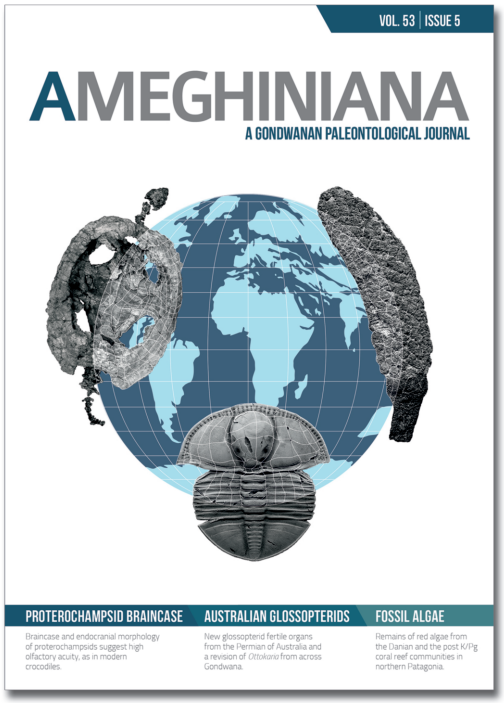
AMEGHINIANA
A GONDWANAN PALEONTOLOGICAL JOURNAL



METACRYPHAEUS TUBERCULATUS AND *METACRYPHAEUS AUSTRALIS* (TRILOBITA, PHACOPIDA) FROM THE DEVONIAN OF THE PARANÁ BASIN: TAXONOMY AND PALEOBIOGEOGRAPHY

FÁBIO AUGUSTO CARBONARO[1]
FELIPE VAN ENCK MEIRA[2]
JULIANA DE MORAES LEME[3]
ELVIO PINTO BOSETTI[4]
RENATO PIRANI GHILARDI[5]

[1]Programa de Pós-graduação em Biologia Comparada, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo – USP, Av. Bandeirantes, 3900, CEP 14040-900, Ribeirão Preto/SP, Brasil.
[2]Programa de Pós-graduação em Geoquímica e Geotectônica, Instituto de Geociências, Universidade de São Paulo – USP, Rua do Lago, 562, CEP 05508-080, São Paulo/SP, Brasil.
[3]Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências, Universidade de São Paulo – USP, Rua do Lago, 562, CEP 05508-080, São Paulo/SP, Brasil.
[4]Universidade Estadual de Ponta Grossa, Laboratório de Estratigrafia e Paleontologia, Departamento de Geociências, UEPG, 84010-919, Ponta Grossa/PR, Brasil.
[5]Departamento de Ciências Biológicas, Faculdade de Ciências de Bauru, Universidade Estadual Paulista Júlio de Mesquita Filho – UNESP, Av. Eng. Luiz Edmundo Carrijo Coube, 14-01, CEP 17033-360, Bauru/SP, Brasil.

Submitted: November 16th, 2015 - **Accepted:** June 23rd, 2016

To cite this article: Fábio Augusto Carbonaro, Felipe Van Enck Meira, Juliana De Moraes Leme, Elvio Pinto Bosetti, and Renato Pirani Ghilardi (2016). *Metacryphaeus tuberculatus* and *Metacryphaeus australis* (Trilobita, Phacopida) from the Devonian of the Paraná Basin: taxonomy and paleobiogeography. *Ameghiniana* 53: 552–564.

To link to this article: http://dx.doi.org/10.5710/AMGH.23.06.2016.2966

PLEASE SCROLL DOWN FOR ARTICLE

ISSN 0002-7014

METACRYPHAEUS TUBERCULATUS AND *METACRYPHAEUS AUSTRALIS* (TRILOBITA, PHACOPIDA) FROM THE DEVONIAN OF THE PARANÁ BASIN: TAXONOMY AND PALEOBIOGEOGRAPHY

FÁBIO AUGUSTO CARBONARO[1], FELIPE VAN ENCK MEIRA[2], JULIANA DE MORAES LEME[3], ELVIO PINTO BOSETTI[4], AND RENATO PIRANI GHILARDI[5]

[1]Programa de Pós-graduação em Biologia Comparada, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo – USP, Av. Bandeirantes, 3900, CEP 14040-900, Ribeirão Preto/SP, Brasil. *fabiocarbonaro@yahoo.com.br*

[2]Programa de Pós-graduação em Geoquímica e Geotectônica, Instituto de Geociências, Universidade de São Paulo – USP, Rua do Lago, 562, CEP 05508-080, São Paulo/SP, Brasil. *fvemeira@gmail.com*

[3]Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências, Universidade de São Paulo – USP, Rua do Lago, 562, CEP 05508-080, São Paulo/SP, Brasil. *leme@usp.br*

[4]Universidade Estadual de Ponta Grossa, Laboratório de Estratigrafia e Paleontologia, Departamento de Geociências, UEPG, 84010-919, Ponta Grossa/PR, Brasil. *elvio.bosetti@pq.cnpq.br*

[5]Departamento de Ciências Biológicas, Faculdade de Ciências de Bauru, Universidade Estadual Paulista Júlio de Mesquita Filho – UNESP, Av. Eng. Luiz Edmundo Carrijo Coube, 14-01, CEP 17033-360, Bauru/SP, Brasil. *ghilardi@fc.unesp.br*

Abstract. Calmoniid trilobites of the genus *Metacryphaeus* Reed include *M. tuberculatus* (Kozlowski), *M. kegeli* Carvalho, Edgecombe and Lieberman, *M. meloi* Carvalho, Edgecombe and Lieberman, *M. rotundatus* (Kozlowski), *M. giganteus* (Ulrich), *M. convexus* (Ulrich), *M. curvigena* Lieberman, *M. branisai* Lieberman, *M. caffer* (Salter), *M. australis* (Clarke), and *M. allardyceae* (Clarke). The geographic distribution of this genus comprises areas of Gondwana, including Bolivia, Peru, Brazil, the Falkland Islands, and South Africa. This study reports a new occurrence of *M. tuberculatus* in the Paraná Basin (Goiás and Paraná states, Brazil), in both the Alto Garças and the Apucarana sub-basins. *Metacryphaeus tuberculatus* was compared with all *Metacryphaeus* species and, especially, with *M. australis*, which also represents a new record for the Paraná Basin. These new records of *M. tuberculatus* imply a different dispersion interpretation from that which is known through the literature. *Metacryphaeus tuberculatus* seems to have originated during the Early Devonian and lived in areas such as Bolivia, Peru, and the Apucarana Sub-basin (Paraná Basin, Brazil). The dispersion between these areas is probably related to the Emsian transgression. During the Givetian, the species presumably migrated towards the Alto Garças Sub-basin (Paraná Basin, Brazil) and the Parnaíba Basin. These facts provide an alternative paleogeographic interpretation to that presented by *Tropidoleptus* Hall and *Exaesiodiscus* Moore and Jeffords in Gondwana and suggest a different pattern of migration during the Devonian of Brazil.

Key words. Alto Garças Sub-basin. Apucarana Sub-basin. Brazil. Dispersion.

Resumen. *METACRYPHAEUS TUBERCULATUS* Y *METACRYPHAEUS AUSTRALIS* (TRILOBITA, PHACOPIDA) DEL DEVÓNICO DE LA CUENCA DEL PARANÁ: TAXONOMIA Y PALEOBIOGEOGRAFÍA. Los trilobites calmónidos del género *Metacryphaeus* Reed incluyen *M. tuberculatus* (Kozlowski), *M. kegeli* Carvalho, Edgecombe y Lieberman, *M. meloi* Carvalho, Edgecombe y Lieberman, *M. rotundatus* (Kozlowski), *M. giganteus* (Ulrich), *M. convexus* (Ulrich), *M. curvigena* Lieberman, *M. branisai* Lieberman, *M. caffer* (Salter), *M. australis* (Clarke) y *M. allardyceae* (Clarke). La distribución geográfica de este género incluye áreas de Gondwana como Bolivia, Perú, Brasil, las Islas Malvinas y Sudáfrica. Este estudio reporta una nueva ocurrencia de *M. tuberculatus* en la Cuenca del Paraná (estados de Goiás y Paraná, Brasil), tanto en la sub-cuenca de Alto Garças como en la de Apucarana. *Metacryphaeus tuberculatus* fue comparado con todas las especies de *Metacryphaeus*, especialmente *M. australis*, que también presenta un nuevo registro en la Cuenca del Paraná. Estos nuevos registros de *M. tuberculatus* implican una dispersión diferente de la que se conoce en la literatura. *Metacryphaeus tuberculatus* parece tener su origen durante el Devónico Temprano en zonas como Bolivia, Perú y en la Sub-cuenca de Apucarana (Cuenca del Paraná, Brasil). Probablemente la dispersión entre estas áreas está relacionada con la transgresión Emsiense. Durante el Givetiense, la especie probablemente emigra a la Sub-cuenca Alto Garças (Cuenca del Paraná, Brasil) y a la Cuenca del Parnaíba, donde tiene registros. Estos hechos proporcionan una interpretación paleogeográfica diferente en comparación con la presentada por *Tropidoleptus* Hall y *Exaesiodiscus* Moore and Jeffords en Gondwana y también sugieren un patrón diferente de migración para el Devónico de Brasil.

Palabras clave. Sub-cuenca Alto Garças. Sub-cuenca Apucarana. Brasil. Dispersión.

DURING the Devonian, some trilobite species were present in the endemic "Austral Fauna" (Clarke, 1913) now referred to as the Malvinokaffric Realm (Richter, 1941; Richter and Richter, 1942; Boucot, 1971, 1974, 1985; Eldredge and Ormiston, 1979). Among the trilobite families contained in this fauna, the Calmoniidae –which includes several genera– were prominent (*e.g.*, *Typhloniscus* Salter, 1856; *Calmonia* Clarke, 1913; *Punillaspis* Baldis and Longobucco, 1977; *Wolfartaspis* Cooper, 1982; *Plesioconvexa* Lieberman, 1993; *Eldredgeia* Lieberman, 1993; *Clarkeaspis* Lieberman, 1993; *Malvinocooperella* Lieberman, 1993). Our study focuses on trilobites of the calmoniid genus *Metacryphaeus* Reed, 1907.

Metacryphaeus occurs in Devonian rocks from the Pragian to the lower Frasnian in Brazil, Bolivia, Peru, the Falkland Islands, and South Africa (Clarke, 1913; Cooper, 1982; Lieberman, 1993; Carvalho *et al.*, 1997; Ghilardi and Simões, 2007; Velazco, 2012). Additionally, in Brazil and Bolivia, it is present in more than one geological unit such in the Paraná and Parnaíba basins in Brazil and in the Belén, Sicasica, Icla, and Limoncito formations in Bolivia (Clarke, 1913; Lieberman, 1993; Carvalho *et al.*, 1997). The represented species include *Metacryphaeus tuberculatus* (Kozlowski, 1923); *Metacryphaeus kegeli* Carvalho, Edgecombe and Lieberman, 1997; *Metacryphaeus meloi* Carvalho, Edgecombe and Lieberman, 1997; *Metacryphaeus rotundatus* (Kozlowski, 1923); *Metacryphaeus giganteus* (Ulrich, 1892); *Metacryphaeus convexus* (Ulrich, 1892); *Metacryphaeus curvigena* Lieberman, 1993; *Metacryphaeus branisai* Lieberman, 1993; *Metacryphaeus caffer* (Salter, 1856); *Metacryphaeus australis* (Clarke, 1913) and *Metacryphaeus allardyceae* (Clarke, 1913).

According to Lieberman *et al.* (1991), intraspecific variation is quite common in *M. tuberculatus*, *M. caffer*, and *M. australis*, and can result in problems when identifying them. However, some characteristics such as the kind of tuberculation, the Large Eye Index, and the position of the anterior margin of the eyes in relation to the axial furrow and the glabellar furrow S2 can be used to differentiate these organisms.

In view of such problems, we reveal that *M. tuberculatus,* recorded from the Devonian of Bolivia and the Parnaíba Basin of Brazil, also occurs in the Paraná Basin of Brazil in both the Alto Garças (Chapada Group Unit 4) and the Apucarana (Ponta Grossa Formation) sub-basins (Figs. 1–2). These new occurrences of *M. tuberculatus* in the Paraná Basin were systematically classified and compared with all other species of *Metacryphaeus* and compared mainly with

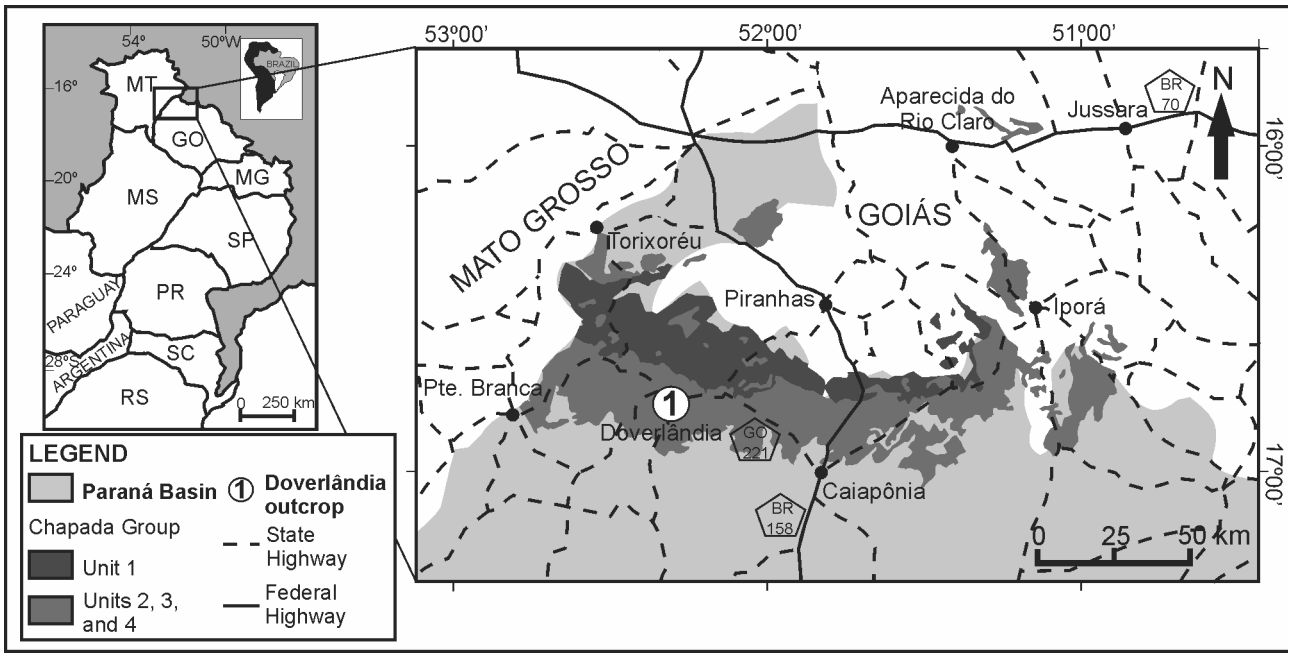


Figure 1. Locality map of the Doverlândia outcrop (Goiás State, Brazil), where ***Metacryphaeus tuberculatus*** was collected (Alto Garças Sub-basin, Paraná Basin).

the new records of *M. australis* in the Paraná Basin.

The presence of *M. tuberculatus* in the Paraná Basin elicited a discussion about the dispersion of this species during the Devonian, which was associated with the transgressive-regressive cycles fairly common in this period (Assine *et al.*, 1998; Assine, 2001; Grahn *et al.*, 2010a; Bosetti *et al.*, 2012). Eustatic high level episodes were more markedly evidenced in the Emsian and Givetian (Assine *et al.*, 1998) and are most probably related to the dispersion of the genus *Metacryphaeus* through marine connections between the basins during the Devonian.

Some organisms, for instance brachiopods and crinoids of the genus *Tropidoleptus* Hall, 1857, and *Exaesiodiscus* Moore and Jeffords, 1968 (Fonseca and Melo, 1987; Scheffler, 2010; Scheffler *et al.*, 2011), prove to be indicators of the aforementioned connections between the Brazilian Paleozoic basins during the Devonian. *M. tuberculatus* provides additional support for such connections.

The present work introduces taxonomic and paleobiogeographic interpretations about the new occurrence of *M. tuberculatus* in the Paraná Basin while establishing a comparison with *M. australis*.

GEOLOGICAL SETTING

The Paraná Basin covers an area of approximately 1.100.000 km^2 of the Brazilian territory and comprises part of the states of Rio Grande do Sul, Santa Catarina (only subsurface), Paraná, São Paulo, Goiás, Minas Gerais, Mato Grosso, and Mato Grosso do Sul (Melo, 1988; Petri and Fulfaro, 1988; Milani *et al.*, 2007). During the Devonian, the exposure area of this basin was marked by a division which was identified through sedimentological studies and subsurface stratigraphic dating. Two sub-basins separated by the Três Lagoas and Campo Grande –also Devonian (Ramos, 1970)– were originated during this period: the Alto Garças (in the north) and the Apucarana (in the south) sub-basins.

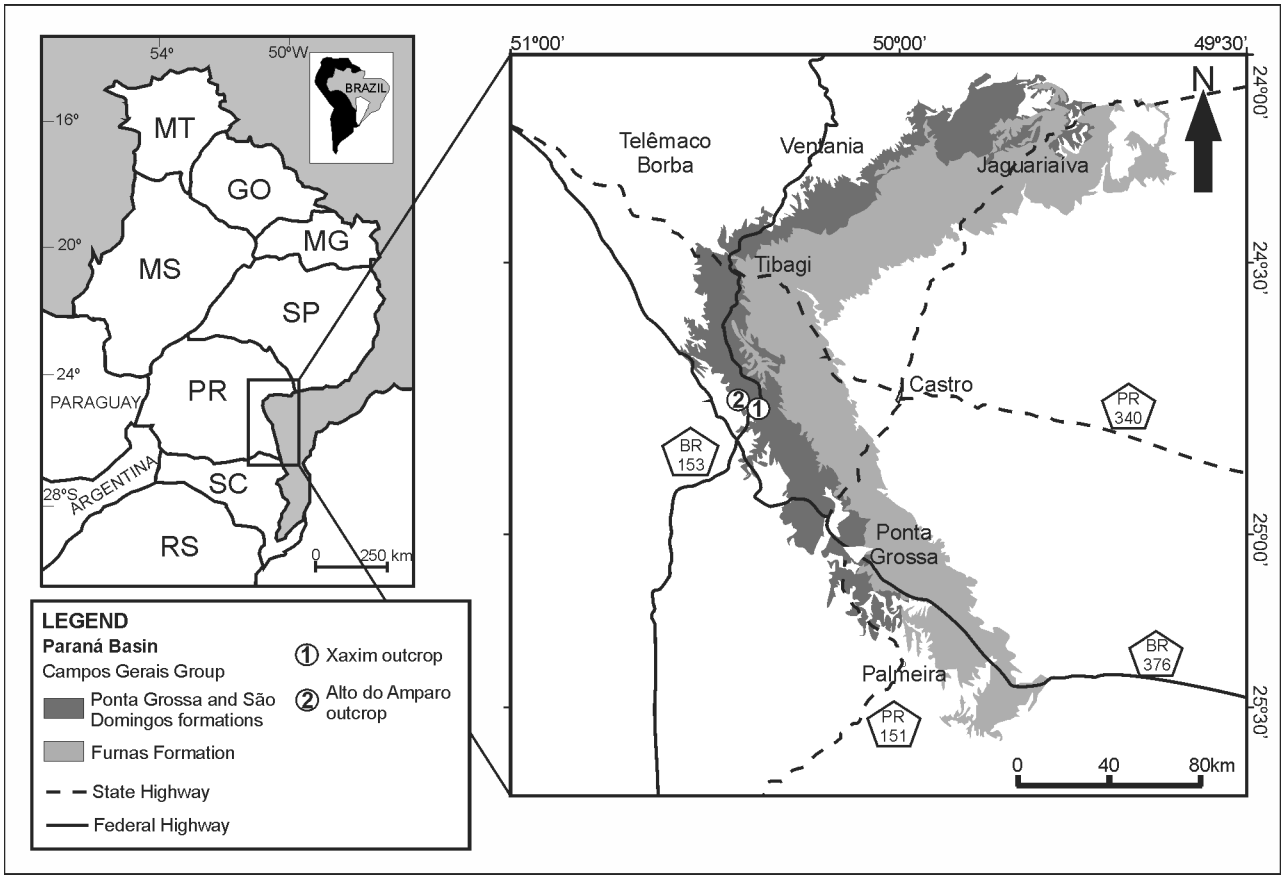


Figure 2. Locality map of Xaxim and Amparo outcrops, where ***Metacryphaeus australis*** occurs (Apucarana Sub-basin, Paraná Basin, Brazil).

According to Melo (1988), the marine connection between these sub-basins opened during the Givetian transgression.

Although the depositional environment of both sub-basins was marine, they evolved differently. The Alto Garças Sub-basin represents a shallow environments with large amount of siltstones and sandstones assigned to Units 1, 2, 3 and 4 of the Chapada Group (Melo, 1988; Grahn *et al.*, 2010b). The units recognized in the Apucarana Sub-basin are the Furnas, Ponta Grossa, and São Domingos formations.

The lithology of Unit 1, which is probably of Lochkovian age according to Grahn *et al.* (2010b), is similar to that of the Furnas Formation of the Apucarana Sub-basin, and comprises fine and coarse sandstones (Melo, 1988).

Unit 2 presents a basal conglomerate covered by fine purple-reddish sandstones with intercalated siltstone and shale. The top of this unit consists of fine- to middle-grained red-grayish bioturbated sandstones (Andrade and Camarço, 1980). This unit was deposited throughout two intervals separated by a depositional gap. While the lower interval is of late Pragian–early Emsian age, the upper interval is of late Emsian–Eifelian age (Grahn *et al.*, 2010b). The lower portion of Unit 2 is coeval with the Ponta Grossa Formation (Apucarana Sub-basin), which includes sandstones interbedded with siltstones and followed by sandy shales (Grahn *et al.*, 2010a).

The lithological composition of Unit 3 comprises to coarse-grained reddish sandstones with conglomeratic levels characteristic of a deltaic deposition in shallow marine environments heavily influenced by waves (Andrade and Camarço, 1980; Grahn *et al.*, 2010b). The transitional beds between the upper portion of Unit 2 and Unit 3 exhibit the same fauna that was found in the Tibagi Member of the São Domingos Formation (Apucarana Sub-basin), thus suggesting a late Emsian age for this contact (Glaser, 1969; Melo, 1988; Grahn *et al.*, 2010b). Unit 3 is of late Emsian–Eifelian age (Grahn *et al.*, 2010b). On the other hand, the São Domingos Formation (Apucarana Sub-basin) predominantly displays clay shales of late Emsian–early Frasnian age (Melo and Loboziak, 2003; Grahn *et al.*, 2013).

Chapada Group Unit 4 usually consists of dark gray shales with intercalations of clay sandstones and siltstones. The upper contact of this unit is erosive and involves diamictites of the Itararé Group (Carboniferous) (Andrade and Camarço, 1980; Grahn *et al.*, 2010b) (Fig. 2). This unit is correlated to the upper portion of the São Domingos Formation (Apucarana Sub-basin; Grahn *et al.*, 2013) and the beginning of its deposition is related to the maximum transgression, which occurred in the early Givetian (Assine, 2001; Grahn *et al.*, 2010a). According to Grahn *et al.* (2010b, 2013), the rocks of this unit are of Givetian–early Frasnian age.

MATERIALS AND METHODS

The new specimens of *Metacryphaeus tuberculatus* from the Paraná Basin were collected from both the Ponta Grossa Formation (Apucarana Sub-basin) and the Chapada Group Unit 4 (Alto Garças Sub-basin). Samples from Unit 4 in association with tentaculitids, brachiopods, ichnofossils, and plant remains (Figs. 1, 3), were collected from the surroundings of Doverlândia city (16° 42′ 43.08″ S; 52° 15′ 46.89″ W, Goiás State, Brazil). This material is deposited in the scientific collection of Laboratório de Paleontologia de Macroinvertebrados (**LAPALMA**) located at Universidade Estadual Paulista (**UNESP**), Bauru Campus, under the numbers CCLP 874a and CCLP 874b.

The specimen of *Metacryphaeus tuberculatus* from the upper part of the Ponta Grossa Formation had been previously classified in Popp's unpublished thesis (1985) as *Metacryphaeus granulata* and is currently being kept in the Universidade Federal do Paraná (**UFPR**) collection under the number NR3130.

The rocks of the São Domingos Formation where *Metacryphaeus australis* was collected present the Givetian age (Melo and Loboziak, 2003; Grahn *et al.*, 2013) and derive from two outcrops located near Tibagi city (Paraná State, Brazil). The Xaxim outcrop is located alongside Highway BR 153 (km 237) and the Amparo outcrop is situated at the Alto do Amparo entrance (Fig. 2). The aforementioned material is held in the collection of DEGEO under the numbers DEGEO/MPI 1535, DEGEO/MPI 1536, DEGEO/MPI 1539 A, DEGEO/MPI 1539 B, DEGEO/MPI 1543, DEGEO/MPI 1555, DEGEO/MPI 1556, DEGEO/MPI 1557, and DEGEO/MPI 8476 B.

Institutional abbreviations. **CCLP,** Coleção científica do Laboratório de Paleontologia de Macroinvertebrados, Universidade Estadual Paulista, Bauru, Brazil; **DEGEO,** Departamento de Geociências da Universidade Estadual de Ponta Grossa, Ponta Grossa, Brazil; **DGM,** Divisão de Geologia e

Mineralogia do Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; **MNHN,** Muséum National d'Histoire Naturelle, Paris, France; **NR,** Coleção da Universidade Federal do Paraná, Curitiba, Brazil.

Anatomical abbreviations. **LEI,** large eye index; **LO,** occipital lobe; **L1, L2, L3,** glabellar lobes; **SO,** occipital furrow; **S1, S2, S3,** glabellar furrows.

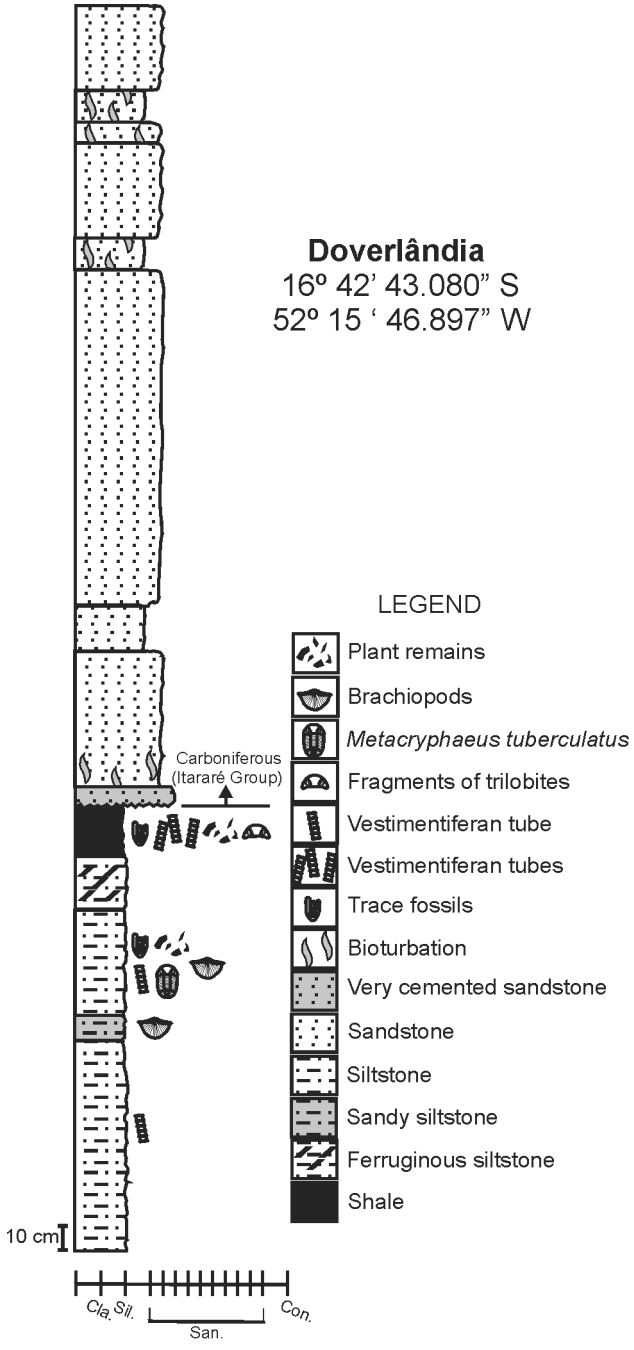


Figure 3. Columnar profile of the Doverlândia outcrop (Chapada Group Unit 4).

SYSTEMATIC PALEONTOLOGY

Order Phacopida Salter, 1864
Family Calmoniidae Delo, 1935
Subfamily Calmoniinae Delo, 1935
Genus ***Metacryphaeus*** Reed, 1907

Type species. *Metacryphaeus caffer* (Salter, 1856).

Metacryphaeus tuberculatus (Kozlowski, 1923)
Figure 4

1923 *Cryphaeus australis* var. *tuberculatus* Kozlowski; p. 43; pl. 3; figs. 20–21.
1965 *Metacryphaeus caffer* var. Braniša; p. 106; pl. 21; figs. 14, 16.
1968 *Metacryphaeus tuberculatus* Wolfart; p. 102; pl. 17; fig. 17; pl. 18; fig. 1.
1991 *Metacryphaeus tuberculatus* Lieberman *et al.*; p. 825–827; fig. 1.1.

Lectotype. MNHN.F.R50817 (Kozlowski, 1923, p. 43–44, pl. 3, fig. 20).

Examined material. CCLP 874a, CCLP 874b, and NR3130.

Geographic and stratigraphic provenance. Upper Belén and Sicasica formations of La Paz Department (Bolivia), Icla Formation of Chuquisaca Department (Bolivia), Limoncito Formation of Santa Cruz Department (Bolivia) and Pimenteira Formation of Parnaíba Basin (Piauí State, Brazil). In the present work, CCLP 874a and CCLP 874b correspond to the Chapada Group Unit 4 (Givetian–Frasnian, Alto Garças Sub-basin, Paraná Basin) while NR3130 derives from the upper part of the Ponta Grossa Formation (lower Emsian, Apucarana Sub-basin, Paraná Basin).

Description. Concave and convex external molds of cephalon (CCLP 874a, CCLP 874b, and NR3130). In CCLP 874a and CCLP 874b, cephalic dimensions are 1.7 cm in length and 3.4 cm in width. NR3130 is 2.2 cm in length and 4.5 cm in width. In other words, cephalic length equals 50% of its width. Cephalic length amounts to 90% of frontal glabellar lobe width. The values of LEI were 0.29–0.31 in the analysed specimens. The cephalon presents a sub-triangular shape with tubercles throughout the glabella, glabellar lobe, palpebral portion, and extra-ocular area. These tubercles also occur on the LO and the proximal half of the posterior border (Fig. 4). The frontal glabellar lobe is inflated and laterally expanded, exhibiting a posterior median impression. The glabellar area is sub-trapezoidal and relatively convex. The frontal glabellar lobe length is 60% of the

glabellar length. The onset of axial furrows occurs on the top of S3 and these are well defined, slightly curved antero-distally, deep, oblique, and marked by diverging toward the antero-distal region. The most well-defined lateral glabellar furrow is S3, which is slightly curved and markedly delimits the frontal lobe. S3 becomes shallower when it joins the axial furrow. S2 is well marked, deep (although to a lesser extent than S3 and S1), wider, and curved where it comes into contact with the axial furrow though narrower and straight toward the glabellar center. S1 is also deep, well-marked and in contact with the axial furrow (more defined than the connection with S2). S1 is curved anteriorly in its proximal margins. The proximal portion of S1 is very close to the proximal portion of S2 and almost contacts it. SO is deep, well-marked, sometimes curved anteriorly, and connects with the axial furrows and posterior border furrows. SO becomes deeper and narrower distally. Glabellar furrows are inflated and present different shapes. L3 is sub-triangular to sub-trapezoidal. L2 is oblong. L1 is concave anteriorly. LO is prominent and its distal portion is slightly arched forward. LO corresponds to 70% of the width of the frontal glabellar lobe. The eyes are relatively small, reniform, and separated from the axial furrows. Some lenses are preserved on the anterior margin of the eyes, thus indicating schizochroal eyes. The anterior margin of the eyes is positioned at the same level as the contact between the axial furrow and S3. The posterior margin is located at half the height of L2. Lateral cephalic border furrow is shallow. Posterior cephalic border furrow is well-marked and laterally follows the posterior border of the cephalon, curving anteriorly and becoming shallower distally. There is a connection between the posterior cephalic border furrow and the lateral cephalic border furrow. Lateral cephalic border is narrow, convex, and in contact with the posterior cephalic border. Genal margins curved anteriorly. Genal spines absent. Posterior cephalic border oblique (in relation to axial furrows) and curved forward distally. Posterior cephalic border wider distally and narrower at the point of contact with the axial furrow.

Discussion. The taxonomic classification of some species of *Metacryphaeus* is –as seen in *M. tuberculatus* and *M. caffer*– arduous because differences are subtle. However, the main features used to identify *Metacryphaeus tuberculatus* in the Paraná Basin are cephalic features such as furrows and glabellar lobes, LEI, and tuberculation patterns.

NR3130 corresponds to the sample classified by Popp (1985) as *Metacryphaeus granulata* (*nom. nud.*). This sample was collected from the upper part of the Ponta Grossa Formation (lower Emsian, Apucarana Sub-basin, Paraná Basin, Paraná State, Brazil). Nevertheless, considering glabellar furrows, glabellar lobes and the tuberculation pattern (Fig. 4.5), we identify NR3130 as *M. tuberculatus*.

Metacryphaeus sedori (*nom. nud.*), as described by Popp (1985), resembles *M. tuberculatus* although it is clearly worn due to taphonomic processes. In addition, *M. sedori* is more similar to *M. australis* in its glabellar lobes and glabellar furrows.

According to Lieberman *et al.* (1991), one of the main differences between *M. australis*, *M. caffer*, and *M. tuberculatus* is the LEI which measures the ratio between eye length and the length of the glabella excluding LO and SO (Wolfart, 1968). However, the values yielded by means of this index represent subtle differences between these species and, in some cases, can partly overlap as observed in *M. caffer* and *M. australis* (0.29–0.39 and 0.38–0.41, respectively). *Metacryphaeus tuberculatus* typically exhibits lower values of LEI (0.26–0.30) though it subtly overlaps those of *M. caffer*. Due to this, LEI can sometimes –albeit not always– be used to differentiate *M. tuberculatus* from *M. caffer* and *M. australis*. The LEI values computed for the analyzed individuals are 0.29–0.31 and correspond to the range of *M. tuberculatus* and *M. caffer*.

Besides the LEI, *Metacryphaeus tuberculatus* presents further differences in relation to *M. australis*, from the Ponta Grossa and São Domingos formations (Apucarana Sub-basin, Paraná Basin, Brazil), and *M. caffer*, from the Bokkeveld Group (South Africa). Such discrepancies occur with respect to S2, which, in *M. australis* and *M. caffer*, does not connect with the axial furrow or only subtly does. Regarding S1, *Metacryphaeus tuberculatus* also stands apart from *M. australis* and *M. caffer* in that, in these, S1 makes tenuous contact with the axial furrow (although more detached than that between the axial furrow and S2). Furthermore, in *M. australis* and *M. caffer*, the glabellar furrows are less marked, L3 may weakly connect with L2 distally, and L2 and L1 are sub-rectangular. Also, glabellar lobes in *M. australis* and *M. caffer* are not inflated as they are in *M. tuberculatus* and the anterior margin of the eyes in *M. tuberculatus* does not reach

the axial furrow, as it does in *M. australis* and *M. caffer*. While the tuberculation of *M. tuberculatus* is coarser, that of *M. australis* is finer and denser. According to Lieberman *et al.* (1991), the tuberculation difference between these species is not related to taphonomic processes as there are *M. australis* samples in excellent preservational conditions displaying fine and dense tuberculation.

The main differences between *M. tuberculatus* and *M. rotundatus*, described from Emsian of the Icla Formation (Bolivia) and the Ponta Grossa Formation (Apucarana Subbasin, Paraná Basin, Brazil), appear regarding the genal spine, which is long and thin in *M. rotundatus*; the absence of tubercles in *M. rotundatus*; the interrelation between glabellar length and frontal lobe width, which is less marked in *M. rotundatus* (85%); the greater length/width ratio of the frontal lobe in *M. rotundatus* (55%); S2 is narrower in its proximal and distal portions in *M. rotundatus*; and the position of the eyes on the cephalon, with posterior and anterior margins closer to the axial furrows in *M. rotundatus*.

When compared with calmoniids from the Paraníba Basin (Brazil), *M. tuberculatus* differs from *M. kegeli* from the Eifelian of the Pimenteira Formation by the absence of shallow depressions on the librigenal field and extra-ocular fixigena. Furthermore, axial and glabellar furrows are more marked in *M. kegeli*, the distance between the eyes is wider in *M. kegeli* and the shape of such structures is also distinct.

Although very similar, *M. tuberculatus* and *M. meloi* from the Passagem Member (Givetian, Pimenteira Formation, Parnaíba Basin, Brazil) differ with respect to their eye size. According to Carvalho *et al.* (1997), what distinguishes *M. meloi* from *M. tuberculatus* is that in *M. meloi* the posterior median impression is less defined, the axial furrows and S3 are narrower, tuberculation is less evident, and the lateral glabellar lobes are less conspicuous.

Metacryphaeus tuberculatus and *M. giganteus*, from the Devonian of the Icla and Belén formations (Bolivia) and the

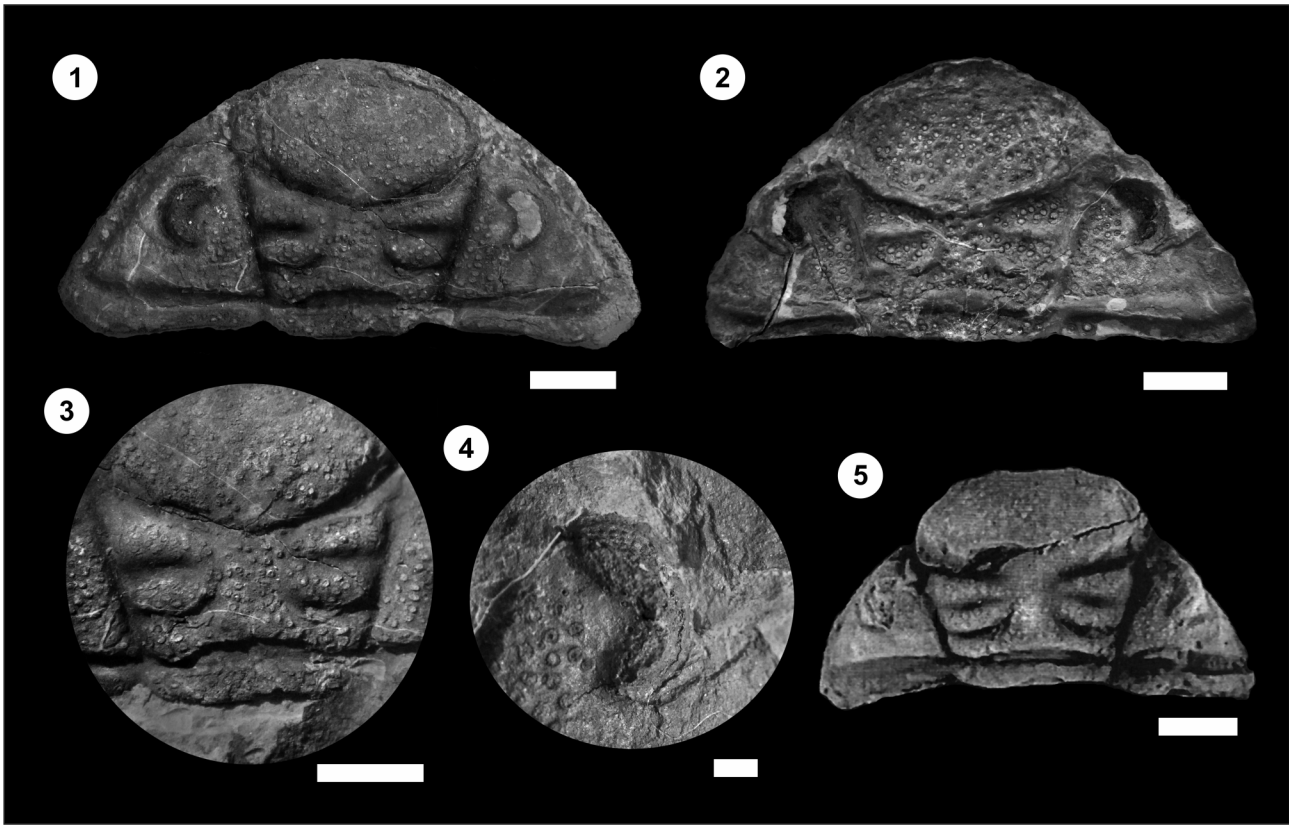


Figure 4. ***Metacryphaeus tuberculatus*****. 1,** external convex mold of cephalon in dorsal view (**CCLP** 874a); **2,** external mold in dorsal view (**CCLP** 874b); **3,** details of the glabellar lobes and furrows (**CCLP** 874a); **4,** eyes with preserved lenses (**CCLP** 874b); **5,** cephalon in dorsal view (**NR**3130; image taken from Stasi, 2013). Scale bars: 1–3, 5= 5 mm; 4= 1 mm.

Cabanillas Formation (Peru), differ in terms of format and position of the eyes (longer and with anterior and posterior margins closer to the axial furrows in *M. giganteus*); regarding the axial furrow, the glabellar furrows, and the posterior border furrow (more prominent in *M. giganteus*); concerning L2 shape (proximal portion is more curved anteriorly in *M. giganteus*), L1 shape (narrower in *M. giganteus*) and the frontal glabellar lobe (more expanded anteriorly in *M. giganteus*); and with respect to the genal spines (long and narrow in *M. giganteus*).

Metacryphaeus tuberculatus differs from *M. convexus* from the Icla Formation given that, in *M. convexus*, the anterior margin of the eyes is connected to the axial furrow; the glabella is more inflated; L2 and L3 are more inflated and larger; the axial furrows, the glabellar furrows, the occipital furrow, and the posterior border furrows are more marked; the proximal portion of S1 is more curved anteriorly; L1 is narrower and smaller; the frontal lobe is more inflated; and the tuberculation pattern proves distinct.

The main differences between *M. tuberculatus* and *M. curvigena* from the Icla Formation reside in the fact that, in *M. curvigena*, the axial furrow and posterior border furrows are more marked, L1 is narrower while S1 is more marked, the posterior median impression is less prominent, L2 and L3 are more inflated and seem to be a single structure, the genal spine is thin and curved inwards on the terminal portion, the anterior margin of the eyes is connected to the axial furrow, and the posterior margin is nearer to the axial furrow.

Compared to *M. branisai*, from the Icla Formation, *M. tuberculatus* presents a more prominent posterior median impression while its L1 is wider, its S3 is more marked, and its L0 is less inflated. Also, the antero-median portion of the lateral cephalic border of *M. branisai* is flexed antero-distally.

Metacryphaeus tuberculatus and *M. allardyceae*, the latter from the Fox Bay Formation (Malvinas Islands), differ in that *M. allardyceae* presents a very long frontal spine and eyes nearer to the lateral cephalic border.

Metacryphaeus australis (Clarke, 1913)

Figure 5

1913 *Cryphaeus australis* Clarke; p. 108–114; pl. 3; figs. 7–14; pl. 4; figs. 1–5.
1925 *Dalmanites australis* Reed; p.145; pl. 11; fig. 9.
1935 *Hadrorachus australis* (Clarke) Delo; p. 415; figs. 34–35.
1942 *Asteropyge australis* Richter and Richter; p. 134.

Lectotype. DGM 35-5 (Clarke, 1913, pl. 4, fig. 5).

Examined material. DEGEO/MPI 1535, DEGEO/MPI 1536, DEGEO/MPI 1539 A, DEGEO/MPI 1539 B, DEGEO/MPI 1543, DEGEO/MPI 1555, DEGEO/MPI 1556, DEGEO/MPI 1557, and DEGEO/MPI 8476 B.

Geographic and stratigraphic provenance. Ponta Grossa and São Domingos formations (Apucarana Sub-basin, Paraná Basin, Paraná State, Brazil). The material presented herein was collected from rocks of the São Domingos Formation (Givetian age, Apucarana Sub-basin, Paraná Basin).

Description. Cephalic portion incomplete (DEGEO/MPI 1556; Fig. 5.1). Cephalic dimensions of 2.25 cm in length and 4.5 cm in width. Cephalic length is equal to 90% of the frontal glabellar lobe width. The estimated value of LEI is 0.40. Small tubercles are present in low numbers. Posterior median impression present. The frontal glabellar lobe length is 55% of the glabellar length. Axial furrow well marked. Lateral glabellar furrow less marked than axial furrow. S3 is more marked than the other lateral glabellar furrows. S2 does not connect with the occipital furrow. S1 slightly curved in its proximal portion. S1 connects the axial furrow distally. SO is well marked and deep. The glabellar lobes present different shapes. L3 is sub-trapezoidal. L2 is sub-rectangular. L1 is sub-rectangular with slight concavity in its anterior portion. The LO is well marked. Only an eye of relatively big size, reniform shape, and with a connection between its anterior margin and the axial furrow was preserved. Thorax incomplete (DEGEO/MPI 1535, DEGEO/MPI 1536, DEGEO/MPI 1555, and DEGEO/MPI 8476 B; Fig. 5.2). Pygidium (DEGEO/MPI 1539 A, DEGEO/MPI 1539 B, DEGEO/MPI 1543, and DEGEO/MPI 1557; Fig. 5.3–4) subtriangular and moderately convex with evident tuberculation. Anterior axial portion wider than posterior portion, tapering towards posterior portion. After the five anterior axial rings of the pygidium, axial furrows become subparallel. Approximately 11 axial rings. Pleural spines (marginal) of pygidium blade-shaped.

Discussion. The diagnostic characters used to identify this species were the LEI, S1 (without connection to the axial furrow), S2 (slightly sinuous), tuberculation (less dense), the connection of the anterior margin of the eyes with the axial

furrow, and the pygidium (with five pairs of pleural lappets). The features of the axial furrows could be interpreted as alterations caused by taphonomic processes, but the cephalon here presented is relatively well preserved which could be observed by the presence of tuberculations and some lenses in the eyes.

Among all species of *Metacryphaeus*, the most similar to *M. australis* are *M. tuberculatus* and *M. caffer*. However, *M. australis* differs from *M. tuberculatus* in terms of the LEI, the tuberculation pattern, and the glabellar furrows. On the other hand, the differences between *M. australis* and *M. caffer* are subtle. *M. australis* presents slightly higher values of LEI (0.29–0.39 in *M. caffer* and 0.38–0.41 in *M. australis*). However, *M. caffer* has a bigger range of LEI.

FOSSILS ASSOCIATED WITH *METACRYPHAEUS TUBERCULATUS* AT DOVERLÂNDIA OUTCROP (GOIÁS STATE)

The record of *Metacryphaeus tuberculatus* in the Chapada Group Unit 4 is associated with a siltstone bed carrying tiny brachiopods, vestimentiferan tubes (quite common at the end of the Middle Devonian; Figs. 3, 6.7–8; Bosetti *et al.*, 2011, 2014), ichnofossils, and plant remains. Among the fossils mentioned above, only the vestimentiferan tubes are abundant.

The associated brachiopods were identified as *Derbyina*, indeterminate *Chonetidina*, and probable indeterminate small Obolidae varying between 1–7 mm in length (Fig. 6.1–5).

Although the cephalon of *M. tuberculatus* is not small, another fragmented trilobite of small size was found (about 10 mm in length without cephalic portion) (Fig. 6.6).

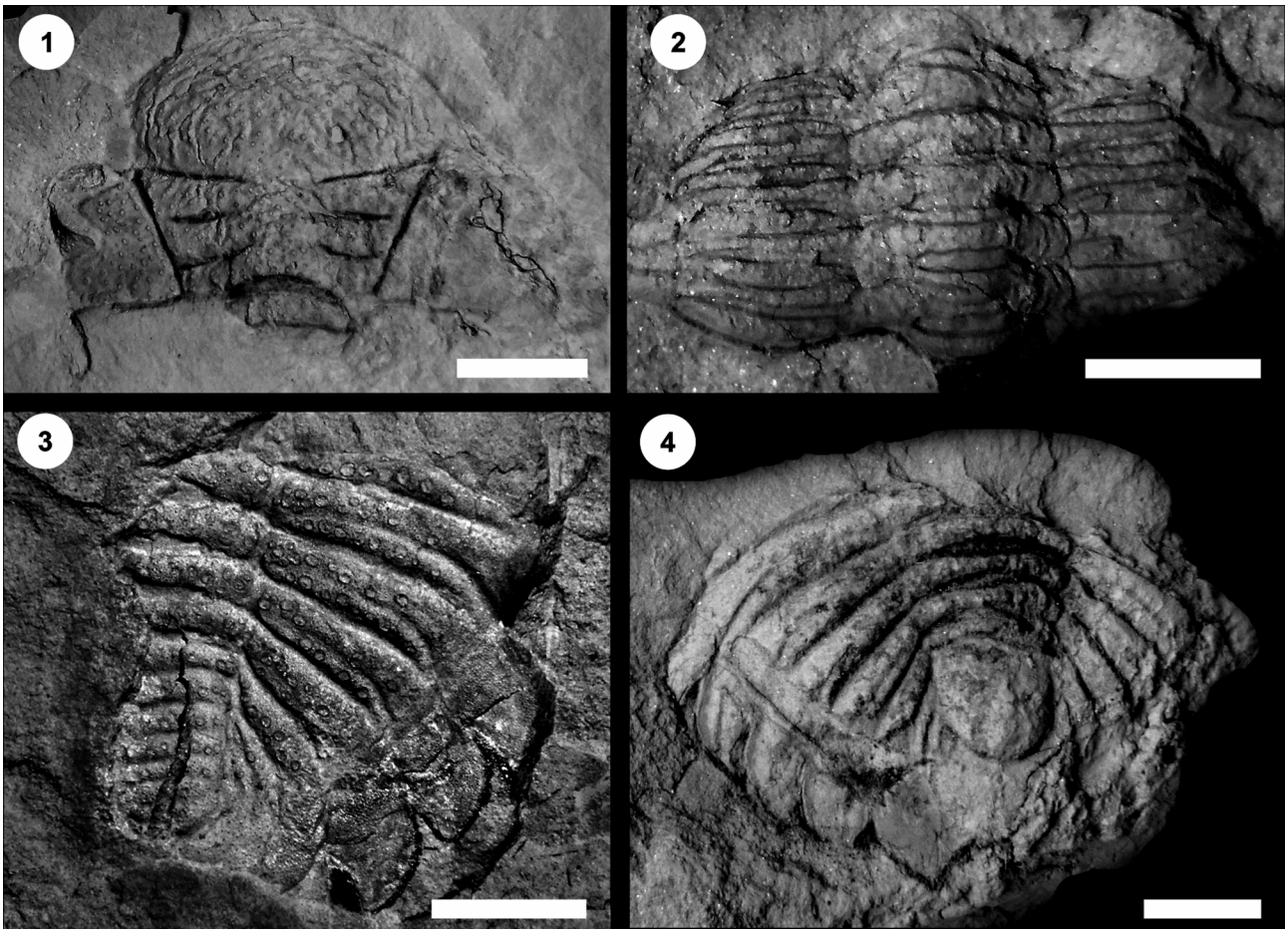


Figure 5. ***Metacryphaeus australis*. 1,** external convex mold in dorsal view (**DEGEO/MPI** 1556); **2,** thoracic portion in dorsal view (**DEGEO/MPI** 1536); **3–4,** pygidium in dorsal view (**DEGEO/MPI** 1557, **DEGEO/MPI** 1539 B). Scale bars= 5 mm.

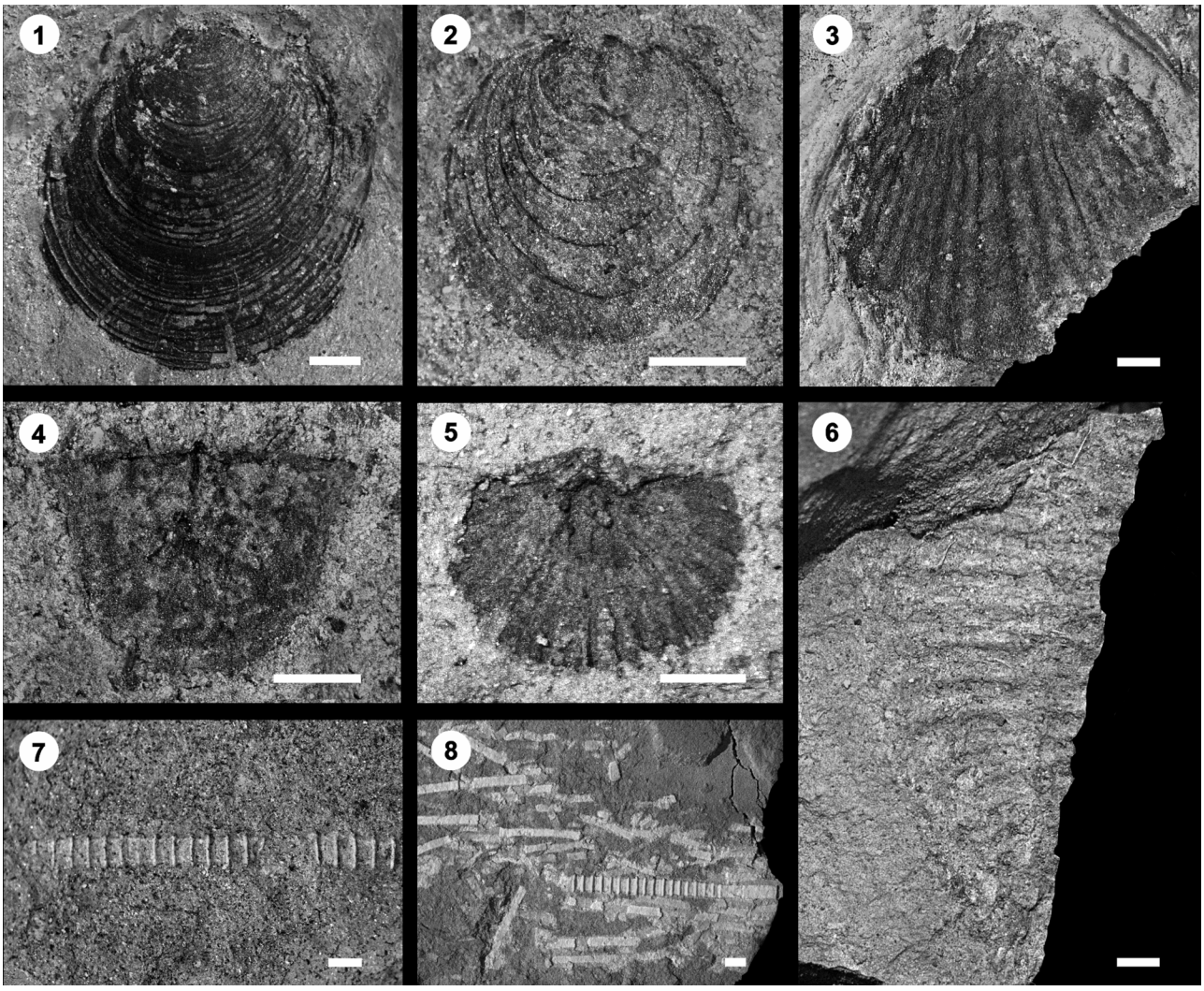


Figure 6. Some fossils found in association with ***Metacryphaeus tuberculatus*** at Doverlândia (GO) outcrop. **1–2,** indeterminate **Obolidae**; **3,** ***Derbyina*** sp.; **4,** indeterminate **Chonetidina**; **5,** indeterminate brachiopod; **6,** trilobite remains; **7,** vestimentiferan tube; **8,** assemblage of vestimentiferans tubes. Scale bars: 1, 3, 6–8= 1 mm; 2, 4–5= 0.5 mm.

The vestimentiferan tubes are preserved in major concentrations at the top of the section, near the area of contact with the Carboniferous Itararé Group (Figs. 3, 6.8). However, these fossils also occur in more basal beds of the outcrop.

PALEOBIOGEOGRAPHY

Metacryphaeus boasts occurrences in many areas of Gondwana and in different Devonian geological units. *Metacryphaeus australis* is endemic of the Paraná Basin and occurs in the Ponta Grossa and São Domingos formations in the Apucarana Sub-basin (Clarke, 1913; Popp, 1985) and in units 2 or 3 (Emsian–Eifelian) and 4 (Givetian) of the Chapada Group in the Alto Garças Sub-basin (Carvalho *et al.*, 1987; Carvalho and Edgecombe, 1991). On the other hand, compared with the other *Metacryphaeus* species, *M. tuberculatus* shows more records distributed in geological units located in Bolivia, Peru, and Brazil.

Bolivian occurrences of *M. tuberculatus* include those of the Icla Formation (Pragian–Emsian), the upper part of the Belén Formation (Emsian–Eifelian), the Sicasica Formation (Eifelian), and the Limoncito Formation (?late Pragian–?Givetian; Lieberman *et al.*, 1991; Lieberman, 1993). Alternatively, Peruvian records are limited to the Cabanillas

Formation (Early Devonian; Velazco, 2012) while Brazilian records include the Paraná Basin (early Emsian of Ponta Grossa Formation, Apucarana Sub-basin; Givetian–early Frasnian of the Chapada Group Unit 4, Alto Garças Sub-basin; in the present work) and the Parnaíba Basin (late Eifelian–early Givetian of the Pimenteira Formation; Lieberman *et al.*, 1991; Lieberman, 1993).

The new Emsian records of *M. tuberculatus* in the Paraná Basin provide a different palaeobiogeographic interpretation from that one established for brachiopods of the genus *Tropidoleptus* and the crinoid *Exaesiodiscus* (Melo, 1985, 1988; Fonseca and Melo, 1987; Petri and Fulfaro, 1988; Scheffler, 2010; Scheffler *et al.*, 2011).

Metacryphaeus tuberculatus was previously recorded in Brazil in the late Eifelian–early Givetian of the Pimenteira Formation (Parnaíba Basin) as well as in some geological units of Peru and Bolivia. However, this new occurrence in the early Emsian of the Apucarana Sub-basin (Paraná Basin) implies that *M. tuberculatus* may have dispersed throughout Bolivia, Peru and Brazil during the Emsian transgression. Later, this species probably migrated to the Alto Garças Sub-basin (Paraná Basin) and the Parnaíba Basin during the Givetian transgression.

On the other hand, it is also possible that the arrival of *M. tuberculatus* in the Parnaíba Basin could have occured as a result of a dispersive event throughout Bolivia, the Amazon Basin (Brazil), and the Parnaíba Basin (Brazil). The connection between these localities has been already explored in the literature by means of studying the fossils of *Tropidoleptus*, *Exaesiodiscus*, *Laudonomphalus* Moore and Jeffords, 1968, *Monstrocrinus* Schmidt, 1941, and *Marettocrinus* Le Menn, 1981 (Fonseca and Melo, 1987; Melo, 1988; Petri and Fulfaro, 1988; Assine, 2001; Scheffler, 2010; Scheffler *et al.*, 2011). However, there are no records evidencing the presence of *M. tuberculatus* and the genus *Metacryphaeus* in the Amazon Basin.

CONCLUSIONS

A new occurrence of *Metacryphaeus tuberculatus* is recorded for the Paraná Basin (Brazil), both in the Alto Garças and the Apucarana sub-basins. This new record is jointly presented with new findings of *M. australis* in the Apucarana Sub-basin, which proved of use for illustrating the differences between *M. australis* and *M. tuberculatus*.

Metacryphaeus tuberculatus, *M. australis*, and *M. caffer* present some morphological similarities while their main differences are observed in the glabellar furrows S1 and S2; the glabellar lobes L1, L2, and L3; their tuberculation pattern; the position of their eyes in relation to the axial furrow; and in the LEI.

The presence of *M. tuberculatus* in the Paraná Basin suggests an alternative paleogeographical interpretation to that presented after studying *Tropidoleptus* and *Exaesiodiscus* (Fonseca and Melo, 1987; Melo, 1988; Petri and Fulfaro, 1988; Scheffler, 2010; Scheffler *et al.*, 2011). Accordingly, *M. tuberculatus* would have arisen in the Early Devonian and inhabited Bolivia, Peru, and Brazil (Apucarana Sub-basin, Paraná Basin). Probably, that migration of *M. tuberculatus* between these areas occurred during the Emsian transgression. In the Givetian, *M. tuberculatus* would have migrated towards the Alto Garças Sub-basin (Paraná Basin) and the Parnaíba Basin, where available records provide evidence for such claim.

In contrast to the paleobiogeographical pattern exhibited by *M. tuberculatus*, *M. australis* is endemic of the Paraná Basin and presents occurrences in both the Apucarana and the Alto Garças sub-basins.

ACKNOWLEDGEMENTS

F. A. Carbonaro would like to thank Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 2013/09683-3) for their financial support and biologist Bruno Francisco dos Santos together with all the LAPALMA team for their collaboration regarding field work in Goiás State (Brazil). F. van E. Meira wishes to thank Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 2012/07075-3) for their financial support. E. P. Bosetti would like to thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 311483/2014-3) for the provided financial support.

REFERENCES

Andrade, S.M., and Camarço, P.E.N. 1980. Estratigrafia dos sedimentos devonianos do flanco nordeste da Bacia do Paraná. *31º Congresso Brasileiro de Geologia* (Balneário de Camboriú), *Anais* 5: 2828–2834.

Assine, M.L. 2001. O Ciclo Devoniano na Bacia do Paraná e correlação com outras bacias Gondwânicas. *Ciência, Técnica, Petróleo*, *Seção Exploração de Petróleo* 20: 55–62.

Assine, M.L., Perinotto, J.A.J., Fulfaro, V.J., and Petri, S. 1998. Progradação deltáica Tibagi no Devoniano Médio da Bacia do Paraná. *Revista Brasileira de Geociências* 28: 125–134.

Baldis, B., and Longobucco, M. 1977. Trilobites devónicos de la Precordillera Noroccidental (Argentina). *Ameghiniana* 14: 145–161.

Bosetti, E.P., Grahn, Y., Horodyski, R.S., Mendlowics Mauller, P., Breuer, P., and Zabini, C. 2011. An earliest Givetian "Lilliput

Effect" in the Paraná Basin, and the collapse of the Malvinokaffric shelly fauna. *Paläontologische Zeitschrift* 85: 49–65.

Bosetti, E.P., Grahn, Y., Horodyski, R., and Mendlowicz Mauller, P. 2012. The first recorded decline of the Malvinokaffric Devonian fauna in the Paraná Basin (southern Brazil) and its cause; taphonomic and fossil evidences. *Journal of South American Earth Sciences* 37: 228–241.

Bosetti, E.P., Horodyski, R.S., Comniskey, J.C., Ghilardi, R.P., and Sedorko, D. 2014. Tubos vestimentíferos no Eogivetiano da Formação São Domingos, Bacia do Paraná?. *2º Simpósio Brasileiro de Paleoinvertebrados* (Ponta Grossa), *Paleontologia em Destaque - Boletim de Resumos*, *Edição Especial,* 107.

Boucot, A.J. 1971. Malvinokaffric Devonian marine community distribution and implications for Gondwana. *Anais da Academia Brasileira de Ciências* 43: 23–49.

Boucot, A.J. 1974. Silurian and Devonian biogeography. *Society of Economic Mineralogists and Paleontologists, Special Publication* 21: 165–176.

Boucot, A.J. 1985. Late Silurian-early Devonian biogeography, provincialism, evolution and extinction. *Philosophical Transactions of the Royal Society of London B* 309: 323–339.

Braniša, L. 1965. Los fósiles guías de Bolivia. I. Paleozoico. *Servicio Geológico de Bolivia, Boletin* 6: 1–282.

Carvalho, M.G.P., and Edgecombe, G.D. 1991. Lower-Early Middle Devonian Calmoniid Trilobites from Mato Grosso, Brazil, and Related Species from Parana. *American Museum Novitates* 3022: 1–13.

Carvalho, M.G.P., Melo, J.H.G., and Quadros, L.P. 1987. Trilobitas devonianos do flanco noroeste da bacia do Parana. *10º Congresso Brasileiro de Paleontologia* (Rio de Janeiro), *Anais* 2: 545–565.

Carvalho, M.G.P., Edgecombe, G.D., and Lieberman, B.S. 1997. Devonian Calmoniid trilobites from the Parnaíba Basin, Piauí State, Brazil. *American Museum Novitates* 3192: 1–11.

Clarke, J.M. 1913. Fósseis devonianos do Paraná. *Monographias do Serviço Geológico e Mineralógico do Brasil* 1: 1–353.

Cooper, M.R. 1982. A revision of the Devonian (Emsian-Eifelian) Trilobita from the Bokkeveld Group of South Africa. *Annals of the South African Museum* 89: 1–174.

Delo, D.M. 1935. A revision of the phacopid trilobites. *Journal of Paleontology* 9: 402–420.

Eldredge, N., and Ormiston, L. 1979. Biogeography of Silurian and Devonian trilobites of the Malvinokaffric Realm. In: A.J. Boucot, and J. Gray (Eds.), *Historical Biogeography, plate tectonics and the changing environment.* Oregon State University Press, Corvallis, p. 147–167.

Fonseca, V.M.M., and Melo, J.H.G. 1987. Ocorrência de *Tropidoleptus carinatus* (Conrad) (Brachiopoda, Orthida) na Formacão Pimenteira, e sua importância paleobiogeográfica. *10º Congresso Brasileiro de Paleontologia* (Rio de Janeiro)*, Anais* 2: 505–537.

Ghilardi, R.P., and Simões, M.G. 2007. History and development of trilobite research in Brazil. *New York State Museum Bulletin* 507: p. 97–104.

Glaser, I. 1969. A formação Furnas no SW de Goiás. *23º Congresso Brasileiro de Geologia* (Salvador), *Anais*: 135–144.

Grahn, Y., Mendlowicz Mauller, P., Breuer, P., Bosetti, E.P., Bergamaschi, S., and Pereira, E. 2010a. The Furnas/Ponta Grossa contact and the age of the lowermost Ponta Grossa Formation in the Apucarana Sub-basin (Paraná Basin, Brazil): integrated palynological age determination. *Revista Brasileira de Paleontologia* 13: 89–102.

Grahn, Y., Mendlowicz Mauller, P., Pereira, E., and Loboziak, S. 2010b. Palynostratigraphy of the Chapada Group and its significance in the Devonian stratigraphy of the Paraná Basin, south Brazil. *Journal of South American Earth Sciences* 29: 354–370.

Grahn, Y., Mendlowicz Mauller, P., Bergamaschi, S., and Bosetti, E.P. 2013. Palynology and sequence stratigraphy of three Devonian rock units in the Apucarana Sub-basin (Paraná Basin, south Brazil): Additional data and correlation. *Review of Palaeobotany and Palynology* 198: 27–44.

Hall, J. 1857. Descriptions of Palaeozoic fóssil. *New York State Cabinet of Natural History, 10th Annual Report:* 4–186.

Kozlowski, R. 1923. Faune devonienne de Bolivie. *Annales de Paléontologie* 12: 1–112.

Le Menn, J. 1981. Les crinoides. *Société Géologique et Minéralogique de Bretagne* 24: 261–273.

Lieberman, B.S. 1993. Systematics and biogeography of the "*Metacryphaeus* Group", Calmoniidae (Trilobita, Devonian), with comments on adaptive radiations and the geological history of the Malvinokaffric Realm. *Journal of Paleontology* 67: 549–570.

Lieberman, B.S., Edgecombe, G.D., and Eldredge, N. 1991. Systematics and biogeography of the "Malvinella group", Calmoniidae (Trilobita, Devonian). *Journal of Paleontology* 65: 824–843.

Melo, J.H.G. 1985. [*A Província Malvinocáfrica no Devoniano do Brasil: estado atual dos conhecimentos*. Tese de doutorado, Universidade Federal do Rio de Janeiro, Instituto de Geociências, Rio de Janeiro, 890 p. Unpublished.].

Melo, J.H.G. 1988. The Malvinokaffric Realm in the Devonian of Brazil. *Canadian Society of Petroleum Geologists* 14: 669–703.

Melo, J.H.G., and Loboziak, S. 2003. Devonian–Early Carboniferous miospore biostratigraphy of the Amazon Basin, Northern Brazil. *Review of Palaeobotany and Palynology* 124: 131–202.

Milani, E.J., Melo, J.H.G., Souza, P.A., Fernandes, L.A., and França, A.B. 2007. Bacia do Paraná. *Boletim de Geociências da Petrobrás* 15: 265–287.

Moore, R.C., and Jeffords, R.M. 1968. Classification and nomenclature of fossil crinioids based on studies of dissociated parts of their columns. *The University of Kansas Paleontological Contributions* 9: 1–86.

Petri, S., and Fulfaro, V.J. 1988. *Geologia do Brasil*. Editorial da Universidade de São Paulo, São Paulo, 631 p.

Popp, M.T.B. 1985. [*Revisão dos trilobitas calmoniideos e comunidades faunísticas da Formação Ponta Grossa, Devoniano do Estado do Paraná Brasil.* Tese de doutorado, Universidade Federal do Rio Grande do Sul, Porto Alegre, 112 p. Unpublished.].

Ramos, A.N. 1970. Aspectos paleo-estruturais da Bacia do Paraná e sua influência na sedimentação. *Boletim Técnico da Petrobrás* 13: 85–93.

Reed, F.R.C. 1907. The fauna of the Bokkeveld Beds. *Geological Magazine* 4: 165–171, 222–232.

Reed, F.R.C. 1925. Revision of the fauna of the Bokkeveld Beds. *Annals of the South African Museum* 22: 27–225.

Richter, R. 1941. Devon. *Geologische Jahresberichte Berlin* 3A: 31– 43.

Richter, R., and Richter, E. 1942. Die Trilobiten der Weismeschichten am Hoen Venn, mit Benerkungen über die malvinocaffrische Provinz. *Senckenbergiana* 25: 156–179.

Salter, J.W. 1856. Description of Paleozoic Crustacea and Radiata from South Africa. *Transactions of the Geological Society of London* 2: 215–224.

Salter, J.W. 1864. The trilobites of the Cambrian, Silurian, and Devonian formations, Part 1 (Devonian and Silurian). *Monograph of the Palaeontographical Society* 67: 1–80.

Scheffler, S.M. 2010. [*Crinóides e blastóides do Devoniano brasileiro.* Tese de Doutorado, Universidade Federal do Rio de Janeiro, Instituto de Geociências, Rio de Janeiro, 278 p. Unpublished.].

Scheffler, S.M., Silva, S.D., Gama Júnior, J.M., Fonseca, V.M.M., and

Fernandes, A.C.S. 2011. Middle Devonian crinoids from the Parnaiba Basin (Pimenteira Formation, Tocantins State, Brazil). *Journal of Paleontology* 85: 1188–1198.

Stasi, A.M. 2013. [*Revisão sistemática dos Calmoniidae (Trilobita, Phacopida) da Formação Ponta Grossa, Devoniano, Bacia do Paraná, Brasil*. Dissertação de Mestrado, Universidade de São Paulo, São Paulo, 91 p. Unpublished.].

Schmidt, W. 1941. Die Crinoïdeen des Rheinischen Devons. II Die Crinoïdeen des Unterdevons bis zur Cultrijugaltus-Zone (mit Asschluss des unsrückschiefers). *Abhandlungen der Reichsstelle für Bodenforschung* 182: 1–253.

Ulrich, A. 1892. Palaeozoische Versteinerungen aus Bolivien. In: G. Steinmann (Ed.), *Beiträge zur Geologie und Paliäontologie von Südamerika*/ Schweizerbart, Stuttgart, p. 1–116.

Velazco, Y.P. 2012. Fósiles del paleozoico de la colección Antonio Raimondi conservados en el Museo de Historia Natural – Universidad Nacional Mayor de San Marcos, Lima-Perú, 1° parte. *Revista del Instituto de Investigación (RIIGEO), FIGMMG-UNMSM* 15: 7–16.

Wolfart, R. 1968. Die Trilobiten aus dem Devon Boliviens und ihre Bedeutung fir stratigraphie und tiergeographie. *Beihefte zum Geologischen Jahrbuch* 74: 5–201.

doi: 10.5710/AMGH.23.06.2016.2966

Submitted: November 16th, 2015

Accepted: June 23rd, 2016