

The Permian Tiaraju bivalve assemblage, Passa Dois Group, southern Brazil: biostratigraphic and paleobiogeographic significance

Assembleia de bivalves permianos de Tiaraju, Grupo Passa Dois, sul do Brasil: significado bioestratigráfico e paleobiogeográfico

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ABSTRACT: Permian bivalves of the Paraná Basin evolved in a large inland sea, under conditions of extreme isolation and environmental stress. Although known since 1918, its evolutionary history is still obscure due to the incomplete and biased information on faunal composition and stratigraphic distribution of various assemblages. Hence, the description of the Tiaraju assemblage, the only known bivalve occurrence in the Passa Dois Group from the southernmost Brazil, adds new key information on the composition, biocorrelation and age of this unique molluscan fauna. *Terraia falconeri*, *Cowperesia emerita*, *Holdhausiella elongata*, and *Terraia altissima* were recorded and described. *T. falconeri* is the commonest species, followed by *C. emerita*, *H. elongata* and *T. altissima*. The faunule is mainly composed by Terrainae, lacking Pinzonellinae. Assemblage is, thus, poorly diversified, both regarding the faunal composition and guild structure (only infaunal, facultatively motile, unattached, suspension feeders present). *Cowperesia emerita* and *T. altissima* strongly indicate biocorrelation with assemblages of the Rio do Rasto and Gai-As formations, Brazil and Namibia, providing an age no younger than the mid-Permian (Wordian-Capitanian). On the light of this information, the current geological map of the Tiaraju region, São Gabriel, and the local boundary between the Teresina and Rio do Rasto formations requires reevaluation.

KEYWORDS: Passa Dois Group, Paraná Basin, Gai-As Formation, Guadalupiano.

RESUMO: Bivalves permianos da Bacia do Paraná evoluíram em um imenso mar interior, sob condições de extremo isolamento e estresse ambiental. Embora conhecidos desde 1918, a história evolutiva desses bivalves é ainda obscurecida pelo conhecimento incompleto e enviesado sobre a composição faunística e a distribuição estratigráfica de várias assembleias. Portanto, a descrição da assembleia de Tiaraju, a única conhecida no Grupo Passa Dois do sul do Brasil, contribui com novas informações-chave sobre a composição, biocorrelação e idade dessa fauna de moluscos únicos. *Terraia falconeri*, *Cowperesia emerita*, *Holdhausiella elongata* e *Terraia altissima* foram registradas e descritas. *T. falconeri* é a espécie mais comum, seguida por *C. emerita*, *H. elongata* e *T. altissima*. A fauna é majormente composta por Terrainae, faltando os Pinzonellinae. A assembleia é, desse modo, pobremente diversificada, no que tange à composição faunística e guildas (somente bivalves de infauna, facultativamente móveis, suspensívoros estão presentes). *Cowperesia emerita* e *T. altissima* sugerem, fortemente, biocorrelação com assembleias das formações Rio do Rasto e Gai-As, Brasil e Namíbia, indicando idade não mais jovem que o Permiano médio (Wordiano-Capitaniano). À luz dessas informações, o mapa geológico da região de Tiaraju, São Gabriel, e o contato local entre as formações Teresina e Rio do Rasto, requerem, ambos, reavaliação.

PALAVRAS-CHAVE: Grupo Passa Dois, Bacia do Paraná, Formação Gai-As, Guadalupiano.

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INTRODUCTION

The Permian bivalve mollusk fauna of the Paraná Basin evolved in a shallow and large landlocked sea, under variable salinity and bottom water ventilation regimes (Runnegar & Newell 1971; Simões *et al.* 1998; Matos *et al.* 2017a, b). Members of the fauna were first described by Holdhaus (1918) and by subsequent authors (see Simões & Fittipaldi 1987, for a literature review), but the fauna was only revised by Runnegar & Newell (1971). Since this benchmark review, most of the following studies aimed to elucidate unsolved issues related to the systematics (Simões *et al.* 1997, 1998, 2010; Mello 1999; Anelli *et al.* 2010), taphonomy (Torello & Simões 1994; Simões *et al.* 1996, 2000; Simões & Kowalewski 1998; Simões & Torello 2003; Neves *et al.* 2010, 2011), paleoecology (Ghilardi 1999; Kowalewski *et al.* 2000; Ghilardi & Simões 2002; Silva 2016; Matos *et al.* 2017a, b) and paleobiogeography (Wesselingh 2007; Simões *et al.* 2010; David *et al.* 2010) of the fauna. However, details of the evolutionary history of this unique bivalve fauna are still obscure because of the biased information on the faunal composition of various assemblages (Simões *et al.* 2010, 2015) (Fig. 1). In the rock succession of the Permian Passa Dois Group, bivalves are recorded in at least seven benthic assemblages including, in ascending order, the Taquaral assemblage, Irati Formation; the *Anhembia froesi* assemblage, Serra Alta Formation; the *Pinzonella illusa* and *Pinzonella neotropica* assemblages, Teresina and Corumbataí formations; the *Terraia curvata* and *Leinzia similis* assemblages, Serrinha Member, Rio do Rasto Formation; and the “*Palaeomutela*” *platinensis* assemblage, Morro Pelado Member, Rio do Rasto Formation (Fig. 1). However, previous studies focused on the fossil assemblages preserved in Teresina and Corumbataí formations (*i.e.*, *P. illusa* and *P. neotropica* assemblages). Indeed, only recently the taphonomy and paleoecology of the bivalves of the Irati (Matos *et al.* 2017b) and Serra Alta formations were studied in detail (Bondioli *et al.* 2015; Silva 2016; Matos *et al.* 2017a). On the contrary, the assemblages of Morro Pelado Member, Rio do Rasto Formation (Rohn 1994), are still poorly studied and described (*i.e.*, those bivalves are forgotten). Additionally, most studies are based on fossils from the eastern border of the Paraná Basin, mainly from the states of São Paulo and Paraná. In this context, the main aim of this contribution was to describe, for the first time, the Tiaraju bivalve assemblage — *i.e.*, informally known as the TB assemblage — (Cunha 1972; Klein 1997), the only one known from Permian rocks of the Passa Dois Group, State of Rio Grande do Sul, southernmost Brazil. This is relevant, since the assemblage can shed a new light into the regional faunal variations of the bivalves that populated the Paraná Basin during the Guadalupian Epoch,

Permian. Yet, it can improve our knowledge on the systematics and biocorrelation of this unique endemic molluscan fauna. As discussed next, the accurate identification of the Permian bivalves of Tiaraju allowed us to compare the TB assemblage with other Gondwanic faunas found in the Huab Basin, Namibia, helping to better constrain its correlation and age.

BACKGROUND

On the regional significance of the Tiaraju bivalve assemblage

As aforementioned, the TB assemblage is the unique Permian bivalve fauna known in rocks of the Passa Dois Group from the State of Rio Grande do Sul, Brazil. Fossils belonging to this assemblage are preserved in carbonate concretions found in the upper part of a succession dominated by laminated mudstones tentatively placed in the Teresina Formation (Klein 1997; Klein & Simões 1998). This fauna was first described by Cunha (1972), who assigned all the specimens to the endemic genus *Cowperesia?* sp. Later, Klein (1997) presented a tentative taxonomic list including the following bivalves: *Pinzonella tiarajuensis* (*nomen nudum*), *Terraia altissima* (Holdhaus 1918), *Jacquesia elongata* (Holdhaus 1918), *Jacquesia* sp., *Pyramus? emerita* (Reed 1929) and *Naidopsis?* sp. Despite this list, the TB assemblage remains undescribed, according to the rules of the International Code of Zoological Nomenclature (ICZN).

During a re-examination of the Permian bivalve faunas of the Passa Dois Group and coeval units from Brazil and Africa (David *et al.* 2010; David 2014), a close resemblance was observed between some of the Tiaraju specimens illustrated by Klein (1997) and those from the Gai-As Formation, Huab Basin, Namibia, which were described by David *et al.* (2010). In this context, this possible biocorrelation is worth of investigation, since the age of the Namibian fossils is well constrained based on radiometric dating (Wanke 2000; Holzförster 2002). In addition, some bivalve species in the compositional faunal list presented by Klein (1997) are not common in that interval of the Passa Dois Group succession. The fauna seems to include a mixture of taxa commonly found in assemblages of the Teresina and Rio do Rasto (Serrinha Member) formations, reinforcing its transitional character.

The nature of Teresina and Rio do Rasto formations boundary

In the Brazilian portion of the Paraná Basin, the upper part of the Permian sedimentary succession encompasses rocks of the 1400-m-thick Passa Dois Group. This unit

includes, from the base to the top, the upper Artinskian Irati Formation, the Kungurian Serra Alta Formation, the upper Kungurian-Roadian Teresina Formation and the Capitanian-Wuchiapingian Rio do Rasto Formation (Rohn 1994, 2007; Holz *et al.* 2010). According to our data (see systematic paleontology below), the TB assemblage has a transitional character, including a mixture of bivalve species that are recorded in benthic assemblages of the Teresina Formation, as well as typical members of the bivalve assemblages of the base of the Serrinha Member, Rio do Rasto

Formation. Therefore, the nature of the contact between these two units is worth mentioning here.

In the vicinities of the city of Lages and along the Rio do Rasto Hill section, Santa Catarina state, the Teresina Formation is a ~160-m-thick (Warren 2006) monotonous sedimentary succession formed by massive and laminated siltstones, interbedded with rare thin sandstone layers. Ellipsoidal- to discoidal-shaped carbonate concretions occur throughout the unit. On the other hand, the Serrinha Member encompasses the lower part of the Rio do Rasto

CHRONO		LITHOSTRATIGRAPHY		BIVALVE ASSEMBLAGES	DEPOSITIONAL SYSTEMS	ENVIRONMENTAL CONDITIONS	
		GROUP	FORMATION				MEMBER
PERMIAN	LOPINGIAN	PASSA DOIS	RIO DO RASTO	MORRO PELADO	FLUVIAL, DELTAIC AND EOLIC SYSTEMS	fresh water oxic siliciclastic	
				" <i>Palaeomutela</i> " <i>platinensis</i>			
	GUADALUPIAN		SERRINHA	<i>Leinzia similis</i>	↑	marginal fresh water oxic mainly siliciclastic	
				<i>Terraia curvata</i>			
	WORDIAN		TERESINA	<i>Pinzonella neotropica</i>		CONFINED INTERIOR SEA	nearshore variable salinity oxic siliciclastic/ carbonatic
				<i>Pinzonella illusa</i>			
	ROADIAN		SERRA ALTA	<i>A. froesi</i>		offshore dysoxic/anoxic siliciclastic	
				IRATI			ASSISTÊNCIA
	KUNGURIAN		TAQUARAL	Taquaral Assemblage			

Figure 1. Schematic chart of the Passa Dois Group, Permian, showing the vertical distribution of the bivalve assemblages in the eastern margin of the Paraná Basin, Brazil (based on Rohn 1994, 2007). Presence of *Cowperesia emerita* and *Terraia altissima*, the absence of pinzonellids and the profuse occurrence of terraidis strongly suggest faunal affinities of the Tiaraju bivalve assemblage with those of the basal part of Rio do Rasto Formation.

Formation and is well exposed in the outcrop belt of the Passa Dois Group, in the State of Santa Catarina, southern Brazil. The unit comprises a ~100-m-thick sedimentary succession with progradational architecture. This is marked, from the base to the top, by gradual changes of thick siltstone and heterolithic facies, by tabular, fine sandstone beds with swaley, hummocky and wave ripples. Plant remains of *Glossopteris* Flora, phosphatized teeth and fish scales, as well as highly bioturbated beds with *Diploclaterion*, *Arenicolites* and *Palaeophycus* icnites, are also common. These evidences indicate that the deposition of this interval of the Passa Dois Group succession occurred under shallow and oxic waters (Warren 2006; Warren *et al.* 2008).

The contact between the upper Teresina and lower Rio do Rasto formations (Serrinha Member) is transitional (Vieira 1973; Riccomini *et al.* 1984; Warren *et al.* 2008) and marked by the gradual change from siltstones to fine sandstone facies. The transition between these units is particularly well-marked by sandstone layers that increase in frequency and thickness from the upper Teresina Formation to the lower part of the Rio do Rasto Formation (Serrinha Member). These reinforce the progradational pattern of the unit (Fig. 2). The lithostratigraphic contact between both units is marked by the first occurrence of a meter-scale, tabular bed of fine sandstone (Warren *et al.* 2008).

Despite the transitional contact between Teresina and Rio do Rasto formations in the State of Santa Catarina, at the borders of the Paraná Basin, that contact can be locally abrupt (Lavina 1991). Available seismic lines and wells drilled by the Brazilian Geological Survey (CPRM) in the 1980's indicate that the contact between these two units is marked by a truncation in seismic reflectors and a sudden increase in the gamma ray values. However, these are probably related to changes in facies association rather than the presence of an erosional discordance (Lavina 1991). Yet, changes in the paleontological content also indicate the occurrence of local diastemas, as evidenced by the sudden disappearance of typical members of the endemic *Pinzonella* fauna, and the appearance of a diverse fauna dominated by bivalves belonging to *Terraia* (Lavina 1991; Simões *et al.* 2015). This is exactly what we can see from the studied fossil material.

GENERAL GEOLOGICAL SETTING

Studied Permian bivalve-rich rocks of the Passa Dois Group were recorded in outcrops located in the State of Rio Grande do Sul, São Gabriel District, ~300 km far from Porto Alegre (state capital), southern Brazil. The main

fossil-rich outcrop (Figs. 3 and 4) can be reached through the unpaved road between Tiaraju and Pau Fincado localities, ~3 km northward from the Sepé Tiaraju Monument, in the Otávio Vargas Farm. The area was originally mapped by Lavina *et al.* (1983) and Klein (1997), and the main geological data are summarized in Klein *et al.* (1999). According to these authors, rocks of Serra Alta, Teresina and Rio do Rasto formations, locally encompassing a 200-m-thick sedimentary succession, are present in the area. The main sedimentary facies recorded in the Tiaraju area are, from the base to the top: laminated, dark gray siltstones with discoidal carbonate concretions and clastic dikes (Serra Alta Formation); heterolytic sediments (siltstones, fine to very fine sandstones) with wavy-linsen bedding; fine sandstones with hummocky cross-stratification with fish remains and intraclasts; laminated siltstones with bivalve-rich carbonate concretions at the top (Teresina Formation); sandstones with planar cross-stratification; and reddish, tabular mudstones (Rio do Rasto Formation) (Klein 1997; Klein *et al.* 1999) (Figs. 4 and 5). The contact between the laminated siltstones (Teresina Formation) and the sandstones with planar cross-stratification (Rio do Rasto Formation) is sharp (Klein *et al.* 1999).

The laminated siltstones with discoidal carbonate concretions were deposited below storm-wave base in offshore settings whereas shallower dysoxic to oxic conditions were indicated by the heterolytic facies. Fine sandstones with hummocky cross-stratification are a record of high energy events (*i.e.*, storms). The laminated mudstones with fossil-rich carbonate concretions that succeed the storm sandstones indicate quiet waters and the return of the day-by-day sedimentation. These are abruptly (discordantly) succeeded by the sandstones deposited in eolian conditions, representing the migration of dune fields on the water body (Klein *et al.* 1999). Reddish, tabular mudstones, sometimes with amphibian remains, intercalated to the sandy facies, indicate deposition under quiet, oxic, continental waters (Klein *et al.* 1999) (Fig. 5).

MATERIAL AND METHODS

Fossil collection and laboratory procedures

Here the Tiaraju bivalve collection was revisited. It is housed in the Museum of Paleontology, Vale do Rio dos Sinos University (UNISINOS), State of Rio Grande do Sul, southern Brazil. The specimens are coded as MPU, comprising up to 100 shells (a precise number cannot be determined, since various shells are inside concretions, but at least 31 specimens were entirely or

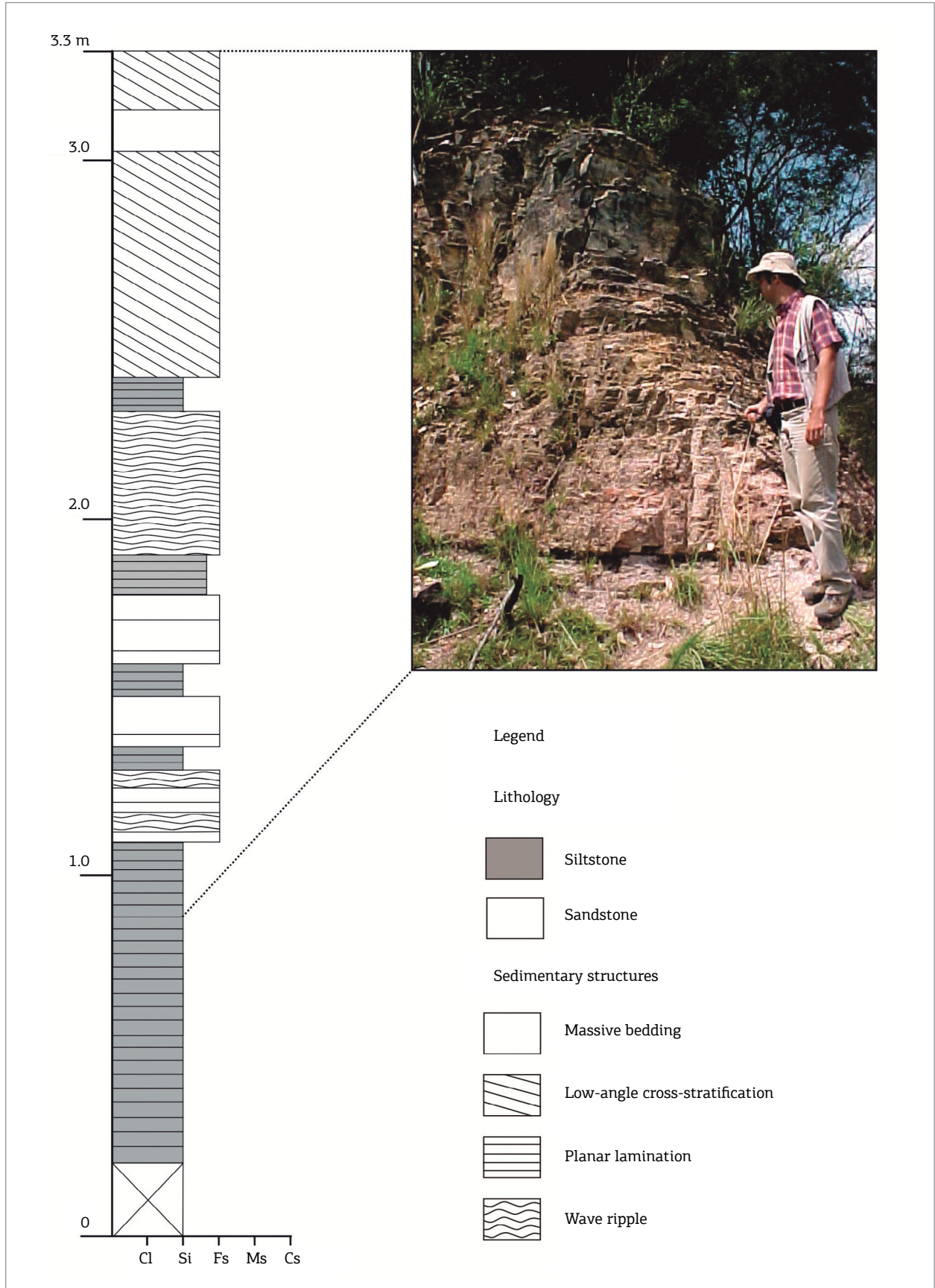


Figure 2. Transitional contact between the upper Teresina and lower Rio do Rasto formations (Serrinha Member), at the Rio do Rasto Hill section, near the city of Lages, Santa Catarina state, southern Brazil.

partially removed from the matrix). These are represented both by shells and molds (internal and external ones). Additionally, we also investigated twenty-nine latex molds that were housed in the scientific collection of the Zoology Department, São Paulo State University, Botucatu Campus, under the code DZP. Preparation of the material included plasticine casts (FIMO brand) and impregnation with magnesium to enhance internal anatomical characters, including possible muscle scars, teeth and sockets (Anelli 1999).

Systematic decisions and ecological guilds

Bivalve species recorded in the Tiaraju assemblage are described in the next section. The suprageneric systematics was based on Morris *et al.* (1991) and Carter *et al.* (2011). The morphological terminology and systematic classification of pachydomids (megadesmids in previous works) were based on Mendes (1952), Runnegar & Newell (1971), Runnegar (1974) and Simões *et al.* (1997). The index of elongation and obesity was interpreted following Stanley (1970). The ecological guilds (*i.e.*, inferred bivalve lifestyle) were determined according to Aberhan & Kiessling (2015, p. 2), including: shallow infaunal, facultatively motile, unattached, suspension feeders (SIFMUSF) and intermediate infaunal, facultatively motile, unattached, suspension feeders (IIFMUSF).

SYSTEMATIC PALEONTOLOGY

Infraclass HETEROCONCHIA (Hertwig 1895)
 Cohort CARDIOMORPHI (Férussac 1822)
 Subcohort CARDITIONI (Dall 1889)
 Order CARDITIDA (Dall 1889)
 Superfamily CRASSATELLOIDEA (Férussac 1822)
 Family *incertae sedis*
Terraia (Cox 1934)

Type species: *Terraia altissima* (Holdhaus 1918).

Terraia falconeri (Cox 1934) (Figs. 6A-F)

Type species: *Pseudocorbula falconeri* (Cox, 1934).

Examined material: Twelve shells (MPU- 2181, 2186, 3507, 3722, 4301, 4309, 4313, 4327a, 4327b, 4341, 4353, 4358) and three internal molds (MPU- 3722, 4317, 4362).

Locality and unit: Tiaraju, Rio Grande do Sul, Passa Dois Group, Teresina Formation, Paraná Basin.

Age: Permian, Guadalupian.

Description: Small, subtriangular, equivalved, equilateral, equant to moderately elongated shell (Table 1). One posterior umbonal carinae is present, extending from the umbonal region to the postero-ventral angle. Parallel to the umbonal carinae, a second carina faintly marked can be observed. Umbones rounded, beaks prosogyrous; well-defined and long escutcheon and lunule, with escutcheon extending entirely through the posterior dorsal margin of the shell. Posterior dorsal margin straight to slightly

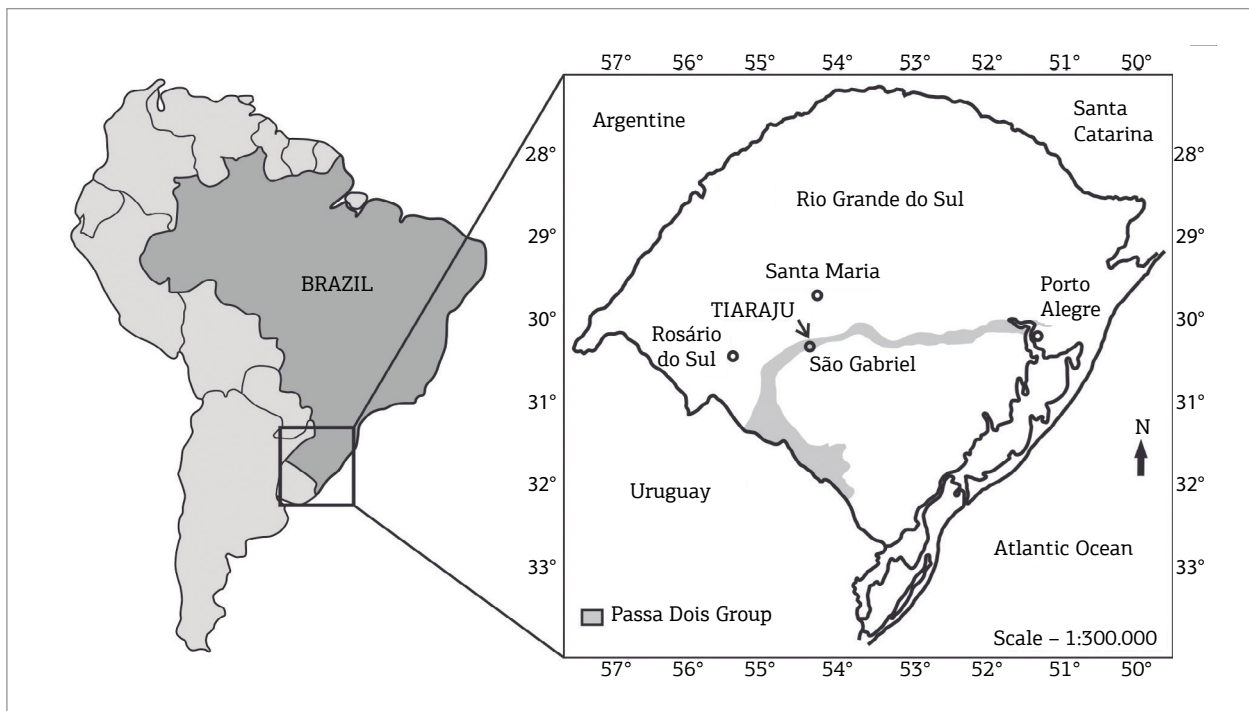


Figure 3. Location maps showing the outcrop belt of the Passa Dois Group, and the Tiaraju fossil site, São Gabriel District, State of Rio Grande do Sul, southern Brazil (based on Klein 1997).

concave; posterior extremity truncated, defining a short and straight respiratory margin; ventral margin rounded; slightly convex anterior dorsal margin. External surface of the shell covered by commarginal growth lines and largely spaced narrow rugae. Hinge plate of the left valve with thick posterior and anterior lateral margins, both ending below umbones as a slightly elevated bump separated by a

well-defined and deep triangular socket located immediately below beak. Muscles scars and hinge features of right valve were not observed.

Discussion: The material here described as *Terraia falconeri* was first interpreted by Cunha (1972), as *Pinzonella tiarajuensis* (*nomen nudum*) (Klein 1997). The shells are externally similar to that of *Pinzonella illusa*, as illustrated

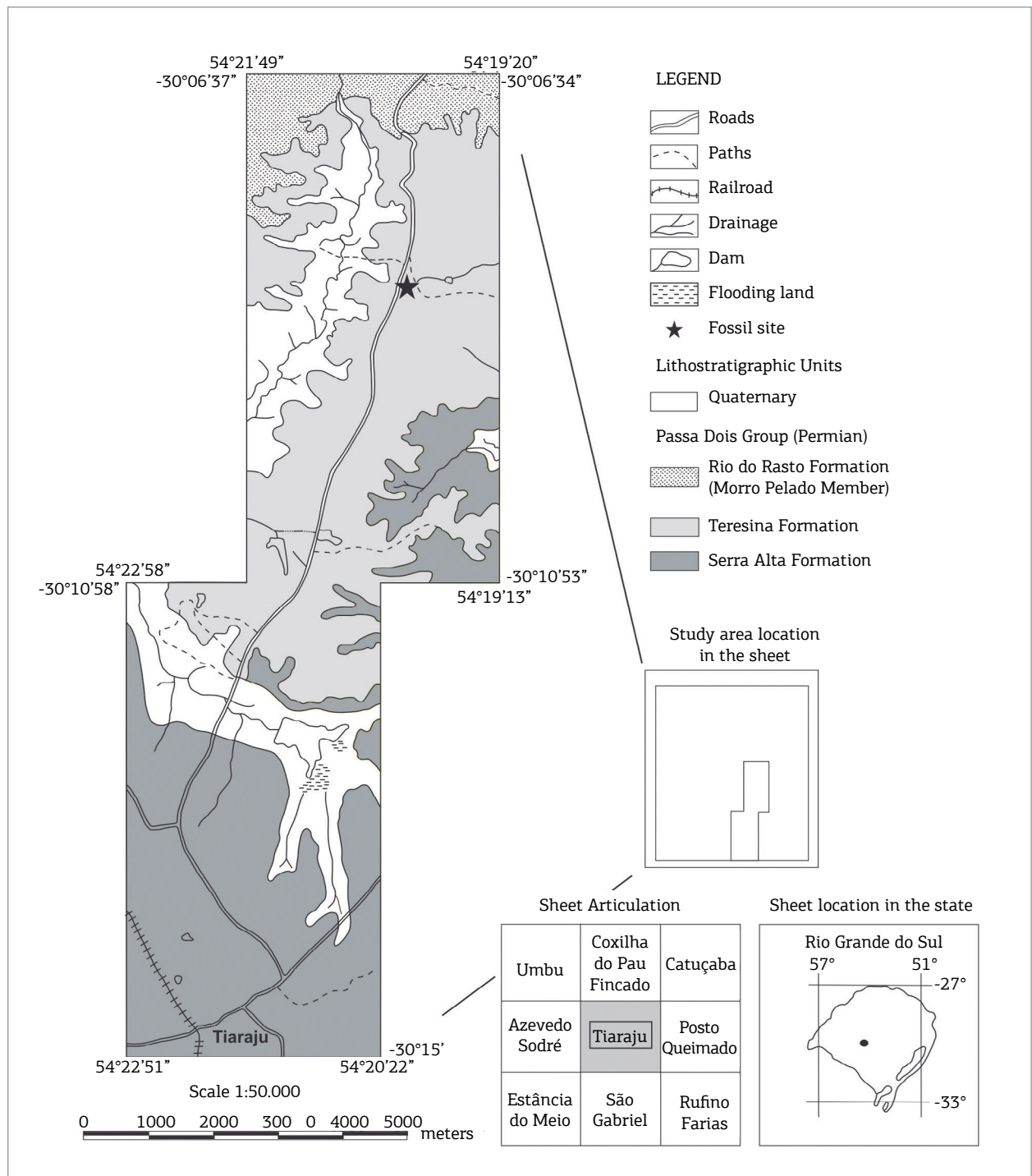


Figure 4. Geological map of the Tiaraju region, São Gabriel District, southern Brazil. The fossil site is highlighted (modified from Klein 1997).

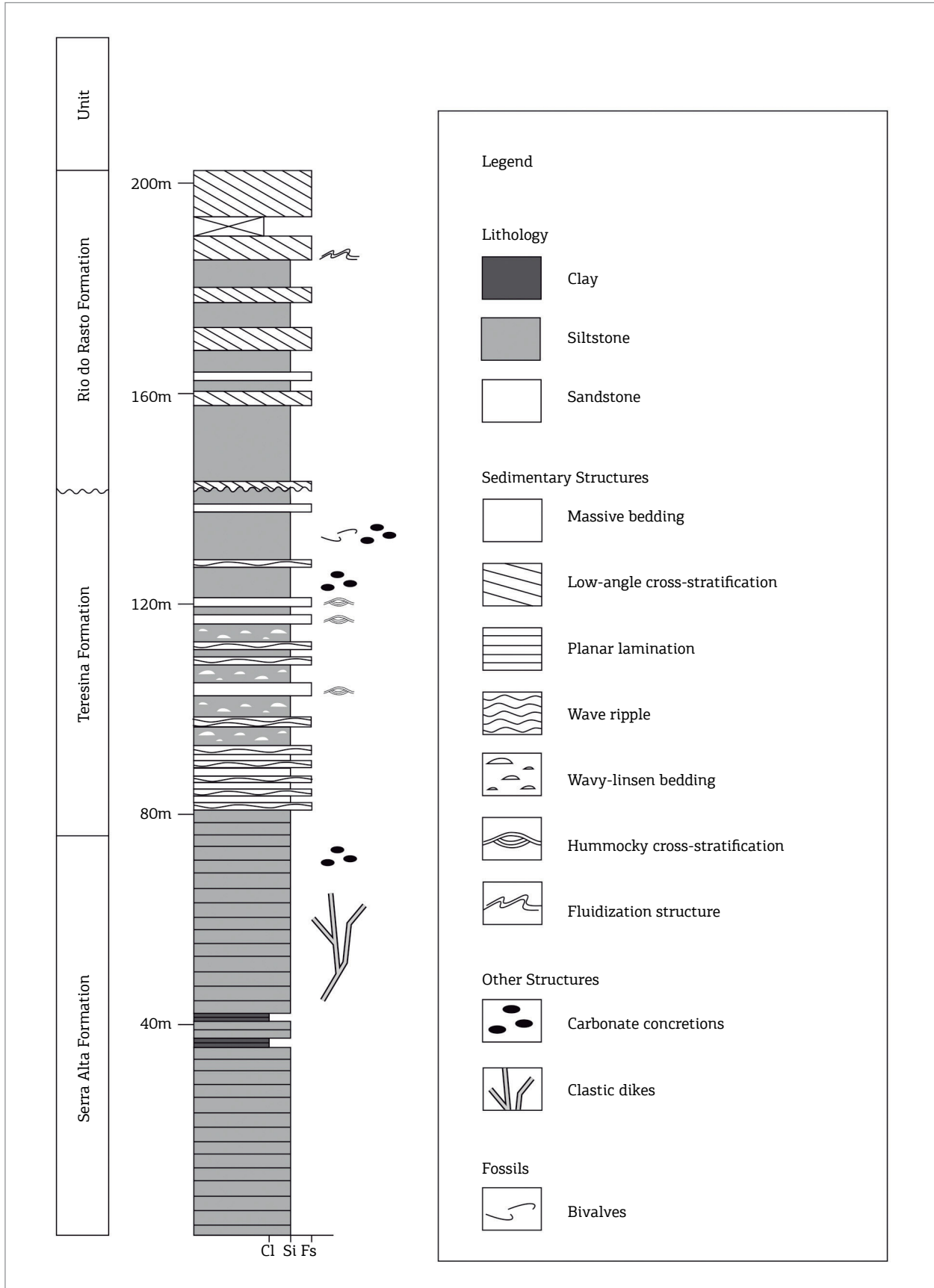


Figure 5. Composite stratigraphic section of the Passa Dois Group, measured at the Tiaraju region. The stratigraphic position of the bivalve assemblage is shown (modified from Klein 1997).

by Runnegar & Newell (1971, Figs. 19B, H, J). Indeed, both shells share a triangular shape, a slightly marked umbonal carinae, and have their external surface ornamented by irregular spaced growth lines. However, in the Tiaraju specimens, the hinge plate of the left valve is not sturdy developed (*i.e.*, thick) and the cardinal and lateral teeth are virtually absent. Additionally, a posterior socket present in the hinge of *Pinzonella illusa* shells is also absent. Hence, these characters and the presence of a well-defined lunule in the Tiaraju specimens (both *P. illusa* and *P. neotropica* show a poorly defined lunule) indicate that these are not related to *Pinzonella*. On the other hand, it is noteworthy that the hinge plate of the left valve of the examined specimens close resembles that of *Terraia falconeri*, as described in Beurlen (1953). Both are characterized by a thickening of the posterior and anterior lateral margins, that ends below umbones, as a slightly elevated bump separated by a well-defined and deep triangular socket located immediately below beak. Also, the external characters of the shells of Tiaraju specimens close resemble *Terraia falconeri* (Beurlen 1953), including the: general valve morphology; prosogyral beaks and presence of a second faintly marked carinae. Based on these characters the specimens are referred to *Terraia falconeri*.

Table 1. Measurements of *Terraia falconeri*.

Specimen	Valve	Length (mm)	Height (mm)	Elongation index
MPU-2181	Left	5.5	5.0	1.10
MPU-2186	Left	-----	4.7	-----
MPU-3507	Left	-----	6.3	-----
MPU-3722a	Right	7.3	7.0	1.04
MPU-3722b	Left	-----	-----	-----
MPU-4301	Right	5.5	6.1	0.90
MPU-4309	Right	-----	5.8	-----
MPU-4313	Left	7.5	6.3	1.10
MPU-4317	Left	4.0	4.8	0.80
MPU-4327a	Left	-----	4.7	-----
MPU-4327b	Left	-----	5.5	-----
MPU-4341	Right	7.1	6.6	1.07
MPU-4353	Right	7.0	6.4	1.09
MPU-4358	Right	7.2	6.5	1.10
MPU-4362	Left	5.7	5.2	1.09

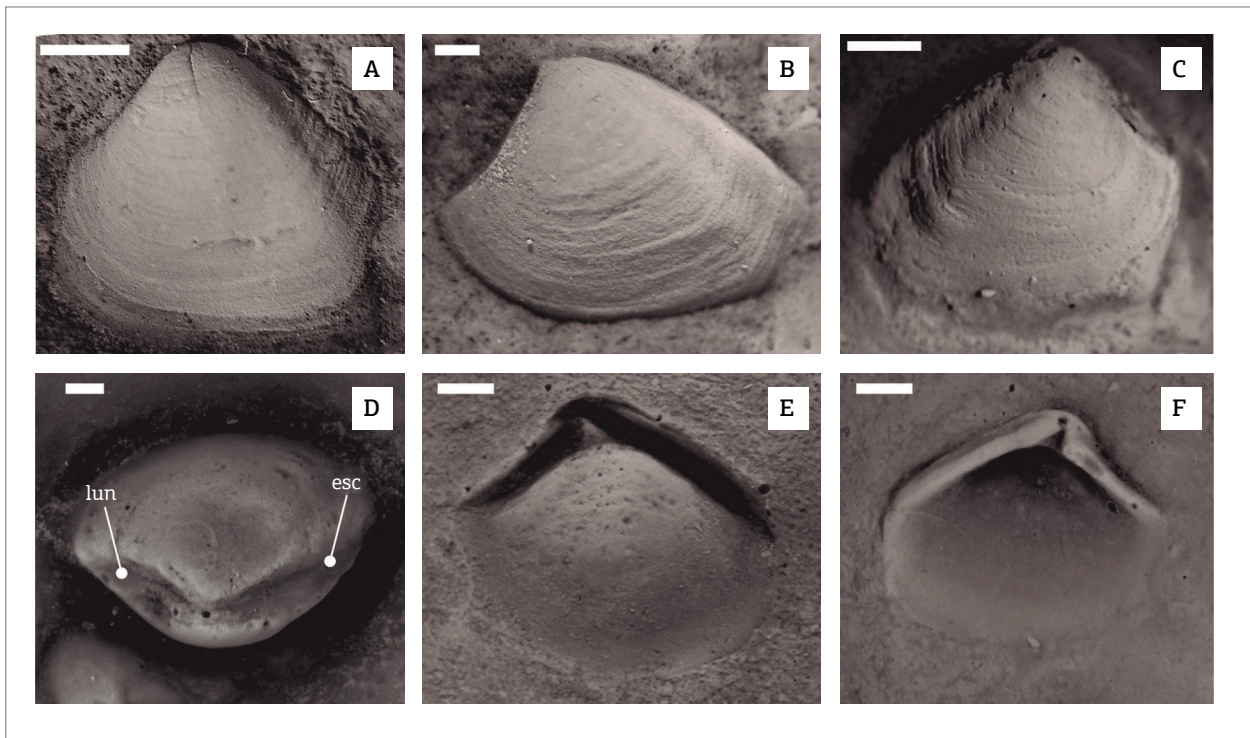


Figure 6. *Terraia falconeri* (Cox, 1934), Tiaraju, Rio Grande do Sul state, Passa Dois Group, Paraná Basin, Brazil. A-B, External view of left valve (MPU 4327a; MPU 4313). C, Internal mold of right valve, MPU 4358; D, Plaster cast of articulated valves, DZP-4337; E, Plaster cast showing the hinge features of left valve, MPU 4362d; F, Cast showing the hinge features of left valve, MPU, 4362b. Explanation: lun= lunule; esc= escutcheon. Scale bars=1mm.

Terraia altissima (Holdhaus 1918) (Figs. 7A-C)

Type species: *Solenomorpha altissima* (Holdhaus 1918).

Examined material: Two internal molds (DZP-4327, 4330).

Locality and unit: Tiaraju, Rio Grande do Sul, Passa Dois Group, Teresina Formation, Paraná Basin.

Age: Permian, Guadalupian.

Description: Small, equivalved, inequilateral, moderately elongated to elongated shell (Table 2). Two well-defined posterior umbonal carinae extend from umbonal region to the postero-dorsal and postero-ventral angles; the ventral carinae bears around seven visible protuberances (knobs). The knobs are faintly visible in the internal mold. The ventral carinae is more pronounced than the dorsal one, which borders the escutcheon ventrally. Umbones low. Anterior dorsal margin slightly convex; anterior margin rounded; posterior margin straight, angular where intercepted by the two posterior carinae. Hinge of right valve partially preserved, showing a well-defined triangular cardinal tooth; anterior and posterior dorsal margins of right valve bordered ventrally by an elongated lateral tooth; immediately above, an elongated socket is present, possibly for receiving the anterior and posterior dorsal edges of left valve. External ornament of faint co-marginal spaced growth lines, which may become distinctly lamellose behind umbonal carinae. Ligament and muscle scars were not observed.

Discussion: The genus *Terraia* has been described from several Permian rocks in Brazil and Uruguay, and more recently in Namibia (David *et al.* 2010; David 2014). The specimens from the TB assemblage bear most of the characters (*i.e.*, absence of lunule, triangular cardinal tooth in right valve, an obscure lateral teeth and socket) present in *Terraia altissima*. In addition, the specimens here described also show most of the diagnostic features listed by Runnegar & Newell (1971), including the: double umbonal carinae; presence of escutcheon; and absence of lunule. Yet, *Terraia* cf. *T. altissima* from the Gai-As Formation, Namibia (David *et al.* 2010), is very similar to the shells described here, regarding its external morphology, including the presence of two well-defined posterior umbonal carinae, an external lamellose commarginal shell ornamentation, and low umbones.

Infraclass HETEROCONCHIA (Hertwig 1895)

Megaorder SOLENATA (Dall 1889)

Order HIATELLIDA (Carter *et al.* 2011)

Table 2. Measurements of *Terraia altissima*.

Specimen	Valve	Length (mm)	Height (mm)	Elongation index
DZP-4327	Left	19.0	12.3	1.54
DZP-4330	Right	25.4	18.5	1.37

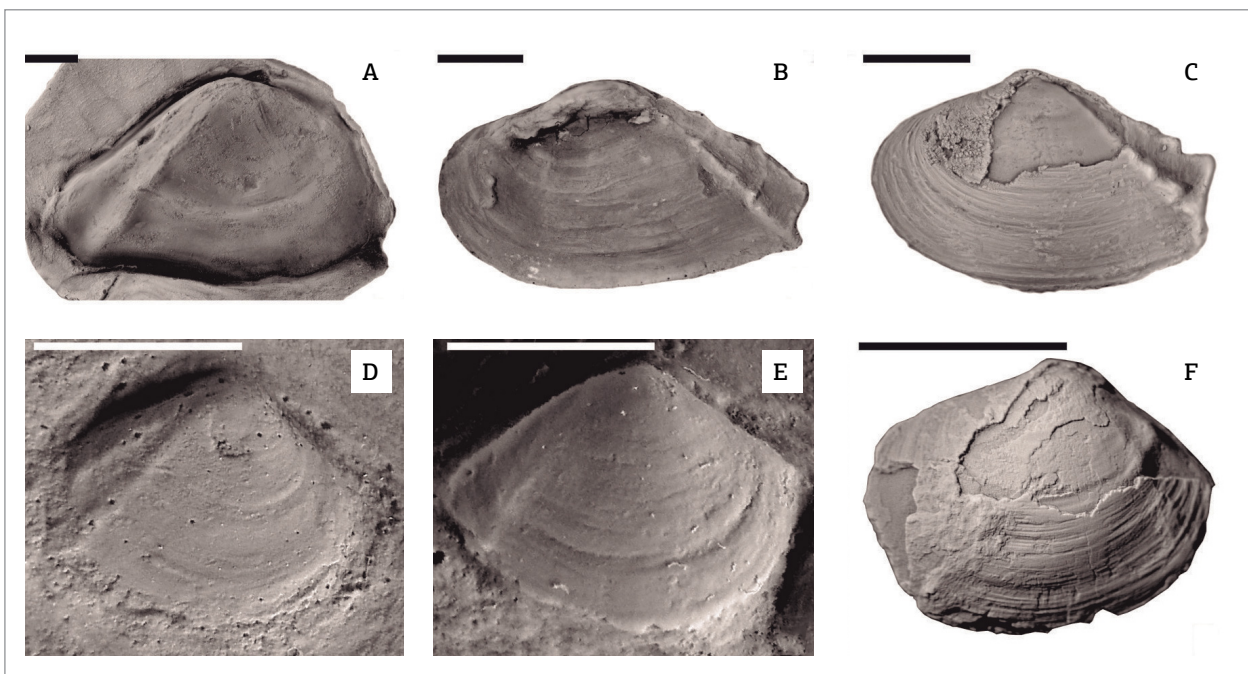


Figure 7. *Terraia altissima* (Holdhaus, 1918) and *Cowperesia emerita* (Reed, 1929), Tiaraju, Rio Grande do Sul state, Passa Dois Group, Paraná Basin, Brazil. A-C, *Terraia altissima*. A, Plaster cast of right valve, showing the triangular cardinal tooth, DZP-4330; B, Plaster cast of left valve, DZP-4327. C, *Terraia* sp. cf. *Terraia altissima* (Holdhaus, 1918), Gai-As Formation, Huab area, Permian, Namibia. External view of silicified left valve, DZP-18711. D-F, *Cowperesia emerita*. D, External view of right valve, MPU 4363. E, Plaster cast of right valve, DZP-4323. F, *Cowperesia emerita* (Reed, 1929), Gai-As Formation, Huab area, Permian, Namibia. Incomplete internal mold of left valve with silicified shell remains, DZP-18700. Scale bars=5mm.

Superfamily EDMONDIOIDEA (King 1850)
 Family PACHYDOMIDAE (Fischer 1887)
 Subfamily PACHYDOMINAE (Fischer 1887)
 Tribe PLESIOCYPRINELLINI (Simões et al. 1997)
Cowperesia emerita (Reed 1929) (Figs. 7D and 7E)

Type species: *Pseudocorbula emerita* (Reed 1929).

Examined material: Four shells (MPU- 4340, 4363, 4595, 5704) and two internal molds (MPU- 4316, 4452; DZP-4323).

Locality and unit: Tiaraju, Rio Grande do Sul, Passa Dois Group, Teresina Formation, Paraná Basin.

Age: Permian, Guadalupian.

Description: Small, subtriangular, equivalved, equilateral, equant to moderately elongated shell (Table 3). Two well defined and slightly curved posterior umbonal carinae are present, one extending from the umbonal region to the postero-ventral angle and the other close to the postero-dorsal margin. Very weak projections are evident where co-marginal growth lines cross the umbonal carinae. Anterior dorsal margin straight; anterior margin rounded; posterior margin straight. External ornament of fine, commarginal growth lines, superimposed by widely spaced, broad co-marginal rugae, also apparent on internal molds. Hinge features and musculature unknown.

Discussion: The shells from Tiaraju close resemble those described by David et al. (2010) as *Cowperesia emerita* from the Gai-As Formation, Huab area, Namibia. Indeed, the external shell characters are very similar, including the: ornamentation; presence of double umbonal carinae; and general shell shape. Yet, it close resembles the specimens of *Cowperesia emerita* found in the Serrinha Member, Rio do Rasto Formation as well (Simões et al. 2015, p. 21, Fig. 5).

Holdhausiella (Mendes 1952)

Type species: *Holdhausiella elongata* (Holdhaus 1918).

Discussion: Runnegar & Newel (1971) considered *Holdhausiella* as junior synonyms of *Jacquesia* Mendes. After this, four species were recognized as belonging

to the genus *Jacquesia*: *Jacquesia brasiliensis* Reed 1929, *Jacquesia arcuata* (= *Favalia arcuata* Mendes 1962), *Jacquesia elongata* [= *Holdhausiella elongata* (Holdhaus 1918)] and *Jacquesia almeidai* (= *Holdhausiella almeidai* Mendes 1952). However, Mello (1999) carried out a cladistic analysis and showed that the synonym proposed by Runnegar & Newell (1971) is not valid. Since they are, indeed, very distinct from the type of material of *Jacquesia*, here we follow Mello's interpretation.

Holdhausiella elongata (Holdhaus 1918) (Figs. 8A and 8B)

Type species: *Sanguinolites elongates* (Holdhaus 1918).

Examined material: Seven internal molds (DZP-4307c, 4324, 4345, 4366, 4335a, b, 4347).

Locality and unit: Tiaraju, Rio Grande do Sul, Passa Dois Group, Teresina Formation, Paraná Basin.

Age: Permian, Guadalupian.

Description: Small to medium-sized, equivalved, inequilateral, elongated to very elongated shell (Table 4), posteriorly expanded, with shallow lateral sulcus and slightly arched carinate umbonal ridge. Umbones low, beaks prosogyrates; posterior umbonal slope slightly concave as seen in internal molds; anterior dorsal margin short and slightly concave; anterior extremity rounded; ventral margin nearly straight; posterior dorsal margin straight. External surface with faint commarginal irregularly spaced rugae. Hinge features and muscle scars not observed.

Table 3. Measurements of *Cowperesia emerita*.

Specimen	Valve	Length (mm)	Height (mm)	Elongation index
MPU-4316	Left	-----	5.1	-----
MPU-4340	Right	7.2	-----	-----
MPU-4363	Right	6.1	5.0	1.22
MPU-4452	-----	-----	-----	-----
MPU-4595	Left	5.5	4.7	1.17
MPU-5704	Right	4.7	-----	-----
DZP-4323	Right	5.4	4.4	1.22

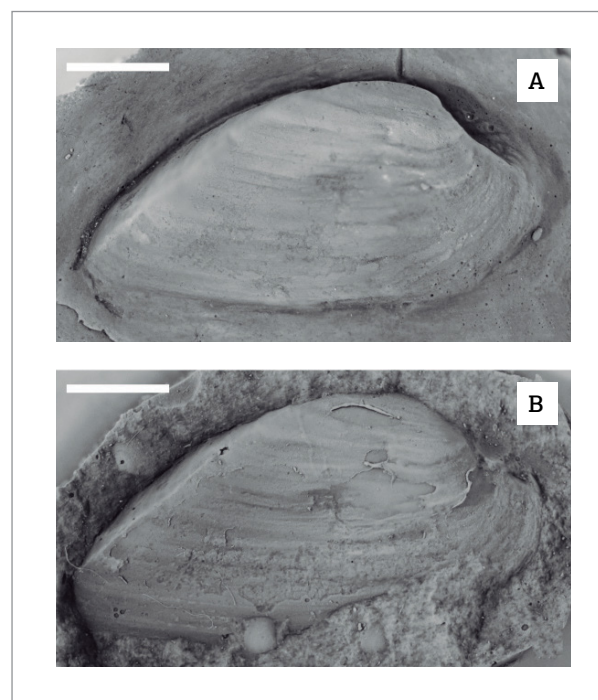


Figure 8. *Holdhausiella elongata* (Holdhaus, 1918), Tiaraju, Rio Grande do Sul state, Passa Dois Group, Paraná Basin, Brazil. A, Latex cast of right valve, DZP-4335a; B, Plaster cast of right valve, DZP-4335b. Scale bars=5mm.

Discussion: The specimen from Tiaraju is very similar in shell shape and external characters to *Holdhausiella elongata*, described and illustrated in Runnegar & Newell (1971, Figs. 16A-J), including the: posterior expanded shell; umbonal carinae; rounded, anterior portion of shell margin; and external surface ornamented by faint commarginal, irregularly spaced, rugae.

RESULTS AND DISCUSSION

Assemblage composition and taphonomy

The Tiaraju assemblage is poorly diversified, both regarding the taxonomic composition and ecological guilds (Tables 5 and 6). However, caution must be taken due to the small sample size (Tables 5 and 6). The identified bivalves are here

Table 4. Measurements of *Holdhausiella elongata*.

Specimen	Valve	Length (mm)	Height (mm)	Elongation index
DZP-4307c	Left	19.8	11.2	1.76
DZP-4324	Left	10.0	7.20	1.38
DZP-4335a	Right	19.7	9.7	2.03
DZP-4335b	Right	19.4	9.5	2.04
DZP-4345	Left	18.7	10.0	1.87
DZP-4347	Right	-----	6.1	----

Table 5. Taxonomic composition and paleoecology of the Tiaraju bivalve assemblage, southern Brazil.

Superfamily	Species	Guilds	n.
Crassatelloidea	<i>Terraia falconeri</i>	SIFMUSF	15
	<i>Terraia altissima</i>	SIFMUSF	2
Edmonдиоidea	<i>Cowperesia emerita</i>	IIFMUSF	7
	<i>Holdhausiella elongata</i>	SIFMUSF	7
	Totals		31

SIFMUSF: shallow infaunal, facultatively motile, unattached, suspension feeders; IIFMUSF: intermediate infaunal, facultatively motile, unattached, suspension feeders.

Table 6. Guild composition of the Tiaraju bivalve assemblage, southern Brazil.

Assemblage	Bivalve guilds	n.
Tiaraju	SIFMUSF	24
	IIFMUSF	7
	Totals	31

SIFMUSF: shallow infaunal, facultatively motile, unattached, suspension feeders; IIFMUSF: intermediate infaunal, facultatively motile, unattached, suspension feeders.

referred to the following species: *Terraia falconeri*; *Cowperesia emerita*; *Holdhausiella elongata*, and *Terraia altissima* (Table 5). *Holdhausiella elongata* is restricted to the Brazilian portion of the Paraná Basin, but *Cowperesia emerita*, *Terraia altissima*, and *Terraia falconeri* are also recorded in other coeval basins of the Central Gondwanic Realm (González 1989). Among the identifiable species, *Terraia falconeri* is the most abundant one, and is followed by *Cowperesia emerita* and *Holdhausiella elongata* (Table 5). Therefore, the Terrainae bivalves are the commonest, lacking the typical members of the preceding assemblages of the Teresina/Corumbataí formations (*i.e.*, Pinzonellinae and Pachydomidae), particularly *Pinzonella* and *Plesiocyprinella*.

According to Klein (1997) and Klein & Simões (1998), which detailed studied the taphonomy of the Tiaraju assemblage, the good preservational quality of the shells and the frequent occurrence of articulated ones indicate that the shells were not exposed to long periods in the sediment-water interface. However, some rare shells were submitted to distinct fossilization processes and were mixed with other non-coeval bioclasts (Klein & Simões 1998). Indeed, the shell infilling in some articulated shells is distinct (sparitic) of the sedimentary matrix (micritic), implying in some degree of time-averaging and shell mixing (Klein & Simões 1998). In summary, the Tiaraju assemblage is a time-averaged, parautochthonous-allochthonous assemblage (Kidwell *et al.* 1986).

Affinities and age

Faunal composition of Tiaraju assemblage, as described above, indicates a mixture of bivalve species that are both found in the Teresina Formation and the overlaying Rio do Rasto Formation. Indeed, *Cowperesia emerita* and *Terraia altissima* are two species that are commonly found in bivalve assemblages recorded in the basal part of the Rio do Rasto Formation (Serrinha Member) (Simões *et al.* 2015), whereas *Terraia falconeri* is only known in assemblages of the upper part of Teresina Formation (*Pinzonella neotropica* assemblage) from Brazil (Beurlen 1953) and Uruguay (Cox 1934). However, the absence of pinzonellids and the profuse occurrence of terrais is a strong indication of faunal affinities with those assemblages of the basal part of the Rio do Rasto Formation. *Cowperesia emerita* and *Terraia altissima* are also recorded in the bivalve assemblages of the Gai-As Formation, Huab area, Namibia (David *et al.* 2010), where they are also associated to *Huabiella compressa* and *Terraia* sp. cf. *T. curvata*. Correlation of the Gai-As bivalve assemblage is well constrained with those of the basal part of the Serrinha Member (Rio do Rasto Formation) (David *et al.* 2010). Hence, despite the absence of deposits the Serrinha Member, basal part of Rio do Rasto Formation, in the geological map of the

Tiaraju region, the bivalve fauna suggests a correlation to those of the basal part of the Serrinha interval of the Passa Dois Group. Yet, in the Permian deposits of the Gai-As Formation, where *Cowperesia emerita* and *Terraia altissima* are common, radiometric dating of zircon grains from tuff beds found in the bivalve-bearing succession provided U/Pb ages of 265 ± 2.5 Ma (Wanke 2000; Holzförster 2002). Therefore, a Wordian-Capitanian age is indicated to the bivalve fauna (David *et al.* 2010). In other words, the TB assemblage deposits could represent an age no younger than the (Guadalupian) Epoch.

Paleobiogeography

The current knowledge about the paleobiogeographic distribution of the Passa Dois Group bivalve species involves occurrences in Brazil (Reed 1929; Mendes 1954; Mezzalira 1957; Maranhão 1986; Rohn 1994), Uruguay (Cox 1934; Morton & Herbst 1990), Paraguay (Reed 1935), Namibia (David *et al.* 2010) and South Africa (Cooper & Kensley 1984). In Brazil, the related occurrences are distributed in the states of São Paulo, Paraná, Santa Catarina and Mato Grosso. The Tiaraju bivalve fauna represents the only known Permian assemblage documented in the Passa Dois Group succession of the State of Rio Grande Sul, adding evidence that during certain times in the geological history of Paraná Basin the bivalve species were not geographically restricted to certain areas (also Simões *et al.* 2010).

The mechanisms involved in the bivalve distribution during the deposition of the Passa Dois Group were discussed by Simões *et al.* (2010). These authors argued that a possible association could exist between bivalve radiation and water level fluctuations, since the widest distribution of some species are usually associated to deposits recording flooding episodes (“transgressions”). On the contrary, faunal isolation correlates with intervals of water level falls (“regressions”). Basin level fluctuations have been recognized with benthic faunal diversity fluctuations and variations in spatial distribution through the Phanerozoic (Newell 1967; Simberloff 1974; Flessa & Sepkoski 1978; Bayer & McGhee 1985; Dockery 1986; Jablonski & Flessa 1986; Hallam 1987, 1992; Brett & Baird 1995; Brett 1998).

In the stratigraphic succession of the Passa Dois Group in the Tiaraju region, the bivalve-rich interval, which is associated to laminated mudstones, records the last “transgressive” event of this unit, which may favor faunal dispersion. In this context, the TB assemblage is a regional example of the poorly diversified benthic assemblages, which populated distinct parts of the Paraná landlocked sea, during the Guadalupian.

CONCLUSIONS

Here we added new and key evidences regarding the nature and faunal composition of the endemic molluscan fauna that thrived in a large, landlocked sea during the Guadalupian. The Tiaraju bivalve assemblage includes the following species *Terraia falconeri*, *Cowperesia emerita*, *Holdhausiella elongata*, and *Terraia altissima*, which were preserved in transgressive deposits previously attributed to the upper part of Teresina Formation. The TB assemblage is poorly diversified, both regarding the taxonomic composition and ecological guilds, suggesting that the bivalves flourished under conditions of high environmental stress. The assemblage includes a mixture of elements that were previously recorded in Teresina Formation, as well as in the basal part of Rio do Rasto Formation, Serrinha Member, showing the transitional character of the faunule. The identified bivalves are also key elements to bio-correlation, constraining the TB assemblage with those of the Gai-As Formation, Huab area, Namibia (David *et al.* 2010), indicating an age no younger than 265 ± 2.5 Ma (Wordian-Capitanian).

CLOSING THOUGHTS

Data presented above indicate that the Tiaraju bivalve fauna is a transitional assemblage between those at the topmost part of the Teresina Formation and at the lowermost part of the Rio do Rasto Formation. Therefore, the absence of lithotypes of the Serrinha Member, Rio do Rasto Formation, in the available regional geological maps is puzzling. Given the transitional character of the fauna, future regional geological studies of the Passa Dois Group deposits in the Tiaraju area, São Gabriel District, State of Rio Grande do Sul, should be viewed under this condition. Hence, the currently accepted geological maps and the boundary between Teresina and Rio do Rasto formations in this area require reevaluation on the light of the paleontological information.

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