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Systematics and Biogeography of the "Malvinella Group," Calmoniidae (Trilobita, Devonian)

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*nia perforator*; *Pseudomera barrandei*; *Cydonocephalus* cf. *C. torulus*; *Ectenonotus* sp.

S-257: *Bathyurus mackenziensis*; *Pseudomera barrandei*

S-260: *Bathyurus mackenziensis*; *Pseudomera barrandei*

S-290: *Xystocrania perforator*; *Bathyurus mackenziensis*; *Ludvigsenella ellipsepyga*; *Cydonocephalus* cf. *C. torulus*

S-369: *Bathyurus angustus*; *Illaenus* sp.

S-475: *Pseudomera barrandei*; *Bathyurus angustus*

#### Section Z

This section was measured in the Sunblood Range on a ridge immediately above Virginia Falls (61°31'N, 125°44'W). A single collection was made from the base of Virginia Falls (BVF). The interval studied here is just a portion of that measured by Ludvigsen (1979a; see Figure 2).

Z-208: *Encrinuroides rarus*; *Bumastoides* cf. *B. lenzi*; *Phorocephala* cf. *P. pinguimitra*

Z-211: *Bathyurus granulosus*; *Amphilichas* sp.; *Isotelus* cf. *I. harrisi*; *Ceraurinella nahanniensis*

Z-240: *Bathyurus granulosus*; *Isotelus* cf. *I. harrisi*; *Illaenid* sp. indet.

Z-284: *Bathyurus granulosus*; *Illaenid* sp. indet.

Z-296: *Isotelus* cf. *I. harrisi*; *Failleana* sp.; *Calyptaulax callirachis*

Z-306: *Bathyurus granulosus*; *Isotelus* cf. *I. harrisi*; *Acanthoparypha evitti*

BVF: *Ludvigsenella ellipsepyga*; *Bathyurus mackenziensis*

#### Section B

This section was measured in the Mary Range (61°19'N, 125°23'W). The interval studied here is just a portion of that measured by Ludvigsen (1979a; see Figure 2).

B-360: *Bathyurus margareti*

B-400: *Bathyurus margareti*

#### Section Y

This section was measured in the Funeral Range, immediately south of the South Nahanni River (61°28'N, 125°04'W).

Y-5: ?*Bathyurus sunbloodensis*; *Isotelus* sp. indet.

Y-30: *Bumastoides* cf. *B. lenzi*; *Cerurina* sp.

Y-32: ?*Bathyurus sunbloodensis*

Y-154: *Bathyurus granulosus*

Y-186: *Bathyurus granulosus*

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## SYSTEMATICS AND BIOGEOGRAPHY OF THE “MALVINELLA GROUP,” CALMONIIDAE (TRILOBITA, DEVONIAN)

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**ABSTRACT**—Phylogenetic parsimony analysis forms a basis for classification of the Siegenian–Eifelian “*Malvinella* group,” a monophyletic taxon within the “*Metacryphaeus* group” of the family Calmoniidae. Fifty-one exoskeletal characters for *Metacryphaeus* Reed and 12 taxa of the “*Malvinella* group” yield a shortest length cladogram with a consistency index of 0.51. A classification based on retrieving the structure of this cladogram recognizes six genera: *Malvinella* Wolfart, *Vogesina* Wolfart, *Palpebrops* n. gen. (type *P. donegalensis* n. sp.), the sister taxa *Parabouleia* Eldredge and *Bouleia* Kozłowski, and *Plesiomalvinella* n. gen. [type *P. pujravii* (Wolfart)]. *Palpebrops* is more closely related to *Vogesina* than to *Malvinella*; Amazonian species are nested within this group as sister taxa to Andean or Amazon/Andean clades. Bolivian Belén Formation *Malvinella buddeae* n. sp. is an allopatric species distinct from Icla Formation *M. haugi* (Kozłowski). “*Metacryphaeus*” of recent revisions is a paraphyletic grade group including primitive species of the “*Malvinella* group.” *Metacryphaeus australis* (Clarke), *M. tuberculatus* (Kozłowski), and *M. caffer* (Salter) are endemic to the Paraná Basin, Andean Bolivia–Paraná Basin, and South Africa, respectively.

#### INTRODUCTION

THE PRESENT paper attempts a systematic study of the “*Malvinella* group,” a clade within the “*Metacryphaeus* group” of Calmoniidae (sensu Eldredge and Braniša, 1980). Included are the genera *Bouleia* Kozłowski, 1923, *Malvinella* Wolfart, 1968, *Vogesina* Wolfart, 1968, *Parabouleia* Eldredge, 1972, and the new genera *Palpebrops* and *Plesiomalvinella*. This clade corresponds to a slightly expanded version of the subfamily Bouleinae Hupé, 1955, as emended by Cooper (1982). As discussed below, informal reference to a “*Malvinella* group” is favored to a formal subfamily, since the group is nested within the subfamily Calmoniinae. Relevant to taxonomy of the “*Malvinella* group” is the current state of the genus *Metacryphaeus* Reed, 1907. A formal revision of *Metacryphaeus* will be the subject of a forthcoming paper; however, some salient comments are appropriate now, as the “*Malvinella* group” includes, and is

within the cladistic structure of, species currently placed in *Metacryphaeus*. In the most recent revisions (Wolfart, 1968; Cooper, 1982), *Metacryphaeus* is a paraphyletic group; certain species of the genus are more closely related to excluded genera and clades such as the “*Malvinella* group” than they are to other species classified as *Metacryphaeus*. Following a discussion of *Metacryphaeus* Reed, parsimony analysis of 51 exoskeletal characters of 12 taxa of the “*Malvinella* group” is outlined. A revision of the group’s taxonomy is based on relationships expressed by minimum-length cladograms.

Morphological terminology generally follows that used by Eldredge and Braniša (1980). Glabellar lobes and furrows are denoted with the prefixes L and S, respectively, and numbered 0 (occipital) to 4 (anterior), as recommended for revision of the Treatise on Invertebrate Paleontology, Part O (Whittington and Kelly, unpublished). The auxiliary impression system of muscle

scars on the frontal glabellar lobe (Eldredge and Braniša, 1980, fig. 2) is abbreviated A.I.S. The abbreviation P.M.I. refers to the posterior median impression in the frontal lobe. Measurement of Large Eye Index follows Wolfart (1968), and is calculated by taking the ratio of the exsagittal length of the eye to the sagittal length of the glabella excluding SO. Points of curvature on the facial suture are as described by Richter and Richter (1949).

Specimens illustrated or cited herein are deposited in the following institutions: Department of Invertebrates, American Museum of Natural History, New York (AMNH); Departamento Nacional da Produção Mineral, Rio de Janeiro (DGM; DNPM); Museu Nacional Rio de Janeiro (MNRJ); New York State Museum, Albany (NYSM); Geology Museum, University of Cincinnati (UCGM); and Department of Paleobiology, United States National Museum of Natural History, Washington (USNM).

#### THE METACRYPHEAUS PROBLEM

Since the inception of its usage, there has been considerable change in the concept of the genus *Metacryphaeus*. Reed (1907) established this genus to unite *M. caffer* (Salter) with a host of South African Bokkeveld Group species now assigned to *Oosthuizenella* Cooper, 1982, *Pennaia* Clarke, 1913, and *Kozlowskiaspis* Braniša and Vaněk, 1973. By 1927, its author had deemed *Metacryphaeus* to be “a type of structure common to several subgenera or genera, a miscellaneous series of species which in light of further knowledge ought to be dissociated and distributed amongst other better limited groups” (Reed, 1927, p. 310). Reed’s comment also seems apt for more recent incarnations of *Metacryphaeus*.

Rennie (1930) revived *Metacryphaeus* (as a subgenus of *Dalmanites* Barrande) by designating *M. caffer* as its type species, and he rejected Reed’s (1925) assertion that this species was appropriately referred to *Asteropyge* Hawle and Corda.

When Delo (1935) erected *Hadrorachus* as a new asteropyginid genus (based on *Cryphaeus australis* Clarke, 1913), he made no direct comparisons to *Metacryphaeus*. However, Struve (1959) regarded *Hadrorachus* to be a junior synonym of *Metacryphaeus* Reed, and provided a lengthy diagnosis to include species occurrences in Brazil, Bolivia, the Falkland (Malvinas) Islands, and South Africa. This concept of *Metacryphaeus* as a speciose, widespread group (with calmonioid, rather than asteropyginid, affinities recognized by Struve, 1959) was enhanced by the transfer of several Bolivian “*Cryphaeus*” species to *Metacryphaeus* (e.g., Braniša, 1965) and Wolfart’s (1968) description of new Bolivian species. Wolfart broadened the generic diagnosis, and discerned two species groups in *Metacryphaeus*; however, he claimed that the two groups (the *giganteus* and *caffer* groups) shared so many similarities that even subgeneric separation was deemed unwarranted. *Metacryphaeus* Reed has not since been rediagnosed.

Wolfart’s generic concept is compatible with that utilized by Eldredge and Ormiston (1979) and Cooper (1982), though both rejected Wolfart’s species groups. Baldis (1979) endorsed the *giganteus* and *caffer* groups (in modified form) as sufficiently distinct for generic separation, and proposed that they correspond to the (Pacific) Austral Andean and (Atlantic) Malvinokaffric Provinces, respectively. That the groups are non-monophyletic, however, renders any “areas of endemism” artifacts of taxonomy. Cooper’s (1982) recognition of *M. cornutus* Wolfart, 1968, as a monotypic subgenus *Wolfartaspis* Cooper, 1982, is based on a subjective weighting of autapomorphies (the presence of a thick, cylindrical pygidial terminal spine and an occipital spine). Removal of the subgenus “*Wolfartaspis*” evi-

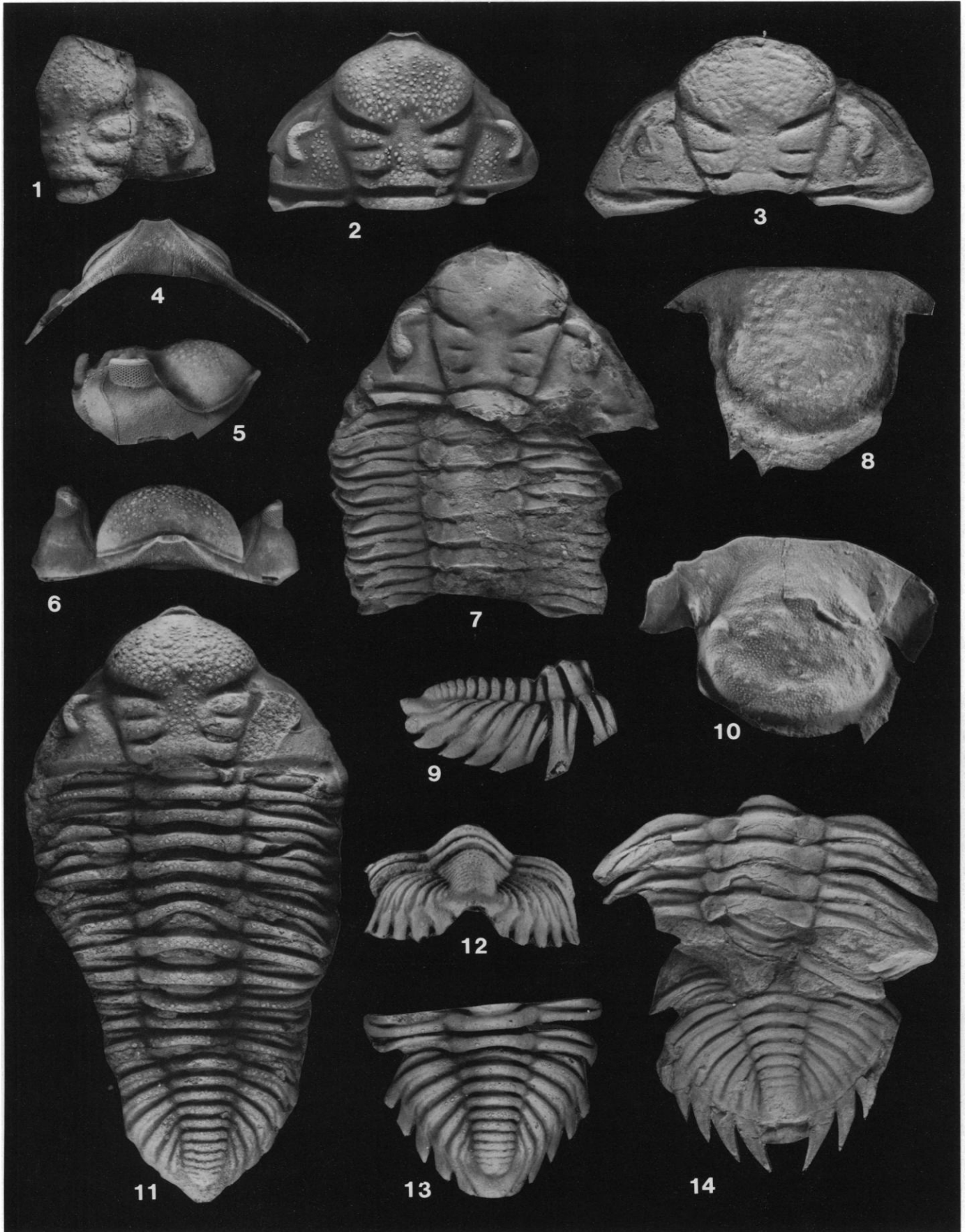
dently renders *M. (Metacryphaeus)* a paraphyletic group, diagnosed by the absence of these derived characters. Accordingly, *Wolfartaspis* is not here recognized. The exclusion of monotypic *Punillaspis* Baldis and Longobucco, 1977, from *Metacryphaeus* is likewise based on weighting uniquely derived features, although *P. argentina* (Baldis, 1967) is certainly (cladistically) nested within “*Metacryphaeus*.”

The following procedures are recommended to make an informative revision of *Metacryphaeus* Reed.

Firstly, *Metacryphaeus* should be restricted to a monophyletic group including the type species, *M. caffer* (Salter, 1856). The following discussion aims to determine the composition of this group, with an assessment of species differentia.

Cooper (1982) suggested that *M. tuberculatus* (Kozłowski, 1923) is probably a junior subjective synonym of *M. caffer*. The Bolivian taxon (*tuberculatus*) was erected as a subspecies of *Cryphaeus australis* Clarke, 1913, but was afforded full specific status by Wolfart (1968). Large collections of Bolivian *M. tuberculatus* (Figure 1.2, 1.4–1.6, 1.9, 1.11–1.14) have been studied; this species occurs at numerous localities in the northern outcrop area discussed by Eldredge and Braniša (1980) (in the Upper Belén–Sicasica Formations), and scarcely occurs in the central outcrop area (Icla Formation). Material from the Limoncito Formation near Chochis, Santa Cruz Department, Bolivia (Petri, 1949), is indistinguishable from these (Figure 1.3, 1.8). *Metacryphaeus* specimens from the Pimenteira Formation in the Parnaíba Basin of northeastern Brazil, figured as *M. australis* (Clarke) by Castro (1968), differ from *M. tuberculatus* only in that L3 is slightly longer exsagittally, and the eyes are sometimes situated closer to the genal margin. An additional nodule collection from the Pimenteira Formation near Picos, Piauí, however, includes specimens in which these characters are expressed as those found in typical Bolivian *M. tuberculatus* (Figure 1.1). Here the species occurs with “*Metacryphaeus*” cf. “*M.*” *venustus* Wolfart, 1968, which differs from Bolivian material only in having L0 longer relative to its width, and S1 more sharply curved forward proximally (Figure 2). The condition of the latter character is comparable to what is found in some South African specimens assigned to “*M.*” *venustus* by Cooper (1982). The association of *M. tuberculatus* and “*M.*” cf. “*M.*” *venustus* suggests that the Pimenteira Formation may be correlated with the uppermost Belén to lower Sicasica formations in western Bolivia. Suarez Soruco (1989, fig. 1), however, has proposed that the Pimenteira Formation is younger than the Andean strata.

Intraspecific variation in *Metacryphaeus tuberculatus* is quite extensive; this confounds any attempts at consistent morphological separation from South African *M. caffer*. Although the South American material sometimes shows L1 to be shorter than in *M. caffer*, this character varies considerably in *tuberculatus* and overlaps other occurrences. The form of the pygidial lappets ranges from short and bluntly rounded to free lobe-like or spinose tips, as Cooper (1982) figured for *M. caffer*. Many Bolivian “*tuberculatus*” pygidia show a less marked anteroposterior change in angle of axial furrow convergence (in *caffer*, strongly convergent against the anterior five rings, subparallel posteriorly); within-species variation, however, precludes the consistent use of this character. The coarse exoskeletal tuberculation characteristic of South American *M. tuberculatus* cannot be discerned on much of Cooper’s (1982) figured *M. caffer* material, although this may in part be a preservational artifact. A cephalon of *M. caffer* from the Bokkeveld Group at Swaatmoed Pass (USNM 12800), however, has several coarse tubercles on the lateral glabellar lobes, with abundant tubercles and coarse granules on the frontal lobe. *Metacryphaeus tuberculatus* is less variable in eye size, and includes individuals with relatively shorter eyes (range of Large Eye Index 0.26–0.30) than



*M. caffer* (range of Large Eye Index 0.29–0.39, measured from photographs in Cooper, 1982). Number of dorsoventral lens files is similar (24–27 in *tuberculatus*; 23–27 in *caffer*). Position of the anterior edge of the eye relative to the axial furrow appears to offer a criterion by which the Bolivian/Parnaíba Basin and South African forms can be distinguished. In *M. tuberculatus* the anterior edge of the eye is distinctly removed from the axial furrow (a thin eye ridge continues to the axial furrow); in *M. caffer* the anterior edge of the eye is immediately adjacent to the axial furrow. Although morphologic differentiation of these taxa is thus slight, we have tentatively retained their specific distinctness.

Photographs of the type material of *M. australis* (Clarke) have been examined, as have additional specimens from the Ponta Grossa Formation (DNPM, NYSM collections). *Metacryphaeus australis* is readily distinguished from *M. tuberculatus* by its large eyes (Large Eye Index 0.38–0.41), which abut the axial furrow anteriorly, relatively longer (exsag.) lateral glabellar lobes, (usually) S2 more strongly isolated from the axial furrow, and prominent, pointed genal spines. This conformation of the genal spine (and its serial repetition in the blade-like triangular pygidial spines; Figure 1.14) also serves to differentiate *M. australis* from Bokkeveld material of *M. caffer*. The latter more typically has lobe-like lappets on the pygidial margin. *Metacryphaeus* from the Fox Bay Formation, Falkland Islands [*M. allardyceae* (Clarke, 1913)] is only weakly differentiated from South African *M. caffer* (see Edgcombe, 1991).

*Metacryphaeus tuberculatus* (including Parnaíba Basin “*australis*” of Castro, 1968) may be distinguished from Paraná Basin *M. australis* (Clarke) by the consistent presence of coarse exoskeletal tuberculation in the former. The presence or absence of tuberculation does not appear to be a mere artifact of nodule versus shale preservation; shale material from the Limoncito Formation is lithologically similar to Ponta Grossa material, yet the former is distinctly tuberculate (like nodule material from Andean localities and the Parnaíba Basin). Some specimens of Ponta Grossa *M. australis* (Figure 1.7, 1.14) lack coarse tuberculation, despite the excellent conditions of preservation; only fine, dense granulation is well preserved. However, some of Clarke’s syntypes (e.g., DGM 35-1; original of Clarke, 1913, Pl. 4, fig. 5) bear distinct exoskeletal tuberculation, as does additional Ponta Grossa material (DNPM 2800, 2807). Material from the Chapada Group on the northwestern flank of the Paraná Basin assigned to *Metacryphaeus* cf. *M. australis* by Carvalho et al. (1987) is also distinctly tuberculate, and is most comparable to the Ponta Grossa form in other features (e.g., the pointed genal spine and thoracic pleural tips).

Hypostomes of *Metacryphaeus australis* (Clarke, 1913, Pl. 4, fig. 3; Figure 1.10) and *M. tuberculatus* (Figure 1.8) are more similar to each other than to other parts of the “*Metacryphaeus*” grade. The *M. australis* hypostome has granulation strongly developed on the middle body, coarser than that found on the borders and anterior wings. The posterior border is of moderate length, with (at least) two pairs of marginal spines positioned

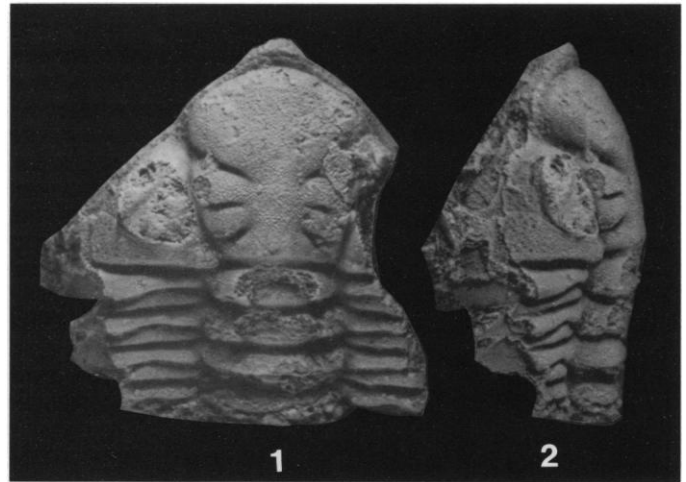


FIGURE 2—1, 2, “*Metacryphaeus*” cf. “*M.*” *venustus* Wolfart, 1968. Pimenteira Formation, 2 km south of Picos, Piauí, Brazil. Dorsal and left lateral view of cephalon and anterior part of thorax, internal mold, UCGM 46411,  $\times 5$ .

posterolaterally; in *M. tuberculatus*, the border is 22 percent of hypostomal length (sag.), with two pairs of triangular marginal spines. Both species have coarse, ovate muscle impression scars densely distributed over the anterior lobe of the middle body. Relatively few scars are present on the posterior lobe, and these are concentrated just behind the middle furrow. The posterior lobe is 35–38 percent of the length of the anterior lobe, which, in *M. australis*, tapers anteromedially. Maculae are of moderate size and strongly defined; in *M. australis* and Limoncito Formation *M. tuberculatus*, they are situated at 45 percent of hypostomal length from the anterior margin to the posterior border furrow. A Belén Formation *M. tuberculatus* hypostome has maculae farther back, at 58 percent of this length.

Secondly, to explicitly recognize that *Metacryphaeus* does not comprise a monophyletic group, the paraphyletic stem group of species conventionally assigned to this genus are referred to as “*Metacryphaeus*,” using the shutter quote convention of Wiley (1979).

Thirdly, to recognize their inclusion within the “*Malvinella* group,” “*Metacryphaeus*” *boulei* (Kozłowski) and “*M.*” *pujravii* Wolfart are excluded from *Metacryphaeus*. They are reassigned to the new genus *Plesiomalvinella*.

Cooper’s informal classification (1982, p. 63) places *Metacryphaeus* and genera here referred to the “*Malvinella* group” in different subfamilies. The former he assigned to a “*Calmonia* plexus” within Calmoniinae. He expanded (originally monotypic) Bouleinae Hupé, 1955, to include *Parabouleia*, *Malvinella*, and *Vogesina*, as well as *Bouleia*. Primitive taxa of the “*Malvinella* group,” such as *Plesiomalvinella pujravii*, display

←  
FIGURE 1—*Metacryphaeus* spp. 1–6, 8, 9, 11–13, *Metacryphaeus tuberculatus* (Kozłowski, 1923). 1, dorsal view of cephalon, UCGM 46408,  $\times 1.5$ . Pimenteira Formation, 2 km south of Picos, Piauí, Brazil; 2, 4–6, dorsal, ventral, right lateral, and anterior views of cephalon, AMNH 44128,  $\times 1.5$ . Belén Formation, Upper Member, Pisakavina, La Paz Department, Bolivia; 3, dorsal view of cephalon, UCGM 46409,  $\times 2$ . Limoncito Formation, near Chochis, Santa Cruz Department, Bolivia; 8, ventral view of hypostome, UCGM 46410,  $\times 4$ , locality as for 3; 9, 12, 13, right lateral, posterior, and dorsal views of posterior two thoracic segments and pygidium, AMNM 44129,  $\times 1.5$ , Belén Formation, Upper Member, Belén, La Paz Department, Bolivia; 11, dorsal view of complete exoskeleton, AMNM 44130,  $\times 1.5$ , locality as for 9, 12, 13. 7, 10, 14, *Metacryphaeus australis* (Clarke, 1913). Ponta Grossa Formation, Ponta Grossa, Paraná, Brazil. 7, dorsal view of cephalon and partial thorax, NYSM 16131,  $\times 1.5$ ; 10, 14, ventral view of hypostome ( $\times 4$ ), and dorsal view of partial thorax and pygidium of disarticulated exoskeleton ( $\times 2$ ), NYSM 16132. All internal molds except 1, latex cast from external mold.



FIGURE 3—Hypostomes of taxa used in parsimony analysis and outgroup rooting. All ventral views, except 3, left lateral view. All from Chacoma, La Paz Department, Bolivia. 1, "*Metacryphaeus*" *cornutus* Wolfart, 1968, Belén Formation, Upper Member, AMNH 44131,  $\times 3$ . 2, 3, *Vogesina lacunifera* Wolfart, 1968, Belén Formation, Lower Member, AMNH 44132,  $\times 3$ . 4, *Plesiomalvinella boulei* (Kozłowski, 1923), Belén Formation, Lower Member, AMNH 44133,  $\times 2$ . 5, "*Metacryphaeus*" *giganteus* (Ulrich, 1892), Belén Formation, Lower Member, AMNH 44134,  $\times 2$ . 6, "*Metacryphaeus*" *venustus* Wolfart, 1968, Belén Formation, Upper Member. 6, AMNH 44135,  $\times 3$ ; 7, AMNH 44136,  $\times 3$ .

a combination of *Metacryphaeus* symplesiomorphies and apomorphies of the "*Malvinella* group" (see below). This provides evidence that *Metacryphaeus* is most closely related (i.e., sister group) to the "*Malvinella* group." Accordingly, Calmoninae sensu Cooper is paraphyletic. While Cooper's emended Bouleiinae finds support as a monophyletic taxon, we are reluctant to restrict this name to the "*Malvinella* group" because a paraphyletic series of "*Metacryphaeus*" species is regarded as successive outgroups. These species are more closely related to Bouleiinae sensu Cooper (1982) than to the subfamily Calmoninae; the former group would require broadening to accommodate them. Accordingly, an informal "*Malvinella* group" is used in favor of Bouleiinae sensu Cooper, slightly broadened to include an additional topologically primitive genus, *Plesiomalvinella* n. gen.

#### CLADISTIC PARSIMONY ANALYSIS

Fifty-one exoskeletal characters, described in the Appendix, were coded for 12 ingroup taxa using "*Metacryphaeus*" *giganteus* (Ulrich) as the first outgroup. The character matrix is mostly complete for Andean species. Certain species from the Maecuru Formation in the Amazon Basin have been recognized by recent investigators as having affinities to the "*Malvinella* group." A comprehensive revision of the group is enhanced by coding "*Phacops*" *goeldi* Katzer, 1903, "*Dalmanites*" *australis* Clarke, 1890, and "*D.*" *gemellus* Clarke, 1890. Each of these species is known from only one or two incomplete cephalons; however, the specific validity of each taxon can be supported. "*Phacops*" *goeldi* is most readily distinguished from the others by light

incision of S2 and S3. The identity of "*D.*" *australis* is problematic, since the small size of the sole cephalon suggests a juvenile growth stage. Nonetheless, it may be differentiated from the glabella representing "*D.*" *gemellus* by a flatter (sag.) profile, less steeply inclined S3, a rather broader frontal lobe, and lack of an elongate P.M.I.

With other parts of the "*Metacryphaeus*" grade as additional outgroups (e.g., "*M.*" *venustus* Wolfart, 1968), it was discovered that *Metacryphaeus* s.s. (e.g., *M. tuberculatus*) shares some characters with the "*Malvinella* group," which can be regarded as apomorphic relative to the condition in the outgroup grade [character (state): 5(1); 37(1)]. *Metacryphaeus tuberculatus* was thus analyzed as part of the ingroup.

Polarization of hypostomal characters 40–44 is aided by new assignments of hypostomes to several species of "*Metacryphaeus*." In each case, at least one hypostome has been observed in association (articulated or slightly displaced) with an identifiable cephalon. Figure 3 illustrates hypostomes of "*M.*" *venustus* Wolfart (cf. Braniša, 1965, Pl. 21, figs. 11, 12), "*M.*" *cornutus* Wolfart, and "*M.*" *giganteus* (Ulrich), used in outgroup coding; those of *M. tuberculatus* (Kozłowski) and *M. australis* (Clarke) have been discussed above. A morphological description is given in the systematic section for the hypostomes of *Plesiomalvinella boulei* (Kozłowski) and *Palpebrops donegalensis* n. sp.

The character data in Table 1 were analyzed with Hennig86 Version 1.5 (Farris, 1988). Most multistate characters were treated nonadditively (i.e., all possible orderings of states allowed). Multistate characters 8, 41, and 44, with one state morphologically intermediate between two others, were treated as



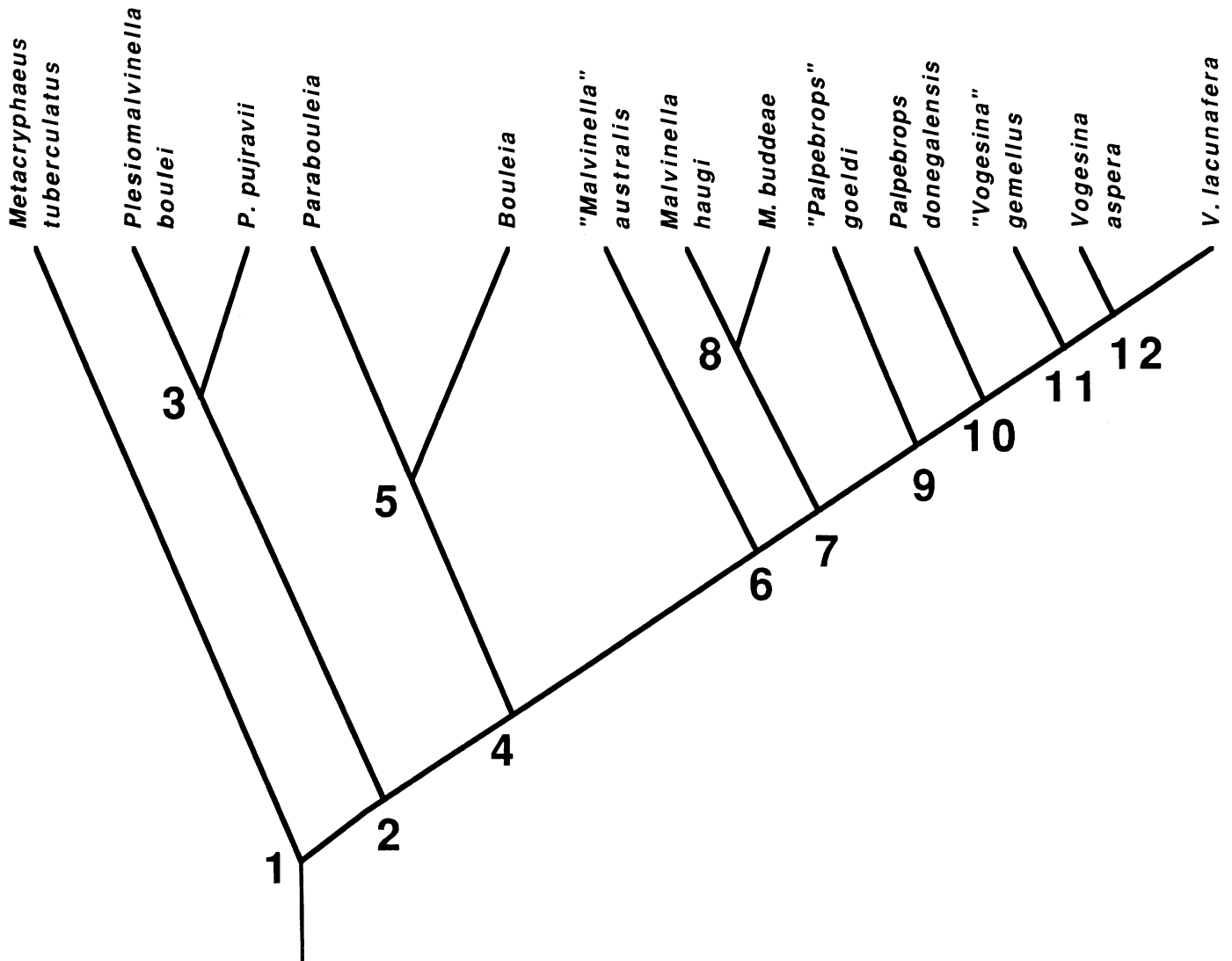


FIGURE 4—Minimum length cladogram (length 118; c.i. 0.51) produced from analysis of character data in Table 1 with Hennig86, version 1.5. Cladogram constructed with implicit enumeration (ie\*); all multistate characters except 8, 41, 44 nonadditive. Character states at nodes as follows (characters as numbered in Appendix, with apomorphic character state in parentheses); square parentheses indicate apomorphies which may be at a more general node but are ambiguous because of missing data or multiple equally parsimonious resolutions: Node 1, 5(1), 37(1); Node 2, 20(1), 27(1), 29(1), 41(1), 44(1), 45(2), 48(1); Node 3, 3(1), 21(1), 24(1); Node 4, 13(1), [15(1)], [35(1)], 36(1), 40(1), 43(1), 44(2), 50(2); Node 5, 1(1), 14(1), 25(1), 29(2), 30(1), 39(1), 46(1), 49(1); Node 6, 7(1), 9(1), 12(1), 17(1), 22(1), 23(1); Node 7, 3(1), 4(1), 34(1), 38(1), [47(1)]; Node 8, [2(1)], [16(1)], [28(1)], 30(1), 33(1), 37(0); Node 9, 8(1); Node 10, 1(1), 9(0), 41(2); Node 11, 5(0), 11(1); Node 12, [0(0)], [3(0)], 8(2), 12(0), 18(1), [20(0)], [27(0)], [29(0)], [32(1)], [36(0)], [45(0)], [48(0)]. This provides minimal number of synapomorphies, i.e., autapomorphic convergences are shown rather than equally parsimonious resolutions with reversals (only unambiguous reversals are shown); reversals and parallelism, however, were allowed equal possibility in calculating the cladogram.

*Type species.*—*Metacryphaeus boulei pujravii* Wolfart, 1968.

*Assigned taxa.*—*Cryphaeus boulei* Kozłowski, 1923.

*Diagnosis.*—Cranial anterior border ridge present; L1 bears one or two spines abaxially; two poorly defined rows of spines on posterior glabellar region (plesiomorphies: S3 well incised adjacent to axial furrow; facial suture recurved forward between  $\epsilon$  and lateral border furrow; hypostome subrectangular, with distinct maculae and posterior margin denticles; pygidial margin with five pairs of lappets).

*Etymology.*—Compounding *plesio*, Greek for primitive, and *Malvinella*, in reference to the basal position of this taxon within the "Malvinella group."

*Discussion.*—Unique grouping of "*Metacryphaeus*" *boulei* and "*M.*" *pujravii* is a component of the minimum-length cladogram in Figure 4. This is compatible with Wolfart's (1968) classification of these taxa as subspecies (by inference, each other's closest relatives). New material of "*M.*" *pujravii*, described below, certainly attests to specific distinctness. However, characters that map on the cladograms as synapomorphies of this group are hypothesized to have arisen at least once elsewhere within the "*Malvinella* group." The presence of discrete tubercles abaxially on L1 also characterizes *Palpebrops*. The rather irregular conformation of the posterior glabellar spine rows may be a primitive condition relative to the well-defined rows of



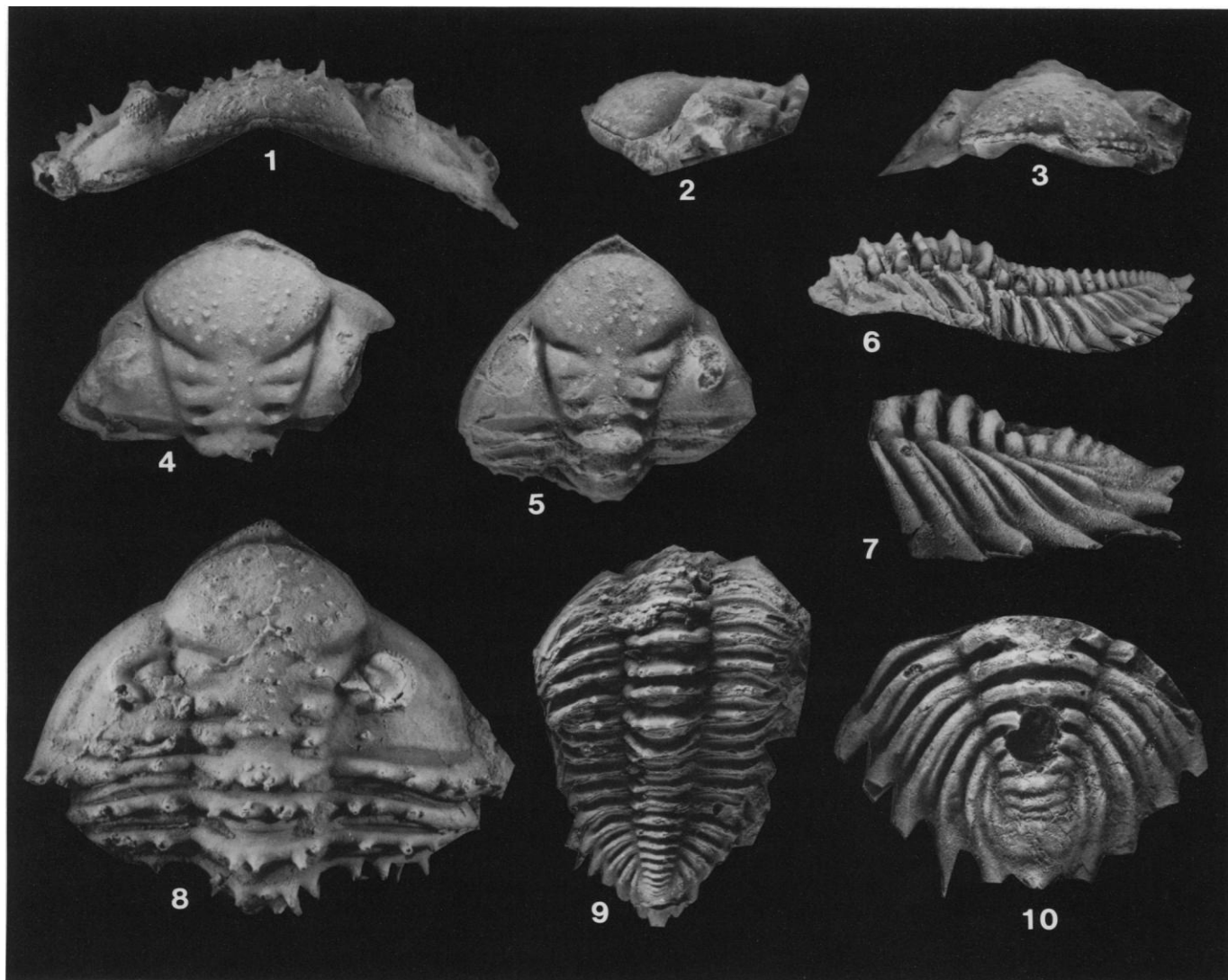


FIGURE 5—*Plesiomalvinella pujravii* (Wolfart, 1968), Icla Formation, Padilla, Chuquisaca Department, Bolivia. 1, 8, anterior and dorsal views of cephalon and anterior part of thorax, AMNH 44137,  $\times 2$ ; 2–4, left lateral, anterior, and dorsal views of cephalon, USNM 449770,  $\times 1$ ; 5, 6, 9, dorsal view of cephalon and left lateral and dorsal views of thoracopygidium of small exoskeleton, AMNH 44138,  $\times 3$ ; 7, 10, left lateral and dorsal views of pygidium, USNM 449771,  $\times 1.5$ . All internal molds except 1, 8, latex cast of external mold.

*Malvinella buddeae* and *Palpebrops donegalensis*. In particular, several characters mapped on the minimum-length topologies as autapomorphies of *Plesiomalvinella pujravii* [characters (states): 2(1); 16(1); 28(1); 37(0)] must be regarded as homoplastic with similar conditions synapomorphic for *Malvinella*. However, all character evidence reveals a greater number of derived similarities to group the clade *Bouleia* + *Parabouleia* with *Malvinella* and *Palpebrops* + *Vogesina*, at the exclusion of *Plesiomalvinella pujravii*. Distinctive primitive homologues retained by *Plesiomalvinella* are listed in the diagnosis under “plesiomorphies.”

Since the character support for *Plesiomalvinella* (i.e., synapomorphies of *pujravii* + *bouleii*) can hardly be regarded as cladistically reliable (sensu Farris, 1969), the diagnosis for the genus is provisional. Should further evidence reveal the group to be non-monophyletic, *Plesiomalvinella* might be restricted to the type species. Unique features of *P. pujravii* (Wolfart), such as long, pointed pygidial spines, would be diagnostic.

#### PLESIOMALVINELLA PUJRAVII (Wolfart, 1968)

Figure 5.1–5.10

*Metacryphaeus boulei pujravii* WOLFART, 1968, p. 92, Pl. 14, fig. 3, Pl. 15, fig. 1.

?*Metacryphaeus boulei pujravii* Wolfart. ELDREDGE AND ORMISTON, 1979, p. 160.

**Occurrence.**—Upper Member of the Belén Formation, Pujraví, La Paz Department, Bolivia (type locality). Also known from the basal Icla Formation at Padilla and Limabamba, Chuquisaca Department, Bolivia (AMNH, USNM collections).

**Description.**—Cephalic length (sag.) 55–60 percent of width. Frontal glabellar lobe projecting beyond semicircular arc of genae. Ventral margin with moderate anterior arch. Axial furrow nearly straight, diverging forward at about 30 degrees, narrow, moderately deep, weakly flexed inward at distal end of S3, with slight but distinct deepening as weak, non-apodemal anterior pit. Cranidial anterior border short exsagittally, lengthening me-

dially as weakly upturned triangular process, extending nearly to cephalic anteromedian margin, bearing numerous small spines. Cranial anterior margin lying in weakly convex (tr.) plane. Preglabellar furrow shallow, narrow. Facial suture running approximately straight anteroventrally between  $\gamma$  and outside anterolateral corner of frontal glabellar lobe. Posterior branch of facial suture approximately straight, inclined anterolaterally (in dorsal orientation) between  $\epsilon$  and lateral border furrow, sharply flexed backward across lateral border;  $\omega$  posterior to  $\epsilon$ . Glabellar length (sag.) 90–100 percent of width across frontal lobe. Frontal lobe subrhomboid, about 60 percent length of glabella, length 55–65 percent of its width. L1–L3 very gently convex (sag.); frontal lobe gently inflated above plane of posterior glabellar region, of relatively low convexity (sag., tr.); anterior part of frontal lobe moderately declined forward. P.M.I. shallow. S3 moderately deep, broad, well incised distally to axial furrow, straight, with branches diverging at about 125 degrees. Sagittal region of L3–L2 nearly flat (tr.), lateral lobes weakly declined abaxially. L3–L1 bearing single spines on each lateral lobe, two crude anteroposteriorly aligned rows of spines on posterior glabellar region (S3–L1). L3 wedge-shaped, lengthening distally, outer edge nearly straight or weakly convex along axial furrow. S2 straight, transverse, each branch moderately deep across about 22 percent of glabellar width (tr.), shallow adjacent to axial furrow. S1 with deep, teardrop-shaped apodemal pit, shortening and shallowing distally, continuous to axial furrow. L1 short (sag., exsag.), flexed forward abaxially, gently convex (tr.), depressed well below L2 exsagittally. S0 longest sagittally, shallow, weakly concave, with deep, transverse apodemal incision distally; anterior margin of S0 broadly arched forward sagittally, posterior margin poorly defined (sag.). L0 60–65 percent width of frontal lobe, moderately arched (tr.), longest sagittally, about 25 percent of its width, most elevated behind midlength, anterior edge with moderate anteroventral slope; row of four large spines near posterior margin, with row of two small spines anterior to these. Large Eye Index 0.28–0.33. Anterior edge of eye weakly separated from axial furrow, opposite anterodistal corner of L3; palpebral lobe moderately oblique (exsag.); posterior edge of eye opposite midlength (exsag.) of L2. Palpebral furrow moderately broad and deep, of rounded V-shape. Thin crescentic ridge along outer edge of palpebral lobe faintly raised above lobe. Eye raised about equal in height to frontal glabellar lobe. Visual surface bearing 22–23 dorsoventral files with a maximum of six lenses per file, outer face gently inclined adaxially dorsally. Fixigena most elevated inward of palpebral lobe, gently sloping posteroventrally to border furrow. Genal field with pervasive dimpling, coarsest abaxially on fixigena. Postocular fixigenal field 55–60 percent length (exsag.) of eye, bearing single spine behind inner edge of eye adjacent to posterior border furrow. Librigenal field moderately declined to lateral border furrow. Posterior border furrow transverse or gently sloping forward distally, anterior margin nearly straight; lengthening (exsag.) between axial furrow and midwidth of gena, shortening and shallowing distally, continuous with lateral border furrow. Posterior border short adjacent to axial furrow, lengthening (exsag.) distally, bearing six or seven coarse spines, densest toward genal angle, posterior margin gently curved backward across inner part of cephalon, border constricted near base of genal spine; genal spine short, angular, projecting posterolaterally. Lateral border furrow shallow; border broad (tr.), gently widening posterolaterally, faintly convex, more gently declined outward than librigenal field, densely granulate. Cephalic anterior border steeply declined beneath cranial anterior border ridge, gently concave, obsolete sagittally, lengthening abaxially. Cephalic doublure with flattened, crescentic medial region, bounded an-

teriorly and anterolaterally by increasing slope; doublure grades into cephalic border ridge anteromedially without topographic break; anterior margin of doublure bluntly pointed.

Thorax of 11 segments. Axial ring about 33 percent width of thorax, shortest medially, length (sag.) about 15 percent of width, lengthening and gently flexed forward distally. Ring furrow longest sagittally, about 70 percent length of ring, shallow, gently concave. Anterior margin of ring poorly defined sagittally, inclined posterodorsally, most elevated near posterior edge, bearing row of four or five coarse spines. Articulating half ring set well below axial ring. Proximal part of pleura transverse, approximately horizontal; anterior segments rather evenly convex (tr.), outer part of pleurae more abruptly flexed downward, straight in posterior segments. Posterior band long (exsag.), gently arched proximal to axial furrow, evenly shortening to break in slope as moderately deep pleural furrow lengthens, then lengthening, flattening abaxially, extending to margin as elongate, tapering spines; spines more strongly flexed backward in posterior segments. Anterior band short (exsag.) across width, depressed well below posterior band proximally, pinching out distally. Posterior band bears three tall spines inward of break in slope on anterior segments, two spines on posterior few segments.

Pygidium broadly triangular in outline (excluding marginal spines), length about 70 percent of width, margin gently convex outward. Axial furrow shallow, narrow, straight, converging backward at about 30 degrees opposite anterior five rings, less convergent posteriorly. Axis 35–40 percent of pygidial width anteriorly, with ten rings, each bearing two spines; rings shortest sagittally, crests in flat, posteriorly declined plane. Ring furrows long, moderately deep medially; deep, transverse apodemes in distal part of anterior four ring furrows, decreasing in size posteriorly, small apodemes in fifth ring furrow. Axial terminus weakly defined, blunt; postaxial region 20 percent of pygidial length (sag.). Anterior five pleurae terminate as long, tapering, gently convex, pointed spines. Seven pairs of pleural furrows, anterior five broad, moderately deep. Anterior band not defined posterior to fifth segment, raised subequal to posterior band at midwidth of pleura in anterior segments. Posterior bands of anterior five pleurae bearing one or two tubercles. Terminal spine triangular, upturned, with doublure gently convex dorsally.

*Discussion.*—Wolfart's (1968) description of this species was based on only two specimens from the Belén Formation, but in these the cephalic anterior border, eyes, thoracic pleural tips, and pygidial terminal region are incompletely preserved. A complete description of *P. pujravii* is accordingly given above. Although this is based on material in part from a considerably lower stratigraphic level in the Icla Formation, it exhibits no discernible differences from the types.

*Plesiomalvinella pujravii* is most readily distinguished from *P. boulei* by the former's less inflated glabella, more divergent cephalic axial furrows, sparser (more regular, symmetrical) cuticular spines, triangular cephalic anteromedian process (with a pointed, rather than rounded, anterior margin of the cephalic doublure), and pygidial pleurae terminating as long, pointed spines.

#### PLESIOMALVINELLA BOULEI (Kozłowski, 1923)

Figures 3.4, 6

*Cryphaeus boulei* KOZŁOWSKI, 1923, p. 46, Pl. 2, fig. 15 (non 16, 17). *Asteropyge? boulei* (Kozłowski). BRANIŠA in Ahlfeld and Braniša, 1960, p. 74.

*Metacryphaeus boulei boulei* (Kozłowski). WOLFART, 1968, p. 88, Pl. 1, figs. 1–3.

*Metacryphaeus boulei boulei?* (Kozłowski). WOLFART, 1968, p. 91, Pl. 10, figs. 7a–c.

*Cryphaeus cf. pentlandi* Salter. KOZŁOWSKI, 1923, p. 46, Pl. 2, fig. 18.  
*Andinapyge spinulosa* BRANIŠA, 1965 [nomen nudum], p. 218, Pl. 77, figs. 3, 4, Pl. 79, fig. 2.

**Occurrence.**—Lower Member of the Belén Formation, Patacamaya (type locality); Hiskachili, Mollepunco-Tal (Wolfart, 1968); Belén, Cahuanota, Chacoma, Colchani, La Paz Department, Bolivia (AMNH, USNM collections); Icla Formation, Padilla, Chuquisaca Department, Bolivia (USNM collection); Quebrada Jarajache (Newell, 1949, fig. 11), Peru. Upper Member of the Belén Formation, Pujravi, La Paz Department (Wolfart, 1968).

**Description.**—Hypostome of elongate shield shape, width (tr.) at midlength about 85 percent of sagittal length. Course of anterior margin (hypostomal suture) gently convex, with large anterior wings positioned far forward. Lateral margin nearly straight behind anterior wings, converging backward slightly. Middle body crudely ovate in outline, broadest near midlength, anterior margin poorly defined; anterolateral margins defined by smooth break in slope, grading down to rather flattened anterior wing. Convexity (tr.) of middle body moderate sagittally; faintly convex (sag.) anterior and posterior lobes separated at about 60 percent of length by broad, shallow middle furrow. Maculae large, low, ovate swellings positioned back about 40 percent sagittal length of hypostome, distinctly abaxial to middle furrow's juncture with shallow lateral border furrow. Posterolateral-posterior border furrows very broad, fairly shallow. Posterolateral border lengthens sagittally, 15 percent length of hypostome posteromedially, gently convex. Posterior margin rounded, apparently lacking spines.

**Discussion.**—Wolfart (1968) provided a detailed description of the cephalon of *Plesiomalvinella boulei* (Kozłowski). The thoracopygidium ascribed to this species by Kozłowski (1923) is that of *Bouleia dagincourti* (Ulrich). The pygidium questionably referred to *P. boulei* by Wolfart (1968) is correctly assigned (cf. Kozłowski, 1923, Pl. 2, fig. 18; Figure 6.3, 6.4 here). Two hypostomes only slightly dissociated from cephalic tergites are known from Chacoma, La Paz Department, and form the basis for the above description.

#### Genus MALVINELLA Wolfart, 1968

**Type species.**—*Anchiopella haugi* Kozłowski, 1923.

**Assigned taxa.**—*Malvinella buddeae* n. sp. *Dalmanites australis* Clarke, 1890, is informally referred to “*Malvinella*” s.l.

**Diagnosis.**—Anterior edge of eye removed from axial furrow, with single spine or discrete spine cluster on interocular fixigena; long, slender genal spine, constricted at its base.

**Discussion.**—The diagnostic characters of *Malvinella* listed above are resolved as synapomorphies grouping Bolivian *M. haugi* (Kozłowski, 1923) and *M. buddeae* n. sp. Since previous workers have subsumed the two Bolivian taxa within a single species, it is hardly surprising that they are identified as a monophyletic group.

Wolfart (1968) assigned *Dalmanites australis* Clarke, 1890 (Maecuru Formation, Pará, Brazil), to *Malvinella* with question. Some of the derived characters shared with *Malvinella* s.s. are most parsimoniously resolved as symplesiomorphic (e.g., L3 flattened exsagittally; anterior margin of cephalic doublure pointed). The pointed cephalic doublure is otherwise known only in *Plesiomalvinella pujravii*, but is interpreted as homoplastic based on fit to other characters. Likewise, the distinctive diamond-shaped frontal glabellar lobe of *Malvinella* is also more generally distributed, retained by “*Palpebrops*” *goeldi* (Katzer),

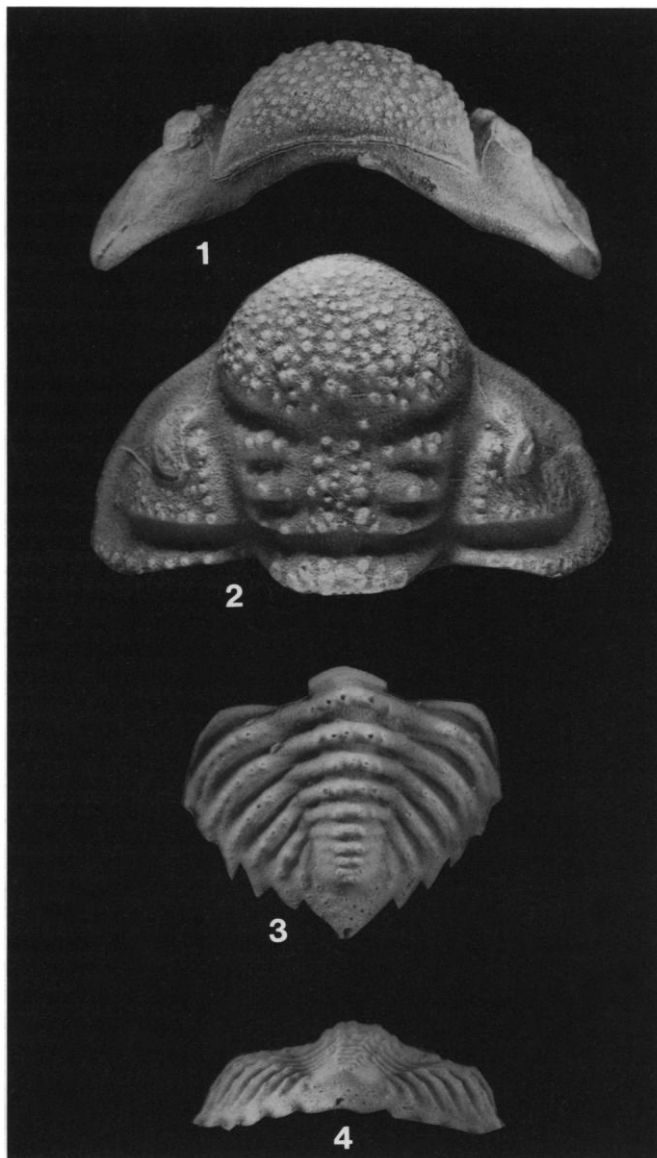


FIGURE 6—*Plesiomalvinella boulei* (Kozłowski, 1923), Belén Formation, Lower Member, La Paz Department, Bolivia. 1, 2, anterior and dorsal views of cephalon, internal mold, AMNH 44139,  $\times 1.5$ . Cahuanota; 3, 4, dorsal and posterior views of pygidium, latex cast from external mold, AMNH 44140,  $\times 1.5$ . Chacoma.

a species that shares additional derived characters with *Palpebrops donegalensis* and *Vogesina*.

#### MALVINELLA BUDDEAE n. sp. Figure 7.9, 7.10, 7.13, 7.15–7.17

*Malvinella haugi* WOLFART, 1968 non KOZŁOWSKI, p. 107, Pl. 18, figs. 2–4, Pl. 19, figs. 1–3, Pl. 20, fig. 1; BRANIŠA AND VANĚK, 1973, Pl. 3, figs. 5, 6; ELDRIDGE AND BRANIŠA, 1980, fig. 39C.

**Diagnosis.**—Cephalic lateral margin moderately divergent; length of cephalon 44–51 percent of width. Anterior part of frontal glabellar lobe nearly vertical (sag.). S2 relatively broad (tr.), convex forward. Anterior edge of eye weakly offset from axial furrow. Prosopon of relatively coarse spines, distinctly symmetrical rows on posteromedian glabellar region and posterior part of frontal lobe; single spine on L2. L0 moderately

high; S0 of moderate depth, length (sag.). Coarse spines on pygidial posterior pleural bands.

*Etymology.*—After Janice Budde, whose collection of excellent exoskeletons includes our type specimens.

*Types.*—Holotype AMNH 44144, internal mold of complete dorsal exoskeleton, from the Upper Member of the Belén Formation near Belén, La Paz Department, Bolivia. Paratypes AMNH 44143, internal mold of complete dorsal exoskeleton, and 44145, counterpart external mold of cephalon and partial thorax.

*Occurrence.*—Lower Member of the Belén Formation at Pujrivi, La Paz Department, Bolivia (Wolfart, 1968); Upper Member of the Belén Formation (*cornutus* Zone) at Belén, Cachuani, Cahuanota, Chacoma, Chiarumani, Letanias, Patacama, Pujrivi, La Paz Department, Bolivia (AMNH, USNM collections).

*Discussion.*—All Bolivian *Malvinella* have previously been referred to a single species, *M. haugi* (Kozłowski, 1923). However, Belén Formation collections (e.g., Wolfart, 1968) can be diagnosed as distinct from Icla Formation material, including specimens from the type locality, Padilla. The former occurrences form the basis for a distinct allopatric species, *M. buddeae* n. sp. The diagnoses list contrasting attributes of the two species. Wolfart's (1968) detailed description of "*M. haugi*" (= *M. buddeae*) is adequate for the new species.

MALVINELLA HAUGI (Kozłowski, 1923)  
Figure 7.1, 7.3, 7.5, 7.7, 7.8, 7.11, 7.12

*Anchiopella haugi* KOZŁOWSKI, 1923, p. 51, Pl. 2, figs. 11–14.

*Diagnosis.*—Cephalon broad (length 37–40 percent of width), with lateral margin strongly divergent. Anterior part of frontal glabellar lobe gently sloping (sag.). Glabella bulged (tr.) across S2–L3. S2 narrow, transverse. Anterior edge of eye distinctly offset from axial furrow. Fixigena swollen between palpebrum and axial furrow, notably in postocular area. Prosopon of densely distributed small spines; indistinct symmetry of spines on posteromedian glabellar region and frontal lobe; several spines on L2. L0 high; S0 long, deeply incised. Indistinct spines on pygidial posterior pleural bands.

*Occurrence.*—Icla Formation at Padilla (type locality), Chuquisaca Department, Bolivia.

*Discussion.*—Since *Malvinella haugi* has been illustrated only in Kozłowski's (1923) original work, additional cephalons from the type area are figured herein. The pygidium of this species is known from a single specimen from Padilla (Figure 7.11, 7.12). This differs from that of Belén Formation *M. buddeae* only in the absence of coarse spines on the posterior pleural bands. Morphology of the visual surface of the eye is only partly preserved on one specimen in our collections, with a maximum of seven lenses in dorsoventral files near the midlength of the visual surface.

#### Genus PALPEBROPS n. gen.

*Type species.*—*Palpebrops donegalensis* n. sp.

*Assigned taxa.*—*Phacops goeldi* Katzer, 1903, is informally referred to "*Palpebrops*" s.l.

*Diagnosis.*—Eye very large, elevated well above glabella. L0 rounded triangular (sag.), raised subequal to highest part of glabella. Short, bluntly angular genal spine.

*Etymology.*—From *palpebrum*, in reference to the raised palpebral lobe of the type species, and *ops*, Greek for eye.

*Discussion.*—A monotypic genus based on *P. donegalensis* n. sp. accommodates the scheme of relationships in Figure 4. This is an alternative to broadening the diagnosis of its sister group, *Vogesina* Wolfart, to include the new species. We have elected

to recognize a separate genus not only to weight the peculiar autapomorphies of *P. donegalensis* (most obvious being the greatly enlarged eyes). Retaining a restricted concept of *Vogesina* (cf. Wolfart, 1968) permits an additional taxonomic statement in the classification (i.e., monophyly of *V. aspera* and *V. lacunifera*, exclusive of *Palpebrops*). Although the pygidium of *P. donegalensis* is not available, the cephalon (including the hypostome) is sufficiently well known to firmly diagnose the taxon and establish its relationships.

Amazonian *Phacops goeldi* Katzer is resolved as sister group to *Palpebrops* + *Vogesina*, sharing the apomorphic convex (sag.) glabellar profile, and is informally referred to "*Palpebrops*" n. gen. Elevation of the palpebrum in "*P.*" *goeldi* is most profoundly expressed on the interocular fixigena, which is steeply inclined to the palpebral lobe. However, the extraocular gena and eye socle of "*P.*" *goeldi* are only raised comparable to that of *Malvinella haugi*. As such, a strongly elevated palpebrum is regarded as an autapomorphy for *Palpebrops donegalensis*.

#### PALPEBROPS DONEGALENSIS n. sp. Figure 8.7–8.13

*Diagnosis.*—As for genus.

*Types.*—Holotype AMNH 44147, internal mold of cephalon and parts of at least five thoracic segments, from the glacial rubble fields of Chacoma, La Paz Department, Bolivia, probably from the Belén Formation (Emsian). Paratype AMNH 44146, internal mold of cephalon, from Cahuanota, La Paz Department, apparently also from the Belén Formation.

*Etymology.*—After the Donegal Inn (now Malachy's), 72nd Street at Columbus Avenue, New York City.

*Description.*—Cephalic length (sag.) 43–46 percent of width (tr.). Frontal glabellar lobe protruding beyond arc of genae; genal margin gently shouldered anterolaterally; lateral margin nearly straight, diverging backward at 35–40 degrees to exsagittal line. Ventral margin with moderate anterior arch. Axial furrow relatively narrow, lightly incised, shallowest opposite L3, diverging at an angle of about 40 degrees posterior to S3, deflected anteriorly into deep, linear axial pit; axial furrow shallow anteriorly, continuing to cephalic border ridge in subparallel course. Preglabellar furrow narrow, shallow. Cranial anterior border ridge short (sag., exsag.), thick, extending to cephalic anterior margin or faintly preceded (sag.) by cephalic anterior border; margin rounded to faintly pointed. Cephalic anterior border reflected dorsally (sag.), nearly confluent with cranial anterior border ridge medially. Glabellar length 105–110 percent of width across frontal lobe. Posterior glabellar region evenly convex (sag.), declined posteroventrally (sag.) at about 20 degrees; L3 and posterior one-third of frontal lobe in roughly flat or weakly convex plane, anterior portion of frontal lobe curving anteroventrally, nearly vertical near preglabellar furrow. Frontal lobe about 60 percent length (sag.) of glabella, transversely ovate, length 65 percent of its width; strongly arched (tr.), bearing numerous small, low spines. Anterior branch of facial suture running immediately abaxial to anterior pits, deflected inward outside anterolateral edge of glabella; weakly flexed dorsally (sag.) bounding cranial anterior border ridge. In dorsal orientation, posterior branch of facial suture gently curved forward between  $\epsilon$  and  $\omega$ ;  $\omega$  just behind  $\epsilon$ . P.M.I. and A.I.S. indistinct. S3 moderately impressed, non-apodemal, nearly straight for most of length, inclined anterolaterally at about 35 degrees to transverse line, proximal end flexed backward. S3 shallow adjacent to axial furrow, distal end weakly meeting axial furrow at anterior part of anterior pits. L3 wedge shaped, weakly convex outward along axial furrow; L3 lateral lobe raised above exsagittal part of frontal lobe, faintly convex (tr.), gently declined abaxially.

ially, sagittal region raised above lateral lobe. S2 short (tr.) apodemal pits, straight, faintly inclined adaxially, with faint incision distally. L2 flattened (tr.), more strongly declined exsagittally than L3. S1 distinctly incised to axial furrow, short (tr.), apodemal, convex backwards, inclined anteromedially. L1 short (sag., exsag.), depressed well below L2 exsagittally; distance between S0–S1 apodemes 50–60 percent of that of S1–S2. Two rows of spines aligned anteroposteriorly on posterior region of glabella; inner pairs between distal ends of S3–S1, on L3–S2. One spine on each of L3–L1 lateral lobes. S0 shallow, about 30 percent length of L0 (sag.), weakly shortening exsagittally and impressed as deep, transverse apodemal grooves, anterior margin gently flexed forward sagittally. L0 longest medially, length 30 percent of width, rounded, strongly convex, raised well above posterior region of glabella, anterior edge less steeply inclined than posterior edge; L0 bearing row of four weak tubercles behind midlength, two smaller tubercles in front of midlength. Interocular fixigena steeply inclined to palpebral lobe, with a subduced spine opposite posterior edge of eye. Large Eye Index 0.47. Anterior edge of eye abutting axial furrow, opposite anterolateral corner of L3; palpebral lobe moderately oblique (exsag.), posterior edge well removed from axial furrow, opposite anterodistal part of S1. Palpebral lobe reniform, strongly raised above fixigena, prominently inflated above visual surface of eye; palpebral furrow well impressed, strongly curved. Visual field bearing 23 dorsoventral lens files, with maximum of six lenses per file; outer face of visual field vertically inclined. Librigena oversteepened beyond vertical beneath short eye socle, with rather abrupt break in slope (“dishing”) and moderate declination to posterior border furrow. Postocular fixigenal field 35 percent length (exsag.) of eye. Posterior border furrow short (sag., exsag.), shallow, nearly straight, transverse, distal part weakly oriented posterolaterally. Lateral border furrow broad (tr.), shallow, very weakly incised posterolaterally, faintly continuous with posterior border furrow. Posterior border short, moderately convex (exsag.) adjacent to axial furrow, set below interocular fixigena, lengthening toward genal angle, bearing a few small tubercles; border weakly constricted near base of genal spine. Genal spine convex, projecting posterolaterally in arc of lateral margin. Lateral border gently convex, narrow anteriorly; gradually flattening, broadening, less steeply declined posterolaterally. Anterior furrow bounding cranial anterior margin, shallowing, shortening medially. Cephalic doublure flattened anteromedially, inclined at 25 degrees to horizontal, set below thick (sag., exsag.), low cephalic anterior border ridge, arched

forward, rounded anteromedially; doublure short, more steeply inclined distally against hypostomal anterior wing, pinching out distal to hypostomal suture. Hypostomal suture gently convex forward. Doublure and dorsal surface of cephalon with pervasive dense granulation.

Hypostomal width about 170 percent of length. Anterior wing broad, wing process absent. Middle body about 85 percent length (sag.) of hypostome, subcircular in outline, rounded posteriorly and laterally, with broadly rounded anteromedian process, moderately arched (tr.), with strongest convexity laterally; nearly flat in lateral view for most of length (sag.), convex posteriorly. Anterior margin of middle body well defined sagittally, with anteromedian process bulging above anterior border. Anterior and lateral border furrow shallow, poorly defined; border furrow obsolete anterolaterally bounding anterior wing. Maculae indistinct. Middle furrow obsolete, definition of anterior and posterior lobes of middle body obscure. Lateral border narrow, separated from middle body by abrupt change in slope. Posterior border very short, of even length (sag., exsag.), lacking marginal spines.

“PALPEBROPS” GOELDI (KATZER, 1903)  
Figure 8.1–8.4

*Phacops goeldi* KATZER, 1903, p. 277, Pl. 15, figs. 6a–d.

*Malvinella goeldi* (KATZER). ELDRIDGE AND ORMISTON, 1979, p. 160.

*Types.*—Lectotype NYSM 9828, internal mold of fragmentary cephalon (figured Katzer, 1903, Pl. 15, figs. 6a, b; Figure 8.1, 8.2, 8.4), from the Maecuru Formation, Lontra Member, Rio Maecuru, Pará, Brazil; designated herein. Paralectotype NYSM 9829, internal mold of glabella (Katzer, 1903, Pl. 15, fig. 6c; Figure 8.3), from same locality.

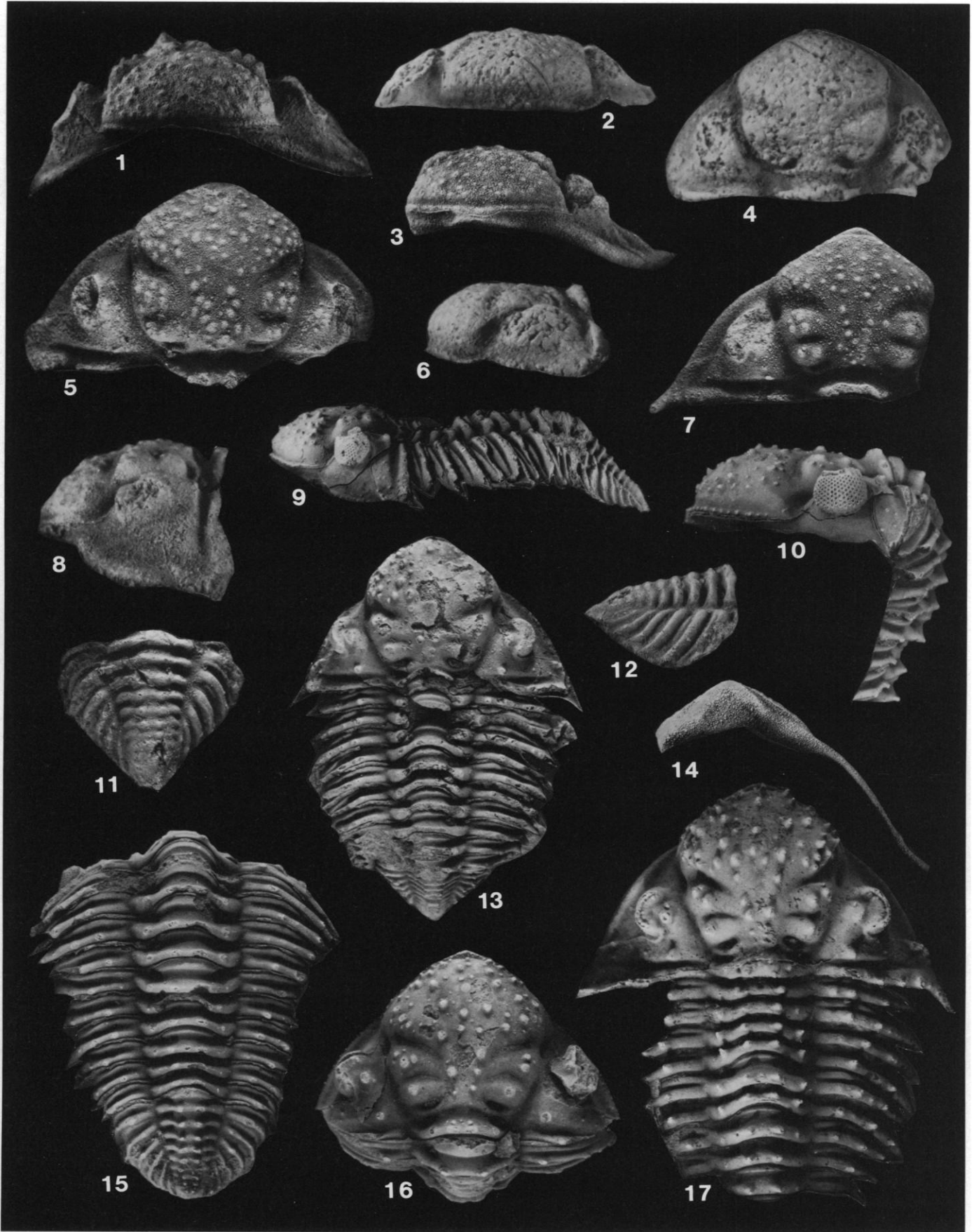
*Remarks.*—Character coding in Table 1 serves as a description of this species, along with illustration of the type specimens. Morphology of the visual surface is partially preserved on the lectotype’s right eye. The number of dorsoventral lens files is inferred to be relatively small; the anterior 10 files appear to represent more than half of the length of the visual surface. At least five lenses are present in files at or near midlength, but the uppermost surface of the visual field is eroded.

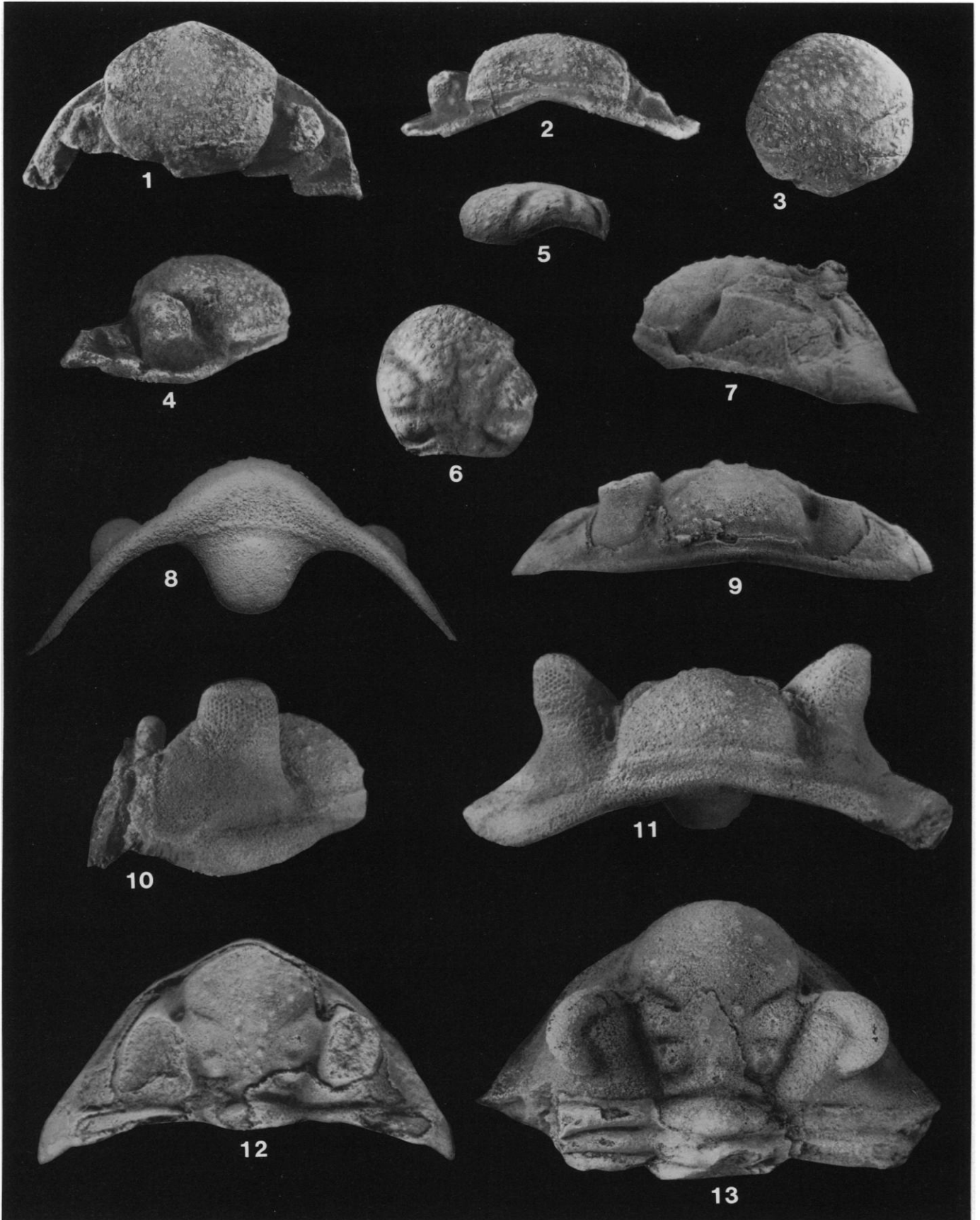
Genus VOGESINA Wolfart, 1968

*Type species.*—*Acaste devonica* Ulrich, 1892. By original designation.

FIGURE 7—*Malvinella* spp. 1, 3, 5, 7, 8, 11, 12, 14, *Malvinella haugi* (Kozłowski, 1923), Icla Formation, Padilla, Chuquisaca Department, Bolivia. 1, 5, 8, anterior, dorsal, and left lateral views of cephalon, AMNH 44141,  $\times 2$ ; 3, 7, 14, anterior, dorsal, and ventral views of cephalon, AMNH 44142,  $\times 2$ ; 11, 12, dorsal and right lateral views of pygidium, USNM 449772,  $\times 2$ . 2, 4, 6, “*Malvinella*” *australis* (Clarke, 1890), Maecuru Formation, Lontra Member, Rio Maecuru, Pará, Brazil, anterior, dorsal, and left lateral views of cast of holotype cephalon (Clarke, 1890, Pl. 2, figs. 11, 13), NYSM 4274 (original MNRJ 3389),  $\times 4$ . 9, 10, 13, 15–17, *Malvinella buddeae* n. sp., Belén Formation, Upper Member, near Belén, La Paz Department, Bolivia. 9, 13, left lateral and dorsal views of paratype exoskeleton, AMNH 44143,  $\times 1.5$ ; 10, 15, 16, left lateral, dorsal thoracopygidial, and dorsal cephalic views of holotype exoskeleton, AMNH 44144,  $\times 2$ ; 17, dorsal view of paratype cephalon and nine thoracic segments, AMNH 44145 (counterpart to 9, 13),  $\times 2$ . All internal molds except 17, latex cast of external mold, 2, 4, 6, plastic cast of internal mold.

FIGURE 8—*Palpebrops* and “*Vogesina*” s.l. 1–4, “*Palpebrops*” *goeldi* (Katzer, 1903), Maecuru Formation, Lontra Member, Rio Maecuru, Pará, Brazil. 1, 2, 4, dorsal, anterior, and right lateral views of lectotype cephalon (Katzer, 1903, Pl. 15, figs. 6a, b), NYSM 9828,  $\times 2$ ; 3, dorsal view of paralectotype glabella (Katzer, 1903, Pl. 15, fig. 6c), NYSM 9829,  $\times 2$ . 5, 6, “*Vogesina*” *gemellus* (Clarke, 1890), Maecuru Formation, Lontra Member, Rio Maecuru, Pará, Brazil, left lateral and dorsal views of plastic cast of syntype glabella (Clarke, 1890, Pl. 2, fig. 14), NYSM 4323,  $\times 1.5$ . 7–13, *Palpebrops donegalensis* n. sp. 7, 9, 12, left lateral, anterior, and dorsal views of paratype cephalon, AMNH 44146,  $\times 3$ , from Cahuanota, La Paz Department, Bolivia, probably from the Belén Formation; 8, 10, 11, 13, ventral, right lateral, anterior, and dorsal views of holotype cephalon and anterior part of thorax, AMNH 44147,  $\times 3$ , from Chacoma, La Paz Department, Bolivia, probably from the Belén Formation. All internal molds except 5, 6, plastic cast of internal mold.





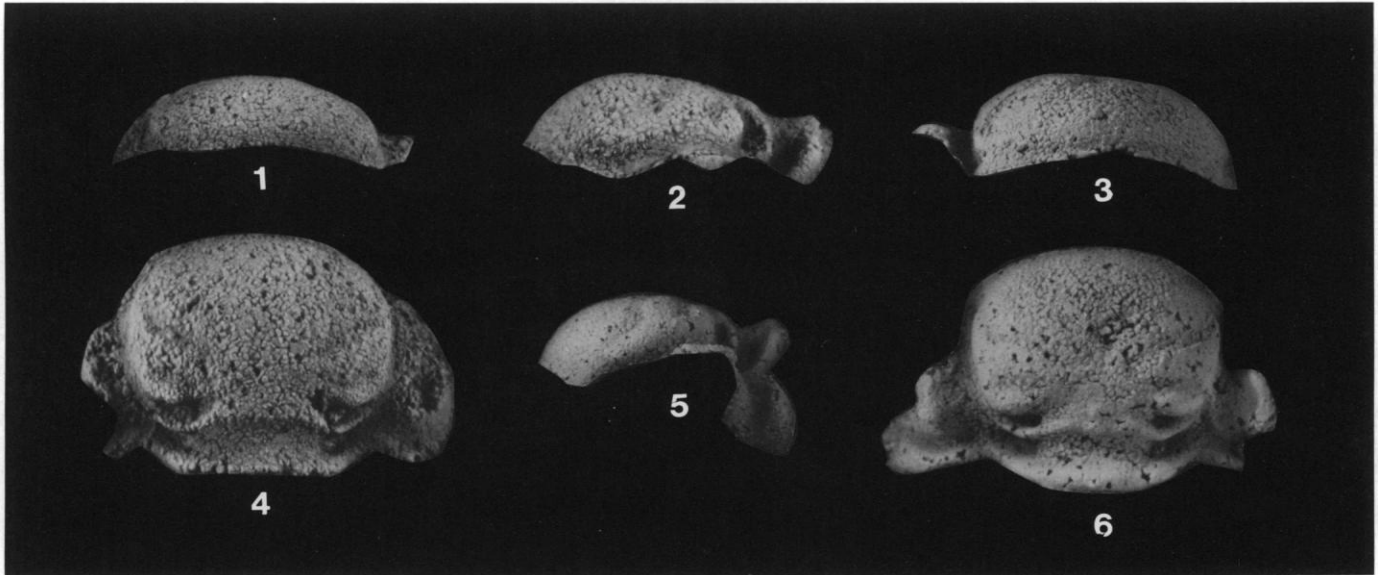


FIGURE 9—Calmoniinae gen. indet. *galea* (Clarke, 1890), Maecuru Formation, Lontra Member, Rio Maecuru, Pará, Brazil. 1, 2, 4, anterior, left lateral ( $\times 3.5$ ), and dorsal views of cephalon, NYSM 16138; 3, 5, 6, anterior, left lateral, and dorsal views of cranium, NYSM 16139. Internal molds,  $\times 3$  except where indicated.

**Assigned taxa.**—*Phacopina (Vogesina) aspera* Wolfart, 1968; *Phacopina (Vogesina) lacunifera* Wolfart, 1968. *Dalmanites gemellus* Clarke, 1890, is referred to "*Vogesina*" s.l.

**Diagnosis.**—Cephalic outline nearly semicircular; cephalon steeply arched (tr.); glabella strongly convex (sag.). Cephalic doublure and anterior border ridge not in contact sagittally. Axial furrow weakly divergent; anterior pit developed as elongate apodemal groove. Glabellar furrows (particularly S3) elongate but weakly incised; S3 steeply inclined exsagittally. Palpebral furrow weak; palpebral rim low. Hypostomal middle body strongly convex, of nearly circular outline, clearly differentiated anteriorly by distinct break in slope. Pygidium elongate, triangular, lacking marginal spines. Pleural field strongly convex, composed of eight or nine ribs; interpleural furrows very shallow. Axis with 11 or 12 rings. Exoskeleton lacks spinose prosopon.

**Discussion.**—The diagnosis of *Vogesina* outlined above might be specified as *Vogesina* s.s. It lists the numerous synapomorphies grouping Bolivian species, and corresponds to Wolfart's (1968) concept of the clade. *Vogesina* s.l. could be broadly diagnosed to include "*Dalmanites*" *gemellus* (Figure 8.5, 8.6), which shares (apomorphic) weakly divergent axial furrows and steeply inclined S3. Many of the shared derived characters of *Vogesina* s.s. are missing data for "*D.*" *gemellus*, rendering their diagnostic value ambiguous.

Wolfart (1968) originally classified *Vogesina* as a subgenus of *Phacopina* Clarke, 1913. Although affording *Vogesina* full generic status, Eldredge and Ormiston (1979) and Eldredge and Cracraft (1980) likewise regarded it as a plesiomorphic calmoniid. Affinities to *Malvinella* were first proposed by Eldredge and Braniša (1980, p. 246). Cooper (1982, p. 63) endorsed this view, citing hypostomal characters and the strong reduction of L1, also shared with *Bouleia* and *Parabouleia*. The discovery of *Palpebrops donegalensis* provides additional evidence, with its combination of *Malvinella*- and *Vogesina*-like character states (and intermediate states in such features as vaulting of the hypostomal middle body). A deep anterior apodemal pit in the cephalic axial furrow provides a distinctive synapomorphy of

*Malvinella*, *Palpebrops*, and *Vogesina*. Figure 4 depicts *Vogesina* nested within the "*Malvinella* group," and outlines a sequence in which characters are transformed and acquired in this clade.

*Dalmanites galea* Clarke, 1890 (Maecuru Formation, Pará, Brazil) was referred to "n. Gen. aff. *Vogesina*" by Eldredge and Ormiston (1979) and Cooper (1982). These affinities would imply that this species is within the "*Malvinella* group." The most obvious derived character shared with *Dalmanites galea* (Figure 9) is shortened (exsag.) L1. However, uniquely grouping this taxon with *Vogesina* would demand reversal or loss of several characters defining nodes of the "*Malvinella* group" outside *Vogesina* (e.g., loss of anterior pits in the cephalic axial furrow; S3 sinuous, with distinct proximal and distal moieties). Many similarities to *Vogesina* are general for Calmoniinae, including the absence of cuticular spines, S2 and S3 weakly impressed, and a weakly defined palpebral furrow. It may be more parsimonious to consider closest relations to certain taxa of "Calmoniidae plesiomorphs" (sensu Eldredge and Ormiston, 1979) such as *Phacopina* Clarke, 1913, or possibly *Schizostylus* Delo, 1935. *Dalmanites galea* resembles *Schizostylus (Curuyella)* Eldredge and Braniša, 1980, in the convex form of S1, short (exsag.) L1, and L0 flexed forward abaxially. The two taxa readily differ, however, in eye position, course of the anterior branch of the facial suture (well removed from the anterolateral corner of the glabella in *D. galea*), and form of the cephalic anterior border. *Phacopina braziliensis* Clarke, 1890, also shares short L1, and likewise has the posterior edge of the palpebral lobe closely approximating the cephalic posterior border furrow. At present, the relationships of *Dalmanites galea* are ambiguous, and the species is regarded as Calmoniinae genus indeterminate.

**Remarks.**—Examination of large collections confirms Wolfart's (1968) distinction of two species of *Vogesina* in the Lower and Upper Members of the Belén Formation. Diagnostic characters of *V. lacunifera* and *V. aspera* listed by Wolfart (1968) allow accurate identification of these species. Coding of morphological characters in Table 1 lists additional differentia.

As Wolfart (1968) observed, *V. devonica* is known only from Ulrich's Chahuarani types. The holotype cephalon most closely



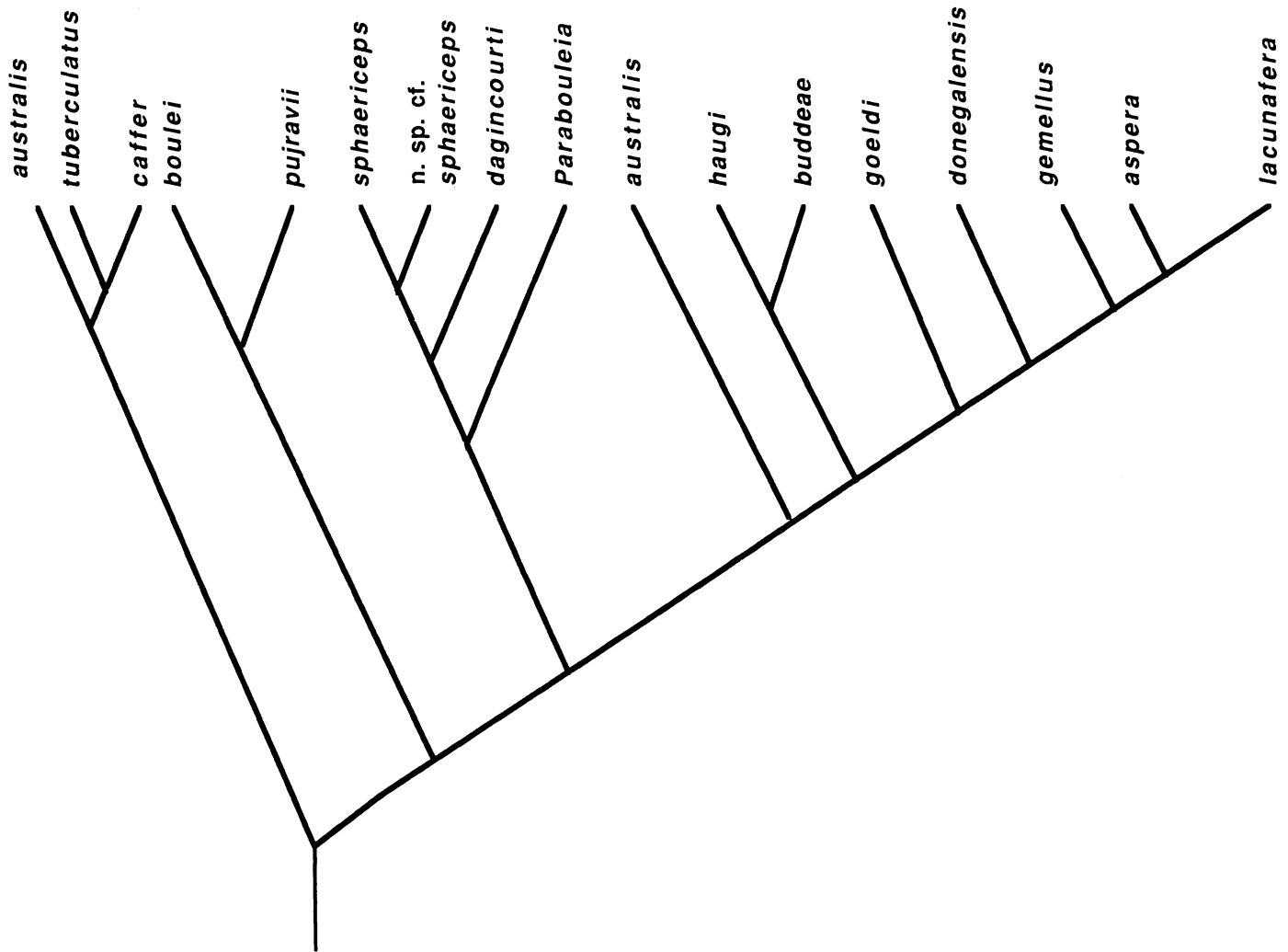


FIGURE 10—Taxonomic cladogram used as basis for constructing area cladograms. Topology is as in Figure 4, with *Metacryphaeus australis* (Clarke) added as sister taxon to *M. tuberculatus* + *M. caffer*, and species differentiation shown for *Bouleia* (*B. sphaericeps* + n. sp. cf. *sphaericeps*) *B. dagincourti*).

resembles *V. lacunafera* Wolfart, but exhibits genal arching beyond the norm for the other two species of *Vogesina*. Although there is considerable variability in this character for both *V. aspera* and *V. lacunafera*, we are unable to find any specimens exhibiting *V. devonica*'s degree of cephalic arching. Several cephalons from the Icla Formation in the region of the type locality of *V. devonica* can, however, be assigned to *V. lacunafera*.

#### BIOGEOGRAPHY

Species cladograms afford a phylogenetic basis for investigating historical biogeography (see Humphries and Parenti, 1986). The minimum length cladogram in Figure 4 serves as a hypothesis against which the spatial differentiation of the "Malvinella group" is examined. A few species in addition to those considered in parsimony analysis have been incorporated into the cladogram (Figure 10); *Metacryphaeus australis* (Clarke, 1913) is interpreted as most closely related to *M. tuberculatus* + *M. caffer*, and *Bouleia* includes at least two species, *B. dagincourti* (Ulrich, 1892) and *B. sphaericeps* (Kozłowski, 1923) (see Eldredge, 1972). This latter group was given a single, basal coding in the parsimony analysis. Cephalons from the Gamonedá-Curuyo region of southern Bolivia assigned to *B. sphaericeps* by

Braniša (1965, Pl. 20, figs. 10, 27) evidently represent a new species. This taxon ("cf. *sphaericeps*" in Figure 10) is regarded as most closely related to *B. sphaericeps*.

When all of these species are considered, *Metacryphaeus* s.s. and the "Malvinella group" have representatives in most of the major basins of the Malvinokaffric Province (Copper, 1977, fig. 1); these include the Paraná Basin (southern Brazil), Malvinas shelf, South Africa, Parnaíba Basin (northeastern Brazil), Amazon Basin (north-central Brazil), and the Andean shelf. Treating these major geographic regions as analytical areas, cladistic relationships of the "Malvinella group" predict the pattern of fragmentation of the Malvinokaffric biota in Figure 11.

The Emsian "Malvinella group" fauna of the Amazon Basin (Maecuru Formation) is most closely related to that of the Andean shelf, indicating that these geographic areas share a more recent history than they do with other areas of the Malvinokaffric Province. This differs from Copper's (1977) interpretation of the Amazon biota as having Appalachian Province affinities, closer to the Devonian faunas of Colombia and Venezuela (see also Melo, 1988, p. 682). However, the Amazon Basin does not map on the area cladogram as a unique area; different Amazonian species are nested within a diverse Andean clade. This

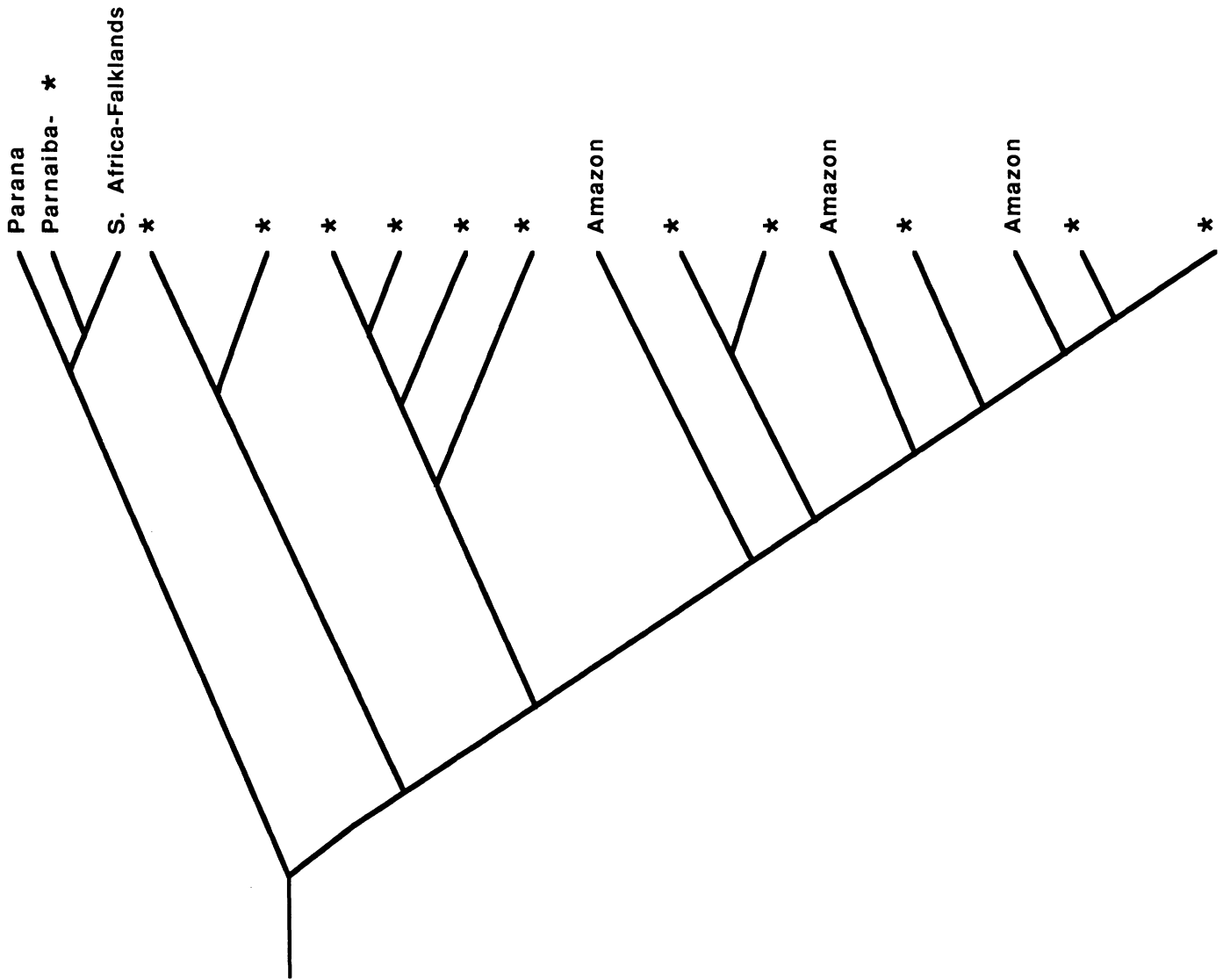


FIGURE 11—Area cladogram for sedimentary basins of the Malvinokaffric Province (Copper, 1977, fig. 1), derived from taxonomic cladogram in Figure 10. Asterisks indicate species endemic to the Andean shelf.

“paraphyletic” topology suggests a complex geological history, extensive taxic dispersal, or missing data.

It is, however, evident that the Amazon should be considered within the “Austral Andean Province” of Baldis (1979). The “*Malvinella* group” does not provide unambiguous support for Baldis’ (1979) Malvinokaffric Province (restricted to southeastern South America, the Falkland Islands, and South Africa) as a natural area, since no monophyletic taxon is endemic to that area. Popp and Baldis (1989) have since split this region into two provinces, Malvinokaffric (South Africa + Falklands) and Brazilian. They also proposed Central Andean and Amazon Provinces, the latter including the Amazon and Parnaíba basins. We conclude that taxa of the “*Malvinella* group” do not provide any evidential support for this grouping; rather, they predict a closer relationship between Amazon and Andean faunas than between Amazon and Parnaíba elements.

The timing of vicariance of the Andean–Amazon region from the rest of the Malvinokaffric Province (in the broad sense of Eldredge and Ormiston, 1979) can be calibrated by the strati-

graphic occurrences of ingroup species. *Parabouleia calmonensis* Eldredge, 1972, is the earliest occurring species considered, known from the late Siegenian (Isaacson, 1977) *Scaphiocoelia* Zone of Bolivia. Figure 10 indicates that *Parabouleia calmonensis* is nested three nodes from the base of the “*Malvinella* group” cladogram. This implies that these (nodal) events of differentiation reflect pre-late Siegenian history. We infer that a widespread undifferentiated fauna would necessarily be of Siegenian or earlier age. Since Siegenian marine sediments are absent in Amazonia (Dineley, 1984, fig. 7.16A), it is most plausible that the Emsian fauna of the Amazon Basin was introduced by the range extension of an Andean biota with an earlier history. “Calmoniid genus and species indeterminate A” of Eldredge and Braniša (1980) appears to be even more closely related to *Malvinella* than is *Parabouleia*, and is also known from the *Scaphiocoelia* Zone. Although the relationships of this poorly known taxon are ambiguous, affinities to *Malvinella* would imply that this group had differentiated from *Palpebrops* + *Vogesina* by the late Siegenian.



FIGURE 12—Geographic location of “areas” used in analysis of Andean shelf historical biogeography. Area 1 (Belén–La Paz–Sicasica), 2 (Icla–Padilla), 3 (Tarija), and 4 (San Juan Province).

The diversity of species within the Andean region begs the question of whether or not more finely resolved biogeographic patterns can be discerned. Eldredge and Braniša (1980) recognized three biogeographic areas in Bolivia for the *Scaphiocoelia* Zone fauna. These (northern) Belén–La Paz–Sicasica, (east-central) Icla–Padilla, and (southern) Tarija regions each have mappably distinct formations (Isaacson, 1977). Species of the “*Malvinella* group” are known from each of these regions, as well as from the San Juan Province, Argentina (*Bouleia dagincourti*; Baldis, 1967). The “Sicasica” fauna from near Lake Titicaca in Peru (Newell, 1949) is comprised only of species known from the Belén–La Paz–Sicasica region (including *Plesiomalvinella boulei* and *Vogesina lacunafera*), and is therefore treated as part of that region. The only record of the “*Malvinella* group” from the Tarija region is *Bouleia* n. sp. cf. *B. sphaericeps* from Curuyo, discussed above. As such, the relationships of four “areas” within the Andean region can be analyzed (Figure 12).

Substituting the geographic occurrences of species into the

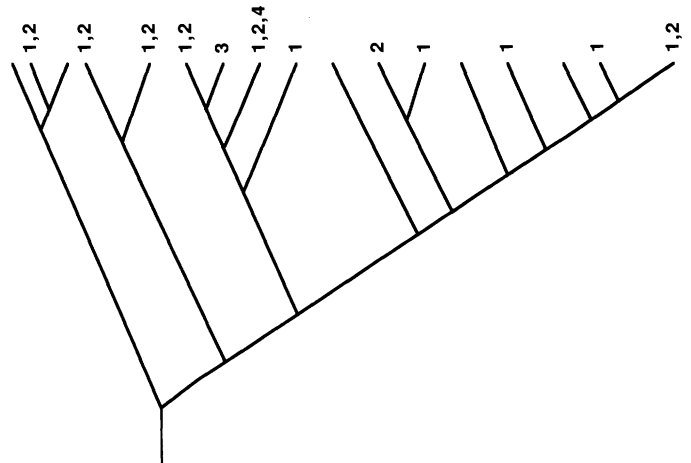


FIGURE 13—Area cladogram for Andean shelf species, based on taxonomic cladogram in Figure 10. Areas 1–4 are as shown in Figure 12. Terminals without numbers are of non-Andean occurrence (cf. Figure 11).

taxonomic cladogram, the resultant area cladogram (Figure 13) does not readily reveal informative patterns. *Malvinella* provides an instance of sister species endemic to either the Belén–La Paz–Sicasica area or to the Icla–Padilla area, suggestive of vicariance of these areas or allopatric differentiation. Species of *Pennaia* Clarke (“*Calmonia* group”) are likewise differentiated in this pattern (Edgecombe, in press). However, the preponderance of redundant areas in a random pattern and several widespread (undifferentiated) species render any general patterns of Andean vicariance unretrievable. Widespread species are particularly concentrated at the basal branches. It is possible that the complex scheme of area relationships reflects complex history (e.g., overprinting of earlier patterns of area relationship by younger ones; interconnectedness of the “areas” might be altered with successive transgressive-regressive cycles. An alternative is that the “areas” used in the analysis are not natural areas for the post-*Scaphiocoelia* Zone faunas, but merely artifacts of present geography (e.g., outcrop areas). Increased collecting and better knowledge of tectonic regional events might allow resolution of the complex scheme of taxonomic differentiation.

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## APPENDIX

Characters used in phylogenetic parsimony analysis, with alternative character states in parentheses. '0' is plesiomorphic state, '1'–'3' apomorphic states. See Table 1 for taxon/character matrix.

0. Course of cephalic margin: (0) protuberant axial region; (1) margin semicircular.
1. Proximity of cephalic anterior border ridge and cranial anterior margin: (0) in contact sagittally; (1) separated by narrow strip of border.
2. Angularity of anterior margin of cephalic doublure: (0) rounded; (1) pointed.
3. Cranial anterior border ridge: (0) absent; (1) present.
4. Anterior apodemal pits in axial furrow: (0) absent; (1) present.
5. Divergence of cephalic axial furrows: (0) weakly divergent (subparallel); (1) strongly divergent.
6. Incision and width of cephalic axial furrows: (0) shallow, narrow; (1) deep, broad; (2) deep, narrow.
7. Course of cephalic axial furrows: (0) straight; (1) curved outward between S1–S3.
8. Convexity (sag.) of glabella: (0) planar; (1) weakly convex; (2) strongly convex, depressed L1 part of even curve.
9. Angularity of exsagittal region of frontal glabellar lobe: (0) smoothly rounded; (1) angular, frontal lobe diamond-shaped.
10. Posterior median impression in frontal lobe: (0) rounded impression; (1) longitudinal groove.
11. Inclination of S3 to transverse plane: (0) gentle; (1) steep.
12. Convexity of S3: (0) straight or sinuous; (1) evenly convex forward, proximal end flexed posteriorly.
13. Incision of distal part of S3, immediately adjacent to axial furrow:

- (0) deep, S3 strongly confluent with axial furrow; (1) shallow, S3 at most weakly confluent with axial furrow.
14. L3 incorporated into strongly inflated frontal glabellar lobe: (0) absent; (1) present.
  15. Topographic separation of frontal glabellar lobe from L3 by incision of S3: (0) present; (1) absent.
  16. Transverse profile of L3: (0) arched, convex; (1) flattened.
  17. Elevation of L2–L3 lateral glabellar lobes (exsag.): (0) low, recessed; (1) raised above exsagittal part of frontal lobe.
  18. Incision of S2–S3: (0) deeply incised; (1) elongate but nearly effaced.
  19. Width (tr.) of S2: (0) transverse; (1) narrow, apodemal pits.
  20. Number of coarse spines on L2 lateral glabellar lobes: (0) 0; (1) 1 or 2.
  21. Two symmetrical rows of sagittal spines on posterior glabellar region: (0) absent; (1) present.
  22. Length of L1 (exsag.): (0) subequal to or slightly shorter than L2; (1) much shorter than L2.
  23. Depression of L1 lateral lobes: (0) level with L2; (1) depressed below L2.
  24. Number of coarse spines on L1 lateral lobes: (0) 0; (1) 1 or 2.
  25. Length of S0 (sag.): (0) long (equal to sagittal length of L0); (1) short (much less than length of L0).
  26. Incision of S0: (0) shallow; (1) deep.
  27. Elevation of L0: (0) not elevated above posterior glabellar region; (1) elevated above posterior glabellar region.
  28. Shape of L0 (sag.): (0) evenly convex or flat; (1) triangular, sloping anteroventrally.
  29. Number of coarse spines on L0: (0) 0; (1) posterior row of 4 spines, with 2 anteriorly; (2) 3 or 5 (with sagittal spine); (3) more than 10.
  30. Eye position (exsag.): (0) proximal (anterior part of palpebrum contacts axial furrow); (1) distal (anterior part of palpebrum does not contact axial furrow).
  31. Eye length: (0) short (posterior margin of eye anterior to distal end of S1); (1) long (posterior margin of eye parallel to or behind distal end of S1).
  32. Definition of palpebral lobe: (0) palpebral furrow strong, palpebral rim swollen; (1) palpebral furrow weak, palpebral rim low; (2) palpebral furrow obsolete, eye set on tall stalk.
  33. Single spine or discrete spine cluster between palpebral lobe and axial furrow: (0) absent; (1) present.
  34. Raised swelling on fixigenal inter-/postocular area: (0) absent; (1) present.
  35. Genal width: (0) wide (cephalon semi-ovate); (1) narrow (cephalon semi-circular).
  36. Course of facial suture between  $\epsilon$  and lateral border furrow: (0) strongly recurved anteriorly; (1) with posterolateral course.
  37. Genal spine: (0) long and slender, constricted at base; (1) blunt or blade-like.
  38. Arching of librigena anterolateral to eye: (0) librigena broad (in dorsal orientation); (1) librigena narrow or concealed beneath eye.
  39. Librigenal/cephalic anterior border spines: (0) absent; (1) present.
  40. Hypostomal outline: (0) long, subrectangular, lateral margins subparallel; (1) short, subtriangular.
  41. Convexity of hypostomal middle body: (0) low (weakly convex); (1) moderate (arched); (2) high (hemispherical).
  42. Incision of hypostomal middle furrow: (0) distinctly defined; (1) effaced.
  43. Maculae: (0) very distinct; (1) weak or indistinct.
  44. Hypostomal marginal spines: (0) long spines; (1) short denticles; (2) absent.
  45. Number of spines on thoracic axial rings: (0) 0; (1) 2; (2) 4 or 5.
  46. Pygidial size: (0) isopygous; (1) micropygous.
  47. Pygidial shape: (0) short, broad; (1) elongate, triangular.
  48. Number of spines on pygidial axis: (0) 0; (1) 2; (2) 3–5.
  49. Depth of pygidial interpleural furrows: (0) much shallower than pleural furrows; (1) much deeper than pleural furrows.
  50. Pygidial pleural terminae: (0) lappets; (1) spinose, non-lappeted; (2) aspinose, non-lappeted.