



FIRST OCCURRENCE OF *BURMEISTERELLA* (TRILOBITA,
HOMALONOTIDAE) FROM THE DEVONIAN OF BRAZIL (PARECIS BASIN),
WITH DESCRIPTION OF A NEW SPECIES¹

(With 3 figures)

MARIA DA GLORIA PIRES DE CARVALHO²

ABSTRACT: A homalonotid trilobite from the Early Devonian (latest Lochkovian?- Pragian) of the Parecis Basin of Brazil is referred to the genus *Burmeisterella*, and represents the first occurrence of this genus in South America. A new species is described, *Burmeisterella braziliensis* n.sp. This form is associated with calmonioid trilobites (*Metacryphaeus australis* (Clarke, 1913) and *Calmonia? triacantha* Carvalho & Edgecombe, 1991) and other fossils characteristic of the Malvinokaffric assemblage, many of which also occur in the lower Ponta Grossa Formation (Pragian-Emsian) of the Paraná Basin. Apart from a possible occurrence of *Burmeisterella* in South Africa, the genus is otherwise known only from the Old World province (e.g. England, Germany, Belgium, Spain, and Algeria).

Key words: Devonian. Parecis Basin. Brazil. Trilobita. Homalonotidae.

RESUMO: Primeira ocorrência de *Burmeisterella* (Trilobita, Homalonotidae) do Devoniano do Brasil (Bacia do Parecis) com a descrição de uma espécie nova.

Um trilobita homalonotídeo do Eodevoniano (Lochoviano sup.? - Praguiano) da Bacia dos Parecis, no Brasil, é atribuído ao gênero *Burmeisterella* e representa a primeira ocorrência deste gênero na América do Sul. Uma nova espécie é descrita, *Burmeisterella braziliensis* sp.n. Esta forma ocorre associada com trilobitas calmoniídeos (*Metacryphaeus australis* e *Calmonia? triacantha*) e outros fósseis característicos da assembléia Malvinocáfrica, muitos dos quais também ocorrem na seção inferior da Formação Ponta Grossa (Praguiano - Emsiano) da Bacia do Paraná. Além de uma possível ocorrência na África do Sul, *Burmeisterella* é conhecido somente na província do Velho Mundo (por ex., Inglaterra, Alemanha, Bélgica, Espanha, Algéria).

Palavras-chave: Devoniano. Bacia dos Parecis. Brasil. Trilobita. Homalonotidae.

INTRODUCTION

A single large specimen of homalonotid trilobite is described from the southeastern border of the Parecis Basin (SIQUEIRA, 1989), in the central region of Brazil. It was collected by L.P.Siqueira, a geologist from Petrobras S.A., and came from a locality known as Morro Vermelho, on Serra Azul Farm, located north of the town of Paranatinga, Mato Grosso State, Brazil (Fig. 1A). The specimen is three-dimensionally preserved, inside an argillaceous concretion. It is referred here to the genus *Burmeisterella* Reed, 1918 (for generic diagnosis see HARRINGTON *et al.*, 1959), and represents the first documented occurrence of this taxon in Brazil and possibly South America. It differs from *Burmeisteria* Salter, 1865 (another homalonotid commonly found in the Devonian of Gondwana) mainly in its pygidial morphology and the arrangement of spines on

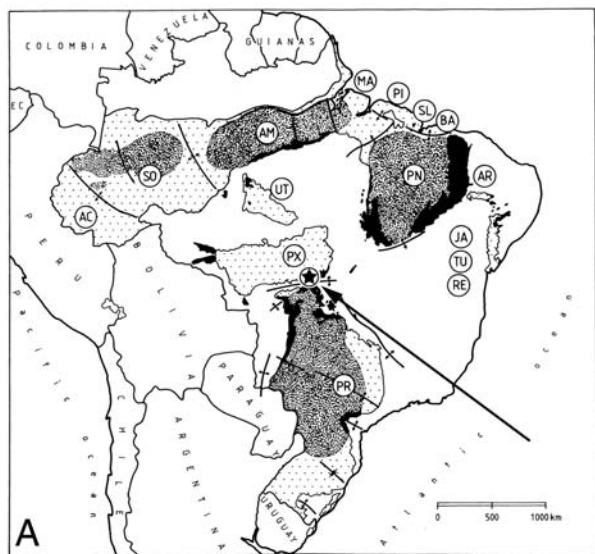
thoracic segments. Well-preserved trilobite fossils are rare in the Devonian of Brazil, and further prospecting at the fossil site would be worthwhile to produce more specimens in order to improve systematic comparison and biogeographic analysis of this interesting taxon.

GEOLOGICAL BACKGROUND

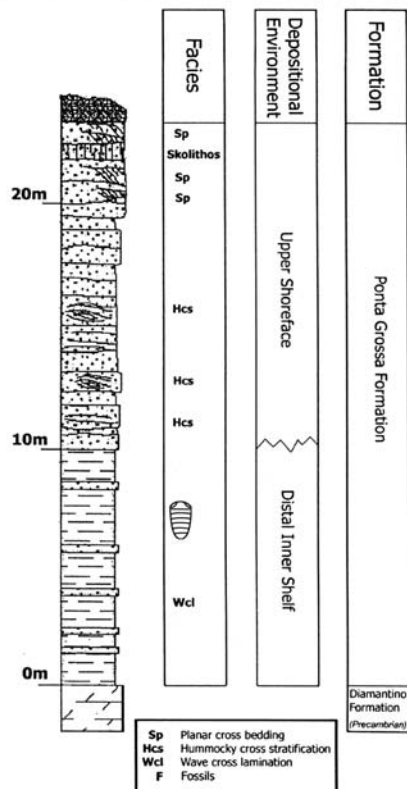
The Morro Vermelho locality is on Serra Azul Farm, north of Paranatinga, Mato Grosso State. The exposure is on a low, flat-topped hill, in an isolated outlier west of the main outcrop belt of Devonian rocks on the southeastern border of the Parecis Basin. The outcrop consists of deeply weathered micaceous shales and ferruginous sandstones, which rest directly on low-grade metasediments of Late Precambrian age (Fig. 1B). The shales of the Paranatinga region, Parecis Basin, are currently

¹ Submitted on April 16, 2004. Accepted on July 22, 2005.

² Universidade Federal do Rio de Janeiro, Instituto de Geociências, Depto de Geologia (Retired Adj. Prof.).
Research Associate of the American Museum of Natural History, NY.



A



B

Fig. 1- (A) Map of Brazil showing the location of the Parecis Basin relative to adjacent basins that include fossiliferous Devonian strata. Outcrop areas in black. Sedimentary basins: (AC) Acre, (AM) Amazon, (AR) Araripe Plateau, (BA) Barreirinhas, (JA) Jatobá, (MA) Marajó, (PI) Pirabas, (PN) Parnaíba, (PR) Paraná, (PX) Parecis/Upper Xingu, (RE) Recôncavo, (SL) São Luís, (SO) Solimões, (TU) Tucano, (UT) Upper Tapajós (from MELO, 1988). (Star) place where the specimen was collected. (B) schematic lithological section of Morro Vermelho locality, modified from BOUCOT *et al.* (2001).

attributed by Brazilian geologists to the Ponta Grossa Formation of the Parana Basin, although the two basins are separated by a structural high of post-Devonian age (Alto Xingu High). These Paranatinga shales are lithologically and paleontologically similar to the lower part of that formation, exposed in the Chapada dos Guimarães area, farther south in Mato Grosso State. They contain an abundant, low-diversity assemblage of marine invertebrates of Malvinokaffric character, including molluscs, several brachiopods such as *Orbiculoidea falklandensis* Rowell, 1965, *Australostrophia mesembria* (Clarke, 1913), *Australocoelia palmata* (Morris & Sharpe, 1846), and *Pleurothyrella Boucot et al.*, 1963 (BOUCOT *et al.*, 2001), and trilobites including *Metacryphaeus australis* and *Calmonia? triacantha* (CARVALHO & EDGEcombe, 1991). The Devonian shales pinch out and disappear toward the west and north along the Parecis Basin's margins, and are quite thin at Paranatinga. They are apparently absent in the subsurface of the central Parecis Basin, thus suggesting that eastern part of the latter originally formed part of the northern Paraná Basin prior to their post-Devonian tectonic separation by the Alto Xingu High (MELO, 1988).

SYSTEMATIC PALEONTOLOGY

Order PHACOPIDA Salter, 1864

Suborder CALYMENINA Swinnerton, 1915

Family Homalonotidae Chapman, 1890

Subfamily Homalonotinae Chapman, 1890

Genus *Burmeisterella* Reed, 1918

Type species *Homalonotus elongatus* Salter, 1865

Burmeisterella braziliensis n.sp.

(Fig.2, A-E)

Diagnosis - Cephalon wider than long, glabella subtrapezoidal, with obsolete glabellar furrows, with median and two paired swollen spine bases; librigena with at least two spines; thoracic with indistinct trilobation; each thoracic segment with four or five pairs of long paired hollow spines, the anteriormost segments with an alternating pattern of four, three, four or five spine pairs; pygidium composed of 10-12 axial rings; pygidial axis slightly waisted, almost reaching posterior margin; fourth to sixth pygidial rings strongly convex anteriorly; paired spines only on first four rings; pygidial pleurae irregularly ornamented, some with a single spine and others without spines.

Holotype – MN 7588-I, Museu Nacional/UFRJ, Department of Geology and Paleontology, Rio de Janeiro, RJ, Brazil. Complete individual preserved in an argillaceous concretion.

Etymology – *Brazil*, the country from which the holotype originates + *-ensis*, Latin adjectival suffix forming an adjective denoting place of origin.

Locality – Morro Vermelho, Serra Azul Farm, north of Paranatinga town, Mato Grosso State, Brazil.

DESCRIPTION

CEPHALON

Although the cephalon has suffered some damage, several features can be described. The cephalon is considerably wider than long (sag.). The anterior border and preglabellar field are extremely narrow (sag.),

although the preglabellar furrow is moderately distinct. The rostral plate is wide but very short (sag.), and has a blunt median process. The facial suture is distinct; the posterior section cuts margin of cephalon in front to genal angle, then curves conspicuously inwards medially defining a narrow posterior area of the fixigena, which is gently convex. There is no clearly defined palpebral area or eye. The glabella is subtrapezoidal in outline, with indistinct segmentation and with bases of a median and two paired spines (these are not well preserved). The librigena has at least two hollow spine bases of different sizes; the larger spine is positioned farther laterally than the smaller one, but both are situated centrally on the librigena rather than at its margin. The posterior border of the cephalon (including the occipital ring) has suffered erosion and is not well preserved. In ventral view parts of the hypostoma and the doublure can be observed (Fig.2, E).

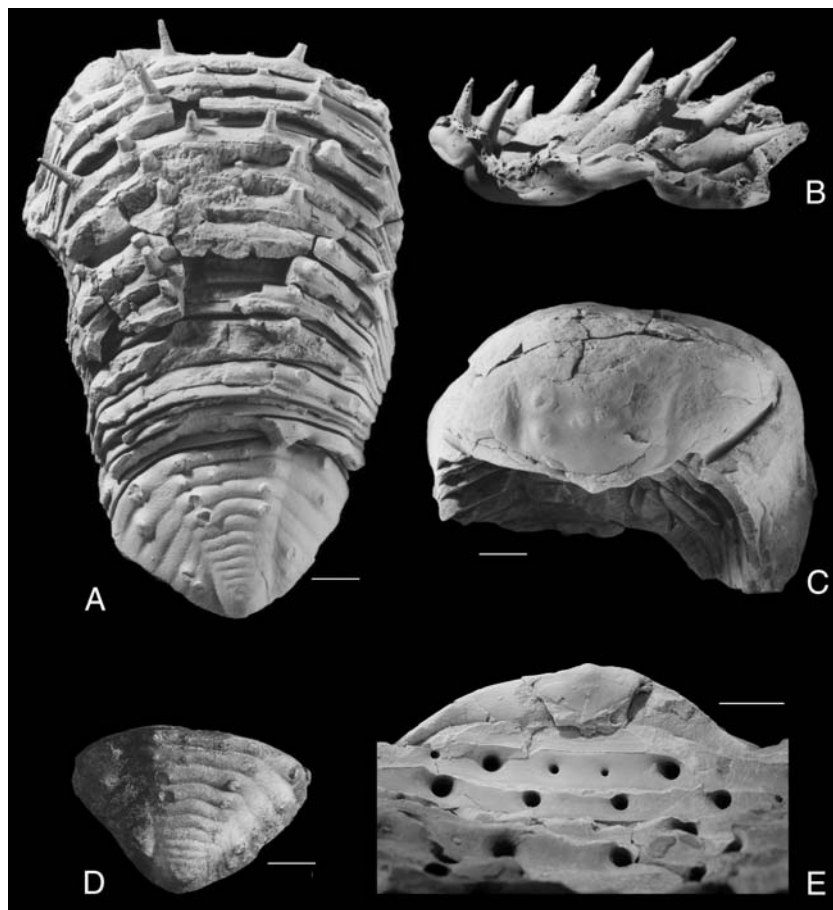


Fig.2- Holotype of *Burmeisterella braziliensis* n.sp., MN 7588-I – (A) dorsal view of thorax and pygidium; (B) latex cast showing thoracic spines; (C) anterior view of cephalon; (D) dorsal view of pygidium; (E) ventral view. A, C, and D are preserved as internal molds; E is an external mold. Scale bars = 10mm.

THORAX

The thorax has a flat and very broad axis, with indistinct trilobation so the axial furrows are not discernible and the axial region and pleurae cannot be clearly distinguished. The articulating furrows are clearly visible. The ornament of the thorax consists of prominent hollow spines preserved as internal molds. As far as can be determined, all the thoracic segments bear spines. The spines are regularly distributed and are always paired, sometimes with a repeating pattern. The first and third thoracic segments have five pairs, of which the first (innermost) and third pairs are distinctly smaller and narrower than the second and fourth (which is lateralmost, presumably on the pleura). The second and fourth segments have only four pairs of spines, all of which are large. The remaining segments are similarly ornamented, and there are clearly longitudinal rows of larger and smaller spines arranged down the length of the entire thorax, but the spine pattern cannot be determined precisely on each segment for preservational reasons. Although the spines nearest to the midline are clearly axial, and those farther laterally are pleural, spines occupying an intermediate position cannot be readily characterized as either because of the indistinct trilobation.

PYGIDIUM

The pygidium is convex, parabolic in outline, with a preserved width of approximately 54mm and length of 35mm. Trilobation of the pygidium is more distinct than on the thorax, and the axial furrow is distinct but shallow. The axial lobe extends the full length of the pygidium as preserved, and there is no evidence of a post-axial field. There are at least 10 to 12 axial rings, although the last few are indistinct. The axial lobe tapers distinctly as far as the seventh axial ring, after which its width remains fairly constant. The first three axial rings are weakly convex forward, while the fourth to sixth rings are conspicuously convex sagittally, and those farther posteriorly are more transverse. Large paired spine bases are present exsagittally on the anteriormost four axial rings of the pygidium. There is an additional pair of smaller tubercles (spine bases?) more medially on the first axial ring, and a single additional one on the left side of the second ring. The remaining axial rings are without ornamentation, and there are no median tubercles or spines. The ring furrows of the pygidium become progressively shallower posteriorly. The pleural field comprises approximately six pairs of ribs, which are separated by shallow and wide interpleural furrows.

The pleurae become slightly wider distally. There is a large tubercle or spine base distally, on the first and second pleurae, distally, and a smaller one adaxially on the fifth and sixth.

DISCUSSION

Burmeisterella and *Burmeisteria* are both representatives of a late homalonotid radiation which occurred in the Silurian (post-Ludlovian) - Devonian (THOMAS, 1977). The generic identification of the trilobite described here is complicated by a controversy surrounding possible synonymy of *Burmeisterella* with *Burmeisteria* (KENNEDY, 1994); this has profound biogeographical implications, as the following remarks will show. Trilobites referred to *Burmeisteria* have been described from Antarctica (Horlick Formation; SAUL, 1965); Argentina (Jachal Formation; THOMAS, 1905); Bolivia (Gamonedá and Belén formations; KOZŁOWSKI, 1923; BRANISA, 1965; WOLFART, 1968; COOPER, 1982; PECK & VANEK, 1991); Brazil (Paraná and Parnaíba Basins - Ponta Grossa and Pimenteira formations respectively; CLARKE, 1913; KEGEL, 1953; CASTRO, 1968; CARVALHO, 1995); Falkland Islands (Fox Bay Formation; CLARKE, 1913; COOPER, 1982); Ghana (from Accra Series; SAUL, 1967); New Zealand (from Reefton Beds; ALLAN, 1935); South Africa (from Bokkeveld Beds; REED, 1925; COOPER, 1982); and Uruguay (from Arroyo del Cordobes and Rincon de Alonso; MÉNDEZ-ALZOLA, 1938). All these records are Gondwanan, suggesting that *Burmeisteria* was a common taxon in Early and Middle Devonian seas of the southern hemisphere.

By contrast, most earlier records of *Burmeisterella* are from the northern hemisphere (England, Belgium, France, Germany, and Algeria), although TOMCZYKOWA (1975) also claimed it is present in South Africa (a questionable occurrence, since no specimen were described and it was not listed by COOPER (1982). Thus, most records of *Burmeisterella* fall within the Old World Realm (BOUCOT & GRAY, 1979).

The specimen described here represents the only other record of a Gondwanan *Burmeisterella*, and is the first reported from South America. Since I have not had an opportunity to examine material previously referred to *Burmeisterella*, a comprehensive investigation of this interesting controversy is beyond the scope of this work, however, a few pertinent remarks can be made. The two most important issues for this work are whether *Burmeisterella* and *Burmeisteria* are synonymous, and whether the Brazilian specimen should be referred to one genus or the other.

Previously, *Burmeisteria* and *Burmeisterella* were distinguished by several features including glabellar shape and lobation, the distinctness of thoracic trilobation, and several features of pygidial morphology (e.g., TOMCZYKOWA, 1975), even though the genera were considered to be very closely related sister taxa. KENNEDY (1994) disagreed with many of these criteria, especially the distinctness of thoracic and pygidial trilobation (arguing that this may represent a preservational difference), glabellar morphology (which is indistinct in *Burmeisterella*) and spiny ornament (which occurs in both *Burmeisteria* and *Burmeisterella*, and which could be influenced by "... environmental or growth factors"; *ibid.*, p.26). KENNEDY (1994) consequently referred some trilobites previously identified as *Burmeisterella* from the Emsian of England and Germany to *Burmeisteria*. Many of the supposed distinctions between these genera are admittedly blurred by variations in

morphology and preservation, and are therefore systematically unreliable. However, certain features of pygidial morphology seem less variable, suggesting that *Burmeisteria* and *Burmeisterella* should continue to be separated (Fig.3). First, the taper of the axial lobe is gradual and unchanged in *Burmeisteria herscheli* (Murchison, 1839) (the type species of that genus), whereas in fossils referred to *Burmeisterella* it decreases posteriorly, so that the last several segments are of subequal width. Second, in *Burmeisteria herscheli* the pygidial axis terminates before it reaches the posterior margin of the pygidium, leaving a short post-axial field (COOPER, 1982, Fig.3A), whereas in *Burmeisterella* the axis reaches the posterior margin or sometimes goes beyond it (Fig.3B). In the new homalonotid from Brazil, the pygidial axis tapers gradually and there is only a very short post-axial field (Fig.2D, Fig.3C), which on basis this form seems closer to *Burmeisterella* than to *Burmeisteria*.

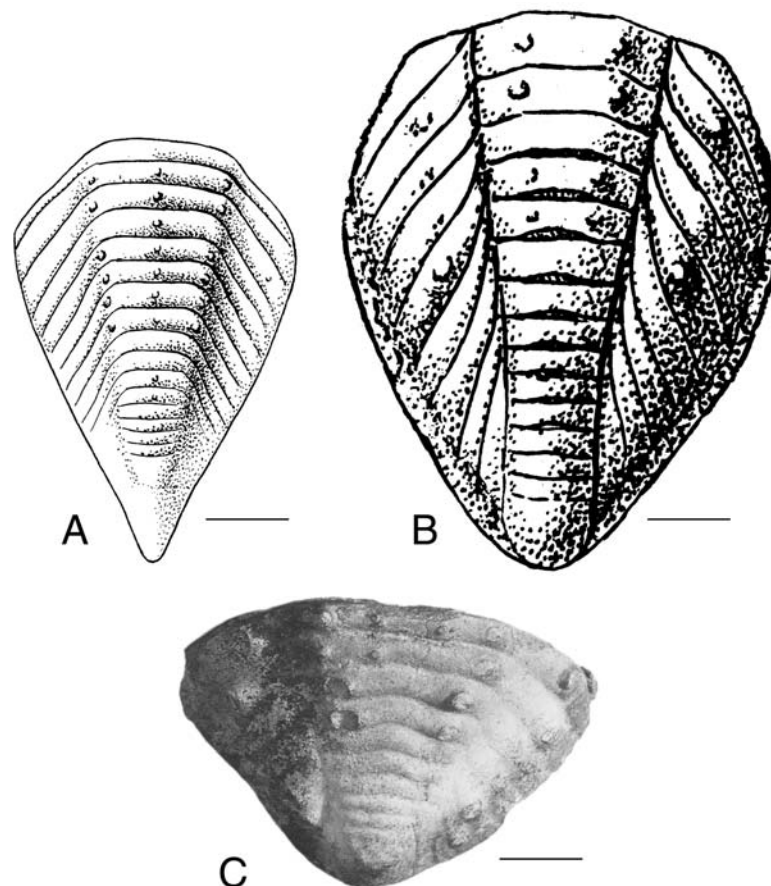


Fig.3- (A) pygidium of *Burmeisteria herscheli* from South Africa; (B) pygidium of *Burmeisterella elongata* from England; (C) pygidium of *Burmeisterella braziliensis*. Drawings (A-B) were taken from HARRINGTON *et al.* (1959). Scale bars = 10mm.

Comparison of the new form with previously described species of *Burmeisterella* and *Burmeisteria* reveal a unique combination of morphological characters, supporting the erection of a new taxon. The new form differs from all of them in having the pygidium much wider than long; in some species the pygidial length is much greater than its width (e.g., *Burmeisterella elongata* (Salter, 1865), *Burmeisteria herscheli*), but in others these dimensions are subequal, with pygidial length only just exceeding its width (e.g., *Burmeisterella armata* (Burmeister, 1843).

Burmeisterella elongata (the type species of that genus) is known only from the pygidium, so features of the cephalon and thorax cannot be compared in this form. Its pygidium is much longer (relative to its width) than in any of the other species referred to this genus, and the pygopleural ribs are more steeply angled posterolaterally. There are 10-12 axial rings (as in the new form), but the axial ring furrows from the fourth ring backward are all arched forward (KENNEDY, 1994), unlike the new form in which only the fourth to sixth axial ring furrows are arched forward. In species referred to *Burmeisteria*, however, the number of axial rings is highly variable (e.g., approximately 16 in *B. herscheli*, but only seven in *B. accraensis* Saul, 1967).

In the new form only the first four axial rings have paired spines; the first and second rings have additional spines. Several of the axial rings have a single pair of spines in *Burmeisterella elongata*, but they lack any additional spines. Paired spines are present on all the axial rings in *B. quadrispinosa* Wenndorf, 1990, with two pairs on first, second and fourth-seventh rings and one pair on the others. The axial rings lack spines in *B. aculeata* (Koch, 1883) and *B. armata* (WENNDORF, 1990). No comparison could be made with *B. champernownei* as its pygidium is badly preserved. In *Burmeisteria* the pygidial axial rings usually lack tubercles or spines, although a few scattered tubercles may be present in *B. herscheli* and may even be arranged in a paired series (COOPER, 1982:24, Fig.12A; 30, Fig.16D).

Pleural spines are characteristically present on the pygidium in *Burmeisterella*, but their number is variable; they occur only on the first and fourth or fifth ribs in *B. elongata* and *B. armata*; on the first, third and fourth in *B. aculeata*; on the first, second, fifth and sixth in the new form; and on each of the first six ribs in *B. quadrispinosa*. To summarize the situation, in material referred to *Burmeisterella*, pleural spines are always present on the first rib, often on the fourth or fifth, and sometimes on the other anterior ribs. By contrast in *Burmeisteria* species the pygidial pleurae are usually smooth, but in *B. herscheli* a few scattered tubercles are

sometimes present (COOPER, 1982).

Although the cephalon and thorax are unknown in the type-species *Burmeisterella elongata*, comparisons can be made with other *Burmeisterella* species. *Burmeisterella aculeata* (KOCH, 1883) differs from *B. braziliensis* in bearing only a single pair of spines on the glabella, positioned on the first glabellar lobe; *B. braziliensis* has a median spine and two pairs of swollen spine bases on the glabella (the posteriormost pair could be on the first glabellar lobe but this is indistinct). *B. aculeata* has three spines on the posterior region of the cephalon, one medially on the occipital ring and paired spines situated more distally on each side of the posterior cephalic border. This region is not well preserved in the holotype of *B. braziliensis*, so only a very limited comparison is possible. Both species have spines on the free cheek; *B. aculeata* has only one, but *B. braziliensis* has at least two. The spine pattern over the thoracic region also differs in these species. *B. aculeata* bears a single pair of spines on each axial ring, whereas in *B. braziliensis* there are at least two pairs (there may be more, but the indistinct trilobation makes this difficult to observe).

Burmeisterella armata (BURMEISTER, 1843) has the same pattern of spines on the posterior region of the cephalon and free cheek as in *B. aculeata*, but differs in having a median bifurcated spine (as in *B. braziliensis*), plus three paired spines on the glabella; the two anteriormost pairs are located more medially, while the posterior pair is more distal and is separated by the median spine. The pattern spine distribution on the thoracic segments is also distinct; unlike in *B. braziliensis* in *B. armata*, the first, second, fifth, eighth, and eleventh thoracic axial rings lack spines (they are also absent on the first, second, eighth, eleventh, and thirteenth pleurae).

Burmeisterella bifurcata Reed, 1920, is readily distinguished from other species of *Burmeisterella* in having its pygidium terminating with a bifurcated terminal spine. The glabella has many tubercles (or spine-bases) arranged into three longitudinal rows, with three tubercles in each row, but this form lacks spines on the occipital ring and posterior cephalic border. The free cheek in *B. bifurcata* has a large rounded tubercle, fewer than in *B. braziliensis*.

Burmeisterella champernownei (Woodward, 1881) also has three longitudinal rows of spines with three spines per row, but apparently has no spines on the free cheek. The anteriormost spine of the median row appears to have been double. The rostrum of *B. champernownei* is much more pronounced than in other *Burmeisterella* species.

Only a small posterolateral part of the cephalon is known in *Burmeisterella quadrispinosa*, but this has three spines on the occipital ring plus one on the cephalic posterior border; unfortunately this region is not well preserved in the Brazilian specimen. The distribution of spines on the thoracic axial rings is very distinctive with two pairs of spines per segment (WENNDORF, 1990:131, Fig.52), not the complex alternating pattern found in *B. braziliensis*. The thoracic pleurae in *B. quadrispinosa* each have a long spine, except for the second and eighth segments where the spine is absent (see the same figure cited above).

Burmeisterella vixarmata Wenndorf, 1990, differs from *B. braziliensis* in having distinct lateral glabellar lobes with very shallow lateral glabellar furrows, the glabella has only a single pair of spines located posteriorly, on the level of the first lateral glabellar lobe, and a pygidium either without spines or with at most only one on the first pleurae.

Although it was not possible to undertake a comprehensive phylogenetic analysis of species included in *Burmeisterella* and *Burmeisteria*, some general observations can be made. There is evidently a common trend for spine rows to be developed on the glabella, thorax and pygidium in both genera, and further studies may reveal phylogenetic patterns among these structures. *Burmeisterella braziliensis* display a unique combination of characters including its pygidial proportions, indistinct thoracic trilobation, and unusual alternation of thoracic spine rows. It is phenetically similar to taxa such as *B. aculeata*, *B. armata* and *B. quadrispinosa* in having a well-ordered pattern of spines over the body. By contrast, in forms referred to *Burmeisteria*, spine distribution is more variable and random. Among Gondwanan homalonotids, spine-bearing forms appear to be restrict to Malvinokaffric areas. The only other *Burmeisteria* with strong ornamentation is *B. huttoni* Allan, 1935 from New Zeland, but this has tubercles and therefore differs from the more spinous forms.

CONCLUSIONS

- 1) *Burmeisteria* and *Burmeisterella* are retained here as distinct genera.
- 2) *Burmeisteria* has a Gondwanan distribution while *Burmeisterella* is more widespread (Old World Realm and Gondwana).
- 3) This is the first time that *Burmeisterella* is recorded from the Devonian of Brazil and South America.

- 4) *Burmeisterella braziliensis* n.sp. from the Devonian of Parecis Basin, Brazil, resembles to *B. aculeata*, *B. armata* and *B. quadrispinosa* in having a spiny body, with the thoracic and pygidium spines distributed regularly, following a well-ordered pattern.

ACKNOWLEDGMENTS

The author thanks the geologists from Petrobras, especially J.H.G.Melo and L.P.Siqueira, who provided the material to study. I would also like to thank staff members of the American Museum of Natural History, including Dr. J.G.Maisey, for useful discussions during the preparation of the manuscript, S.Klofak, for preparing the specimens and latex casts, and S.Thurston, for producing the illustrations. Suggestions by the reviewers are appreciated.

REFERENCES

- ALLAN, R.S., 1935. The fauna of the Reefton Beds (Devonian), New Zealand; with notes on Lower Devonian animal communities in relation to the base of the Devonian System. **Palaeontology Bulletin**, Wellington, **14**:1-72.
- BOUCOT, A.J.; ROWELL, A.J.; RACHEBOEUF, P.R.; PEREIRA, E.; MELO, J.H.G. & SIQUEIRA, L.P., 2001. Position of the Malvinokaffric Realm's northern boundary (Early Devonian) based on newly discovered brachiopods from the Parecis Basin (Brazil). **Journal of the Czech Geological Society**, Prague, **46**(3/4):109-120.
- BOUCOT, A.J. & GRAY, J., 1979. Epilogue. A Paleozoic Pangea? p.465-482. In: GRAY, J. & BOUCOT, A.J. (Eds.) **Historical biogeography, plate tectonics and the changing environment**. Corvallis: Oregon State University Press.
- BRANISA, L., 1965. Los fosiles guias de Bolivia. I. Paleozoico. **Boletin del Servicio Geologico de Bolivia**, La Paz, **6**:1-282.
- BURMEISTER, H., 1843. **Die organisation der Trilobiten aus ihren lebenden Verwandten entwickelt; nebst einer systematischen Uebersicht aller zeither beschriebenen Arten**. Berlin. 147p.
- CARVALHO, M.G.P., 1995. **Trilobitas devonianos da Bacia do Parnaíba (Formações Pimenteira, Cabeças e Longá)**. Rio de Janeiro. 151p. (PhD Thesis, Rio de Janeiro Federal University).
- CARVALHO, M.G.P. & EDGEcombe, G.D., 1991. Lower-Early Middle Devonian calmonioid trilobites from Mato Grosso, Brazil, and related species from Paraná. **American Museum Novitates**, New York, **3022**:1-13.

- CASTRO, J.S., 1968. Trilobitas da Formação Pimenteira, Devoniano do Estado do Piauí. **Anais da Academia Brasileira de Ciências**, Rio de Janeiro, **40**(4):481-489.
- CLARKE, J.M., 1913. Fósseis devonianos do Paraná. **Serviço Geológico e Mineralógico Brasileiro**. Monografia 1, Rio de Janeiro, 353p.
- 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**, Cape Town, **89**: 1-174.
- HARRINGTON, H.J.; HENNINGSMOEN, G.; HOWELL, B.F.; JAANUSSON, V.; LOCHMAN-BALK, C.; MOORE, R.C.; POULSEN, C.; RASETTI, F.; RICHTER, E.; RICHTER, R.; SCHMIDT, H.; SDZUY, K.; STRUVE, W.; STØRMER, L.; STUBBLEFIELD, C.J.; TRIPP, R.; WELLER, J.M. & WHITTINGTON, H.B., 1959. Family Homalonotidae, p.454-461, figs.360-361. In: MOORE, R.C. (Ed.) **Treatise on Invertebrate Paleontology**. Lawrence: The Geological Society of America, Inc.; University of Kansas. Arthropoda 1. Trilobite - Part O, p.38-540.
- KEGEL, W., 1953. Contribuição para o estudo do Devoniano da Bacia do Parnaíba. **Boletim da Divisão de Geologia e Mineralogia**, Rio de Janeiro, **141**:1-48.
- KENNEDY, R.J., 1994. British Devonian Trilobites. **Monography of the Paleontographical Society**. London, Part 1, 1-33, pls.1-5. (Publ. No.595, part of Vol.148 for 1994).
- KOCH, C., 1883. Monographie der *Homalonotus* - Arten des Rheinischen Unterdevon. **Abhandlungen der geologischen Spezialkarte von Preussen und den Thüringischen Staaten**, Berlin, **4**:2, 71p.
- KOZLOWSKI, R., 1923. Faune Dévonienne de Bolivie. **Annales Paléontologie**, Paris, **12**(1/2):1-112.
- MELO, J.H.G., 1988. The Malvinokaffric Realm in the Devonian of Brazil. p.669-703. In: McMILLAN, N.J.; EMBRY, A.F. & GLASS, D.J. (Eds.) **Devonian of the World. Vol. I Regional syntheses**. CalgaryCan. Soc. Petrol. Geol.
- MENDEZ-ALZOLA, R., 1938. Fósiles Devónicos del Uruguay. **Instituto Geológico del Uruguay**, Montevideo, **24**:3-80.
- PEK, I. & VANEK, J., 1991. On some Silurian and Devonian Trilobites of Bolivia. **Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium Geographica-Geologica XXX**; Prague, **103**:75-104.
- REED, F.R.C., 1918. Notes on the genus *Homalonotus*. **Geological Magazine**, London, **5**:263-276; 314-327.
- REED, F.R.C., 1920. Notes on the fauna of the Lower Devonian beds of Torquay. **Geological Magazine**, London, **57**:299-306; 341-347, pl.4.
- REED, F.R.C., 1925. Revision of the fauna of the Bokkeveld Beds. **Annals of the South African Museum**, Cape Town, **22**:27-225.
- SAUL, J.M., 1965. Trilobita. p.269-271. In: HADLEY, J.B. (Ed.) **Geology and palaeontology of the Antarctic. Antarctic Research. Ser. 6**. Washington, D.C.
- SAUL, J.M., 1967. *Burmeisteria (Digonus) accraensis*, a new homalonotid trilobite from the Devonian of Ghana. **Journal of Paleontology**, Lawrence, **41**:1126-1136.
- SIQUEIRA, L.P., 1989. Bacia dos Parecis. **Boletim de Geociências da Petrobras**, Rio de Janeiro, **3**:3-16.
- THOMAS, A.T., 1977. Classification and phylogeny of the homalonotid trilobites. **Palaeontology**, London, **20**:159-178.
- THOMAS, I., 1905. Neue Beiträge zur Kenntnis der devonische Fauna argentinien. **Zeitschrift der deutschen geologischen Gesellschaft**, Berlin, **57**:233-290.
- TOMCZYKOWA, E., 1975. The trilobite subfamily Homalonotinae from the Upper Silurian and Lower Devonian of Poland. **Acta Paleontologica Polonica**, Warszawa, **20**:1-46, pls.1-6.
- WENNDORF, K.W., 1990. Homalonotinae (Trilobite) from the Lower Devonian of the Rheinische Schiefergebirge. **Palaeontographica A**, Stuttgart, **121**:1-184, pls.1-15.
- WOLFART, R., 1968. Die Trilobiten aus dem Devon Boliviens und ihre Bedeutung für stratigraphie und Tiergeographie. **Beihefte zum Geologischen Jahrbuch**, Hannover, **74**:5-201.
- WOODWARD, H., 1881. Note on a new English *Homalonotus* from the Devonian, Torquay, South Devon. **Geological Magazine**, London, **8**(2):489-491, pl.13.