax, and pygidium. These features collectively support inclusion of the new species in the genus *Eldredgeia*.

Eldredgeia eocryphaea is most readily distinguished from the younger *E. venusta* (the type species, also from Bolivia) by its hypostome having more pronounced maculae (fig. 3D) and a substantially shorter (sag.)



posterior border (see Lieberman et al., 1991: figs. 3.6, 3.7 for E. venustus). In addition, the genal angle is blunter (versus more spinelike in *E. venusta*) and the visual surface has a lower number of dorsoventral files (24 versus 26–27 in *E. venusta*), although the maximum number of lenses per file (nine) is the same in both species.

Eldredgeia venusta has also been reported from the Middle Devonian (Eifelian) of Brazil and South Africa; in South Africa the species is even said to characterize an *E. venusta* Zone (Cooper, 1982). Lieberman (1993: 554) suggested that the South African and two Brazilian forms probably represent additional, distinct species of *Eldredgeia*. *Eldredgeia eocryphaea*, n. sp. differs from the South African form in having a higher number of dorsoventral files on the visual surface (24 versus 18), more lenses per file (nine; the South African form has six or seven), the shape of the genal angles (blunt rather than pointed), and glabellar lobes (more inflated in the form from South Africa).

The Brazilian form attributed to *Eldredgeia* from the Amazon Basin (*E. paituna* (Hartt and Rathbun) from the Ererê Formation; see Lieberman, 1993: 554) can be distinguished from *E. eocryphaea*, n. sp. in having a longer (sag.) frontal lobe and S1 with an accentuated crescent shape. In the other Brazilian form (from the Parnaíba Basin, Pimenteira Formation; see Lieberman et al., 1991: fig. 2), S1 is more strongly curved (adaxially) and L0 is longer (sag.). We endorse Lieberman's (1993) suggestion that the South African and Brazilian material represents additional species of *Eldredgeia*, and the new form described in the present work appears to be distinct from all of them.

Eldredgeia eocryphaea significantly extends the range of *Eldredgeia* into earlier stratigraphic intervals than previously known. It also represents the earliest occurrence of the *Metacryphaeus* morphotype (i.e., the dalmanitiform cephalic morphology and five-lappeted pygidial form shared by *Metacryphaeus* and allied genera as revised by Lieberman, 1993). This morphotype has not previously been known from the *Scaphiocoelia* Assemblage Zone. On the basis of a late Lochkovian occurrence of *Parabouleia*, a member of the *Malvinella* subgroup of the *Metacryphaeus* group, in Argentina, Edgecombe et al. (1994) inferred that lineages of the *Metacryphaeus* group predated their known occurrences in Bolivia. *Eldredgeia* was one of several lineages in the *Metacryphaeus* group that was inferred to have an unsampled range extension (or ghost lineage) that considerably preceded its first observed appearance (in late Emsian or Eifelian strata in the Upper Member of the Belén Formation). The discovery of *Eldredgeia eocryphaea* in the lower part of the Lower Member of the Belén Formation and equivalent strata in the Gamoneda Formation (both representing the *Scaphiocoelia* Assemblage Zone) closes one of the stratigraphic gaps in the *Metacryphaeus* group.

Wolfartaspis Cooper, 1982

TYPE SPECIES: *Metacryphaeus cornutus* Wolfart, 1968, from the lower part of the Upper Member of the Belén Formation (late Emsian), La Paz Department, Bolivia.

Wolfartaspis liebermani, new species

Figures 4A–F, 5A–F

DERIVATION OF NAME: For Bruce S. Lieberman, who has made valuable contributions to systematics and biogeography of calmoniid trilobites.

DIAGNOSIS: Cephalic anterior border weakly pointed medially; ventral view of cephalon triangular in outline. Eyes less than one-third glabella length (Large Eye Index 31%); vi-

←

Fig. 3. *Eldredgeia eocryphaeus*, n. sp. **A–C, H, I,** Gamoneda Formation, Cerro Picacho, Tarija Department. All scales 5 mm. A–C, AMNH 47147, dorsal, lateral, and anterodorsal views of cephalon and articulated thorax, internal mold; H, I, AMNH 47146, dorsal and posterior views of pygidium, internal mold. **D–G,** holotype MHNC 8129, internal mold of cephalon, Belén Formation, Tikani, La Paz Department. All scales 5 mm. D, ventral view of hypostome; E–G, lateral, anterior, and dorsal views of cephalon; **J–L,** MHNC 12900, dorsal, posterior, and lateral views of pygidium. All scales 5 mm.

sual surface with 25–26 dorsoventral files with a maximum of 10 lenses per file. Occipital ring strongly arched in cross section, wide medially, with pronounced convex anterior margin and robust median spine tapering dorsally.

TYPES: Holotype: MHNC 8132, external mold of an incomplete cephalon, Icla Formation, equivalent to basal part of Upper Member at Icla type locality (see Discussion below), Kochis Hills (approximately 3 km north of the Rio Grande, on the border between Chuquisaca and Cochabamba Departments), Bolivia. Paratypes: AMNH 47148, internal mold of thorax and pygidium; AMNH 47149, internal mold of a cephalon; AMNH 47150, external mold of pygidium; AMNH 47151, external mold of an incomplete pygidium; AMNH 47401, hypostome in situ beneath cephalon; AMNH 47403, internal mold of almost complete cephalon; MHNC 12749, internal mold of incomplete pygidium. All type specimens are from the Icla Formation, Kochis, Cochabamba Department.

OTHER MATERIAL: Some additional topotype specimens collected within the same stratigraphic interval as the types are referred to *Wolfartaspis liebermani*, but they are not well preserved. Most are from broken concretions and include three internal molds and two external molds of pygidia, an internal mold of four or five thoracic segments, an external mold of some pleurae, and two internal molds of cephala. In addition, however, there is a single, well-preserved, small pygidium in part and counterpart. This additional material is housed in the MHNC collection.

DESCRIPTION: The cranidial length (sag.) is about 29.7 mm in AMNH 47403. The anterior cephalic border is narrowest medially, where the upturned doublure nearly contacts the cranidial margin; the anterior cephalic border projects only slightly in front to the glabella medially in dorsal view; the anterior border gently widens abaxially, but remains narrow (exsag.) in dorsal view, and is steep along its entire width. The cephalic anterolateral margin is nearly straight in dorsal view and is rounded medially. The axial furrow is deep, wide, straight, slightly divergent forward. Glabellar length (sag., excluding S0) in AMNH 47403 is 23.4 mm, with the frontal lobe having marked independent convexity from the posterior glabellar region, which has a flat sagittal profile. The frontal glabellar lobe is inflated, about 60% of glabellar length, and gradually expands anteriorly and laterally, with its anteromedian margin rounded. The anterior section of the facial suture circumscribes but does not transect the frontal glabellar lobe. The frontal lobe has a well- developed circular to slightly elongated posterior median impression (PMI) and auxiliary impression system (AIS) of muscle scars. The latter is most clearly preserved on the left side and the median part of AMNH 47403 (fig. 5A) as small rounded pits on the internal mold, forming divergent rows. Medially, the AIS does not seem to have a defined pattern. The lateral glabellar furrows are well developed. S3 is wide, deep, oblique, straight, with its proximal part weakly bent posteromedially, lengthening abaxially, and distinctly confluent with the axial furrow. S2 is transverse, narrower and shallower than S1 and S3; it becomes abruptly shallow distally and has only faint impression against the axial furrow on the external cuticular surface (fig. 4A). S1 is deeper than S2 and S3; it sharply narrows distally but is distinctly confluent with the axial furrow on the external mold; the posterior margin of S1 is concave. L3 is wedge-shaped; L2 is approximately trapezoidal; L1 is slightly shorter (exsag.) than L2 and L3, with its posterior margin markedly convex backward and then continuing inward, forming a short (sag.) transglabellar lobe that is weakly curved anteriorly; this feature makes the glabella slightly higher at L1 than at L3. S0 is long and relatively shallow (sag.), becoming shorter and deeper as it approaches the axial furrow. Where the cephalic posterior furrow meets S0, both have approximately the same width; the posterior furrow becomes wider (exsag.) toward the fulcrum, and is then gently flexed forward and shallows distally. L0 is strongly arched in its transverse section, wide medially, with a pronounced convex anterior margin, and bearing a robust median spine that tapers dorsally; the median spine is weakly declined posteriorly. The eye is high, less than one-third glabellar length (Large Eye Index 31%). Its anterior edge is

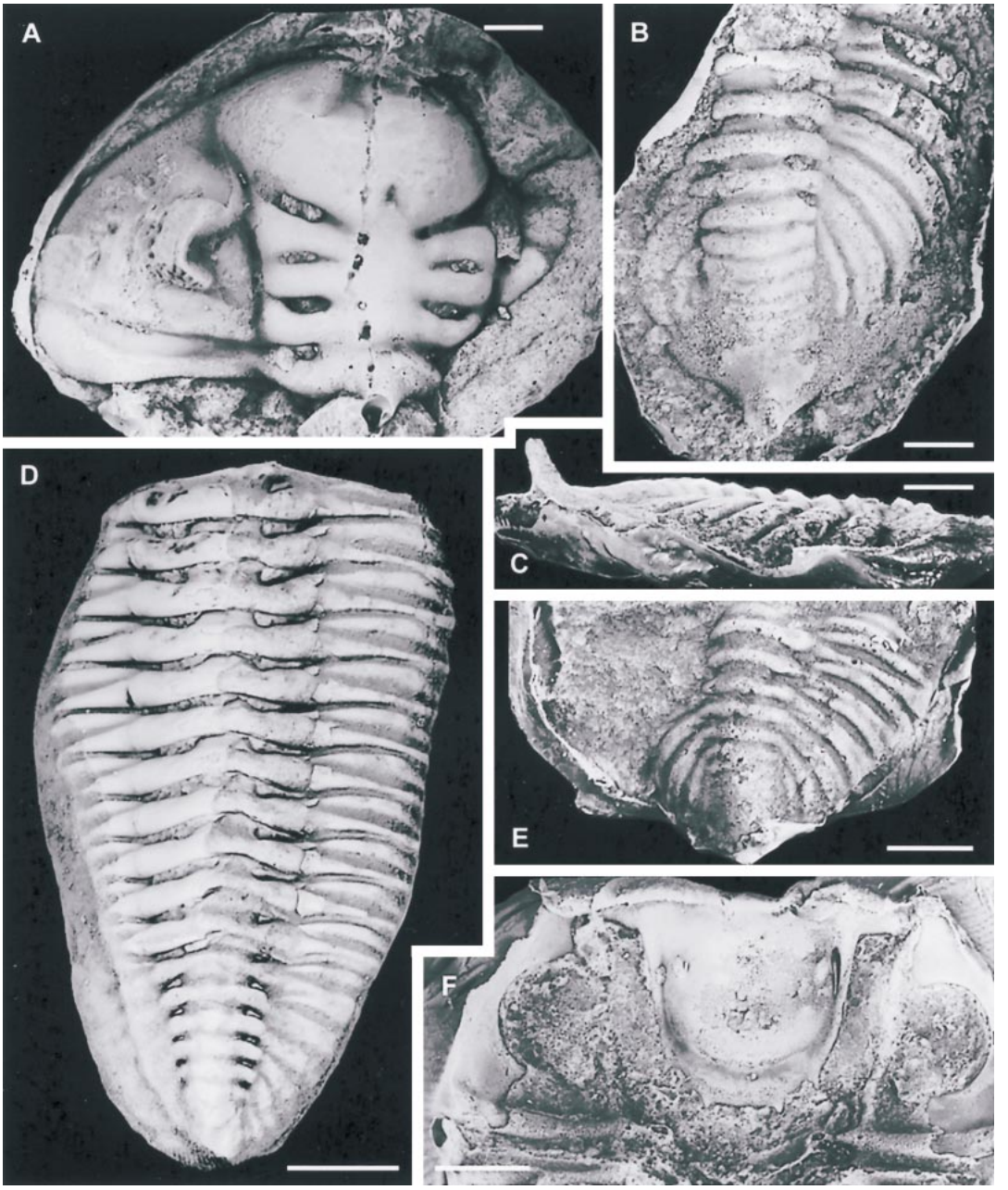


Fig. 4. *Wolfartaspis liebermani*, n. sp. Icla Formation, Kochis, Cochabamba Department. All scales 5 mm. **A,** holotype MHNC 8132, dorsal view of cephalon, latex cast from external mold; **B, C,** dorsal and lateral views of pygidium, AMNH 47150, latex cast from external mold; **D,** dorsal view of thorax and pygidium, AMNH 47148, internal mold; **E,** dorsal view of pygidium and posterior part of thorax, AMNH 47151, latex cast from external mold; **F,** ventral view of hypostome in situ beneath cephalon, AMNH 47401, latex cast from external mold.

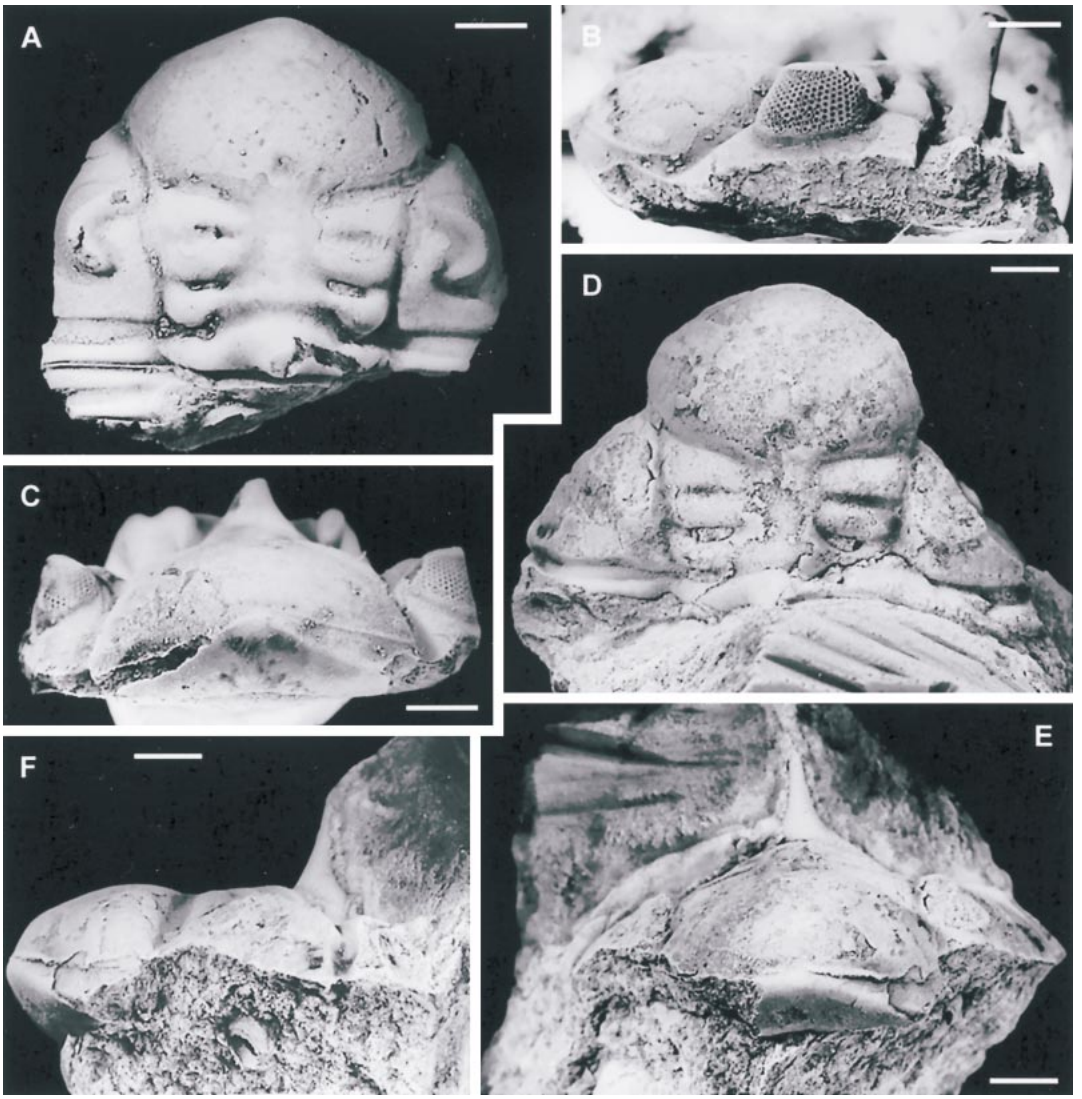


Fig. 5. *Wolfartaspis liebermani*, n. sp. Icla Formation, Kochis, Cochabamba Department. All scales 5 mm. **A–C,** dorsal, lateral, and anterior views of cephalon and part of first thoracic segment, AMNH 47403, internal mold; **D–F,** dorsal, anterior, and lateral views of cephalon, AMNH 47149, internal mold.

opposite the anterolateral corner of L3, and its posterior edge is opposite the posterolateral margin of L2 and at a considerable distance from the posterior cephalic border furrow (approximately 4 mm in the holotype). In anterior view, the visual surface is straight from top to bottom, gradually becoming wider toward its base, with 25–26 dorsoventral lens files, and a maximum of 10 lenses per file. The interocular fixigena slopes upward as it approaches the narrow, C-shaped palpebral lobe; the palpebral furrow is moderately deep. The lateral cephalic border furrow is faint. The posterior cephalic border is narrow proximally, about equal in width (exsag.) to the posterior border furrow at the fulcrum, and widened distally; none of the available specimens preserves the genal angle.

The hypostome is preserved in situ beneath the cephalon in one specimen (fig. 4F). Its anterior margin is largely missing, but its

course against the moderately wide anterior wings suggests a transverse hypostomal suture. The middle body is roughly circular and gently convex (tr., sag.). The maculae are strong, forming a pair of ovoid protuberances positioned abaxially, near to the junction of the faint middle furrow and the lateral border furrow, anterior to the midlength of the middle body. The border furrow is obscure anterolaterally (against the wings), becoming moderately impressed at the macula, maintaining moderate depth and width posterolaterally and posteromedially. The lateral border is narrow, with the lateral margins gently converging between the anterior wing and first of two pairs of short, sharp posterolateral marginal spines; the inner pair of spines (on posterior border) is separated by slightly greater than the distance between the two spine pairs. The posterior border is fairly long and gently convex (sag.); the posteromedian margin is faintly convex backward between the inner pair of marginal spines.

The thorax consists of 11 segments. The relative width of the axial rings and thorax cannot be determined, as the distal ends of the pleurae are not preserved in any specimens, but in AMNH 47148 (fig. 4D) the axial rings appear to be wider than the pleural fields. The axial furrow is shallow and narrow, weakly diverging back to the sixth ring, then gently converging. In lateral view, the axial rings are faintly convex, raised well above the pleurae. The anteriormost axial rings are spatulate distally, but this is less marked in the more posterior rings. Small but distinct apodemal pits lie between the axial rings abaxially. The pleural furrows are narrow and moderately impressed adjacent to the axial furrow, becoming wider distally, with a straight, oblique course across the rib; the anterior margin of the pleural furrows is gently convex anteriorly, while the posterior margin of the furrows is straight.

The pygidium is triangular, moderately arched in lateral view, wider than long, with a pointed posterior tip. The axial furrow is narrow and moderately deep. The axis is slightly waisted, the axial furrow moderately convergent against the first five axial rings, weakly converging posterior to this; the axial terminus is blunt, lacking impression of the axial furrow, lying well in advance of the pygidial posterior margin. There are 10–11 axial rings, but the last few are indistinct; the first five rings are gently arched anteriorly, but the subsequent ones are transverse or weakly bowed backward. The axial rings are separated by wide ring furrows that become progressively narrower posteriorly; the first five ring furrows have narrow, groovelike apodemal pits distally. The pleural field includes six pairs of strongly furrowed ribs plus a small seventh pair that parallels the axis. The pleural furrows are deep and wide, though gradually narrowing on more posterior segments; they are moderately curved. The interpleural furrows are narrow, moderately deep proximal to the fulcrum between the anterior few ribs, progressively shallow between more posterior ribs such that fifth interpleural furrow is last distinct one on external mold. The lateral margin of the pygidium is not well preserved in any of the material (fig.4E); the fifth lappet is small, flat, and wide (fig.4B), with a curved anterior margin and straight posterior margin. The posteromedian margin of the pygidium is an elongate, tapering, upturned spine (its basal part is preserved in AMNH 47150; fig. 4B, C).

DISCUSSION: The monotypic *Wolfartaspis* was erected by Cooper (1982) as a subgenus of *Metacryphaeus*, but recent usage (Lieberman, 1993) recognizes it at the generic rank. According to Lieberman, *Wolfartaspis* differs from *Metacryphaeus* in having an enlarged occipital spine and an upwardly curved pygidial spine. The material described here includes both of these features, and it is therefore assigned to the genus *Wolfartaspis*. We place our material in a new species, based on the following differences from *W. cornutus*: (1) the ventral view of the cephalon has a rounded shape in *W. cornutus*, but is more pointed in our form; (2) the Large Eye Index in *W. cornutus* is 34%, but is less in our material (31%); (3) the occipital spine in *W. cornutus* (Lieberman, 1993: fig. 2.8) is stouter than in our material (fig. 5E, F) and does not taper from its base. Differences are also noted in the stratigraphic levels of the two forms. *Wolfartaspis cornutus* occurs in the basal part of the Upper Member of the Belén Formation, in strata overlying the layer of *Francovichia branisi* (= layer of

Odontochile branisi sensu Wolfart, 1968, in the upper part of Lower Member of Belén Formation). At Kochis, *Francovichia* occurs stratigraphically above the beds with *Wolfartaspis liebermani*.

Granadocephalus, new genus

DERIVATION OF NAME: Combination of type locality (Villa Granado, Cochabamba Department) and ''cephalon''.

TYPE SPECIES: *Granadocephalus hannibali*, n. gen. and sp.

REFERRED SPECIES: Monotypic.

DIAGNOSIS: Cephalon moderately convex (tr.), subsemicircular in outline; ventral margin with moderate anterior arch. Profile of glabella evenly curved, steepening anteriorly; frontal lobe not distinctly separated from rest of glabella; posterior median impression weakly developed. Axial furrow moderately impressed, divergent especially from S2, with small, rounded fossular depression near anteromedial corner of palpebral lobe. Glabellar furrows not reaching axial furrow on internal mold; S3 lightly impressed, narrow, faintly sinuous; S2 shallow but deeper than S3, weakly directed backward at its inner tip; S1 deeper, weakly concave anteriorly, directed anteromedially; S0 with strongly convex anterior margin. L3 and L2 not inflated; L1 about two- thirds length (exsag.) of L2. L0 slightly shortened abaxially. Anterior section of facial suture not transecting anterolateral corner of glabella. Palpebral area slopes downward abaxially, lying entirely below interocular fixigena; palpebral furrow weak. Librigenal field relatively strongly pitted. Posterior cephalic border furrow straight. Entire cephalon covered by very fine granular ornament on internal mold.

DISCUSSION: We were hesitant to create a new genus and species on the basis of such a limited sample. However, the material displays a unique combination of characters within the Calmoniidae (e.g., ventral margin with moderate anterior arch; a peculiar convex [sag.] profile of the glabella; PMI weakly developed; distinctive shape and development of the glabellar furrows and lobes; anterior section of the facial suture does not transect the frontal lobe; visual surface low, lying entirely below the interocular fixigena) that does not permit it to be placed in any of the described calmoniid genera. We consider that the pygidium and the cephalon included here belong to a single species. Both were collected at the same locality and stratigraphic level, they correspond in size, the pygidium has appropriate proportions of the axis and pleurae relative to the cephalon, they have similar depth and width of the pleural furrows on the thorax (fig. 6E) and pygidium (fig. 6F), and the pygidium cannot be assigned to any other calmoniid taxon. Still, since the association of the pygidium is not certain, the generic diagnosis is restricted to cephalic characters.

The affinities of *Granadocephalus* are difficult to determine. Of suprageneric groups identified in previous work (Eldredge, 1979; Eldredge and Ormiston, 1979; Eldredge and Braniša, 1980), *Granadocephalus* lacks the diagnostic characters of either the *Probolops* group or the *Malvinella* subgroup, and membership in the *Calmonia* group is most probable. In the *Metacryphaeus* group, the only obvious comparison is with the topologically primitive genus *Plesioconvexa* Lieberman, 1993, which has an evenly convex glabellar profile reminiscent of *Granadocephalus* (compare *Plesioconvexa praecursor* in Lieberman, 1993: fig. 3.8 with *G. hannibali*, here fig. 6C). However, *Plesioconvexa*, like other members of the *Metacryphaeus* group, has much deeper incision of S2 and S3 than does *Granadocephalus*. In *Plesioconvexa*, S2 has the characteristic transverse, apodemal impression shared by other members of the *Metacryphaeus* group. Furthermore, *Plesioconvexa*, and indeed all members of the *Metacryphaeus* group except for deeply nested, highly modified taxa such as *Vogesina*, has a much deeper palpebral furrow than does *Granadocephalus*. Character states such as light impression of S2 and S3, the former being weakly convex forward and the latter sinuous, as well as a shallow palpebral furrow, are shared by *Granadocephalus* and members of the *Calmonia* group. These similarities, however, may be primitive characters for Calmoniidae. Eldredge and Braniša (1980) noted that axial morphology of the *Calmonia* group displays conservative characters for Calmoniidae, whereas the various genera of that group are more variable in

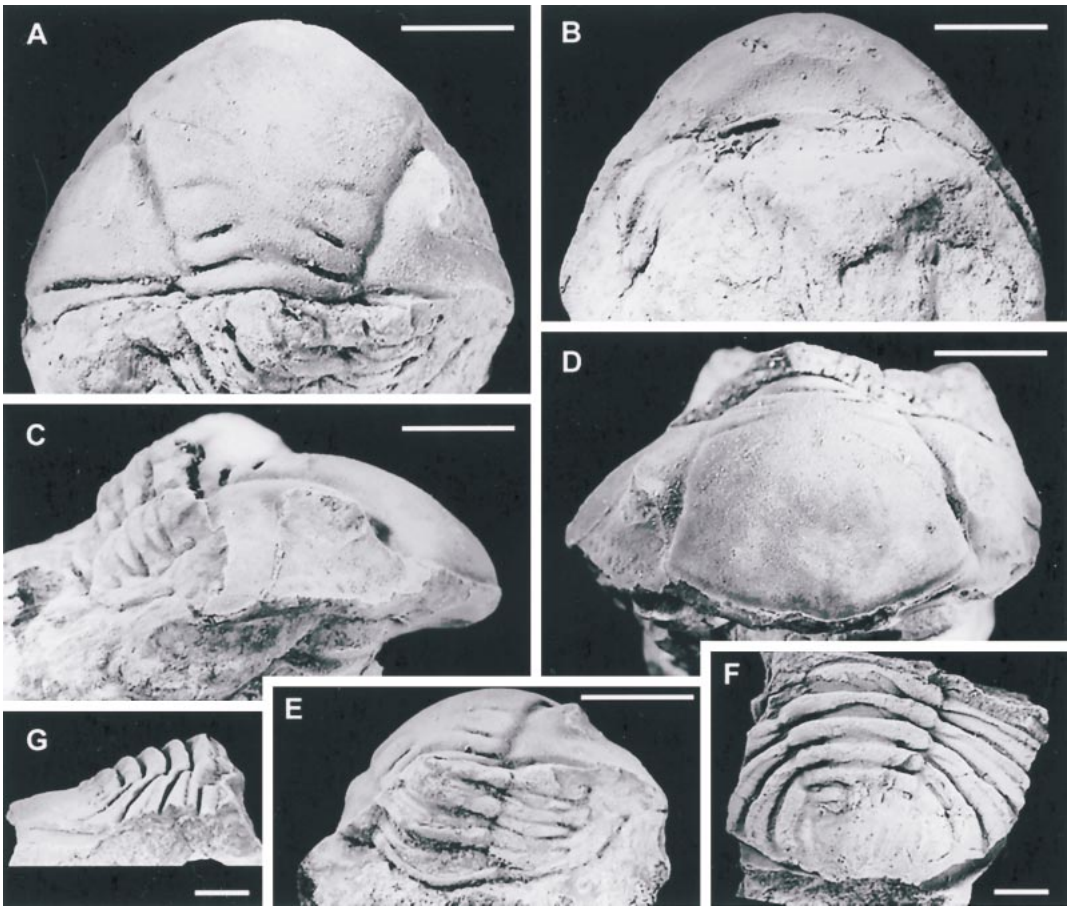


Fig. 6. *Granadocephalus hannibali*, n. gen. and sp. Icla Formation, 5 km east of Villa Granado, Cochabamba Department. All scales 10 mm. **A–E,** holotype MHNC 8131, cephalon with a few articulated thoracic segments (internal mold): (A) dorsal; (B) ventral; (C) lateral; (D) anterodorsal; and (E) oblique posterodorsal views (orientations with respect to cephalon); **F, G,** dorsal and lateral views of pygidium, MHNC 9451, internal mold.

their features of the exoskeletal margin (e.g., genal spines, thoracic pleural spines, pygidial marginal spines). The state of these characters is not known for *Granadocephalus*.

Granadocephalus hannibali, new species

Figure 6A–G

DERIVATION OF NAME: The species name expresses our appreciation to Dr. Joseph T. Hannibal (Cleveland Museum of Natural History), who has made significant contributions to the knowledge of Bolivian paleontology, and who collected the holotype.

DIAGNOSIS: As for genus.

TYPES: Holotype: internal mold of cephalon with a few displaced, articulated thoracic segments, MHNC 8131 (cast AMNH 47150) (fig. 6A–E). Paratype: internal mold of pygidium, MHNC 9451 (fig. 6F, G). Both from the Icla Formation, layer of *Francovichia branisi* (Emsian, inferring equivalence to layer of *F. branisi* sensu Wolfart (1968) in the Belén Formation in the Altiplano), on a hillside 5 km east of Villa Granado, Cochabamba Department, Bolivia, near the highway leading from Aiquile to Santa Cruz de la Sierra.

DESCRIPTION: The cephalon is moderately arched (tr.), subsemicircular in outline. Its maximum width is 45 mm (across the pos-

terior border) and its sagittal length is 30 mm. The ventral margin is moderately arched anteriorly, with at least two pairs of low, widely spaced protuberances. The anterior cranidial border is uniformly narrow, set off by a sharp anterior cranidial border furrow. The anterior cephalic border is also narrow, especially medially. The axial furrow is moderately impressed, moderately wide, divergent forward especially from S2, with a small, rounded fossular pit situated opposite S3 (exsag.) and near the anteromedial corner of the eye. The anterior section of the facial suture circumscribes the frontal glabellar lobe, passing around its anterolateral corner without transecting it. Glabellar length (sag.) is 25 mm (excluding S0) and its maximum width is 27 mm. In longitudinal profile, the glabella is curved, without a break in slope between the frontal lobe and S0 medially; the frontal lobe is steepest anteriorly. The glabellar median region is almost flat (tr.). The posterior median impression (PMI) is weakly developed as a faint elongate groove that extends back nearly opposite the inner tips of S3. The three pairs of glabellar furrows are not connected with the axial furrow. S3 is narrow, lightly impressed, and faintly sinuous; S2 is shallow but deeper than S3, weakly convex anteriorly, in part by a gentle posterior curvature at its inner tip; the overall course of S2 is approximately transverse, effacing well inward of the axial furrow; S1 is deeper impressed as gently concave, anteromedially directed apodemal grooves, abruptly shallowing distally, at most faint immediately adjacent to axial furrow. S0 is well developed, with a strongly convex anterior margin and a gently convex posterior margin, such that S0 is longest sagittally; medial part of S0 moderately deep, distal part incised as faintly concave apodemal grooves that parallel apodemes in S1. L2 and L3 lack independent inflation; L3 is wedge-shaped, expanded distally; L2 is more conspicuous than L3, and slightly narrowed medially. L1 is about two- thirds the length (exsag.) of L2. L0 is of even length across much of its width, with slight shortening distally, behind the apodemal part of S0; its width is 15 mm. The gena is subtrigonal, moderately convex. The palpebral area slopes downward laterally to the border furrow. The eye, though not well preserved, is relatively small, with the visual surface about 8 mm long and not elevated, lying entirely below the interocular fixigena; midlength of the palpebral furrow is opposite S2, its posterior edge opposite the posterolateral corner of L2. The anterior edge of the palpebral lobe is very close to the axial furrow, but the distance between them increases posteriorly such that the posterior edge of the eye is equidistant between the axial furrow and the posterior cephalic border furrow. The librigenal field slopes steeply down to the lateral cephalic border furrow, with the field bearing numerous strong pits. The lateral border of the cephalon and the genal angle are not preserved. The posterior cephalic border furrow is narrow, deep, and transverse; its anterior margin is straight. The posterior border gradually widens (exsag.) distally, more strongly widening distal to the fulcrum. The cephalon is ornamented with fine granulation, which is especially dense on the glabella.

Only an internal mold of a laterally incomplete pygidium is known. The axial furrow is shallow, narrow, and rather strongly converging posteriorly. The axis appears to be slightly wider than the inferred width of the pleurae (excluding marginal spines, if present). In lateral view the axis is gently raised above the pleural field. Five axial rings are strongly developed, plus parts of a sixth. The first two rings are moderately arched anteriorly and the succeeding ones are more gently arched. Medially the rings are widely separated from each other, with a pseudoarticulating half ring in the first two ring furrows; these rings are shortest sagittally and distinctly spatulate distally. Apodemal pits are developed in the distal parts of the ring furrows. The axis terminates far in advance of the posteromedian margin of the pygidium, with the postaxial region defined by a change in convexity rather than distinct impression of the axial furrow posteromedially. Five pleurae are preserved on the right side, but only parts of four are present on the left. The pleurae are gently arched (tr.), the ribs lengthening abaxially; the anteriormost ribs are gently and evenly curved laterally, but the last ones bend back more abruptly. The first interpleural furrow is narrow but sharply impressed, the succeeding furrows are simi-

larly narrow, but shallow; the fourth is the last discernible interpleural furrow on the internal mold. The pleural furrows are deep and relatively wide, maintaining their impression to the inner edge of the doublure. The lateral and posterior margins are not preserved, though the even outer margin of the doublure beneath the fourth and fifth ribs suggests that marginal spines or lappets were probably lacking on those segments at least.

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