# A new Pennsylvanian Oriocrassatellinae from Brazil and the distribution of the genus *Oriocrassatella* in space and time

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ABSTRACT

*Oriocrassatella* Etheridge Jr., 1907 is a long range crassatellid bivalve genus well recognized in shallow waters of epeiric seas throughout the upper part of Paleozoic. The first occurrences of this genus are recorded in the sedimentary successions of the Gondwana, both in Australia and South America. However, the geographic and age distribution of *Oriocrassatella* in Late Mississippian deposits of Australia and Argentina may indicate an earliest Visean or even a pre-Visean origin for the genus. Following its origin in Early Carboniferous a complex paleobiogeographic history from Southern to Northern Hemisphere took place in the Permian. During its initial dispersal phase from Late Carboniferous to the Early Permian the genus thrived in cold water environments associated to the Late Paleozoic Gondwana glaciation. Shallow-water bottoms of the warm waters of the central Gondwana fringe and Laurussia were colonized by *Oriocrassatella* only during Early Permian times when the genus became cosmopolitan. A new species of this genus is described herein, *Oriocrassatella piauiensis* n. sp., recorded from the Piauí Formation, Pennsylvanian of the Parnaíba Basin. This new species may represent an early adaptation to warm waters. However, based on available data, species of this genus seem to have adapted definitely to warm water environments probably related the Late Pennsylvanian interglacial phases. In these phases, climatic barrier were interrupted allowing the faunal interchange and larval dispersion following a South to North migration route through the eastern margins of Gondwana and the eastern Paleotethys.

**KEY WORDS**
*Oriocrassatella*, bivalve, Gondwana, Upper Paleozoic, glaciation, paleobiogeography, new species.

**RÉSUMÉ**
*Nouvel Oriocrassatellinae du Pennsylvanien du Brésil et distribution spatio-temporelle d'*Oriocrassatella.

*Oriocrassatella* Etheridge Jr., 1907 est un crassatellidé à large distribution stratigraphique, bien connu dans les mers épicontinentales en eaux peu profondes, caractéristique du Paléozoïque supérieur. Ce genre apparaît pour la première fois dans des dépôts sédimentaires du Gondwana, en Australie et en Amérique du Sud. D'après sa distribution spatio-temporelle dans des dépôts du Mississippien supérieur, *Oriocrassatella* serait originaire du début du Viséen, ou même pré-viséenne. Par la suite, depuis le Carbonifère inférieur jusqu'au Permien, ce genre a eu une histoire paléobiogéographique complexe allant de l'hémisphère Sud vers l'hémisphère Nord. Pendant la phase initiale de dispersion à partir du Carbonifère supérieur jusqu'au Permien inférieur, ce genre a prospéré dans un milieu dominé par des eaux froides du Gondwana, suite à la glaciation du Paléozoïque supérieur. Les eaux littorales chaudes du Gondwana central et de Laurussia ont été colonisées par *Oriocrassatella* uniquement durant le Permien inférieur, parce que ce genre est devenu cosmopolite. Une espèce nouvelle, *O. piauiensis* n. sp., est décrite de la Formation Piauí du Pennsylvanien du bassin du Parnaíba ; elle pourrait représenter une première adaptation aux eaux chaudes. En outre, et en s'appuyant sur les données disponibles, d'autres espèces d'*Oriocrassatella* se seraient aussi définitivement adaptées à des milieux en eaux chaudes au cours des périodes interglaciaires du Pennsylvanien tardif, car des barrières climatiques ont disparu, favorisant des échanges de faune avec dispersion des larves, et migration du sud vers le nord le long des bordures est du Gondwana et de la Paléotéthys.

**MOTS CLÉS**
*Oriocrassatella*, bivalve, Gondwana, Paléozoïque supérieur, glaciation, paléobiogéographie, espèce nouvelle.

## INTRODUCTION

Due to its paleoecological significance and paleogeographical distribution, the importance of *Oriocrassatella* Etheridge Jr., 1907 was highlighted by various authors (Boyd & Newell 1968; Dickins 1996; Archbold *et al.* 1996; Larghi 2005). Bivalve molluscs belonging to the cosmopolitan, long range genus *Oriocrassatella* were first described by Etheridge Jr. (1907) from the Lower Permian of Western Australia. Later, Yakovlev (1928) erected the genus *Procrassatella*, a very similar crassatellacean from Russia, subsequently regarded by Newell (1958) as a junior subjective synonym of *Oriocrassatella*. At the present time, *Oriocrassatella* is a crassatellacean well-characterized by a hinge area with strong septate nymphs, a large, well-defined triangular resilium and two cardinal teeth in each valve.

Until 1968, 19 occurrences of the genus were known, with only two species recognized in western Pangea (Boyd & Newell 1968: 29, table 1). In that contribution, the subfamily Oriocrassatellinae was erected to accommodate members of the family Crassatellidae Férussac, 1822, characterized, among other features, by the overlap of the left valve on right valve in front of beaks. In addition, these authors briefly discussed a possible evolutionary pathway for the genus referring to the presence of members of the family Crassatellidae in pre-Carboniferous times. However, the origin of the *Oriocrassatella* lineage is still uncertain due to its questionable phylogenetic affinity with the Devonian genera *Cypricardella* Hall, 1858 and/or *Crassatellopsis* Beushausen, 1895.

Boyd & Newell (1968) were also the first authors to analyze the distribution of the genus in space and time. They suggested a possible Gondwanan origin in the Lower Carboniferous, and the dispersion to northern portions of Pangea during Permian times. Based on an extensive stratigraphical revision including new chronostratigraphic data, as well as about 18 newly recognized species, Archbold *et al.* (1996) reassessed the distribution of this genus asserting its Gondwanan origin in Lower Carboniferous and the posterior migration throughout Pangea. However, afterwards three new carboniferous species of *Oriocrassatella* were identified in South America (González 1997, 2002; Sterren 2005; see Figs 1, 2). A new species of *Oriocrassatella* is described herein from the Pennsylvanian of the Parnaíba Basin, Brazil, the tenth occurrence of the genus described in South America. A thorough revision of the records of this genus is presented based on their updated ages, including Argentinean and Australian data, offering new interpretations on the distribution of this Crassatellidae taxon in space and time, with significant paleobiogeographic implications.

## *ORIOCRASSATELLA* IN SPACE AND TIME

According to the available data, around 42 occurrences of *Oriocrassatella* are known at the present

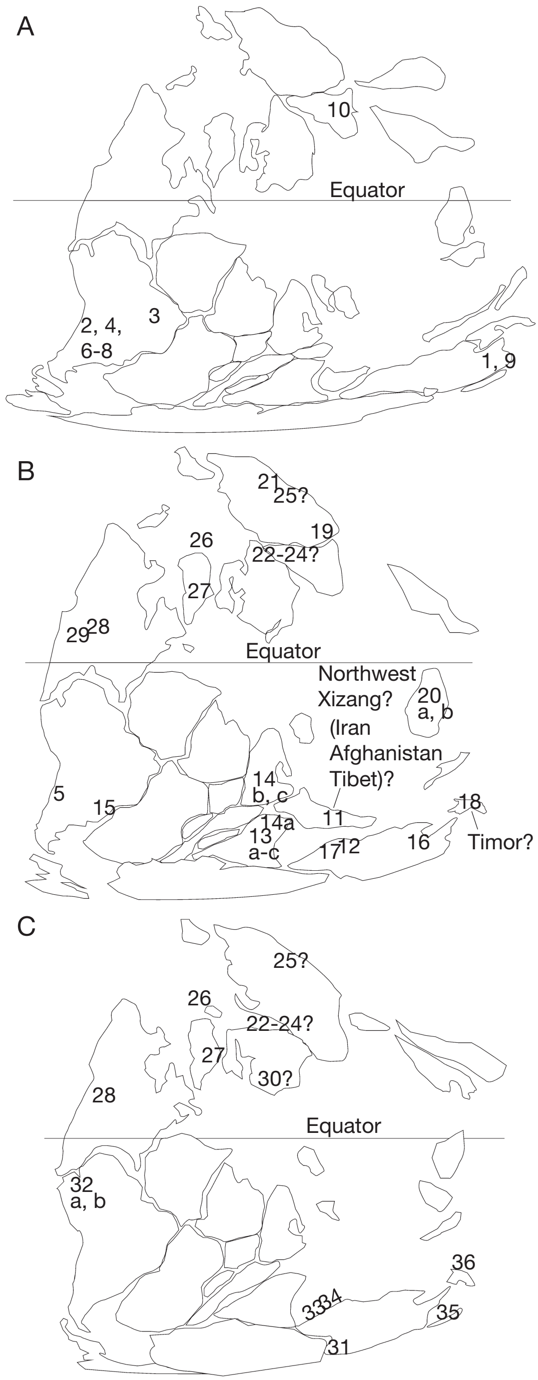



Fig. 1. — Paleogeographic distribution of *Oriocrassatella* Etheridge Jr., 1907 in the: **A**, Carboniferous; **B**, Lower Permian; **C**, Upper/Middle Permian. Paleogeography according to Scotese's Climate Story at www.scotese.com. Numbers according to references in Figure 2.

time. The genus was recorded in nearly 24 localities throughout the Pangea in Carboniferous and Permian strata (see Figs 1; 2).

Figure 2 displays the distribution of *Oriocrassatella* in space and time together with the Permo-Carboniferous glacial events. A simplified correlation of the Late Palaeozoic brachiopod zones from Argentina and eastern Australia is also shown. In this context we discuss the issues related to time and region of origin of the genus, and possible pathways that lead *Oriocrassatella* to reach and widespread in warm water environments throughout the Late Paleozoic.

### The Carboniferous fossil record of *Oriocrassatella* in the Gondwana

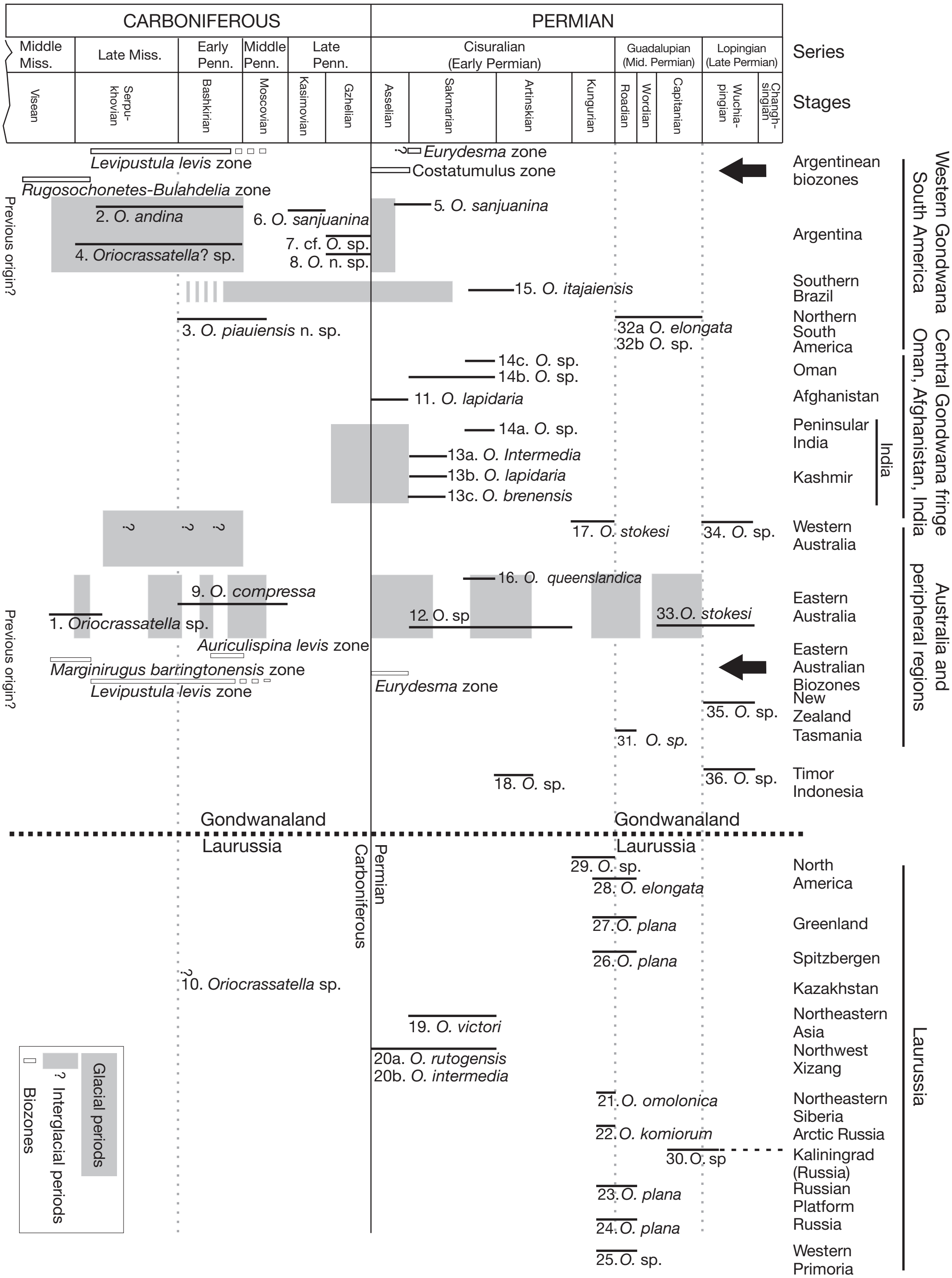
Nine occurrences are restricted to the Carboniferous, eight from Gondwanaland and one from Early Pennsylvanian Carboniferous in northern Laurussia (Muromtzeva 1974 *in* Biakov 2005). This record is puzzling, since all other Carboniferous occurrences are invariably recorded in Gondwana terrains (Figs 1; 2).

#### *Australia*

Two occurrences were described from Carboniferous strata in Australia. Records of *Oriocrassatella compressa* Maxwell, 1964, from Rands (Carboniferous) and Burnet formations (Lower Permian) were long considered to be the oldest for the genus in Gondwana (see Boyd & Newell 1968; Archbold *et al.* 1996). The Burnett Formation is probably Permian – it has *Eurydesma burnettensis* Waterhouse, 1986 that looks moderately close to *E. cordatum* Morris, 1845, and both are considered to be Early Asselian in age (Waterhouse pers. comm.). Overlying beds with *Bandoproductus macrospina* Waterhouse, 1986 are either latest Asselian (as generally favored for South Asian occurrences) or Early Tastubian (Sakmarian) (Waterhouse pers. comm.). In the Rands Formation *O. compressa* occurs below *Auriculispina levis*, and above *Levipustula levis* zones. *Auriculispina levis* appears to be the youngest known Carboniferous occurrence in eastern Australia, but the precise age of this record is open to conjecture. It could be Gzhelian or probably post-Moscovian, and certainly not as old as Namurian (Waterhouse pers. comm.). Hence, these data confine *O. compressa* to Upper Early to Middle Pennsylvanian beds. However, if *O. compressa* occurs within the post-Moscovian Rands Formation as well as in the upper part of the *Marginirugus barringtonensis* zone in the Faulkland Formation (Namurian after Peou & Engel 1979), the range of the species may be limited from Bashkirian to Moscovian, respectively Early to Middle Pennsylvanian.

Based on data above, the small *Oriocrassatella* sp. of Peou & Engel (1979) probably is the oldest known occurrence of this genus. This is because *Oriocrassatella* sp. occurs within the upper part of the *Marginirugus barringtonensis* zone of Faulkland Formation in the Rawdon Valley region (Australian Gondwana; Peou & Angel 1979; see Figs 1A, 2), being considered by Roberts *et al.* (1976) Upper Visean to Lower Early Serpukhovian in age.

Fig. 2. — Distribution of *Oriocrassatella* Etheridge Jr., 1907 in space and time: **1**-**37**, occurrences and ages according to: **1**, Peou & Engel (1979); **2**, González (2002); **3**, *Oriocrassatella piauiensis* n. sp. described here, Campanha & Rocha-Campos (1979); **4**, Sterren (2005), Azcuy *et al.* (2007); **5**, González (1982); **6**, González (1976), Sabattini *et al.* (1990), Azcuy *et al.* (2007); **7**, Manceñido *et al.* (1976), Azcuy *et al.* (2007); **8**, González (1997); **9**, Maxwell (1964) (Bruce Waterhouse pers. comm. 2009); **10**, Muromtzeva (1974); Biakov (2005, and written communication 2009); **11**, Termier *et al.* (1974), Archbold *et al.* (1996); **12**, Dickins (1963), Vanderhor *et al.* (2006); **13a**-**c**, Reed (1932), Veevers (1995), Honegger *et al.* (1982); **14a**, Dickins & Shah (1979), Stephenson *et al.* (2007); **14b**, Dickins & Shah (1979), Angiolini *et al.* (2006); **14c**, Larghi (2005); **15**, Rocha-Campos (1970), Holz *et al.* (2008, 2010); **16**, Dickins (1961, 1996); **17**, Dickins (1963), Archbold *et al.* (1996); **18**, Dickins & Skwarko (1981), Archbold *et al.* (1996), Charlton (2001); **19**, Biakov (2005); **20a**, **b**, Liu & Cui (1983), Archbold *et al.* (1996), Jin (2002); **21**, Muromtseva & Guskov (1984), Archbold *et al.* (1996); **22**, Kanev (1994), Shi *et al.* (2002); **23**, Yakovlev (1902), Archbold *et al.* (1996); **24**, Newell (1958); **25**, Lobanova (1961), Archbold *et al.* (1996); **26**, Boyd & Newell (1977), Archbold *et al.* (1996); **27**, Newell (1955), Archbold *et al.* (1996); **28**, Boyd & Newell (1968), Archbold *et al.* (1996); **29**, Ciriacks (1963), Boyd & Newell (1968); **30**, Suveizdas *et al.* (1975), Archbold *et al.* (1996); **31**, Clarke (1987); **32a**, **b**, Sanchez (1984 and pers. comm. 2009); **33**, Newell (1958); **34**, Dickins *et al.* (1989), Archbold *et al.* (1996); **35**, Archbold *et al.* (1996); **36**, Wanner (1940), Archbold *et al.* (1996). Ages for glacial periods: in Argentina, according to González (1981, 1990, 2002) and González & Díaz-Saravia (2007); in Australia, to Roberts *et al.* (1995), Dickins (1996) and Fielding *et al.* (2008a, b); in Brazil, to Holz *et al.* (2008); in India, to Veevers & Tewari (1995) and Maejima *et al.* (2001). Ages for Biozones in Argentina and Australia from Kelly *et al.* (2001); for *Marginirugus barringtonensis*, Roberts *et al.* (1976).


CARBONIFEROUS
PERMIAN
Middle Miss.
Late Miss.
Early Penn.
Middle Penn.
Late Penn.
Cisuralian (Early Permian)
Guadalupian (Mid. Permian)
Lopingian (Late Permian)
Series
Visean
Serpu-khovian
Bashkirian
Moscovian
Kasimovian
Gzhelian
Asselian
Sakmarian
Artinskian
Kungurian
Roadian
Wordian
Capitanian
Wuchia-pingian
Changh-singian
Stages
Levipustula levis zone
Eurydesma zone
Costatumulus zone
Argentinean biozones
Rugosochonetes-Bulahdelia zone
2. O. andina
6. O. sanjuanina
5. O. sanjuanina
4. Oriocrassatella? sp.
7. cf. O. sp.
8. O. n. sp.
Argentina
Previous origin?
15. O. itajaiensis
Southern Brazil
3. O. piauiensis n. sp.
32a O. elongata
32b O. sp.
Northern South America
Western Gondwana South America
14c. O. sp.
14b. O. sp.
Oman
11. O. lapidaria
Afghanistan
14a. O. sp.
Peninsular India
13a. O. Intermedia
13b. O. lapidaria
13c. O. brenensis
Kashmir
India
Central Gondwana fringe Oman, Afghanistan, India
17. O. stokesi
34. O. sp.
Western Australia
16. O. queenslandica
9. O. compressa
1. Oriocrassatella sp.
12. O. sp
33. O. stokesi
Eastern Australia
Auriculispina levis zone
Marginirugus barringtonensis zone
Levipustula levis zone
Eurydesma zone
Eastern Australian Biozones
35. O. sp.
New Zealand
31. O. sp.
Tasmania
18. O. sp.
36. O. sp.
Timor Indonesia
Australia and peripheral regions
Gondwanaland
Laurussia
Permian
Carboniferous
29. O. sp.
28. O. elongata
North America
27. O. plana
Greenland
26. O. plana
Spitzbergen
10. Oriocrassatella sp.
Kazakhstan
19. O. victori
Northeastern Asia
20a. O. rutogensis
20b. O. intermedia
Northwest Xizang
21. O. omolonica
Northeastern Siberia
22. O. komiorum
Arctic Russia
30. O. sp
Kaliningrad (Russia)
23. O. plana
Russian Platform
24. O. plana
Russia
25. O. sp.
Western Primoria
Laurussia
Glacial periods
? Interglacial periods
Biozones

*South America*

Coeval marine deposits in South America are found in western Argentina referred to the *Rugosochonetes-Bulahdelia* zone (Taboada 1997; see also Fig. 2), but *Oriocrassatella* was not found in these rocks, perhaps due to incomplete sampling or poor preservation. In western Argentina (San Eduardo Formation) the *Rugosochonetes-Bulahdelia* fauna occurs in beds immediately above the glacial phase El Paso II, and underlay the *Levipustula levis* zone (González 1990). In fact, Sterren (2005) identified as *Oriocrassatella*? sp. a specimen from the upper portion of the *Rugosochonetes-Bulahdelia* fauna (see Figs 1, 2), but it shows an incomplete hinge and an unusual profile for the genus.

The earliest known record of the genus in South America could be *Oriocrassatella andina* González, 2002, described from Serpukhovian-Bashkirian deposits of Western Argentina (see Figs 1A, 2; González 2002). *Oriocrassatella andina* is the only Oriocrassatellinae species known from the *Levipustula levis* zone (Serpukhovian-Bashkirian).

*Oriocrassatella* sp. (González 1997) from the Río del Peñón Formation belongs to the *Kochiproductus-Heteralosia* assemblage, the youngest faunal assemblage of the informal Aguanegran faunal stage. The same is also true for *Oriocrassatella* sp. (Manceñido *et al.* 1976). Both species are restricted to the Gzhelian (see Fig. 2[7; 8]).

*Oriocrassatella sanjuanina*? (González 1982) from the Agua del Jaguel Formation (southern Uspallata-Iglesia Basin) is probably a new species. It is much younger than *O. sanjuanina* (González 1976) from the Cerro Agua Negra Formation and belongs to the *Costatumulus amosi* fauna, restricted to the Upper Asselian-Lower Sakmarian, subsequent to the Early Permian glacial sequence, that should be restricted to early Asselian in western Argentina.

In Brazil, *Oriocrassatella piauiensis* n. sp., which is described below, was found in the Piauí Formation (Upper Carboniferous), Parnaíba Basin, Northeastern Brazil. The Piauí Formation crops out in a large area at the northeastern part of the Parnaíba Basin (Fig. 3A), Piauí State, Brazil. Several fossiliferous dolostones beds occur near the José de Freitas village, and are associated with sandstones, siltstones, and mudstones deposited in a shallow-marine carbonatic shelf (Lima Filho 1991, 1999). One of the dolostones, informally named Mucambo (Fig. 3A-C), together with other three beds located in the region (see Anelli *et al.* 2006), contains the most diverse bivalve fossil record known from the Upper Paleozoic rocks of South America (Anelli 1999; Anelli *et al.* 2002, 2006, 2009). The Mucambo dolostone bed is Lower to Middle Pennsylvanian in age (Bashkirian to Lower Moscovian; Campanha & Rocha-Campos 1979). The fauna also includes commonly many gastropods, cephalopods, brachiopods and bryozoans. Trilobites are less common (Anelli 1999). The associated fauna shows clear affinities to other Upper Pennsylvanian South and North American warm water faunas. A Bashkirian to Lower Moscovian age attributed to the Piauí Formation is also supported by palynomorphs, from subsurface material (Dino & Playford 2002; Souza *et al.* 2010). An age younger than Middle Moscovian to this unit is discarded, taking into account the glacial event in Paraná Basin (Itararé Subgroup), that occurred after these times. Then, a significant gap separates the Piauí Formation and the overlying Pedra de Fogo Formation, comprising the Late Moscovian to Carboniferous/Permian boundary (Melo J.H.G. pers. comm.).

## The Permian fossil record of *Oriocrassatella* in Gondwana

The early portion of Early Permian was marked by an intense period of glaciation both in Argentina (Asselian to Early Sakmarian, González 2002) and Brazil (Asselian-Sakmarian; Holz *et al.* 2008; see Fig. 2) that may have restricted the occurrences of *Oriocrassatella* in southern South America. During the Early Permian (Cisuralian) there are only two scattered occurrences of the genus, being one in the post- glacial interval in western Argentina (Upper Asselian-Lower Sakmarian) and a second one in Brazil in post-glaciation rocks (Upper Sakmarian-Lower Artinskian, see both occurrences in Figures 1B and 2[5, 15]).

During the Early Permian, *Oriocrassatella* is well recorded in deposits of central Gondwana fringe (Oman, Afghanistan and India; Figs 1B, 2[11, 13a-c, 14a-c]) with seven species assigned. Species described in Oman and Afghanistan occur out of glacial areas of perigondwanan regions during the Asselian and Sakmarian (Angiolini *et al.* 2007, 2009). Larghi (2005) described a dubious *Oriocrassatella* (see Figs 1B, 2[14c]) in the *Dickinsartella* fauna of the Saiwan Formation, Oman. According to this author, this fauna is indicative of climatic amelioration in North-Eastern Gondwanan fringe after the end of the Early Permian glacial events. Angiolini *et al.* (2006) stated that the progressive increase of carbonate deposits (Haushi Formation) where *Oriocrassatella* was recorded by Dickins & Shah (1979; see Figs 1B, 2[14b]) is correlative to this time of climatic warming during the Upper Sakmarian. Indeed, based on oxygen isotope composition of brachiopod shells Angiolini *et al.* (2009) suggested that low-latitude Early Permian ocean waters did not undergo significant cooling during the final episode of Gondwanan glaciations (Glacial III).

The Carboniferous and Permian glacial interval in India is just roughly understood from the contributions of Sen (1991), Sen & Banerji (1991) and Maejima *et al.* (2001). It seems that all occurrences known from India are present in rocks deposited after the glacial interval (Figs 1B, 2[13a-c, 14a]).

Three occurrences of *Oriocrassatella* are scattered throughout Permian in Eastern Australia in both glacial and interglacial intervals. However, this should be viewed with caution since the dating of some occurrences is not precise, lacking resolution to attribute them to worldwide accepted Permian stages (Figs 1B, C, 2[12, 16, 33]). In Western Australia and peripheral regions the genus is known only from post-glaciated deposits (Figs 1B, C, 2[17, 31, 34-36]), except by the Early Permian occurrence from Timor (Figs 1, 2[18]) an area apparently free from glaciers during this time (Angiolini *et al.* 2009).

### The Permian fossil record of *Oriocrassatella* in Laurussia

The oldest known record of the genus in the Laurussia refers to an isolated Middle Carboniferous occurrence in Kazakhstan (Muromtzeva 1974; Figs 1A, 2[10]), followed by an extensive hiatus throughout the entire Pennsylvanian. During the Early Permian (Asselian to Sakmarian) *Oriocrassatella* is present in only two localities in Laurussia (see Figs 1B, 2[19, 20a, b]). After that, another gap in the stratigraphical distribution of the genus occurs during the entire Artinskian to Early Kungurian.

During the Upper Kungurian and Roadian the genus reached its maximum paleobiogeographic distribution in Laurussia (Figs 1B, 2[21-29]). Only one species was recorded in deposits of Early Lopingian age (Figs 1C, 2[30]) in the end of the Middle Permian and beginning of the Upper Permian. Indeed, the genus is declined significantly in the Upper Permian rocks of Laurussia.

## SUMMARY AND FINAL REMARKS

The geographic and age distribution of the occurrences in Late Mississippian deposits of Australia and Argentina may indicate an earliest Visean or even a pre-Visean origin in Gondwana for the genus *Oriocrassatella* (see Fig. 2). Hence, the current knowledge of its distribution in space and time strongly supports Archbold *et al.* (1996) view, indicating a complex history of migration through time, from the Southern Hemisphere to Northern Hemisphere during the Permian.

Although the earliest known stratigraphic record of the genus appears in eastern Australia, a greater number of species is known from Lower and Upper portions of Carboniferous in South America indicating a putative South American origin for the genus during the earliest (Tournasian-Visean) Carboniferous times (see Fig. 2).

The earliest but isolated occurrence of the genus in eastern Gondwana (eastern Australia, see Figs 1A, 2[1]) during Early Carboniferous (Upper Visean-Lower Serpukhovian) may equally indicate Australia as the site of origin of *Oriocrassatella*. The genus appears to have originated during the Carboniferous in cold waters as seen by its distribution during this time in Argentina and Australia (see Mississippian occurrences in Fig. 1A). However, after this, during Pennsylvanian and Permian times the genus appears to have dispersed to warm waters of the Gondwana peripheral regions and Laurussia. However, exceptions to the pattern above are also known. For example, occurrences are recorded from Carboniferous and Permian of eastern Australia (Figs 1, 2[1, 9, 12, 16, 36]) within glacial intervals. This may indicate that species of this genus did not obligatory avoided cold water settings. Indeed, González (2002) included *Oriocrassatella* as a genus commonly present in both cold and warm waters in faunas from the Pennsylvanian of western Argentina. In accordance to this interpretation, *Oriocrassatella piauiensis* n. sp. from the Piauí Formation is associated with a well diversified warm water fauna (Anelli *et al.* 2002, 2006, 2009). Moreover, Permian occurrences of *Oriocrassatella* in South America fit well with non glaciated areas during the upper part of Sakmarian stage in Argentina (Figs 1, 2[5]), Brazil (Figs 1, 2[15]) and Middle Permian in Venezuela (Northern South America; Figs 1, 2[32a, b]).

For that reason, the existence of the oldest known species of *Oriocrassatella* in Gondwana (*Oriocrassatella* sp., *O. compressa*, *O. piauiensis* n. sp. and *O. andina*) during the Carboniferous glacial period, in proximity to the glaciated areas (as *O. piauiensis* n. sp.), suggests that the origin of this genus was close to the cold seas of the southern hemisphere. This is not surprising as many lineages of bivalves appeared during the Carboniferous glaciations within the *Levipustula levis* fauna in central Patagonia, especially the endemic genera *Pyramus* Dana, 1847, *Megadesmus*? Sowerby, 1839, *Myonia* Dana, 1847, *Aphanaia* de Koninck, 1877, *Kolymia* Likharev, 1941, *Merismopteria* Etheridge, 1892 (see González 1972, 2002) and more rarely in Australia (Runnegar 1972). Also the precursors of the atomodesmids appear to have adapted to warm sea waters, during their migration to the northern hemisphere in the Permian (González & Waterhouse 2012). Similarly, *Oriocrassatella* younger species are everywhere associated with warm climate (Archbold *et al.* 1996; Figs 1, 4). We cannot rule out the possibility that the first species could be more tolerant to different temperatures, or perhaps *O. piauiensis* n. sp. was an early adaptation to warm waters, but certainly species of this genus adapted definitely to warm water environments during the Late Pennsylvanian interglacial. This warming eliminated the climatic barrier that interrupted the faunal interchange during the "Middle" Carboniferous glacial period and favored larval dispersion following a South to North migration route through the eastern margins of Gondwana and the eastern Paleotethys (Shi & Grunt 2000; González & Waterhouse 2012). It should be noted, however, that the lack of fossil evidence in intermediate regions (as in western Antarctica, see Kelly *et al.* 2001) is not an evidence of absence. Through the western margin of Gondwana migratory sense may have varied in the course of the Late Paleozoic.

The Late Pennsylvanian time elapsed without records of *Oriocrassatella* (and the Gondwana fauna), except for occurrences in Argentina (see Fig. 1[6-8]), may be related to the generalized marine regressions in Gondwana (see Roberts *et al.* 1995; Dickins 1996). In addition, the pattern of occurrences described above for the Late Pennsylvanian may be a result of taphonomic bias and/or incomplete sampling. However, a preservational bias is difficult to conceive in some cases, as in the lack of *Oriocrassatella* records during the Serpukhovian-Moscovian stages in Australia, because the fossil record is accompanied by marine deposits yielding members of the *Levipustula levis* zone (see Fig. 1A). It is noteworthy that *Oriocrassatella* is also apparently absent in the same interval in Carboniferous deposits of the Alexander Island, Antarctica (Kelly *et al.* 2001).

The Carboniferous *Oriocrassatella* from Kazakhstan, Laurussia (Muromtzeva 1974 *in* Biakov 2005) may indicate a pre-Permian migration from Gondwana to northern Laurussia, but Early Carboniferous occurrences half way in central Pangea sequences are still missing. Hence, *Oriocrassatella* has a patchy distribution during Carboniferous. Finally, only during Permian times the genus spread-out through Pangea when the worldwide distribution was reached.

## A NEW CARBONIFEROUS SPECIES OF *ORIOCRASSATELLA* FROM BRAZIL

### General observations

Specimens of Oriocrassatellinae described here were found in a dolostone bed informally named as "Mucambo", which crops out near the village of José de Freitas (Fig. 3), Piauí. The specimens were collected and prepared according to standard paleontological techniques (Feldmann *et al.* 1989). For all

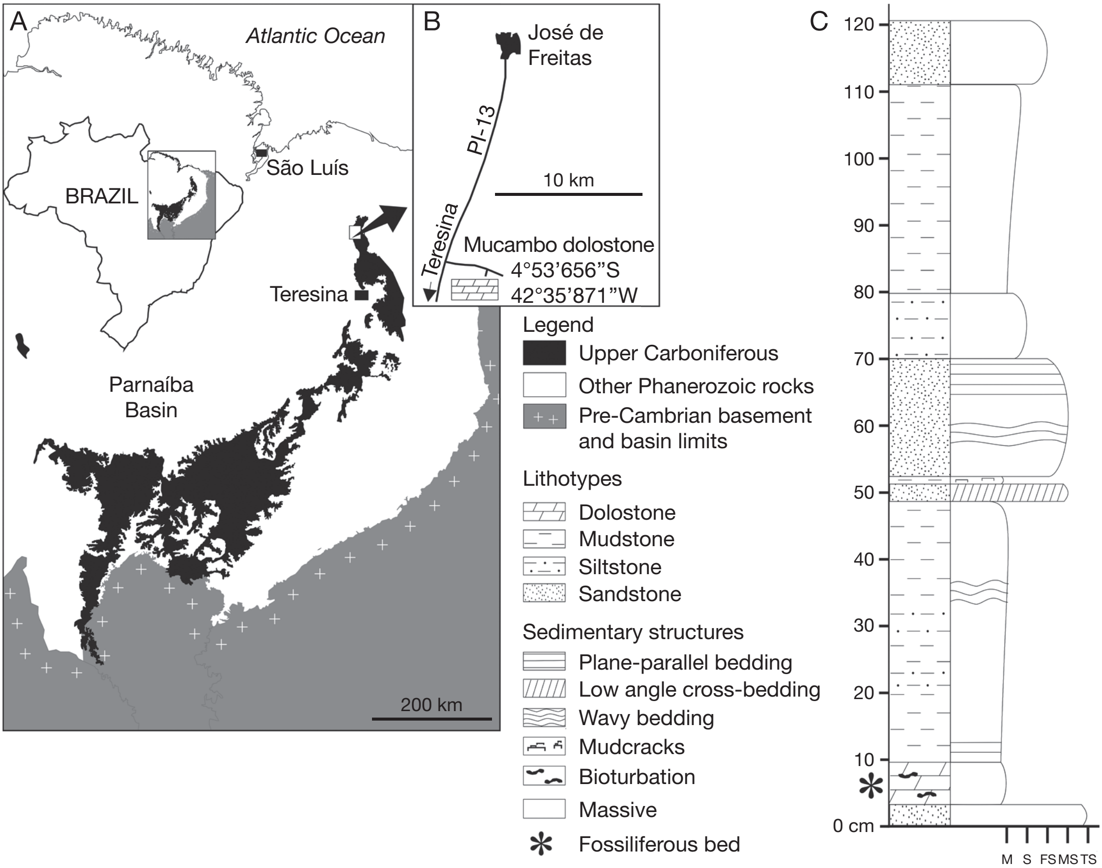



Fig. 3. — **A**, map showing the area of occurrence of the Upper Carboniferous Piauí Formation (in black) in the Parnaíba Basin, northeastern Brazil; **B**, localization of the outcrop of Mucambo dolostone; **C**, stratigraphic section showing the Mucambo dolostone.

specimens, latex casts were prepared for assessment of muscle scars and especially for hinge features. Additionally, some latex casts of hinge features were photographed with scanning electronic microscope (SEM). The studied specimens are housed in the scientific collection of the Instituto de Geociências, Universidade de São Paulo, under the code GP/1T. In addition, some specimens belonging to the Departamento Nacional da Produção Mineral (DNPM), Rio de Janeiro, were also analyzed. The suprageneric systematics is based on Boyd & Newell (1968) and Amler (1999). The elongation and obesity indexes were calculated according to Stanley (1970).

## SYSTEMATIC PALEONTOLOGY

Family Crassatellidae
Férussac, 1822
Subfamily Oriocrassatellinae
Boyd & Newell, 1968

Genus *Oriocrassatella* Etheridge Jr., 1907

*Procrassatella* Yakovlev, 1928: 114 (type species: *Schizodus planus* Golovkinsky, 1868, by monotypy).

Type species. — *Oriocrassatella stokesi* Etheridge Jr., 1907, by monotypy.

TABLE 1. — Dimensions (in mm) of *Oriocrassatella piauiensis* n. sp. Abbreviations: **l**, length; **h**, height; **w**, width; *****, approximate for incomplete valve.

| specimen | valve | length | height | width | elongation l/h | obesity h/w | umbonal angle (°) |
|---|---|---|---|---|---|---|---|
| GP/1T 2026 | L | 24 | 17.5 | 4 | 1.37 | 2.1 | 132 |
| DNPM 219 | L | 24 | 17 | 4 | 1.41 | 2.1 | 124 |
| DNPM 271 | R | 23 | 15.5 | 4 | 1.48 | 1.94 | 130 |
| GP/1T 2022 | R | 21 | 13 | 4 | 1.61 | 1.62 | 132 |
| DNPM 220 | L | 20 | 14.9 | 3 | 1.41 | 2.5 | 131 |
| DNPM 148 | – | 20 | 13 | 3 | 1.54 | 2.2 | 131 |
| GP/1T 2023 | R | 17 | 13 | 3 | 1.30 | 2.2 | 125 |
| DNPM 234 | R | 17* | 13 | 3 | 1.31* | 2.2 | 129 |
| GP/1T 2028 | L | 17 | 11 | 2.5 | 1.54 | 2.2 | 134 |
| GP/1T 2024 | R | 14.5 | 10 | 2.5 | 1.45 | 2.0 | 129 |
| DNPM 221a | L | 14.2 | 9.5 | 2.5 | 1.49 | 1.90 | 129 |
| GP/1T 2027 | L | 14 | 9 | 2 | 1.55 | 2.2 | 128 |

***Oriocrassatella piauiensis*** n. sp.
(Fig. 4)

TYPE MATERIAL. — Holotype GP/1T 2022. — Paratypes GP/1T 2023, 2024, 2026-2028; DNPM 148, 219, 220, 221a, 234, 271.

ETYMOLOGY. — The specific epithet refers to Piauí State, northern Brazil, where the species was found.

TYPE HORIZON. — Mucambo dolostone, Piauí Formation, Parnaíba Basin.

AGE. — Bashkirian to Moscovian. The time-range assigned herein comprises the more reliable relative ages to the Piauí Formation, obtained from palynological data (Dino & Playford 2002; Souza *et al.* 2010) and comparisons with the palynostratigraphical scheme erected to the neighbor Amazonas Basin (Playford & Dino 2000).

MATERIAL EXAMINED. — Six internal molds of left valves and six of right valves; two external molds of left valves.

MEASUREMENTS. — See Table 1.

TYPE LOCALITY. — José de Freitas, (4°53'656"S, 42°35' 871"W), Piauí, Brazil.

DIAGNOSIS. — *Oriocrassatella* with lateral teeth absent; non bifid cardinal tooth 2; ornamentation of regularly spaced lamellae with flattened surfaces showing rare bifurcation in anterior and posterior regions of shell.

DESCRIPTION

Internal and external molds up to 24 mm in length, and up to 17.5 mm in height. Shell thick based on internal molds, oval in shape, elongate, very compressed. Umbones depressed, beaks prosogyrate slightly elevated above hinge. Umbonal carina weak and rounded, running from beaks to posterior ventral angle, defining a large respiratory margin. As seen in casts of external molds, anterior dorsal margin straight; anterior extremity convex; ventral margin slightly convex; posterior extremity slightly truncated; posterior dorsal margin straight. Ornamentation of concentric lamellae, regularly spaced, about two per millimeter, some showing bifurcating pattern anteriorly and posteriorly. Pedal or siphonal gapes absent. Lunule and escutcheon absent.

Hinge formula as follows:

| | | | | | | |
|---|---|---|---|---|---|---|
| Posterior | RV | /nsr | – | 3b | – | 3a/ |
| Anterior | LV | /nsr | 4b | – | 2 | –/ |

Left anterior cardinal (2) strong, non arched or bifid; left posterior cardinal (4b) weak, laterally compressed, vertical, sometimes showing sigmoid shape. Right anterior cardinal (3a) well defined, separated from the anterior dorsal margin by shallow depression. Right posterior cardinal (3b) straight, vertical, slightly inflated in both extremities. Resilifer (r) in left valve placed behind posterior cardinal (4b), cover deck absent; septum (s) strong, well developed in both valves, originating immediately posterior to beak, bounding resilifer posteriorly; nymph (n) well-defined in posterior wall of septum, close to beak. Ligament furrow (lf) very narrow, located posterior to the septum. Lateral teeth absent.

Adductor muscles scars similar in size. Anterior scar positioned close to anterior dorsal angle, twice higher than long, with irregular shape at posterior

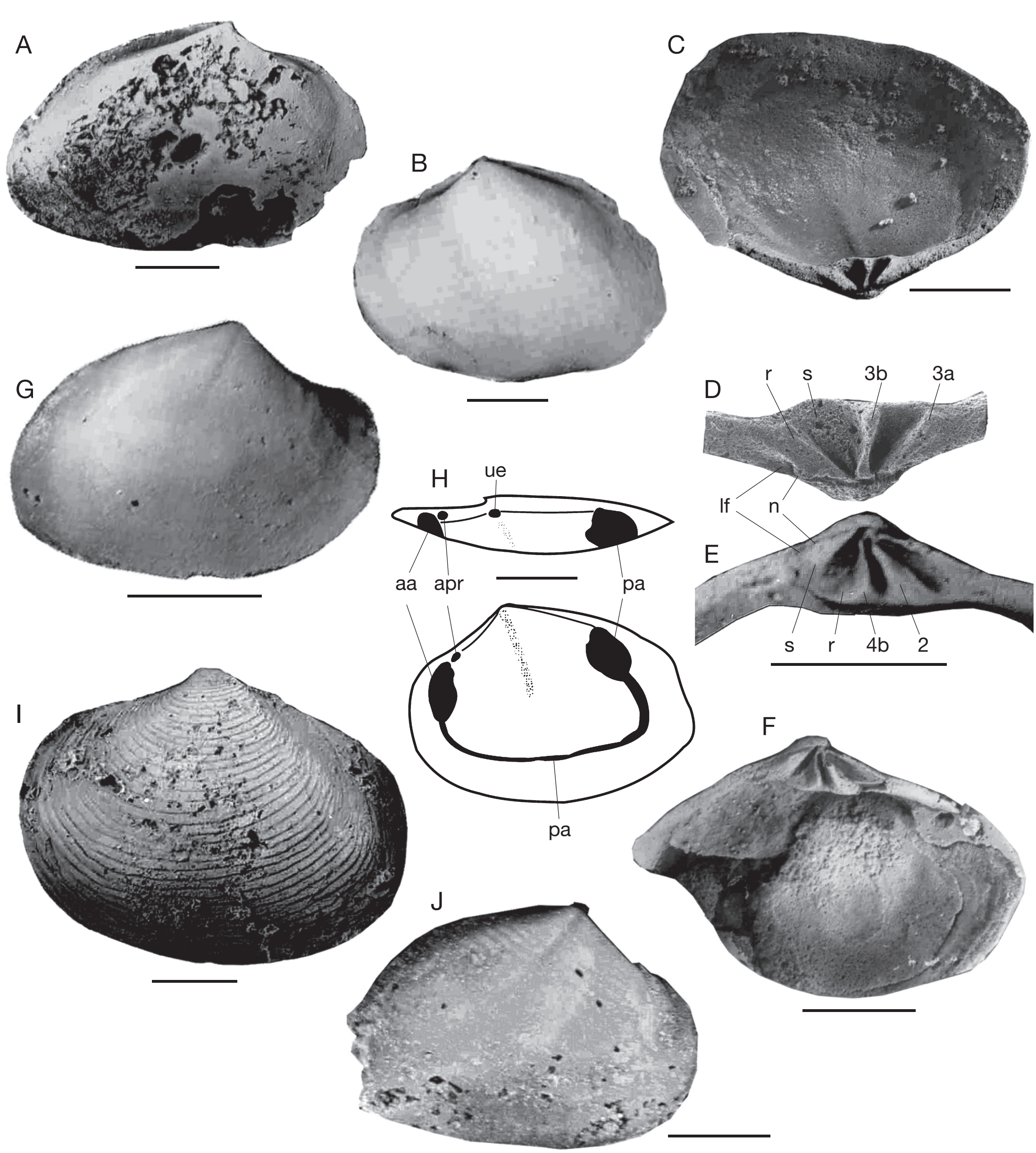



Fig. 4. — *Oriocrassatella piauiensis* n. sp., Mucambo limestone; **A**, holotype, internal mold of right valve, GP/1T 2022; **B**, internal mold of left valve, DNPM 076; **C**, latex cast, internal mold of right valve, DNPM 234; **D**, latex cast, magnified hinge area, internal mold of right valve, same specimen; **E**, latex cast, internal mold of left valve, magnified hinge area, DNPM 221b; **F**, latex cast, internal mold of left valve, same specimen; **G**, internal mold of right valve, GP/1T 2024; **H**, muscle scars based in specimen DNPM 076; **I**, latex cast, external mold of left valve, DNPM 220; **J**, internal mold of right valve, DNPM 234. Abbreviations: **aa**, anterior adductor; **apr**, anterior pedal retractor; **lf**, ligament furrow; **n**, nymphs; **pa**, posterior adductor; **pl**, pallial line; **r**, resilifer; **s**, septum; **ue**, umbonal elevator; **2**, left anterior cardinal; **3a**, right anterior cardinal; **3b**, right posterior cardinal; **4a**, left posterior cardinal. Scale bars: 0.5 cm.

margin. Anterior pedal retractor small, well marked, not fused but placed close to dorsal extremity of the adductor. Posterior adductor located above posterior dorsal angle, nearly circular in shape. Posterior pedal retractor apparently fused to dorsal end of posterior adductor. Pedal elevator scar well-marked, located at tip of beaks. Pallial line well defined, without sinus.

## DISCUSSION

Boyd & Newell (1968: 28, 30) included among the diagnostic features for the genus *Oriocrassatella* the presence of a cover deck over the apical part of the resilifer and of a more or less bifid cardinal tooth 2 in left valve. Although both features may be easily removed from shell by taphonomic processes as abrasion or corrosion, our observations of several well preserved specimens from the Piauí Formation indicate that these features are absent in *Oriocrassatella piauiensis* n. sp. Furthermore, the cover deck feature was recorded only in the type species and *O. stokesi* (Newell 1958) from the Upper Permian of Eastern Australia. In the same way, the bifid cardinal tooth 2 is only observed in the type species and a few other Permian species of this genus (*O. itajaiensis* [Rocha-Campos 1970, Brazil], *O. stokesi* [Dickins 1963, Western], and *O. stokesi* [Newell 1958, Eastern]). Therefore, both the cover deck and bifid cardinal tooth 2 are known only in Permian species. If the presence of these characters are used to characterize species of *Oriocrassatella* then we must remove from this genus all species in which those characters are absent. Since both characters are present only in extremely well preserved Permian specimens we decide to assign our species to *Oriocrassatella* rather than erect a new genus.

*Oriocrassatella* species from Argentina comparable to *O. piauiensis* n. sp., include *O. sanjuanina* González, 1976, from Upper Carboniferous, which has very similar general profile, but differs by its more posteriorly developed resilifer in right valve, and by the presence of the anterior lateral tooth AII. *Oriocrassatella andina*, from the Late Mississippian-Early Pennsylvanian La Capilla Formation (González 2002) differs also by the presence of the lateral tooth AII and by its ornament of concentric striations. *Oriocrassatella* sp. from Rio del Peñón Formation (González 1997) does not show hinge features for close comparison, but has a more elongated shell and more strongly truncated posterior extremity. The anterior pedal retractor is fused to the anterior adductor. *Oriocrassatella* sp. from Del Salto Formation (Manceñido *et al.* 1976) is more circular in shape and has all four lateral teeth in left valve.

*Oriocrassatella itajaiensis* described by Rocha-Campos (1970: 11, 12, fig. 3), has a more expanded septum in hinge, and although not completely visible, may have anterior and posterior lateral teeth in left valve. Finally, *O. elongate* Boyd & Newell, 1968 described from Permian rocks of Venezuela (Sanchez 1984) and North America (Boyd & Newell 1968) is more elongated in shape, and presents the complete set of lateral teeth in both valves.

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