

**Devonian trilobites from the Amazonas Basin: systematic diversity,
taphonomy, and biogeographic significance**
Trilobitas devonianos da Bacia do Amazonas: diversidade sistemática,
tafonomia e importância biogeográfica

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Abstract: Although the Devonian invertebrate biota of the Amazonas Basin is incompletely known, its unusual mixture of supposedly Malvinokaffric and Appalachian taxa is of considerable biogeographical interest. The history of research on Devonian trilobites from the Amazonas Basin is summarized. These fossils occur in the Maecuru (latest Emsian – early Eifelian) and Ererê (latest Eifelian – early Givetian) formations, representing the families Homalonotidae, Dalmanitidae, and Calmoniidae. Trilobite diversity is higher in the Maecuru (nine named plus six indeterminate *taxa*) than the Ererê Formation (with only two named *taxa*), which displays faunal impoverishment generally. None of the Devonian Amazonas Basin trilobite species is known from other Malvinokaffric sites, suggesting very high endemism within this basin. A taxonomic revision of "*Homalonotus*" *derbyi* (Clarke, 1890) is presented and a lectotype is designated. A lectotype and paralectotype are also designated for *Eldredgeia paituna* (Hartt & Rathbun, 1875). Some taphonomic observations of fossils from the Maecuru Formation are made, and a brief biogeographic synopsis of the Devonian Amazonas biota is also given.

Keywords: Amazonas Basin. Devonian. Homalonotidae. Dalmanitidae. Calmoniidae. Trilobites.

Resumo: Embora a fauna de invertebrados devonianos da Bacia do Amazonas ainda não seja completamente conhecida, sua excepcional mistura de taxa de afinidades Malvinocáfricas e Apalachianas é de considerável interesse biogeográfico. A história da pesquisa sobre os trilobitas devonianos da Bacia do Amazonas é resumidamente apresentada. Estes fósseis ocorrem nas formações Maecuru (Emsiano terminal – Eoefeliano) e Ererê (Eifeliano terminal – Eogivetiano), estando representados pelas famílias Homalonotidae, Dalmanitidae e Calmoniidae. Na Formação Maecuru, a diversidade de trilobitas é maior (nove *taxa* identificados, além de outros seis *taxa* indeterminados) do que na Formação Ererê (com apenas dois *taxa* identificados), esta última apresentando um empobrecimento da fauna de um modo geral. Nenhuma das espécies de trilobitas devonianos da Bacia do Amazonas é encontrada em outras regiões Malvinocáfricas, o que sugere um alto grau de endemismo nesta bacia. Uma revisão taxonômica de "*Homalonotus*" *derbyi* (Clarke, 1890) é apresentada, e um lectótipo é designado. Também são designados um lectótipo e um paralectótipo para *Eldredgeia paituna* (Hartt & Rathbun, 1875). São realizadas algumas observações tafonômicas dos fósseis da Formação Maecuru, assim como um breve resumo sobre a biogeografia da fauna devoniana da Bacia do Amazonas.

Palavras-chave: Bacia do Amazonas. Devoniano. Homalonotidae. Dalmanitidae. Calmoniidae. Trilobitas.

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INTRODUCTION

Of all the Paleozoic sedimentary basins in Brazil, the remoteness of Amazonas Basin, coupled with the paucity of exposures, has imposed severe limitations upon research on its Devonian fossils. Despite this, past investigations nevertheless suggest that the Amazonas Basin was extremely important biogeographically during the Devonian, as a transitional “biogeographic boundary mixing area” (Boucot & Racheboeuf, 1993) characterized by the co-occurrence of Eastern Americas brachiopods and Malvinokaffric trilobites. Unfortunately, the literature dealing with these fossils (especially trilobites) is widely scattered. In an attempt to rectify this situation, the present paper reviews the history of research on, and the systematic diversity of Devonian trilobites from the Amazonas Basin. Additionally, taphonomic observations are provided in order to improve understanding of the depositional environments in which these fossils occur, especially regarding the Maecuru Formation. Finally, a brief biogeographic synopsis of the Amazonas Devonian biota is presented, with emphasis on similarities and differences from Andean and Appalachian biotas.

The first Devonian trilobites described from the Amazonas Basin were *Dalmania paituna* Hartt & Rathbun (1875) and *Homalonotus oiara* Hartt & Rathbun (1875), collected during the Morgan Expeditions, in 1870 and 1871, around the village of Ererê, in the State of Pará, Brazil. At that time, the Ererê sandstone was considered to be of Middle Devonian age and was correlated with the Hamilton Group of New York. Modern palynological data indicate that the Ererê Formation is latest Eifelian to early Givetian (Grahm & Melo, 2004).

Another expedition, undertaken by the “Comissão Geológica do Império do Brasil” (1876), carried out a further examination of the Ererê district and resulted in the discovery of richly fossiliferous Devonian deposits along the Maecuru and Curuá rivers.

Marine invertebrate macrofossils occur in the upper part of the Maecuru Formation [(*sensu stricto* after Derby (1878) and Cunha *et al.* (2007))] and in the lower level of the Ererê Formation.

Clarke (1890) described the trilobites from Maecuru and Ererê formations. For many years afterward, no taxonomic revision was made for the Amazonian trilobites and subsequent papers used only Clarke's original designations.

Clarke (1913) coined the generic name *Phacopina* with the type species *Phacops braziliensis* Clarke, 1890. Other supposed *Phacopina* species from North America included by him, are no longer considered to belong to this genus (Eldredge & Branisa, 1980, p. 240). Eldredge & Ormiston (1979) presented a “Master List” with all the known genera and subgenera of Malvinokaffric trilobites, and discussed their phylogenetic affinity, including species from the Devonian of the Amazonas Basin. Tomczykowa (1975), Copper (1977), Melo (1988), Lieberman (1993), Lieberman *et al.* (1991), Sandford (2005) and Rustan & Vaccari (2012) also discussed Devonian Amazonian trilobites in their works. Carvalho & Fonseca (2007) reviewed the taxon “*Dalmanites*” *maecurua* and erected the new genus *Amazonaspis*.

MATERIAL AND METHODS

Specimens studied and figured herein are housed in the paleoinvertebrates collection of the Museu Nacional/UFRJ (MN) and Departamento Nacional de Produção Mineral (DNPM/RJ), Rio de Janeiro, and in the New York State Museum (NYSM), New York. They are from the Maecuru and Ererê formations, State of Pará (for locality map, see Carvalho & Fonseca, 2007). The trilobites are represented by internal and external molds of disarticulated, mostly incomplete and poorly preserved specimens. Morphological terminology follows Whittington & Kelly (1997) and Eldredge & Branisa (1980).

SYSTEMATIC PALEONTOLOGY

Order Phacopida Salter 1864
 Suborder Calymenina Swinnerton 1915
 Family Homalonotidae Chapman 1890
 Subfamily Homalonotinae Chapman 1890
 Genus *Digonus* Gurich, 1909

Type species: *Homalonotus gigas* Roemer, 1843, from the Lower Devonian (Emsian) Kahleberg Sandstone, Germany, by original designation.

Digonus derbyi (Clarke, 1890) (Figure 1A-1C)

1890 – *Homalonotus derbyi* Clarke, 1890: 7-11, plate I, figure 4 and 7; non figure 19.

1913 – *Homalonotus derbyi* Clarke. Mon. Serv. Geol. Mineral. Brasil, 1: 72, 92.

1923 – *Homalonotus derbyi* Clarke. Kozłowski, R. Ann. Paleont., 12(1/2): 24-25.

1933 – *Homalonotus derbyi* Clarke. Katzer, F. Bol. Mus. Para. Emílio Goeldi, 9: 186, est. 15, figure 1 (translated from the German original: Grund. der Geol. des unt. Amazonasgebietes..., Leipzig, 1903).

1975 – *Digonus? derbyi* (Clarke). Tomczykowa, E. Acta Palaeont. Polonica, 20(1): 11.

1982 – “*Homalonotus*” *derbyi* Clarke. Cooper, M.R. Ann. S. Afr. Mus., 89(1): 43.

2005 – *Digonus? derbyi* (Clarke). Sandford, A.C. Mem. of Mus. Victoria 62(1): 21.

Type material: from Clarke's syntypes, MN 3370-I, an external mold of an almost complete cephalon (figured by Clarke, 1890, plate I, figure 4), is designated here as the lectotype. MN 3371-I, Clarke, 1890, plate I, figure 7, small incomplete internal mold of cephalon, here designated the paralectotype.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Diagnosis: cephalon subtriangular in outline; glabella subtrapezoidal, convex (sag. and tr.), with sides weakly concave, indistinct lobation, glabellar's antero-lateral angles broadly rounded and postero-lateral angles acute; preglabellar field produced conspicuously, well below the level of the glabella. Rostral suture slightly concave. Palpebral and postocular fixigena areas bulged, depressed abruptly in front of them. Anterior branch of facial suture slightly sigmoidal. Eyes quite small, situated at the summit

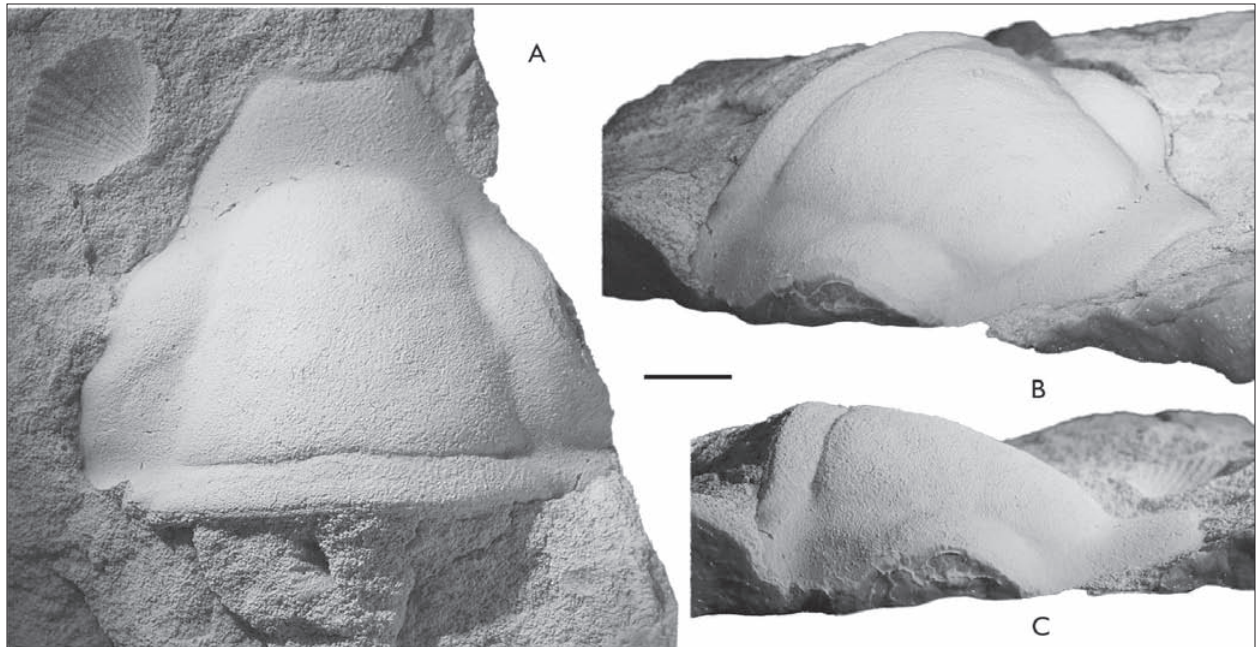


Figure 1. Homalonotidae. *Digonus derbyi* (Clarke, 1890), Lectotype, MN 3370-I: A) dorsal, B) oblique, C) lateral views of internal mold of cephalon. Scale bar = 10 mm.

of the palpebral lobe, away from axial glabellar furrow. Paraglabellar area distinct. Occipital furrow well developed, narrow, nearly transverse, curving slightly forward at the axial line. Posterior border furrow wide and very shallow. Occipital ring moderately broad and convex (sag. and tr.), above the level of the glabella.

Remarks: the available material is represented by an external mold of an almost complete cephalon, described originally by Clarke (1890) as *Homalonotus derbyi*. He suggested that this species was a representative of the "subdivision *Trimerus*". Subsequent authors (e.g. Katzer (1897); Clarke (1913); Kozłowski (1923) followed Clarke, but Cooper (1982) considered that *H. derbyi* may be a species of *Trimerus*. Tomczykowa (1975) and Sandford (2005) tentatively referred the Amazonian species to *Digonus*. In reality, the allocation of this species to one or another genus of Homalonotinae is somewhat problematic, because of the incompleteness and paucity of material. Nevertheless, some cephalic characters are shared with other species of *Digonus*.

The specimen figured by Clarke (1890, plate I, figure 19, MN 3372-I) is not a homalonotid. It may instead belong to the family Dalmanitidae (Figure 2C). The incompleteness of the material does not allow more accurate taxonomic placement and it is here regarded as gen. and sp. indet.

Genus *Burmeisteria* Salter, 1865

Type species: *Homalonotus herscheli* Murchison, 1839, by original designation, from the Gydo Formation of the Bokkeveld sequence, Lower Devonian, South Africa.

Burmeisteria oiara (Hartt & Rathbun, 1875)

1875 – *Homalonotus oiara* Hartt & Rathbun. Ann. Lyc. Nat. Hist. N.Y., 11(13): 114.

Occurrence: Ererê Formation, Middle Devonian (latest Eifelian; Grahn & Melo, 2004), State of Pará, Amazonas Basin, Brazil.

Type material: internal mold of a fragment of a cephalon. According to Clarke (1890), the material collected by the Morgan expeditions of 1870 and 1871 "is in the museum of the Cornell University, Ithaca" but apparently it was transferred to the New York State Museum (NYSM 4494).

Remarks: based on Clarke's description (1890), the glabella is subrectangular with a strong incurvature of the lateral margins (= urceolate) and smooth non-lobate surface, which are all characteristics of *Burmeisteria*.

Family Dalmanitidae Vogdes, 1890

Genus *Dalmanites* Barrande, 1852

Type species: *Trilobus caudatus* Brunnich, 1781 from the Wenlock (mid-Silurian), England.

Dalmanites? infractus Clarke, 1890

1890 – *Dalmanites infractus* Clarke. Arch. Mus. Nac. Rio de Janeiro, 9: 34, plate 2, figures 8, 16.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Type material: small internal and external molds of a single glabella. The material is lost and for this reason we could not provide the catalogue number of the MN (RJ) where it was originally deposited.

Remarks: according to Eldredge & Ormiston (1979, p. 163) this sp. could be considered a Dalmanitidae *sensu lato*, or perhaps a true dalmanitid. We did not see the original material and left the species as Dalmanitidae gen. indet.

Genus *Amazonaspis* Carvalho & Fonseca, 2007

Amazonaspis maecurua (Clarke, 1890) (Figure 2A, 2B)

Type material: *Dalmanites maecurua* Clarke, 1890: 23-29, plate II, figures 1-3; 6-7; 10; 15, from the Maecuru Formation, Pará State, Brazil. Clarke's syntypes:

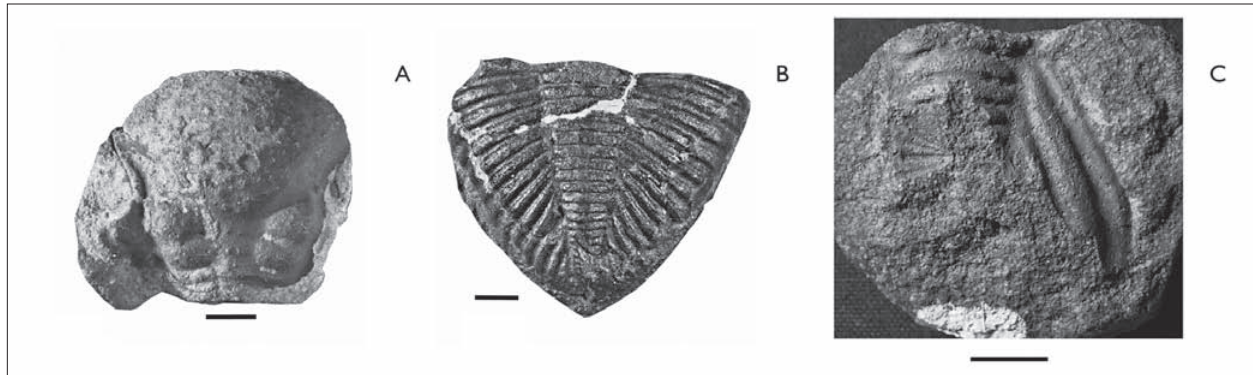


Figure 2. A-B) Dalmanitidae. *Amazonaspis maecurua* (Clarke, 1890): A) Lectotype, MN 3383-I, dorsal view of an incomplete cephalon; B) Paralectotype, MN 3387-I, dorsal view of internal mold of pygidium (from Carvalho & Fonseca, 2007); C) Dalmanitidae gen. and sp. indet., MN 3372-I, internal mold of incomplete pygidium. Scale bar = 10 mm.

MN 3382-I, MN 3383, MN 3384, MN 3385, MN 3386, and MN 3387.

Lectotype: MN 3383-I, internal mold of glabella plus a small part of the left fixigena (figured by Clarke, 1890, plate II, figure 2; in Carvalho & Fonseca, 2007, figure 3C-3E).

Paralectotypes: MN 3382-I, internal mold of part of the left librigena including genal spine; MN 3384-I, incomplete internal mold of hypostome; MN 3385-I, internal mold of an incomplete thoracic segment; MN 3386-I and MN 3387-I, external and internal molds respectively of an almost complete pygidium (figured by Clarke, 1890, plate II, figures 1, 3, 7, 10, 15; in Carvalho & Fonseca, 2007, figure 3G, 3F, 3H, 3A).

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Remarks: for complete description, as well as a diagnosis, see Carvalho & Fonseca (2007), who designated the lectotype and paralectotypes.

Family Calmoniidae Delo, 1935

Subfamily Calmoniinae Delo, 1935

Genus *Acastoides* Delo, 1935

Type species: *Acaste henni* R. Richter, 1916, Lower Devonian, Germany.

Acastoides? menurus (Clarke, 1890) (Figure 3A)

1890 – *Phacops menurus* Clarke, Arch. Mus. Nac. Rio de Janeiro, 9: 17, plate 1, figure 15.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Type material: MN 3377-I, internal mold of pygidium.

Remarks: Eldredge & Ormiston (1979) and Eldredge & Branisa (1980) did not consider this species belonged the boreal genus *Acastoides*, Delo (1935), but did not erect a new genus for it, referring it instead to *Acastoides?*. For further explanation see Eldredge & Branisa (1980, p. 235).

Genus *Eldredgeia* Lieberman, 1993

Type species: *Metacryphaeus venustus* Wolfart, 1968 from Sicasica strata, locality of Cruz Loma, Devonian of Bolivia.

Eldredgeia paituna (Hartt & Rathbun, 1875) (Figure 3B)

1875 – *Dalmania paituna* Hartt & Rathbun, Ann. Lyc. Nat. Hist. N.Y., 11 (13): 111.

1890 – *Dalmanites* (*Cryphaeus*) *paituna* (Hartt & Rathbun). Clarke, Arch. Mus. Nac. Rio de Janeiro, 9: 39, plate 1, figures 13, 14, 16, 17.

Occurrence: Ererê Formation, Middle Devonian (latest Eifelian; Grahn & Melo, 2004), Municipality of Monte Alegre, State of Pará, Amazonas Basin, Brazil.

Type material: Lectotype: MN 3394- I, internal mold of partial cephalon (erected here; Figure 3B). Paralectotype: MN 3395- I, internal mold of glabella (erected here). DNPM - MCT 2799-I; DNPM - MCT 2807-I and DNPM - MCT 2791-I were also analyzed.

Remarks: Lieberman (1993) included the Amazonian species “*paituna*” to the new genus *Eldredgeia*. *Eldredgeia paituna* differs from *E. venustus* in the greater convexity (sag.) of the glabella and the greater dorsoventral expansion of the frontal lobe (see Lieberman, 1993, p. 553-554). The genus *Eldredgeia* is known from Amazonas and Parnaíba basins and Bolivia, but not from other Malvinokaffric areas.

Genus *Malvinella* Wolfart, 1968

Type species: *Anchiopella haugi* Kozłowski, 1923 from the Devonian of Bolivia.

Malvinella australis (Clarke, 1890) (Figure 3C)

1890 – *Dalmanites australis* Clarke, Arch. Mus. Nac. Rio de Janeiro, 9: 29, plate 2, figures 11, 13.

Type material: Holotype, MN 3389-I, internal mold of an almost complete cephalon.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Diagnosis: cephalon small, wider than long (sag.) with depressed surface. Glabella subpentagonal in outline with flattened surface; frontal glabellar lobe subrhomboidal in outline, sloping abruptly, almost vertically, to the antero-lateral margin. Glabellar furrows

S3 and S2 are shallow and wider; S3 slightly convex, S2 small and weakly straight; S1 is reduced to a deep adaxial apodemal pit. S0 wide and moderately deep. L0 narrow, in profile is above of the glabella.

Remarks: Wolfart (1968) assigned *Dalmanites australis* Clarke, 1890, to *Malvinella* with question. Eldredge & Ormiston (1979) considered the taxon from Maecuru Formation cf. *Malvinella*, n. gen. Lieberman *et al.* (1991) informally referred *D. australis* to “*Malvinella*” s.l. Here, *D. australis* is assigned to *Malvinella*.

The genus *Malvinella* is known from the Amazonas Basin and Bolivia, but not from other Malvinokaffric areas.

Malvinella? tumiloba (Clarke, 1890) (Figure 3D)

1890 – *Dalmanites tumilobus* Clarke, Arch. Mus. Nac. Rio de Janeiro, 9: 35, plate 2, figures 9, 12.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Type material: syntypes, MN 3391-I, 3392-I, and 3393-I, internal molds of cranium and several glabellas.

Remarks: we did not make a revision of this material and have left it in open nomenclature. This material will be studied in the future.

Genus *Palpebrops* Lieberman *et al.*, 1991

Type species: *Palpebrops donegalensis* Lieberman, Edgecombe, Eldredge, 1991, from the Devonian of Bolivia.

Palpebrops? goeldi (Katzer, 1903)

Type material: *Phacops goeldi* Katzer (1903), internal mold of fragmentary cephalon. Lieberman *et al.* (1991) designated the lectotype NYSM 9828, internal mold of fragmentary cephalon (figured by Katzer, 1903, plate 15, figures 6a, 6b; and by Lieberman *et al.*, 1991, figure 8-1, 2, 4) and paralectotype NYSM 9829, internal mold of

glabella (figured by Katzer, 1903, plate 15, figure 6c; and by Lieberman *et al.*, 1991, figure 8, 3).

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Remarks: Lieberman *et al.* (1991, p. 835) informally referred this Amazonian taxon to "*Palpebrops*" and designated the lectotype and paralectotype. Eldredge & Ormiston (1979) placed this species within the genus *Malvinella* but, according to Lieberman *et al.* (1991), it is phylogenetically closer to *Palpebrops* and *Vogesina* than to other members of the "*Malvinella* group", although it could not be assigned confidently either to *Palpebrops* or *Vogesina*.

Genus *Phacopina* (Clarke, 1890)

Type species: *Phacops braziliensis* Clarke, 1890, from Devonian of Brazil, Amazonas Basin.

Phacopina braziliensis (Clarke, 1890) (Figure 3E)

Type material: type species: syntypes, *Phacops braziliensis* Clarke, 1890, p. 15, plate 1, figures 1, 2. MN 3375-I and MN 3376-I.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Remarks: Clarke (1913) erected the genus *Phacopina*. Eldredge & Branisa (1980, p. 165) made a revision of this taxon but did not designated lectotype or paralectotype. These will be provide in the future work. *Phacopina* is another genus that is known so far only from the Amazonas Basin and Bolivia.

Genus *Homalonotus?* (*Calymene*) *acanthurus* Clarke, 1890

Type material: holotype MN 3374-I (Figure 3F. Clarke, 1890, p. 11, plate 1, figures 9, 10).

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Remarks: definitely this taxon is not a homalonotid. The specimen is represented by an internal mold of pygidium, the morphology of which suggests affinity with the *Metacryphaeus* Group. However, we do not assign it to a particular genus, and leave it in open nomenclature as a Calmoniidae gen. indet.

Genus *Vogesina* Wolfart, 1968

Type species: *Acaste devonica* Ulrich, 1892 by original designation, from Devonian of Bolivia.

Vogesina gemellus (Clarke, 1890)

Dalmanites gemellus Clarke, 1890, p. 38, plate 2, figure 14.

Type material: syntypes (lost), however, there is a cast of the original material in the collection of NYSM 4323 (figured by Lieberman *et al.*, 1991, figure 8-5, 6).

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Remarks: according to Lieberman *et al.* (1991), this species is phylogenetically closest to *Vogesina*, but was left in open nomenclature. This is yet another example of genus that occurs only in the Amazonas Basin and Bolivia.

Dalmanites? galea Clarke, 1890

Dalmanites galea Clarke, 1890, p. 31, plate 2, figures 4, 5

Type material: syntypes MN 3390-I, represented by internal molds of two small, almost complete cephalons and several glabella, catalogued under one number.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

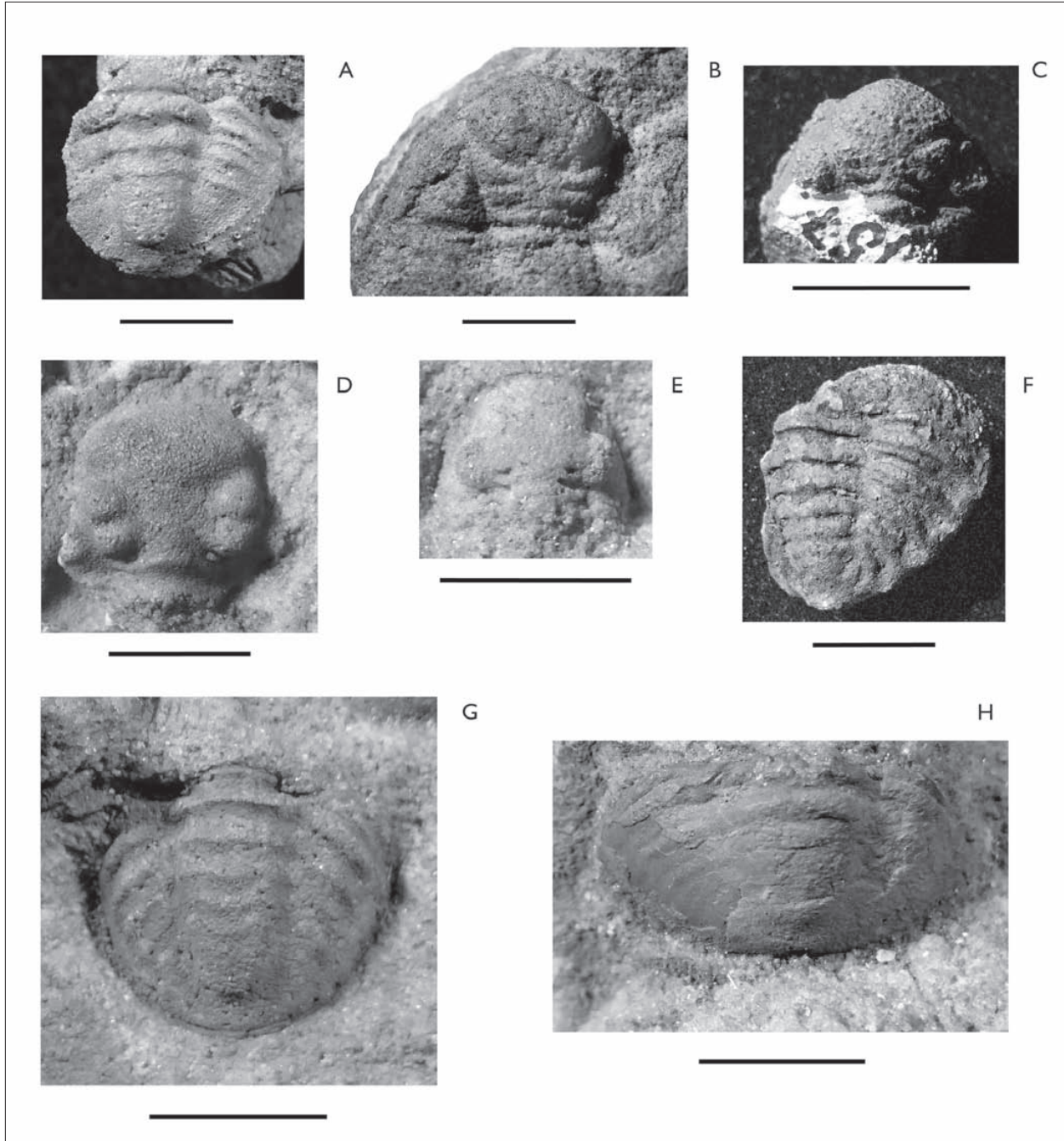


Figure 3. Calmonidae: A) *Acastoides? menurus* (Clarke, 1890). Type material: MN 3377-I; B) *Eldredgeia paituna* (Hartt and Rathbun, 1875), Lectotype, MN 3394-I, dorsal view of internal mold of partial cephalon; C) *Malvinella australis* (Clarke, 1890), Holotype, MN 3389-I, dorsal view of internal mold of cephalon; D) *Malvinella? tumiloba* (Clarke, 1890), Syntype, MN 3392-I, internal mold of partial cranium; E) *Phacopina braziliensis* (Clarke, 1890), Syntype, MN 3375-I, internal mold of cephalon; F) *Calmoniid* gen. ind. *acanthurus* (Clarke, 1890), Holotype, MN 3374-I, dorsal view of an incomplete pygidium; G) "*Phacops*" *macropyge* Clarke, 1890, Syntype, MN 3380-I, dorsal view of internal mold of pygidium; H) Uncertain fam., *Phacops? pullinus* Clarke, 1890, Syntype, MN 3379-I, dorsal view internal mold of pygidium. Scale bar = 10 mm.

Remarks: Eldredge & Ormiston (1979) considered this taxon as a "Calmoniidae Plesiomorph" and suggested that it may represent a new genus close to *Vogesina*, possibly a morphological link between *Vogesina* and *Acastoides*?. Lieberman *et al.* (1991, p. 838, figure 9-1, 6) considered its phylogenetic position ambiguous, and left it as Calmoniinae gen. indet.

Phacops? scirpeus Clarke, 1890

Phacops scirpeus Clarke, 1890, p. 18, plate 1, figure 6

Type material: Holotype MN 3378-I, internal mold of an entire pygidium.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Remarks: Eldredge & Ormiston (1979) included this taxon within the *Metacryphaeus* Group and suggested that it could be a new genus, or aff. *Malvinella*, along with *Dalmanites gemellus* Clarke, 1890 (see above), but Lieberman *et al.* (1991) did not comment on its affinity.

The elongated shape of this pygidium is not typical of the genus *Phacops*, in which the pygidium is usually short (micropygous). It is conceivable that this taxon represents a new genus. A revision of this material is required.

Phacops? macropyge Clarke, 1890 (Figure 3G)

Phacops (Dalmanites) macropyge Clarke, 1890, p. 21, plate 1, figure 11

Type material: syntypes, MN 3380-I (figured) and MN 3381-I, internal molds of several pygidia.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Remarks: the presence of small pygidial lappets definitely excludes this taxon from *Phacops*, but suggests calmonioid affinity.

Phacops? pullinus Clarke, 1890 (Figure 3H)

Phacops? pullinus Clarke, 1890, p. 20, figure 12

Type material: syntypes, MN 3379-I, several internal molds of pygidia.

Occurrence: Maecuru Formation, Middle Devonian (early Eifelian, Grahn & Melo, 2004), Amazonas Basin, Maecuru River, State of Pará, Brazil.

Remarks: the identification of these pygidia is problematic and they are left as uncertain family.

DISCUSSION

Calmoniids (which are endemic to marine cold waters of the southern hemisphere Malvinokaffric Realm) include *Acastoides? menurus* (Clarke, 1890), *Eldredgeia paituna* (Hartt & Rathbun, 1875), *Malvinella australis* (Clarke, 1890), *Malvinella? tumiloba* (Clarke, 1890), "*Palpebrops*" *goeldi* (Katzer, 1903), *Phacopina braziliensis* (Clarke, 1890), *Calmonioidgen. ind. acanthurus* (Clarke, 1890), *Vogesina gemellus* (Clarke, 1890), and calmoniids gen. indet., *galea* (Clarke, 1890), *scirpeus* (Clarke, 1890). Although homalonotids and dalmanitids are cosmopolitan groups, their Malvinokaffric representatives are highly endemic at genus and species level. Homalonotids from the Amazonas Basin include *Digonus derbyi* (Clarke, 1890) and *Burmeisteria oiara* (Hartt & Rathbun, 1875); dalmanitids include *Amazonaspis maecurua* (Clarke, 1890), *Dalmanites? infractus* Clarke, 1890, plus a Dalmanitidae gen. and sp. indet.

From the list of the original and current nomenclature for the Devonian trilobite species from the Amazonas Basin, it is evident that diversity at genus level is far greater than was originally suspected (growing from six to eleven named genera, plus six additional indeterminate taxa) (Table 1).

TAPHONOMIC CONSIDERATIONS

In the Amazonas Basin, the taphonomic analysis of the macrofossils from Maecuru and Ererê formations is limited. First of all, the fossiliferous sandstones were not *in situ* when they were collected by the Petrobras expedition in 1986 (they were already moved away from the original site),

Table 1. Initial and current nomenclature of trilobites from the Amazon Basin.

Generic and specific original designation	Current nomenclature
<i>Homalonotus oiara</i> Hartt & Rathbun, 1876	<i>Burmeisteria oiara</i> (Hartt & Rathbun, 1876)
<i>Homalonotus derbyi</i> Clarke, 1890	<i>Digonus derbyi</i> (Clarke, 1890)
<i>Homalonotus derbyi</i> Clarke, 1890	Dalmanitidae gen. and sp. indet.
<i>H. (Calymene) acanthurus</i> Clarke, 1890	Calmoniid gen. indet.
<i>Dalmanites maecurua</i> Clarke, 1890	<i>Amazonaspis maecurua</i> (Clarke, 1890)
<i>Dalmanites infractus</i> Clarke, 1890	<i>Dalmanites? infractus</i> Clarke, 1890
<i>Dalmanites gemellus</i> Clarke, 1890	<i>Vogesina gemellus</i> (Clarke, 1890)
<i>Phacops menurus</i> Clarke, 1890	<i>Acastoides? menurus</i> (Clarke, 1890)
<i>Dalmania paituna</i> Hartt & Rathbun, 1876	<i>Eldredgeia paituna</i> (Hartt & Rathbun, 1876)
<i>Dalmanites australis</i> Clarke, 1890	<i>Malvinella australis</i> (Clarke, 1890)
<i>Dalmanites tumiloba</i> Clarke, 1890	<i>Malvinella tumiloba</i> (Clarke, 1890)
<i>Phacops goeldii</i> Katzer, 1903	<i>Palpebrops? goeldi</i> (Katzer, 1903)
<i>Phacops braziliensis</i> Clarke, 1890	<i>Phacopina braziliensis</i> (Clarke, 1890)
<i>Dalmanites galea</i> Clarke, 1890	Calmoniid gen. indet. (Clarke, 1890)
<i>Phacops scirpeus</i> Clarke, 1890	Calmoniid gen. indet. (Clarke, 1890)
<i>Phacops (Dalmania) macropyge</i> Clarke, 1890	Calmoniid gen. indet. Clarke, 1890
<i>Phacops? pullinus</i> Clarke, 1890	Uncertain Fam. " <i>P.</i> " <i>pullinus</i> Cl., 1890

while previous expeditions collected only small samples that are even more inadequate for taphonomic analysis.

Ponciano & Machado (2007) made some taphonomic observations of the Maecuru Formation and observed that many brachiopods and bivalves still had their valves articulated, but were associated with disarticulated specimens, and lacked preferred orientation. They also observed many bivalve and brachiopod shell edges without apparent modifications, suggesting possibly a low grade of transportation, although it was sufficient to result in disarticulation of trilobite exoskeletons (poorly preserved as incomplete cephalon and pygidium molds). Disarticulation of trilobites also may reveal the disturbance of the exuvium after molting (inference corroborated by the absence of *in situ* librigenae and hypostomes, because these sutures open during exuviation). Other delicate fossil invertebrates, as bryozoans, corals and conulariids present low to intermediate degrees of fragmentation, suggesting low energy in the marine depositional environment. According to

Caputo (1984), the Maecuru Formation represents a major river-dominated fan-delta system progradation interrupted by a fast, short-lived transgression followed by another fan-delta system progradation. Much like the sedimentological studies (Caputo, 1984), the combination of taphonomic signatures also corroborate the influence of episodic events as storms or floods on the genesis of the Maecuru fossil assemblages, suggesting that the fossils are parautochthonous and were deposited in a shallow marine environment.

PALEOBIOGEOGRAPHIC CONSIDERATIONS

The Devonian trilobites of the Amazonas Basin are important paleobiogeographically. Calmoniids were apparently endemic to the Malvinokaffric Realm, a region in the southern hemisphere characterized by cold water, siliciclastic beds and an endemic fauna. Besides calmoniids, two other more cosmopolitan groups (homalonotids and dalmanitids) also occur, but these are represented by species that were apparently restricted to the Malvinokaffric Realm.

Nevertheless, *Amazonaspis maecurua* shows affinity with dalmanitids from Appalachia (Carvalho & Fonseca, 2007), and the homalonotid *Digonus* is known from the Old World. These trilobites may have migrated into the Amazonas Basin during a widespread Eifelian transgression from the northeast.

Eldredge & Ormiston (1979) divided the Malvinokaffric Realm into three Provinces, based on trilobite distribution patterns: an Andean Province, including Peru, Bolivia, Paraguay, and Argentina; a Brazilian Province, including Brazil and possibly Uruguay; and a South African-Malvinan Province, possibly including Antarctica.

The calmoniid species from the Amazonas Basin differ from those from the Paraná Basin, with no genera or species shared by these two basins. However, all the calmoniid genera recorded from the Devonian of the Amazonas Basin are also present in the Devonian of Bolivia, although they are represented by different species. As Lieberman *et al.* (1991) noted, representatives of the “*Malvinella* group” from the Maecuru Formation are most closely related to Andean taxa, suggesting that a marine connection probably existed between the Amazonas Basin and Bolivia or southern Peru during the Middle Devonian.

Boucot (1988) proposed two major Devonian Units in the northern hemisphere, based on the distribution of brachiopods: the Old World Realm and the Eastern Americas Realm. He divided the latter into four sub-provinces: Nevadan, Appohimchi, Colombian and Amazon. He also suggested that Malvinokaffric brachiopods were more closely related to early Devonian brachiopods of the Appohimchi Subprovince of the Eastern Americas Realm (except for *Australocoelia*). Curiously, this pattern of relationships is not observed among the trilobites in the Amazonas Basin.

The association of Malvinokaffric trilobites with Eastern Americas brachiopods in the Amazonas Basin suggests that these taxa had somewhat different physiological or environmental tolerances that rarely coincided except in this region (a “biogeographic boundary mixing area”; Boucot & Racheboeuf, 1993). This concept is also supported by paleogeographical reconstructions for

the late Emsian and late Eifelian/Givetian in Brazil (Melo, 1988), as well as by reconstructions of Pangea in the late Early Devonian and Middle Devonian (Boucot, 1988).

CONCLUSIONS

Despite the paucity of Devonian fossils from the Amazonas Basin, increased systematic diversity among its trilobites has been recognized over the past century, particularly in the Maecuru Formation and especially at genus level (eleven named genera, plus six additional indeterminate taxa). This increase has resulted only from revisionary studies of existing collections, rather than from new collecting, suggesting that the true diversity of Amazonas trilobites may be seriously underrepresented and that many new forms could be revealed with renewed efforts to collect and describe fossils from this intriguing region, especially from the Maecuru Formation.

Moreover, because the Devonian biota of the Amazonas Basin seems to include biogeographically mixed taxa of Malvinokaffric trilobites and Appalachian brachiopods, renewed collecting is imperative in order to elucidate and further expand our understanding of this still largely unexplained situation.

We have attempted here to review the known occurrences of trilobites in the Maecuru and Ererê formations, to examine some taphonomic aspects of Maecuru fossils, and to summarize the biogeographical conundrum revealed by them. The point of this exercise was to provide a snapshot of current understanding rather than to offer new interpretations, and to emphasize the urgent need for further research (especially new collecting) in the Devonian of the Amazonas Basin. We are confident that such investigations will yield important new data that will greatly clarify the contemporaneous biogeographical relationships of the Malvinokaffric Realm to other regions of the world.

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