



A PERMIAN MIXOHALINE OSTRACOD ASSOCIATION OF THE TERESINA FORMATION, PARANÁ BASIN, BRAZIL

CRISTIANINI TRESCASTRO BERGUE

Departamento Interdisciplinar, Universidade Federal do Rio Grande do Sul, Campus Litoral Norte, Av. Tramandaí, 976, 95625-000, Imbé, RS, Brazil. ctbergue@gmail.com (corresponding author)

MARIA DA SAUDADE ARAÚJO SANTOS MARANHÃO

Instituto Geológico, Secretaria de Infraestrutura e Meio Ambiente do Estado de São Paulo, Rua Joaquim Távara, 822, 04015-011, São Paulo, SP, Brazil. mmaranhao@sp.gov.br

CHRISTIANO NG

Centro de Pesquisa e Desenvolvimento Leopoldo Américo Miguez de Mello, Petrobras, Avenida Horácio Macedo, 950, 21941-915, Rio de Janeiro, RJ, Brazil. ng.christiano@gmail.com

MARIA A. NAUMCHEVA

Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznayaulitsa, 123, Moscow 117647, and Kazan (Volga Region) Federal University, Kremlyovskayaulitsa, 18, Kazan 420008, Russia. m.zhokina@gmail.com

ABSTRACT – New ostracod species are described for Middle to Upper Permian (Guadalupian) rocks of the Teresina Formation, Paraná Basin, from two localities in the São Paulo State, southwestern Brazil: Xavante Dam and Pau Preto Quarry. *Paranacythere nigripallus* gen. nov. and sp. nov., *Velatomorpha xavante* sp. nov., and *Velatomorpha pseudoaltilis* sp. nov. are herein described. The association *Velatomorpha–Paranacythere* is proposed as typical of Permian mixohaline environments of the Teresina Formation, and is the most abundant in the two studied localities. *Paranacythere nigripallus* gen. nov. and sp. nov. is proposed to accommodate a very abundant species with typically cytheroidean characteristics, and tentatively ascribed to the family Cytheruridae. Some ecological remarks are presented based on ostracod population age structure, biostratinomy and taxonomic composition of assemblages. The diagnosis of *Velatomorpha* Tibert & Dewey is emended.

Keywords: evolution, marginal marine environments, paleoecology, Teresina Formation, taxonomy.

RESUMO – Novas espécies de ostracodes são propostas para rochas do Permiano Médio a Superior (Guadalupiano) da Formação Teresina, Bacia do Paraná, em duas localidades no Estado de São Paulo, sudeste do Brasil: Represa Xavante e Pedreira Pau Preto. *Paranacythere nigripallus* gen. nov. e sp. nov., *Velatomorpha xavante* sp. nov., and *Velatomorpha pseudoaltilis* sp. nov. são descritas. A associação entre os gêneros *Velatomorpha* e *Paranacythere* é interpretada como típica de ambientes mixoalinos da Formação Teresina, e são os ostracodes mais abundantes nas localidades aqui estudadas. *Paranacythere nigripallus* gen. nov. e sp. nov. é proposto para acomodar uma espécie com características tipicamente cytheroides e tentativamente atribuído à família Cytheruridae. Aspectos ecológicos são discutidos com base na estrutura populacional etária, biostratinomia e composição taxonômica das assembleias. É proposta uma emenda à diagnose de *Velatomorpha* Tibert & Dewey.

Palavras-chave: ambientes marginais marinhos, evolução, Formação Teresina, paleoecologia, taxonomia.

INTRODUCTION

Ostracods constitute the arthropod lineage with the most abundant and diversified fossil record, which ranges from the Ordovician to the Holocene (Rodríguez-Lázaro & Ruiz-Munhoz, 2012). Marine faunas were dominated initially by paleocopids, but towards the Late Paleozoic podocopids and

platycopids became gradually more diverse, while paleocopids became extinct at the end-Permian extinction (EPE). By the Early Carboniferous these crustaceans began to colonize marginal marine and lacustrine waters, reaching considerable diversity in these environments in the Late Carboniferous and afterwards (Williams *et al.*, 2006; Bennett *et al.*, 2011; Iglíkowska, 2014). Horne (2003)

and McGairy *et al.* (2021), however, argue that the colonization of mixohaline environments by paleocopids, platycopids and leperditicopids might have begun during the Silurian.

The ecological diversity of ostracods allows their use as reliable environmental proxies (Carbonel *et al.*, 1988), which requires detailed taxonomic knowledge. In South America, research on Permian ostracods lags behind the post-Paleozoic one, and taxonomic knowledge is, therefore, very limited. Studies in Chile (Breitkreuz *et al.*, 1992), Paraguay (Zabert, 1985), and Uruguay (Díaz-Saravia & Herbst, 2001), revealed typical lacustrine assemblages. In Brazil, Sohn & Rocha-Campos (1990), Maranhão & Petri (1996) and Bergue *et al.* (2020), on the other hand described the occurrence of assemblages with some degree of marine influence in the Passa Dois Group. Those papers supply invaluable data for the understanding of non-marine ostracods diversification in southern Pangea. This paper aims to contribute towards the knowledge on Brazilian Paleozoic ostracods describing a new genus and three new species of the Teresina Formation, and presenting brief discussion on their evolutionary and paleoecological significance.

GEOLOGICAL SETTING

In this work, two localities in the southern São Paulo State corresponding to rocks of the Teresina Formation, Passa Dois Group, are studied (Figure 1). The Passa Dois Group records mainly Middle to Upper Permian rocks (Holz *et al.*, 2010; Ng *et al.*, 2019), and represents a complete cycle of continentalization divided in Irati, Serra Alta, Teresina and Rio do Rasto formations (Milani *et al.*, 1998).

These units comprise mixed carbonate-siliciclastic microfacies where part of the carbonate rocks is associated to episodic marine incursions (Ng *et al.*, 2019). Especially in the Teresina Formation, the limestones are more abundant at the middle and upper portions of the unit, and usually present cm to dm-scale layers of bivalve and ostracod bearing limestones and microbialites. The typically pure ones correspond to oolitic calcarenites (Ng *et al.*, 2019) cemented by sparite, and calcilitites, which may present bivalves and ostracods with

disarticulated shells (Rohn, 2001; Rohn *et al.*, 2003). The ostracod assemblage described herein was recovered in peloidal calcisiltites from the Pau Preto Quarry and Xavantes Dam outcrops, correlated to middle to upper portion of the Teresina Formation, respectively (Mello & Sousa, 1985; Maranhão, 1995; Maranhão & Petri, 1996; Rohn & Fairchild, 2015; Bergue *et al.*, 2020).

These mixed microfacies, and particularly calcisiltites in the depositional context of the Passa Dois Group, can be accumulated in a wide spectrum of marginal marine paleoenvironments (*e.g.*, lagoons, estuaries, deltas). It is reflected in rich fossil assemblages, which include, for instance, fishes (*e.g.*, Würdig-Maciel, 1975), ostracods (Sohn & Rocha-Campos, 1990; Bergue *et al.*, 2020), temnospondyls (*e.g.*, Dias *et al.*, 2020), conchostraceans (*e.g.*, Ferreira-Oliveira & Rohn, 2010), bivalvia (*e.g.*, Simões *et al.*, 2017) and palynomorphs (*e.g.*, Mori & Souza, 2012).

Previous studies in the Xavantes Dam outcrop reported also bivalves from the *Pinzonella neotropica* Biozone, vertebrate remains, sponge spicules, charophytes (Maranhão & Petri, 1996) and stromatolites (Rohn & Fairchild, 2015). Plant remains such as charophytes and the presence of microphylls of lycophytes are related to the *Lycopodiopsis derbyi* Phytozone, coeval to the Pinzonellinae bivalve biozones (Holz *et al.*, 2010; Ng *et al.*, 2019). Upper in this section (~ 40 m) lay rocks of the Rio do Rasto Formation, with beds rich in *Glossopteris* leaves and *Leinzia similis* bivalves (Rohn, 1997; Rohn & Fairchild, 2015). The Pau Preto Quarry contains similar fossil assemblage, but the carbonate rocks are mainly composed by dm to m-scale oolitic grainstones and stromatolites beds (Suguio *et al.*, 1974; Maranhão & Petri, 1996; Callefo *et al.*, 2015). The presence of fossil footprints (Andreis & Carvalho, 2001) and well-documented huge desiccation cracks, ripple marks and geochemical analysis converge to a shallow evaporitic-dominated paleoenvironment (Suguio *et al.*, 1974). Elementary and strontium ratio analysis in the charophyte bearing bed of the Xavantes Dam outcrop also suggest freshwater affluence (Maranhão, 1995). On the other hand, agglutinated foraminifers were reported to the

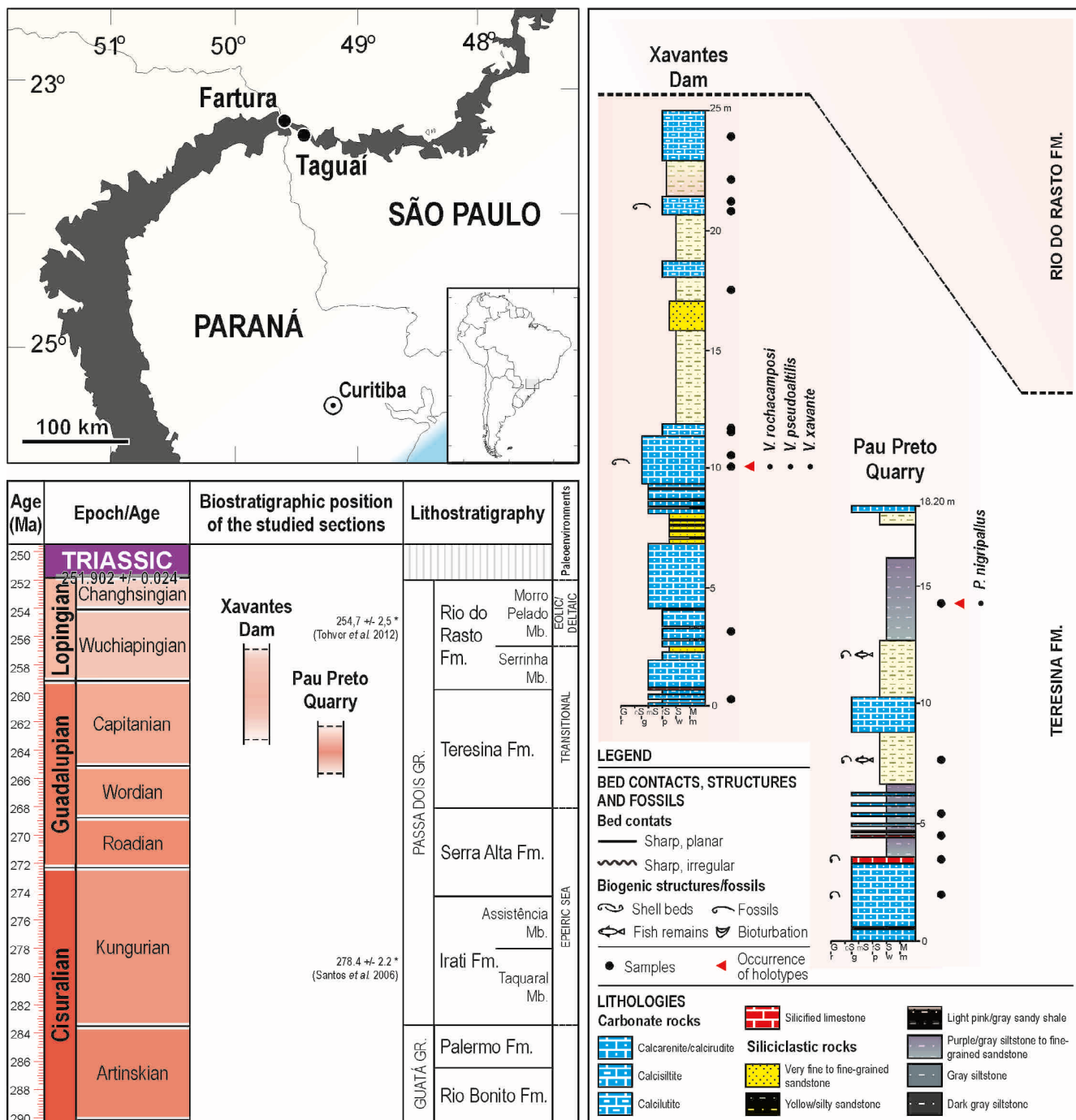


Figure 1. Map of the Passa Dois Group outcrops between São Paulo and Paraná, location and stratigraphic position of study areas and samples. Sources: Ages and chronostratigraphic division according to Lucas & Shen (2018) and chronostratigraphic chart after Ng et al. (2019). Complementary radiometric age determination of bentonic ash falls beds from Irati Formation and Araguinha impact structure according to Santos et al. (2006) and Tohver et al. (2012), respectively.

Teresina Formation facies to the composed section between these two localities (Mello & Sousa, 1985).

These fossil assemblages characterize marginal environments with variable marine influence. According to Bergue et al. (2020), the ostracod assemblages, at least in some levels, characterize mixohaline waters due to the low richness

and high abundance of some taxa, particularly *Velatomorpha*. In the absence of reliable global marine biostratigraphic markers (e.g., conodonts), the position of the Teresina Formation is still not defined but lies possibly between either the Guadalupian–Lopingian or the Lopingian–Triassic boundaries (Ng et al., 2019). Isotopic analysis

carried out in the Araguinha Dome and seismic structures coeval to the Teresina Formation reinforce a Guadalupian–Lopingian age for these stratigraphic interval (Tohver *et al.*, 2012, 2018).

MATERIAL AND METHODS

The 18 samples (approximately 500 g each) were obtained in exposed sections from two localities of the São Paulo State, southwestern Brazil, as follows: 11 samples from the Xavantes Dam (Fartura municipality, 23°19'52.22"S; 49°36'7.07"W), and seven samples from the Pau Preto Quarry (Taguaí municipality, 23°17'28"S; 49°18'12"W) (Figure 1). The samples were disaggregated in oxygen peroxide, washed in meshes between 0.25 and 1.0 mm, and oven dried. All ostracod specimens were picked under stereomicroscope and assembled in micropaleontological slides for taxonomic analysis. SEM images were carried out in a Phenom XL equipment at Laboratório de Micropaleontologia Aplicada of Departamento de Geologia, Universidade Federal de Pernambuco. The genus *Velatomorpha* Tibert & Dewey, 2006 is very abundant in the studied material, represented both as adult and juvenile specimens, but in many of them identification at species level was not possible due to poor preservation. So, only specimens that could be assigned to any of the species described herein or in previous studies are counted at the item “Material” on the taxonomy chapter.

SYSTEMATIC PALEONTOLOGY

The suprageneric taxonomy herein adopted follows mostly Tibert *et al.* (2013). All specimens illustrated are held at the Museu de Paleontologia Irajá Damiani Pinto, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, under the prefix MP-O. Morphological terminology follows Scott (1961) and Sylvester-Bradley & Benson (1971).

Abbreviations: C, carapace; H, height; L, length; LV, left valve; RV, right valve; W, width.

Order PODOCOPIDA Sars, 1866

Suborder CYTHEROCOPINA Gründel, 1967

Superfamily CYTHEROIDEA Baird, 1850

Family CYTHERURIDAE? Müller, 1894

Paranacythere gen. nov.

urn:lsid:zoobank.org:act:183E3B7C-4685-43AE-A72C-800D4E5DEEB9

Type-species. *Paranacythere nigripallus* sp. nov., by monotypy.

Diagnosis. A small sized genus with elongate sub-rectangular outline. Carapace preplate, surface thoroughly reticulated with polygonal fossae. Duplicature moderately wide at the anterior region. **Etymology.** In allusion to the basin name (Paraná) + cythere, the first marine ostracode genus proposed (Müller, 1785) in allusion to the Greek island Cythera.

Remarks. The monotypic genus *Paranacythere* is proposed to accommodate a very abundant species of the Teresina Formation. *Paranacythere* gen. nov. differs significantly from any Paleozoic or post-Paleozoic genera (*e.g.*, Benson *et al.*, 1961; Abushik, 1990). The impossibility of studying in detail the internal morphology does not permit to ascribe with certainty this genus to any family, although the conspicuous duplicature clearly indicates its podocopid affinity. Based on its chronostratigraphic position and general macroevolutionary aspects of podocopids, however, *Paranacythere* gen. nov. is probably among the Permianidae, Limnocytheridae, Bythocytheridae and Cytheruridae (Whatley & Mognilevsky, 1998; Whatley & Boomer, 2000). Permianids and limnocytherids are typically non-marine taxa and characterized by a median sulcus in carapace. The marine bythocytherids also present a conspicuous median sulcus, which is absent in *Paranacythere* gen. nov. Therefore, Cytheruridae, seems to be a reasonable classification for the genus herein proposed. Despite being predominantly marine, and diversified from Mesozoic onwards, Whatley & Boomer (2000) argue that the earliest cytherurids might have inhabited marginal marine environments.

Paranacythere gen. nov., however, differs from the two Permian cytherurids discussed by Whatley & Boomer (2000). From *Judahella* Sohn, 1968 differs in outline and the absence of swellings and nodes on the surface. From *Gruendeliclythere* Kozur, 1971

differs in the absence of reticulated nodes and sulci in the lateral surface.

Paranacythere nigripallus sp. nov.

urn:lsid:zoobank.org:act:1E02CB7A-E271-4A3A-B757-702BACE400A5

(Figures 2A–I)

2020 *Editia?* sp. Bergue *et al.*, p. 312, pl. 4, figs. 7–11.

Etymology. *L.* in allusion to the name of the type-locality, the Pau Preto Quarry (Pau = *pallus* + Preto = *nigrus*).

Holotype. MP-O-2912 male C L = 0.52 mm, H = 0.28 mm, W = 0.22 mm.

Paratypes. MP-O-2913 female LV L = 0.55 mm, H = 0.33 mm; MP-O-2914 male C L = 0.51 mm, H = 0.28 mm, W = 0.23 mm; MP-O-2915 female LV L = 0.55 mm; H = 0.33 mm; MP-O-2869 female LV L = 0.53 mm, H = 0.33 mm; MP-O-2870 female C L = 0.50 mm, H = 0.30 mm, W = 0.22 mm; MP-O-2871 male C L = 0.50 mm, H = 0.26 mm, W = 0.20 mm (all adult specimens).

Type-locality and horizon. Pau Preto Quarry (23°17'28"S; 49°18'12"W), Taguaí municipality, São Paulo State, Brazil. Teresina Formation (Guadalupian).

Material. 36 C and 210 V, both of adults and juveniles.

Diagnosis. Carapace preplate, elongated, subrectangular, and slightly inflated in the middle. Surface thoroughly reticulated with polygonal fossae. Dorsal margin not seen due to preservation, but with outline slightly sinuous anteriorly in males, and slightly convex in females. Anterior and posterior margins equicurvate.

Description. Carapace elongated, preplate, and subrectangular. Maximum height at the anterior cardinal angle; maximum length and width at the middle. LV slightly larger than RV. Both anterior and posterior margins equicurvate. Dorsal margin not seen due to preservation, but with outline slightly sinuous anteriorly in males, and slightly convex in females; ventral outline very sinuous in males and less sinuous in females. Reticulation with low muri and polygonal fossae, mostly with

pentagonal or hexagonal pattern. Internal view: Hinge and central muscle scars not seen due to diagenetic alteration; anterior duplicature fairly well developed, and with homogeneous width. Sexual dimorphism conspicuous: females higher and slightly longer than males.

Geographic and stratigraphic distribution. Known only for the type-locality (Teresina Formation, Guadalupian).

Remarks. In a previous study this species was tentatively ascribed to *Editia* Brayer, 1952 based on its cytheroidean characteristics (Bergue *et al.*, 2020). However, the revisions by Weber & Becker (2004) and Sobolev (2019) clearly demonstrate that the absence of ridges and caudal process rule out any affinity to *Editia*. The specimens of the type-series present some degree of variation in length (0.5 to 0.55 mm) and width. These length variations are ascribed to intraspecific variation, which would be expected in time-averaged assemblages. Variations in width, on the other hand, are considered sexual dimorphism. The sexual dimorphism herein proposed is based on the general pattern observed in podocopids where males are usually lower and narrower than females.

Order PLATYCOPIDA Sars, 1866

Suborder METACOPINA

Sylvester-Bradley, 1961

Superfamily HEALDIOIDEA Harlton, 1933

Family CARBONITIDAE Sohn, 1985

Velatomorpha Tibert & Dewey, 2006

Type-species. *Carbonia fabulina* var. *altilis* Jones & Kirkby, 1889.

Remarks. In previous work, Bergue *et al.* (2020) adopted Liebau's (2005) classification and placed *Velatomorpha* among the Podocopida (Suborder Darwinulocopina). However, the absence of duplicature and the aggregate cluster of adductor muscle scars diverge from the diagnosis of other podocopids, and are more congruent with Platycopida, as originally proposed by Tibert & Dewey (2006, p. 56). The diagnosis of *Velatomorpha*, however, presents inconsistency.

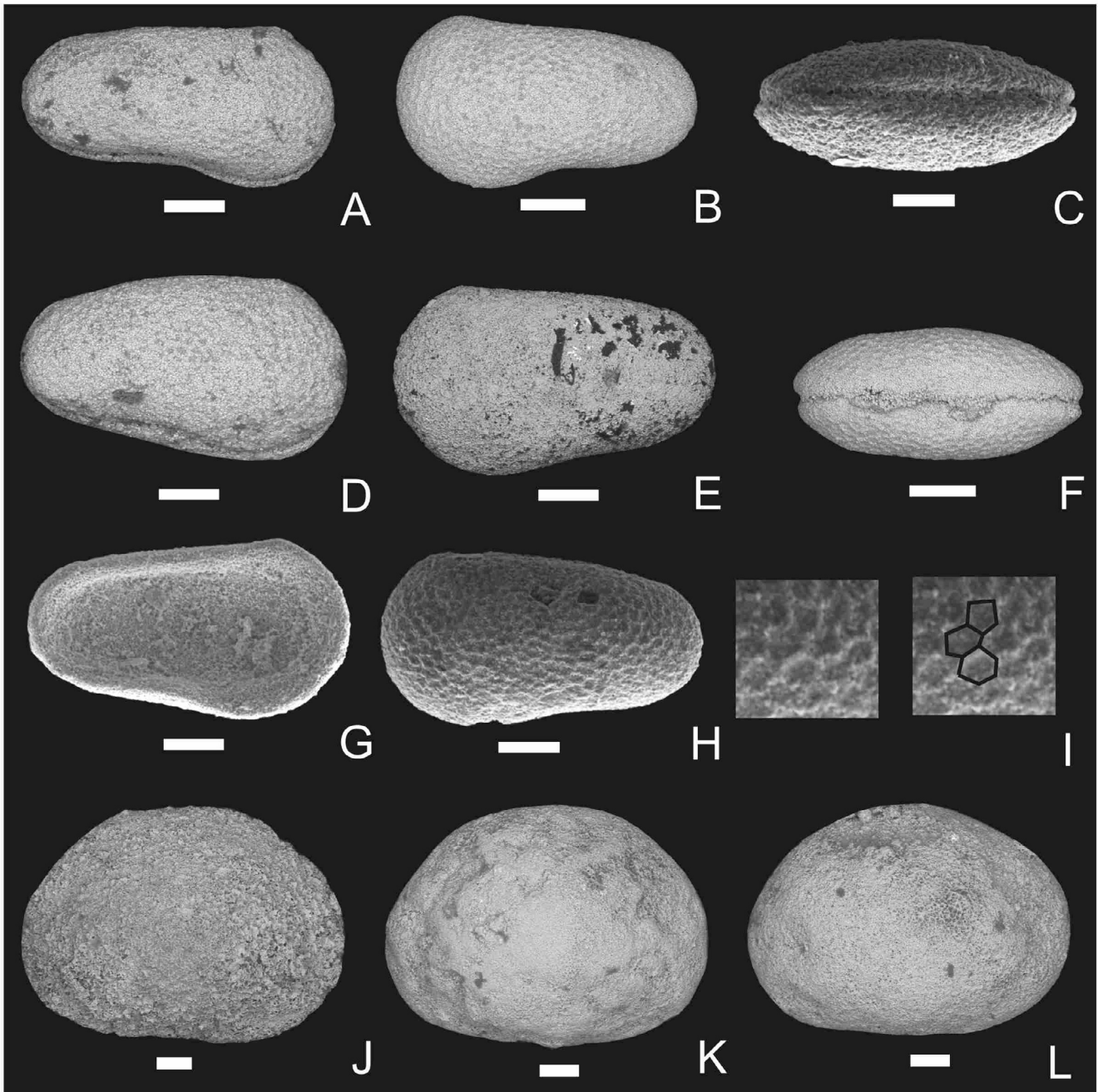


Figure 2. A–I, *Paranacythere nigripallus* gen. nov. and sp. nov.; A, male C right view. Holotype (MP-O-2912); B, male C left view (MP-O-2871); C, male C dorsal view (MP-O-2914); D, female C right view (MP-O-2870); E, female LV (MP-O-2869); F, female C ventral view (MP-O-2870); G, female LV inner view (MP-O-2869); H, female C left view (MP-O-2913); I, detail of reticulation of MP-O-2913; J–L, *Velatomorpha rochacamposi* Bergue *et al.*, 2020; J, RV lateral view (MP-O-2872); K, A-1 RV lateral view (MP-O-2873); L, A-1 LV lateral view (MP-O-2874). Scale bars = 0,1 mm.

Although it states that the greatest height lies at the anterior, the table 1 of Tibert & Dewey (2006, p. 57) of that same paper indicates that the greatest height is at the posterior. Based on the specimens figured by Tibert & Dewey (2006) it is possible to see that the greatest height is actually in the posterior and, therefore, an emended diagnosis is herein proposed.

Emended diagnosis. Sub-ovate; strong right over left valve overlap; postplete or amplete; gentle sloping posterior; 6–8 inner stigmata surrounded by 19–20 stigmata; AMS field is bi-arcuate with a rearward facing convex arch; contact margin is a ridge and groove on the left valve most prominent at anterior and posterior areas; adont hinge as described for the superfamily Healdioidea.

Velatomorpha rochacamposi Bergue,
Maranhão & Ng, 2020
(Figures 2J–L)

p 2020 *Velatomorpha rochacamposi* Bergue *et al.*,
p. 306, pl. 2, figs. 9, 10, 14–16. [non figs. 11–13].

Figured specimens. MP-O-2872 RV L = 0.90 mm, H = 0.65 mm; MP-O-2873 A-2 RV L = 0.83 mm, H = 0.60 mm; MP-O-2874 A-2 LV L = 0.80 mm, H = 0.58 mm.

Locality. Xavantes Dam, Fartura municipality, São Paulo State, Brazil.

Remarks. The study of additional material from type-locality and review of the type-series of *Velatomorpha rochacamposi* resulted in the exclusion of the specimens MP-O-2932 and MP-O-2935 (see description of *V. pseudoaltilis* in this section).

Velatomorpha xavante sp. nov.

urn:lsid:zoobank.org:act:DB6D8C04-B947-41F2-93E9-1D8BCE1E2D56

(Figures 3A–D)

Etymology. In allusion to the type-locality, the Xavantes Dam outcrop.

Holotype. MP-O-2875 male RV L = 1.03 mm, H = 0.70 mm.

Paratypes. MP-O-2876 male RV L = 1.00 mm; H = 0.68 mm; MP-O-2877 female RV L = 0.95 mm, H = 0.65 mm; MP-O-2878 A-2 RV L = 0.90 mm, H = 0.60 mm; MP-O-2879 LV L = 0.79 mm, H = 0.51 mm; MP-O-2880 LV L = 0.8 mm, H = 0.53 mm.

Type-locality and horizon. Xavantes Dam, Fartura municipality, São Paulo State, Brazil. Teresina Formation (Guadalupian).

Material. 36 V, adults and juveniles.

Diagnosis. Carapace large, amplete moderately inflated, RV suboval in lateral view; LV subtrapezoidal in lateral view and slightly smaller than RV.

Description. Carapace large, amplete suboval in right lateral view; somewhat angulose in the anterior and posterior margins in juveniles. Slightly inflated in the ventrolateral region. Both dorsal and ventral margins short and straight. Anterior margin broad and equicurvate; posterior margin slightly

angulose at upper and lower portions resulting in more acuminate median outline compared to the anterior one. Surface finely and thoroughly punctuated with puncta more easily seen in instars. Internal features poorly preserved due to filling or nesting. Adductor muscle scars not seen, but externally a group of small scars with carbonitid-like pattern occurs in the center area of some specimens. Hinge short and straight, but elements not seen due to incrustation. Contact margin well developed in the RV. Sexual dimorphism present, but subtle: females higher than males.

Geographic and stratigraphic distribution. Known only for the type-locality (Teresina Formation, Guadalupian).

Remarks. *Velatomorpha xavante* sp. nov. is easily distinguished from *V. rochacamposi* Bergue *et al.*, 2020 in having subrectangular outline with dorsal and ventral areas straighter. Small differences assigned to sexual dimorphism reinforce the occurrence of this characteristic in the genus as proposed by Tibert & Dewey (2006).

Velatomorpha pseudoaltilis sp. nov.

urn:lsid:zoobank.org:act:0B366460-0F5C-4C9C-AA24-AFECB3FF4AAF

(Figures 3E–I)

2020 *Velatomorpha* sp. 2 Bergue *et al.*, p. 308, pl. 3, fig. 3.

p 2020 *Velatomorpha rochacamposi* Bergue *et al.*, p. 306, pl. 2, fig. 12. [non figs. 9, 10, 14–16].

Etymology. *L.* in allusion to the morphological similarity to *V. altilis* (Jones & Kirkby, 1889).

Holotype. MP-O-2940 RV L = 0.95 mm, H = 0.61 mm.

Paratypes. MP-O-2932 RV L = 0.89 mm, H = 0.60 mm; MP-O-2935 juvenile broken C, L = 0.83 mm, H = 0.62 mm, W = 0.55 mm; MP-O-2881 RV L = 0.93 mm, H = 0.62 mm; MP-O-2882 RV L = 0.9 mm, H = 0.59 mm; MP-O-2909 RV L = 0.9 mm, H = 0.59 mm; MP-O-2910 juvenile LV L = 0.78 mm, H = 0.53 mm.

Type-locality and horizon. Xavantes Dam, Fartura municipality, São Paulo State, Brazil. Teresina Formation (Guadalupian).

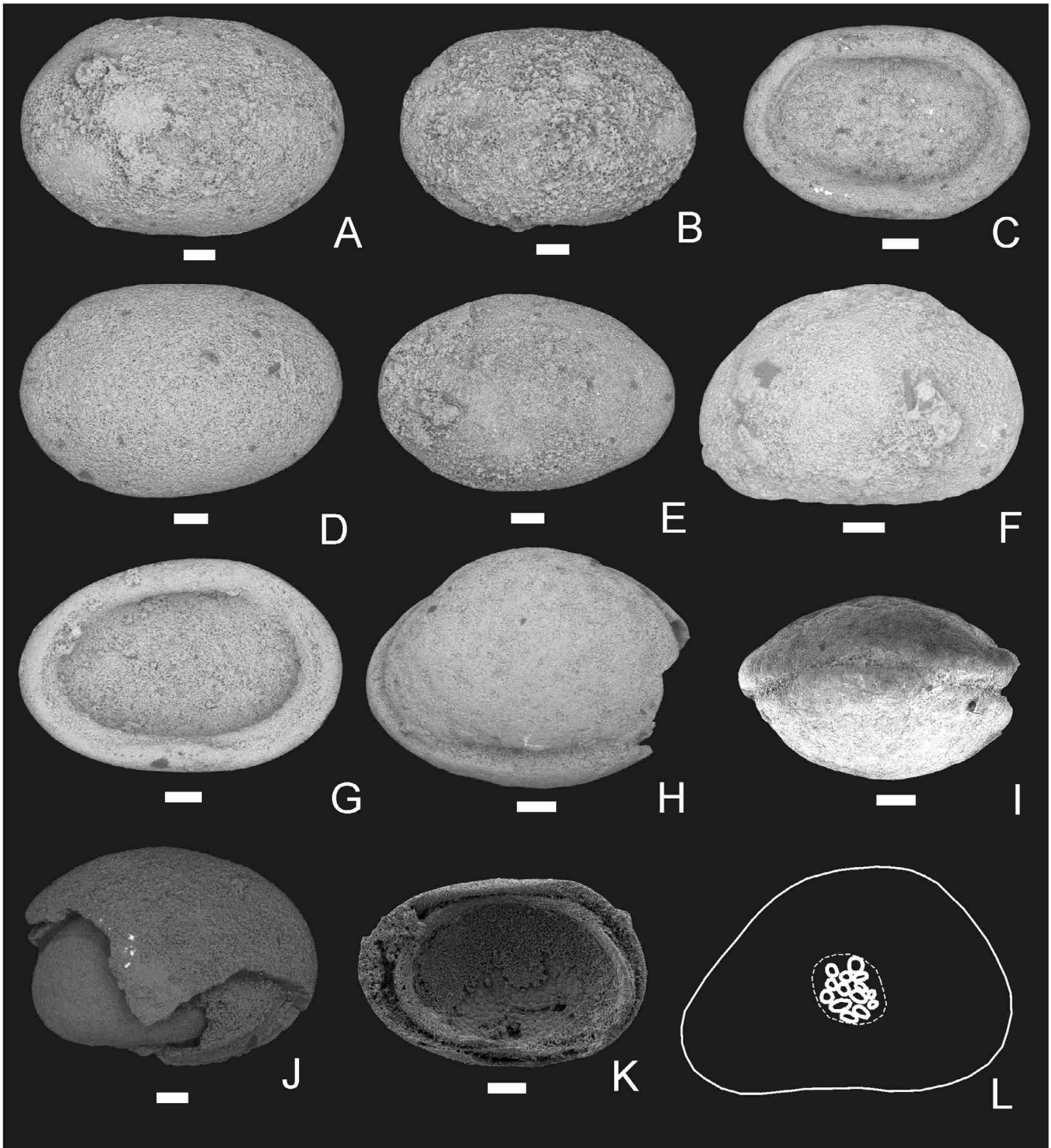


Figure 3. A–D, *Velatomorpha xavante* sp. nov.; A, RV lateral view (MP-O-2875), holotype; B, RV A-1 lateral view (MP-O-2876); C, RV inner view (MP-O-2878); D, LV external view (MP-O-2880); E–I, *Velatomorpha pseudoaltitilis* sp. nov.; E, RV external view (MP-O-2940), holotype; F, Juvenile LV external view (MP-O-2910); G, RV inner view (MP-O-2932); H, C in left view (MP-O-2935); I, C in dorsal view (MP-O-2935); J–K, valve nesting in indeterminate species of *Velatomorpha*; J, MP-O-2911; K, MP-O-2939; L, Camera lucida sketch of an instar of *Velatomorpha rochacamposi* (MP-O-2937) showing the position and part of the adductor muscle scars. Scale bars = 0,1 mm.

Material. 21 V adults and juveniles, and one C juvenile.

Diagnosis. Carapace postplate strongly inequivalve and smooth. LV subtrapezoidal and higher than the RV at median region; RV subelliptical overlapping

LV along the free margins, but that LV overreaches RV along dorsum.

Description. Carapace postplate strongly inequivalve. LV subtrapezoidal outline with dorsal margin short and oblique, and ventral margin short

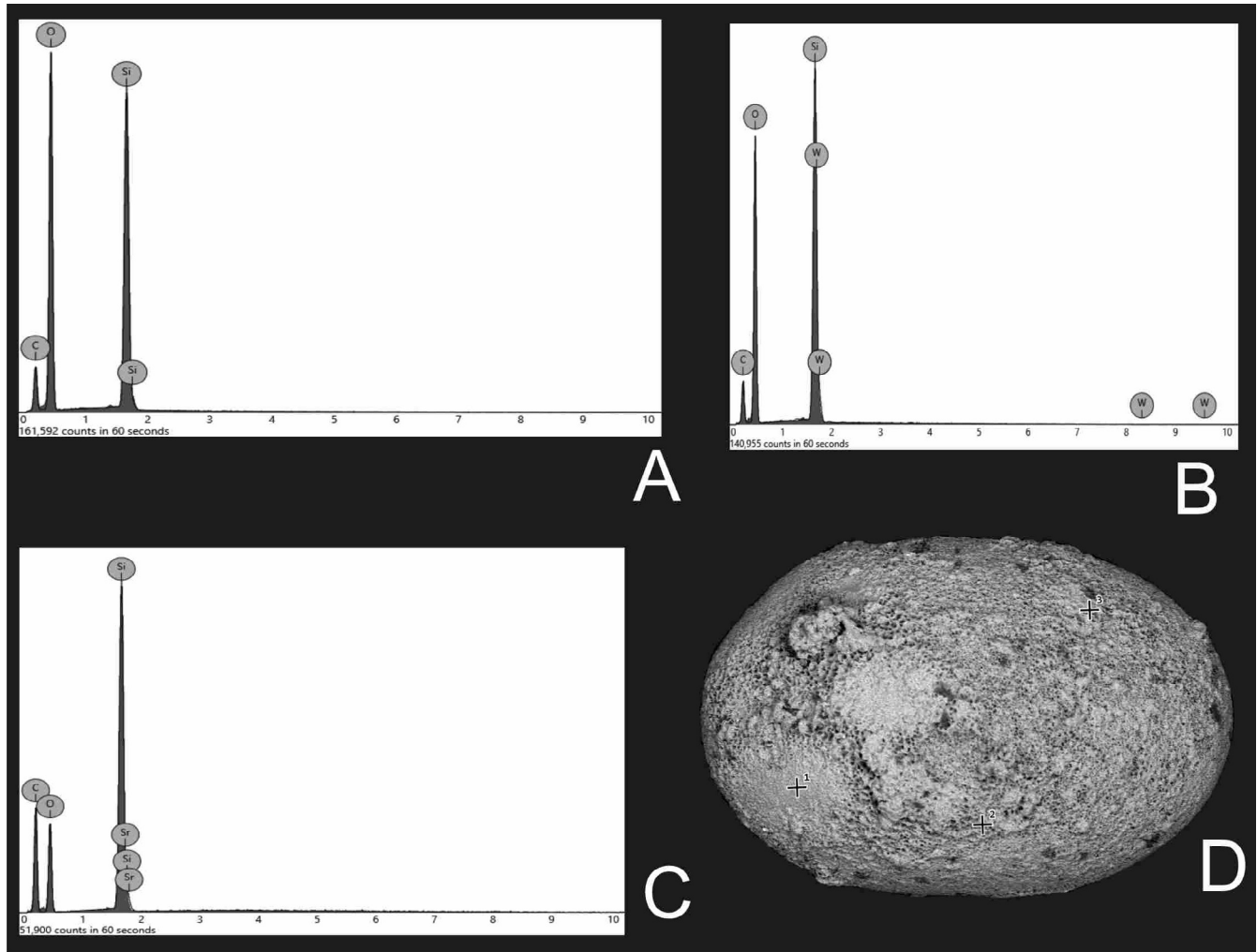


Figure 4. Energy-dispersive X-ray spectroscopy (EDS) analysis carried out in three regions of the valve MP-O-2875 (*Velatomorpha xavante* sp. nov.).

and straight. Anterior and posterior margins oblique at upper half. RV subelliptical with both dorsal and ventral outlines convex, enclosing LV around the free margins; anterior and posterior margins equicurvate. Surface predominantly smooth in adults, but thoroughly punctuated in juveniles. Internal features poorly known due to filling or nesting. Hinge and adductor muscle scars not seen. Contact margin well developed in the RV, slightly projected outward in the middle portion of the ventral margin. Sexual dimorphism not observed.

Geographic and stratigraphic distribution. Known only for the type-locality.

Remarks. *Velatomorpha pseudoaltilis* sp. nov. differs from *V. xavante* sp. nov. in having the outline of the RV markedly oval. In spite of the similarity to *V. altilis*, these species differ in the posterior outline of the RV and in the outline of the LV. Another

similar species, *V. fittsi* (Kellet, 1935), differs in having the LV completely enclosed by the RV.

ASSEMBLAGES COMPOSITION AND TAPHONOMIC REMARKS

Velatomorpha spp. and *Paranacythere nigripallus* gen. nov. and sp. nov. are the dominant taxa both in Xavantes Dam and Pau Preto Quarry. The Xavantes site is characterized by high incidence of *Velatomorpha*, whose specimens are usually preserved as two or three nested valves of several instars, possibly up to A-5. Carapaces, on the other hand, are very rare and exclusively juveniles. In the Pau Preto Quarry assemblages are dominated by *Paranacythere nigripallus* gen. nov. and sp. nov., but *Velatomorpha* spp. are also common.

Different from *Velatomorpha*, carapaces of *Paranacythere nigripallus* gen. nov. and sp. nov. are common, although valves are dominant. In part, the predominance of valves over carapaces in *Velatomorpha* is explained by the hinges poorly developed or even absent in most Paleozoic ostracods (Scott, 1961). In the species herein described hinge structures were not observed, and the valves junction occurs simply (at least in *V. pseudoaltilis* sp. nov.) through a smooth contact margin without interlocking devices.

The valve:carapace and adult:juvenile ratios in fossil assemblages might indicate environmental energy level and have, therefore, paleoecological potential. Reyment (1960) discussed briefly the adult:juvenile relation in ostracod assemblages, but this issue was detailed only some decades later by Whatley (1988), who represented population age structures in three histogram types (A, B, and C). Whatley's histogram type A represents assemblages composed both by adults and multiple instars indicating autochthony and low environmental energy. Types B and C, in turn, depict assemblages whose original composition has been altered by transport. The assemblages from Xavantes Dam composed by adults and several instars fit in Whatley's assemblage Type A (*i.e.*, low environmental energy), which is consistent with marginal marine areas. In Pau Preto, the predominance of adults over juveniles of *Paranacythere nigripallus* gen. nov. and sp. nov. cannot be ascribed either to selective transport or preservation bias based on the available data.

Valve nesting (also called cup-in-cup), another conspicuous biostratinomic trait seen in several samples of both sections herein studied, is usually assumed as indicative of gentle water movements in very shallow marginal areas (Wakefield, 1995; Carignano & Varella, 2011; Bergue *et al.*, 2011, 2015). Alternative explanation for the origin of this pattern is the stacking in the digestive tract of predators (Retrum & Kaesler, 2005). Notwithstanding, a more plausible explanation links nesting to two factors: size and abundance of valves, *i.e.*, nesting would occur whenever high incidence of large valves takes place (Guernet & Lethiers, 1989; Wakefield, 1995). This reasoning is supported by Fontana & Ballent (2005) who

observed in an ephemeral lake in the Buenos Aires Province (Argentina) the occurrence of nesting only in the largest species: *Amphicypris argentinensis* Fontana & Ballent, 2005.

Last but not least, carapace incrustation must be pointed as another important thaphonomic feature in the studied assemblages. In most cases it hampered the morphological analysis of specimens and, consequently, their due identification. The incrusting mineral deposited over valves and carapaces produces in some instances honeycomb-like structures, whose analysis through energy dispersive X-ray spectroscopy (EDS) revealed to be of carbonatic composition (Figure 4). The paleoenvironmental significance of these incrustations, however, could not be interpreted in the present study, and constitute a potential theme of investigation in future works.

THE TERESINA FORMATION ASSEMBLAGES IN THE CONTEXT OF THE WORLD PERMIAN OSTRACOD RECORD

Research on Permian ostracods mostly reports marine assemblages (*e.g.*, Honigstein *et al.*, 2006; Chitnarin *et al.*, 2008; Crasquin *et al.*, 2010; Tanaka *et al.*, 2013; Forel, 2018, *inter alia*). Some important studies, however, have also been carried out in assemblages from mixohaline and freshwater paleoenvironments of North America (*e.g.*, Retrum & Kaesler, 2005; Tibert *et al.*, 2011, 2013), France (Lethiers *et al.*, 1993, 1997), China (Pang & Jin, 2004; Chu *et al.*, 2015), Russia (Kashevarova & Molostovskaya, 1986; Molostovskaya, 2000, 2005; Naumcheva & Golubev, 2020), and South America (Zabert, 1985; Sohn & Rocha-Campos, 1990; Breitzkreuz *et al.*, 1992; Maranhão & Petri, 1996; Díaz-Saravia & Herbst, 2001; Bergue *et al.*, 2020).

The studies above mentioned supply important data on the origin and radiation of non-marine (*i.e.*, mixohaline and freshwater) ostracod faunas in several parts of Pangea. Adaptative radiations, irrespective of the animal group considered, result mostly from opportunities. Species do not necessarily have fixed ecological traits, which would permit ecological shift and occupation of new niches (Mayr, 1963). Yet, opportunities do not ensure *per se* adaptative radiation, and factors such

as lack of speciation, lack of ecological resources and lack of evolvability, might turn some clades more prone to radiating than others (Losos, 2010). The diversity of environments in marginal marine areas during the Late Paleozoic in different regions of Pangea lay the pathway for understanding the adaptive irradiation of ostracods (Bennett *et al.*, 2011).

Although records of the initial phase of freshwater colonization by ostracods might be biased by preservational restraints, it is assumed that the oldest freshwater faunas date from Early Carboniferous (Horne, 2003; Williams *et al.*, 2006; Bennet, 2008). Details and timing of these radiations – that might have occurred repeatedly (see Retrum & Kaesler, 2005) – are not completely known. Notwithstanding, they were certainly influenced both by intrinsic (*e.g.*, physiologic adaptations) and extrinsic factors (*e.g.*, sea level changes and coastal morphodynamics) during the Carboniferous and which continued along the Permian (Bennett *et al.*, 2011; Iglukowska, 2014).

Whatever the events experienced by some marine lineages, which allowed the radiation into non-marine domains in the Carboniferous, these ostracod faunas were dominated by darwinuloidean, carbonitoidean and limnocytherids (Horne, 2003). The evolutionary processes which took place in the Late Paleozoic influenced the forthcoming Meso–Cenozoic freshwater faunas which became dominated by cypridoideans, besides darwinuloideans and the cytheroidean family Limnocytheridae (Whatley & Mognilevsky, 1998; Horne, 2003). Mixohaline faunas, in turn, are usually less diverse than freshwater ones, and characterized instead by high abundance of a few species. A cytheroidean family – the Cytherideidae – became important in post-Paleozoic mixohaline environments in Jurassic (*e.g.*, Boomer *et al.*, 2001), Cretaceous (*e.g.*, Tibert *et al.*, 2003; Piovesan *et al.*, 2015), and Neogene (*e.g.*, Nogueira *et al.*, 2011; Gross *et al.*, 2014; Nogueira & Ramos, 2016).

The absence of marine ostracod taxa (such as bairdiids, bythocytherids and healdiids) in the Teresina Formation might be explained by the evolutive phase of the Paraná Basin during the Carboniferous and Permian. After the Late Paleozoic Ice Age (Pennsylvanian), a sea level

rise trend is registered in the Supersequence Gondwana I (Milani *et al.*, 2007; Cagliari *et al.*, 2016). The Serra Alta Formation represents its maximum marine influence, and the overlaid Teresina Formation registers pelites with tide influenced structures, which characterizes the inception of new ecological conditions (Milani *et al.*, 2007). According to Simões *et al.* (2017) and Guerrini *et al.* (2020), these processes represent the establishment of a confined epeiric sea, followed by a trend of shallowing and continentalization in the basin. In marginal areas of this epeiric sea, several types of environments with variable salinity gradients might have been established (Ng *et al.*, 2019), such as estuaries, bays, lakes, lakes with occasional marine influence, and lagoons as discussed by Bennett *et al.* (2011).

Hence, the absence of typical marine cytheroidean, and the freshwater limnocytherids and darwinulids, permit to characterize the assemblages herein studied as mixohaline, where *Velatomorpha–Paranacythere* constitutes the typical association. This association is considered ecologically analogous to others composed by Cytherideidae in the Mesozoic and Cenozoic. Other occurrences in the northwestern Pangea sustain *Velatomorpha* as a taxon widespread and diverse in mixohaline environments (Tibert & Dewey, 2006; Gray *et al.*, 2012; Tibert *et al.*, 2013). The continentalization trend observed in this sector of the Paraná Basin and the repeated events of climatic changes prompted the evolution of the endemic ostracod assemblage herein studied.

CONCLUSIONS

The association *Velatomorpha–Paranacythere* characterizes mixohaline environments of the Guadalupian Teresina Formation and is proposed as ecological analogous of the cytherideid associations *Fossocytheridea–Perissocytheridea* in the Mesozoic and *Cyprideis–Perissocytheridea* in the Cenozoic. Ostracod assemblages from the Teresina Formation record important evolutionary step on the diversification of non-marine ostracods in the southern Pangea. The genus *Velatomorpha* with three species formally described for the Teresina Formation represents an important ecological index

for mixohaline environments. Other morphotypes of *Velatomorpha*, which could not be thoroughly studied in the present work due to the scarcity of specimens, possibly correspond to new species, and in this case a biostratigraphical potential for the genus might be expected.

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