

# The morphology and systematics of the clam shrimp *Platystheria* gen. nov. *abaetensis* (Cardoso) (Crustacea, Spinicaudata) from the Lower Cretaceous of the Sanfranciscana Basin, southeast Brazil

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## ABSTRACT

New specimens of the clam shrimp '*Pseudestheria*' *abaetensis* Cardoso, 1971 (Spinicaudata) are described. The material was collected from the Quiricó Formation (Lower Cretaceous of the Sanfranciscana Basin), at the same locality as the type series of the species. The carapaces are very large, oval and elongated, with anteriorly located and slightly projected umbo, straight dorsal margin, with flattened growth bands and 15–20 serrated growth lines. Details of the microscopic structure of the carapace were analysed under scanning electron microscope for the first time, disclosing a unique reticular pattern of ornamentation. This species is similar to some Early Cretaceous taxa from South America, Africa and China. Yet, the peculiarities in the shape and ornamentation of the carapace support its reassignment to a new genus (*Platystheria* gen. nov.), within the Superfamily Eosestherioidea. In addition, an energy-dispersive X-ray spectroscopy analysis of the multiple stacked growth bands revealed that the valves are enriched in calcium and phosphorus, similar to those of modern spinicaudatans. Minor amounts of silicon, iron and aluminium suggest that the carapaces were preserved partly through the input of ions from the environment during the diagenesis.

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## 1. Introduction

Spinicaudatans are widespread components of both recent and ancient ephemeral continental aquatic environments around the world (Mattox, 1959; Williams, 1987; Chen, 2008). Species of that clade have been recovered in strata dating back to Devonian, and they were diverse during the Mesozoic (Chen, 2008). In the Cretaceous of the Sanfranciscana Basin, spinicaudatans have been known since early 1970s, when Cardoso (1971) described *Palaeolimnadiopsis freybergi*, '*Pseudestheria*' *abaetensis* and reported the presence of '*Pteriograpt*' cf. *reali* and '*Pseudograpt*' cf. *barbosai*

from the lacustrine strata of the Quiricó Formation, cropping out in São Gonçalo do Abaeté and Carmo do Paranaíba, northwest Minas Gerais state (see also Tasch, 1987). Some authors have reassigned '*Ps.*' *abaetensis* to *Cyzicus* (*Lioestheria*) *abaetensis* or *C.* (*Euestheria*) *abaetensis* (Tasch, 1987; Carvalho, 1993). Additional supposed records of that species include specimens from the Lower Cretaceous of the Araripe, Parnaíba, and Uiraúna basins (Carvalho, 2014).

According to Cardoso (1971), the type specimens of both *Palaeolimnadiopsis freybergi* and '*Pseudestheria*' *abaetensis* were housed in the Museu de História Natural e Jardim Botânico of the Universidade Federal de Minas Gerais (MHNJB). However, the whereabouts of these specimens are presently unknown.

Following recent fieldwork to the localities explored by Cardoso (1971), new specimens of '*Pseudestheria*' *abaetensis* were recovered from its type locality and are described herein. Ornamentation details of the carapace are evidenced for the first time with

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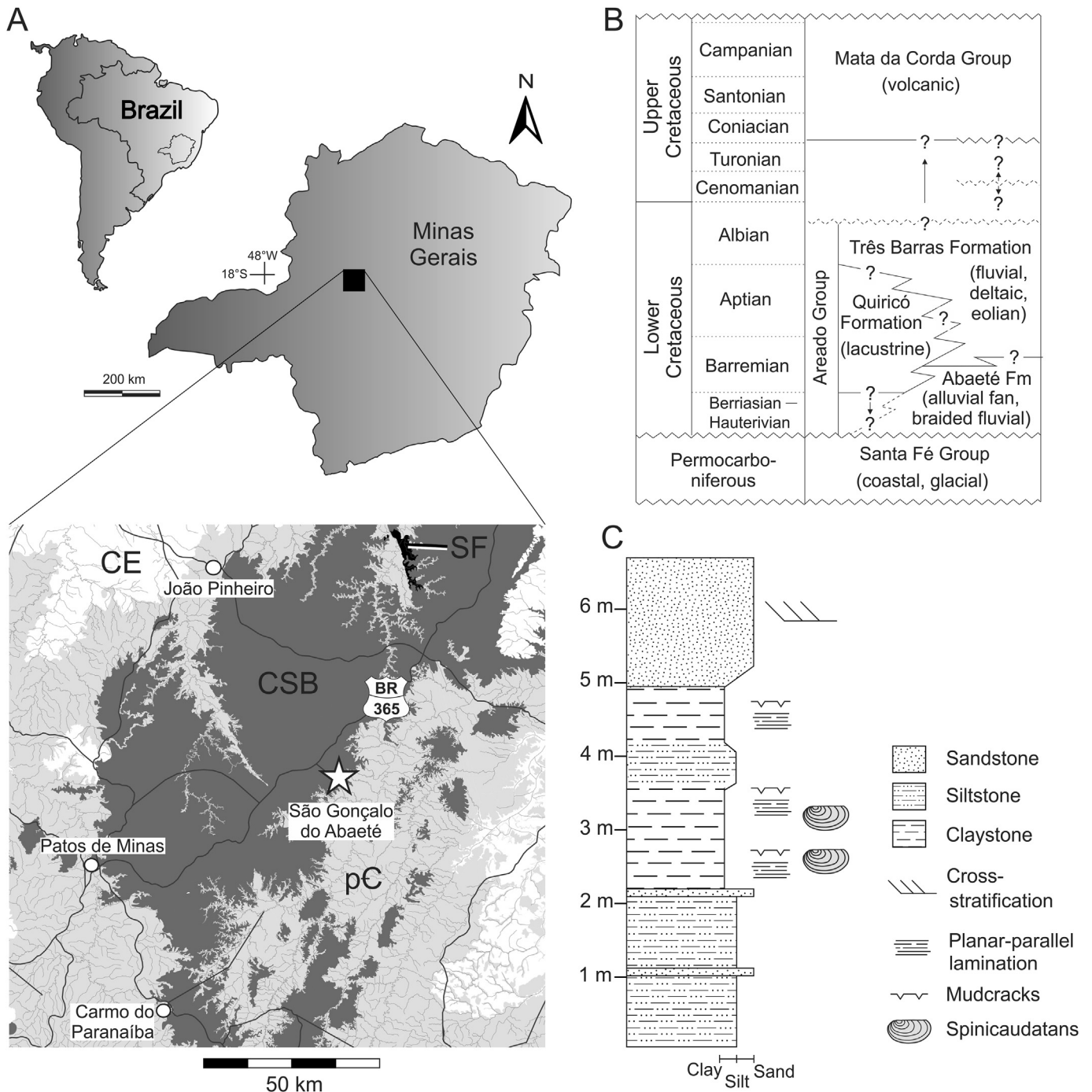
E-mail addresses: [bittencourt.paleo@gmail.com](mailto:bittencourt.paleo@gmail.com) (J.S. Bittencourt), [rohn@rc.unesp.br](mailto:rohn@rc.unesp.br) (R. Rohn), [ofgallego@live.com.ar](mailto:ofgallego@live.com.ar) (O.F. Gallego), [monfdm@gmail.com](mailto:monfdm@gmail.com) (M.D. Monferran), [auhlein@gmail.com](mailto:auhlein@gmail.com) (A. Uhlein).

scanning electron microscope. Data gathered from this new material allowed the reassignment of that species to a new genus. In addition to the taxonomic assessment, we performed a semi-quantitative energy-dispersive X-ray spectroscopy analysis for an exploratory study of the elemental composition of the spinicaudatan carapaces.

## 2. Geological setting

The Sanfranciscana Basin (sensu Campos and Dardenne, 1997) encloses c. 150,000 km<sup>2</sup> of sedimentary and volcanic rocks

spanning over the states of Minas Gerais, Goiás, Tocantins, Bahia, Piauí and Maranhão (see also Sgarbi et al., 2001). In the region studied for this paper, the strata of the Sanfranciscana Basin overlie discordantly the Precambrian basement (Fig. 1A; Campos and Dardenne, 1997; Sgarbi et al., 2001) and comprises the glacial levels of the Santa Fé Group (Fig. 1B; Carboniferous–Permian), the Early–Late Cretaceous fluvial, lacustrine and eolian deposits of the Areado Group, and the Late Cretaceous volcanic Mata da Corda Group (Ladeira and Brito, 1968; Grossi Sad et al., 1971; Campos and Dardenne, 1997; Sgarbi et al., 2001).



**Fig. 1.** Location and stratigraphic section of the *Platystheria abaetensis* comb. nov. site. A, Geological map of the area (CPRM/CODEMIG, 2014), showing the location of the outcrop in São Gonçalo do Abaeté (star) and neighbour municipalities with relevant fossil occurrences (see text). Abbreviations: CE, Cenozoic cover; CSB, Cretaceous units of the Sanfranciscana Basin (basically Areado and Mata da Corda groups); SF, Santa Fé Group; pC, Precambrian basement. B, Chrono- and lithostratigraphy of the southern Sanfranciscana Basin (after Campos and Dardenne, 1997; Sgarbi et al., 2001; Maraschin et al., 2016). C, Stratigraphic section of the outcrop showing the vertical position of the spinicaudatans described herein.

The specimens described herein were collected in São Gonçalo do Abaeté, at the road leading to the route BR-365 (Fig. 1A). The location and lithology of the outcrop is compatible with the type locality of '*Pseudestheria*' *abaetensis* (Cardoso, 1971, p. 21). The fossils include abundant carapaces of '*Ps.*' *abaetensis* and '*Pterio-grapta*' cf. *reali*, but rare *Palaeolimnadiopsis freybergi*. These occur in the same level of reddish, carbonate-cemented and finely laminated silty claystone, locally interbedded with clayey siltstone (Fig. 1C). The claystone bears millimeter-sized fractures obliquely oriented to the layer, and mud cracks filled with poorly sorted sandstone. The clayey and silty levels are overlain by 1.5 m thick, fine, reddish, silty sandstone with cross-stratification. The lithology is typical of the Quiricó Formation (Fig. 1B), which corresponds to the middle interval of the Areado Group (Campos and Dardenne, 1997). This formation yields most of the fossil record of the Sanfranciscana Basin (Sgarbi et al., 2001; Bittencourt et al., 2015), including palynomorphs, gymnosperms and angiosperms, insects, ostracods, spinicaudatans, elasmobranchs, actinopterygians, coelacanthiforms and dinosaurs (Scorza and Silva Santos, 1955; Cardoso, 1971; Santos, 1971; Lima, 1979; Martins-Neto, 1996; Duarte, 1997; do Carmo et al., 2004; Carvalho and Maisey, 2008; Zaher et al., 2011; Bittencourt et al., 2017; de Carvalho and Santucci, 2018).

Additional spinicaudatans in the Quiricó Formation occur within the ostracod-rich pelitic beds at Carmo do Paranaíba (Cardoso, 1971; do Carmo et al., 2004) and João Pinheiro (Delicio et al., 1998; Carvalho and Maisey, 2008) (Fig. 1A). Ostracods and palynomorphs recorded in the Quiricó Formation support a Barremian-Aptian age (Arai et al., 1995; Campos and Dardenne, 1997; do Carmo et al., 2004), but lower levels of this formation can be older than Barremian (Leite et al., 2016). The fossiliferous sections of the Quiricó Formation are reconstructed as a lacustrine to fluvio-lacustrine and playa lake paleoenvironment by most authors (Moraes et al., 1986; Sgarbi et al., 1993; Campos and Dardenne, 1997; Sgarbi et al., 2001; Fragoso et al., 2011; Mescolotti et al., 2015).

### 3. Material and methods

Tens of carapaces compatible with the diagnosis of '*Pseudestheria*' *abaetensis* (Cardoso, 1971) were recovered in close association. The samples are housed in the Instituto de Geociências of the Universidade Federal de Minas Gerais (IGC-P), either as isolated specimens or as sets of specimens in reddish claystones. In the second case, each specimen is identified sequentially, e.g. IGC-P 0026/1, 0026/2.

Carapace morphometry followed Defretin-Le Franc (in Tasch, 1987, p. 35; Gallego and Covacevich, 1998), including the parameters L: valve length; H: valve height; Ch: hingeline length; Cr: distance from beak to anterior end of the valve; Av: distance from anterior end of the dorsal margin to the anterior end of the valve; Arr: distance from the posterior end of the dorsal margin to the posterior end of the valve; a: distance from maximum anterior bulge to dorsal margin; b: distance from maximum posterior bulge to dorsal margin; c: distance from maximum ventral bulge to the anterior end of the valve. The comparative parameters of size, shape and relative position of the umbo were based on the paper by Scholze and Schneider (2015).

Although the term 'conchostracan' is widespread in the scientific literature, we use the updated Spinicaudata, which includes most representatives of the traditional 'Conchostraca', except for laevicaudatans and cyclotheriids, in accordance with the most recent phylogenetic hypothesis (Negrea et al., 1999; Stenderup et al., 2006; Olesen, 2009; Gallego, 2010; Gallego et al., 2013; Olesen and Richter, 2013).

Details of the ornamentation of the carapaces were analysed under scanning electron microscopy (SEM) and semi-quantitative determinations of the elemental composition of the fossils and rock matrix were obtained by energy-dispersive X-ray spectrometry (EDSX). The equipment used for SEM and EDSX data was a scanning electron microscope JEOL JSM-6510 and a JEOL JSM-6360LV with an energy-dispersive spectrometer attached (Thermo Noran System 7). Samples were carbon-coated before examination. Elements with atomic numbers greater than five were detected with a resolution of 129.2 eV for the Mn-K $\alpha$  line. An acquisition live time of 60 s, nominal incident beam energy  $E_0 = 15$  keV, and a 15 mm working distance were used in all cases.

Point measurements by EDSX were used for monitoring trends in elemental distributions (major and minor components). The measurements were performed on different sample areas, including several points on the thin, whitish, remnant layers of the carapace, and the rock matrix. Locations of measurement points were chosen at preset intervals. However, in some cases, point positions were manually modified to an adjacent area in order to avoid fossil or rock pore spaces. This adjustment assures a sufficiently flat surface area for the electron beam. At each point the weight percent of the following elements was obtained: C, O, F, Na, Mg, Al, Si, P, S, K, Ca, Ti, and Fe. The estimated reproducibility was within 10%.

### 4. Systematic paleontology

Phylum Arthropoda von Siebold, 1848

Subphylum Crustacea Brünnich, 1772

Class Branchiopoda Latreille, 1817

Order Diplostraca Gerstaecker, 1866

Suborder Spinicaudata Linder, 1945

Superfamily Eosestherioidea Zhang and Chen (in Zhang et al., 1976)

Family ?Loxomegaglyptidae Novojilov, 1958

Genus *Platyestheria* gen. nov.

Type species: *Pseudestheria abaetensis* (Cardoso, 1971)

*Derivation of name.* From ancient Greek *plātýs*: broad, and *estheria*: traditional suffix to names of spinicaudatan genera.

*Diagnosis.* Spinicaudata with very large and elongated oval carapace, long almost straight dorsal margin and sharply curved anterior and posterior margins; anterior submarginal small umbo; growth lines with setae pits and pointed, sharply curved serrations; relatively wide growth bands displaying extensive reticular ornamentation, characterized by uniform small alveoli (pit-like subunits of the reticular ornamentation), sometimes grouped into larger, irregular polygons, or concentrically stretched, or size-graded from punctae (growth band perforations smaller than alveoli) to alveoli within some growth bands.

*Platyestheria abaetensis* (Cardoso, 1971) comb. nov.

(Figs. 2–5)

1971 *Pseudestheria abaetensis* Cardoso, p. 32–35, text-fig. 8, Pl. I, fig. 4.

1987 *Cyzicus* (*Lioestheria*) *abaetensis* (Cardoso, 1971) in Tasch, p. 104.

1993 *Cyzicus* (*Euestheria*) *abaetensis* (Cardoso, 1971) in Carvalho, p. 204–206.

1996 *Cyzicus* (?*Lioestheria*) *abaetensis* (Cardoso, 1971) Tasch, 1987, in Rohn and Cavalheiro, p. 163.

2006 *Pseudestheria abaetensis* Cardoso, in Gallego and Martins-Neto, p. 234.

*Type material.* Left valve (Museu de História Natural da UFMG nº 005) figured by Cardoso (1971, Plate 1, fig 4.) and designated as lectotype by Tasch (1987). Paralectotypes include five non-figured



specimens mentioned by Cardoso (1971, p. 33). The whereabouts of the type specimens are presently unknown.

**Referred material.** Complete carapaces, isolated left and right valves registered as IGC-P 0025–0042, 0054–0060. Some of these, as 0026, 0033, 0034, 0035, 0037, 0054, 0055, are claystone fragments with a varied number of individuals (from two to more than five). **Type locality.** Outcrop c. 1 km away from São Gonçalo do Abaeté downtown (18° 19' 57.66"S; 45° 50' 15.34"W), at the road (MG-60) leading to the route BR-365 (formerly MG-51) (Cardoso, 1971).

**Stratigraphic horizon and age.** Pelitic layers of the Quiricó Formation, Areado Group, Sanfranciscana Basin, dated as Early Cretaceous, Barremian–Aptian or older (Campos and Dardenne, 1997).

**Diagnosis emended.** Spinicaudata with very large and elongated oval carapace, length on the order of 1 cm, height–length ratio (H/L) of c. 0.55, height of the carapace is maximal at the anteroposterior midlength; long, almost straight dorsal margin and sharply curved anterior and posterior margins; anterior, submarginal small umbo; growth lines with setae pits and pointed, sharply curved serrations; relatively wide growth bands with flat surfaces, displaying extensive reticular ornamentation, usually characterized by uniform small alveoli, sometimes grouped into larger irregular polygons, or concentrically stretched, or size graded from punctae to alveoli within each growth band; alveoli of the reticular ornamentation with 4–7  $\mu\text{m}$  in diameter.

**Measurements (mm).** L: 6.6–9.5; H: 3.3–5.3; H/L: 0.50–0.56; Ch: 4.2–5.9 (based on the type series, Cardoso, 1971, p. 33). L: 8.0–11.5; H: 4.3–6.17; H/L: 0.53–0.57; Ch: 5.3–8.9; Av: 1.04–1.48; Arr: 0.74–1.8; Cr: 1.82–3.5; a: 1.49–2.59; b: 1.72–2.32; c: 3.15–5.88 (based on the seven most complete specimens of the referred material).

**Description.** The carapaces are very large (according to Scholze and Schneider, 2015), elongated, oval, with telliniform outline, the length is slightly less than twice the height, with anterior and faintly pronounced, submarginal umbo (Figs. 2 and 3A). The valves' maximal height is located on the anteroposterior midlength of the carapace. The dorsal margin is subhorizontal and elongated, comprising three quarters of the carapace length. The anterodorsal margin sharply curves ventrally, merging with the anterior margin, which is shorter and lower than the posterior one. The posterodorsal margin smoothly slopes ventrally. Both the anterior and posterior margins are very sharply curved, and their points of maximal projection are closer to the dorsal than to the ventral margin of the valve. Ventrally, the carapace is elongated and smoothly convex. In the larger carapaces (IGC-P 0025; Fig. 2A and B), the ventroposterior margin is more rounded than in smaller ones (e.g. IGC-P 0028, 00054; Fig. 2C and D). There are 15–20 irregularly spaced, serrated growth lines (Fig. 2–4). The first growth line reveals a small larval valve (=umbo). The marginal serrations are sharply pointed and curved, distributed by 40 'denticles' per millimeter (Figs. 4 and 5). Rounded to elliptical pits for the insertion of setae (Shen, 2003) are seen at the base of each 'denticle'. Growth bands are flattened and broader at the central region than in the ventral portion of the carapace (Figs. 2 and 3A).

Patterns of microscopic ornamentation revealed by SEM are extensive and slightly variable in distinct lamellae (i.e., stacked growth bands) within the same individual (Figs. 3–5). The reticular ornamentation is more common, and defined by dense, uniformly-sized sub-hexagonal to almost circular alveoli (4–7  $\mu\text{m}$  in diameter). In middle to ventral portions of the carapace, the alveoli are concentrically elongated in the proximal area of the growth bands (Figs. 4B–C, 5A). In some growth bands, the ornamentation is formed by almost indiscernible punctae, grading ventrally to alveoli (Fig. 5D). On adjacent layers (or on their respective molds), the alveoli are grouped into larger and irregular polygons measuring

40–50  $\mu\text{m}$  in diameter, which are distinguishable across the entire growth band, or only on its proximal half (IGC-P 0038, Figs 3B–D; IGC-P 0037/1, Fig. 4).

SEM images revealed additional minor local variations of ornamentation. A worth-mentioning pattern occurs on an apparently more internal growth band at the ventral region of the specimen IGC-P 0038 (Fig. 3C). This pattern is also reticular, but characterized by a little larger and non-alveolar, equidimensional subunits. At the distal portion of one of these layers, these subunits becomes fringe-like and oblique towards the posteroventral side of the valve (Fig. 3D, 2).

## 5. Taxonomic discussion

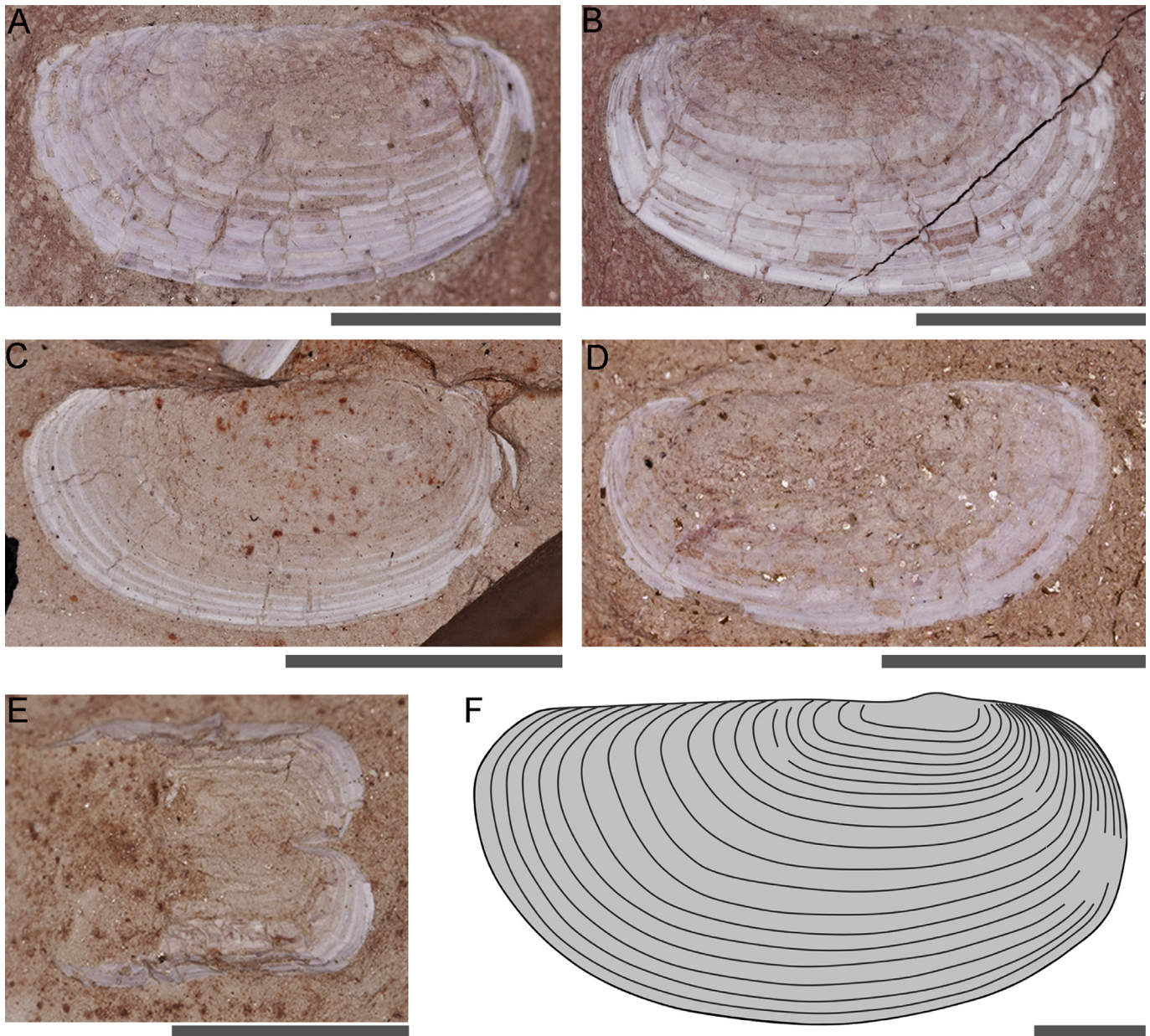
### 5.1. Affinities to Pseudestheria/Cyzicus

Cardoso (1971) described '*Pseudestheria* *abaetensis*' with basis on six specimens, one of which (N° 005) has been figured (Cardoso, 1971, Plate I, fig. 4, p. 45). The assignment to *Pseudestheria* Raymond, 1946, a predominantly Palaeozoic genus (Raymond, 1946; Tasch, 1987; Cuvelier et al., 2015), was supported by the oval outline of the carapaces, their straight hinge line and reticular ornamentation (Cardoso, 1971). Raymond (1946, p. 243) defined this genus as "Lioestheriidae with oval carapace, engirdled by concentric lirae or costellae separated by spaces equal or greater than their own width. No sculpture, except punctuation, is present in the intervals". Such characters are common to a plethora of spinicaudatan genera (Tasch, 1987; Cuvelier et al., 2015), and are not diagnostic to genus-level taxa. Indeed, the author himself recognized that this genus is stratigraphically meaningless and "must inevitably become a sort of dumping ground for not too well preserved fossils" (Raymond, 1946, p. 243). Accordingly, '*Ps.* *abaetensis*' cannot be assigned to that genus on the basis of the characters mentioned by Cardoso (1971), which are also seen in phylogenetically distant species of clam shrimps (Tasch, 1987).

Tasch (1969) considered *Pseudestheria* as junior synonymy of *Cyzicus* Audouin, 1837, an extant, highly variable genus defined according its soft part characteristics not preserved in fossil forms. Several species of clam shrimps collected in rocks dated since the Devonian have been assigned to *Cyzicus*. Tasch (1987) recombined '*Ps.* *abaetensis*' as *Cyzicus* (*Lioestheria*) *abaetensis*, referring the figured specimen N° 005 as lectotype. Yet, as also stated for *Martinsstheria codoensis* (Cardoso, 1962) (Lower Cretaceous of Parnaíba, São Luís-Grajaú and Araripe basins), '*Ps.* *abaetensis*' cannot be assigned to the typically Paleozoic subgenus *Lioestheria* either, as it lacks the presence of an umbonal nodule and rib, which is typical of that taxon (Kozur et al., 1981; Martens and Lucas, 2005; Gallego et al., 2013).

Until recently, most fossil spinicaudatans from Brazil, as well as many specimens from Lower Cretaceous, were assigned to *Cyzicus* (Tasch, 1987; Carvalho and Viana, 1993; Carvalho, 1995; Rohn and Cavalheiro, 1996; Delicio et al., 1998; Rohn et al., 2005; Gallego and Martins-Neto, 2006; Gallego et al., 2013), following the tendency of lumping several morphotypes into the genus *Cyzicus* as a "Western" taxonomic system. However, critical discussions concerning the characters that support these assignments are rarely provided, hinting that taxonomic review for several fossil Spinicaudata from Brazil is required (Rohn et al., 2005; Gallego and Martins-Neto, 2006; Gallego et al., 2013).

The carapaces of *Platystheria abaetensis* are, in general, distinct from other species of *Cyzicus*, which was diagnosed by Jones (1863) by the presence of reticulated ornamentation, occasionally modified with vertical bars, unequal to subequal valves; umbo usually subtriangular to suboval, anterior or occasionally central; the curvature of the valves and growth lines are larger on its posterior



**Fig. 2.** *Platystheria abaetensis* comb. nov. A–B, IGC-P 0025, right valve separated in two parts; C, IGC-P 0054, right valve, note the variation in the posterior margin of the carapace, which is slightly posteriorly projected; D, IGC-P 0028, left valve; E, IGC-P 0036, open articulated valves in dorsal view; F, Drawing based on the specimens depicted herein. Scale bars: A–E = 5 mm; F = 2 mm.

portion rather than on the anterior; ventral margin frequently semicircular. However, these diagnostic features are vague and may be applied to distinct genera of clam shrimps, particularly those referred to Eosestherioidea (e.g. *Pseudestheria* Raymond, 1946, *Euestheria* Depéret and Mazeran, 1912, *Tenuestheria* Chen and Shen, 1977).

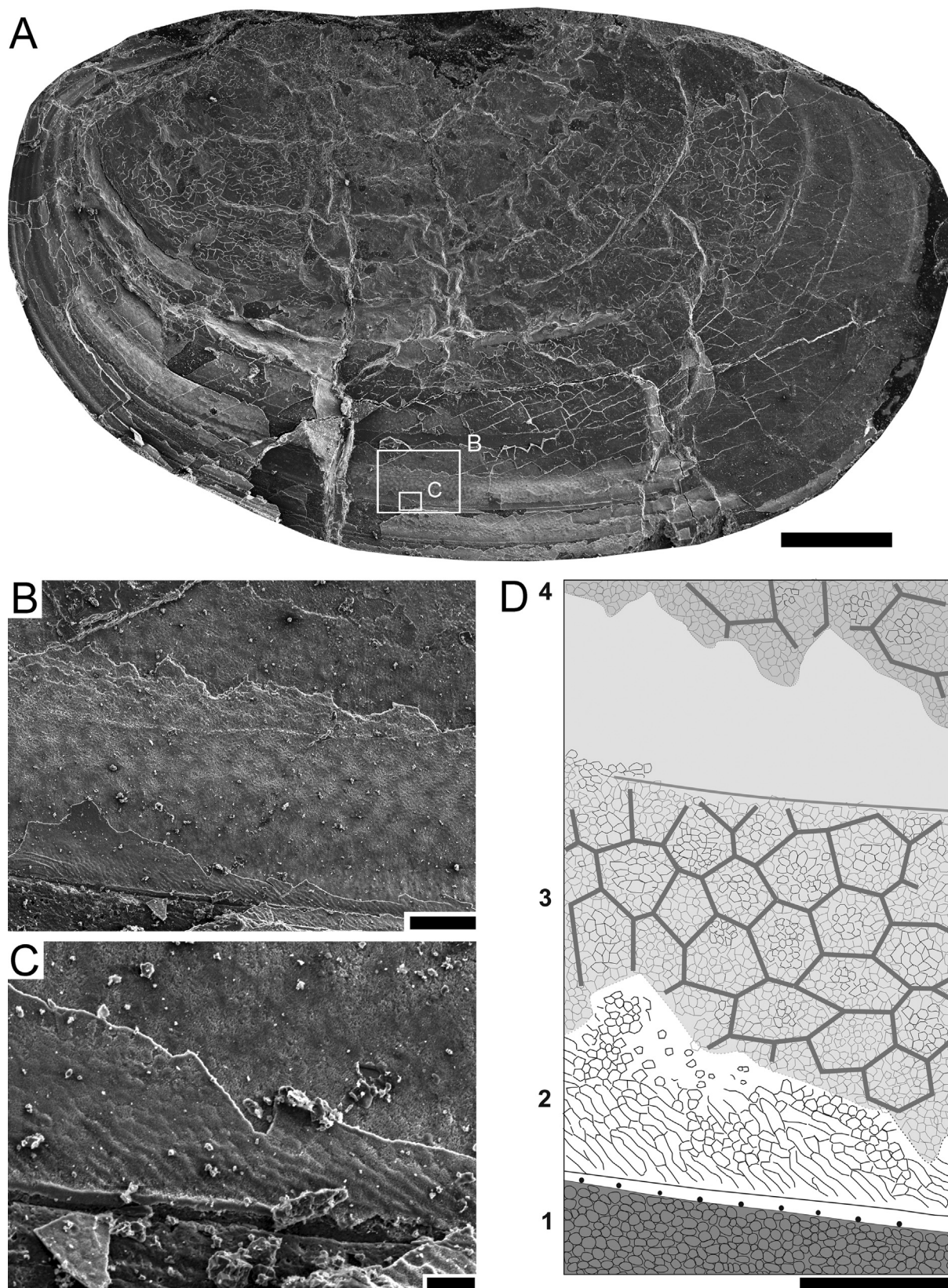
A comparison with several taxa already assigned to *Cyzicus* from the Brazilian Mesozoic [e.g. *C. pricei* (Cardoso, 1966), *C. brauni* (Cardoso, 1966), *C. mirandibensis* (Cardoso, 1966), *C. cassambensis* (Teixeira, 1960), *C. iphygenioi* (Cardoso, 1966), *C. mawsoni* (Cardoso, 1966), *C. erichseni* (Cardoso, 1966), *C. cf. barbosai* (Almeida, 1950) and *Martinsesstheria codoensis*] revealed that no individual attributed to these taxa bears an equivalent anteroposterior elongation, straight dorsal margin, the maximal height of the carapace at the anteroposterior midlength, and its faintly projected umbo

(Cardoso, 1966; Tasch, 1987; Carvalho, 1996, 2001a,b, 2006; 2014; Arai and Carvalho, 2001; Srivastava and Carvalho, 2007; Gallego et al., 2013). Likewise, that combination of features, including here the telliniform carapace, is lacking in other species of spinicaudatans from Brazil: *Estheriina* Jones, 1897b, *Bauruestheria* Rohn, Shen, Dias-Brito, 2005, several *Palaeolimandriopseidae*, *Macrolimnadiopsis* Beurlen, 1954 and *Graptoesstheriella* Cardoso, 1965 (= *Camerunograptia* Novojilov, 1958) (Jones, 1897a; b; c; Cardoso, 1966; 1962; 1971; Mezzalana, 1974; Tasch, 1987; Carvalho and Srivastava, 1996; Cunha Lana and Carvalho, 2001; Rohn et al., 2005).

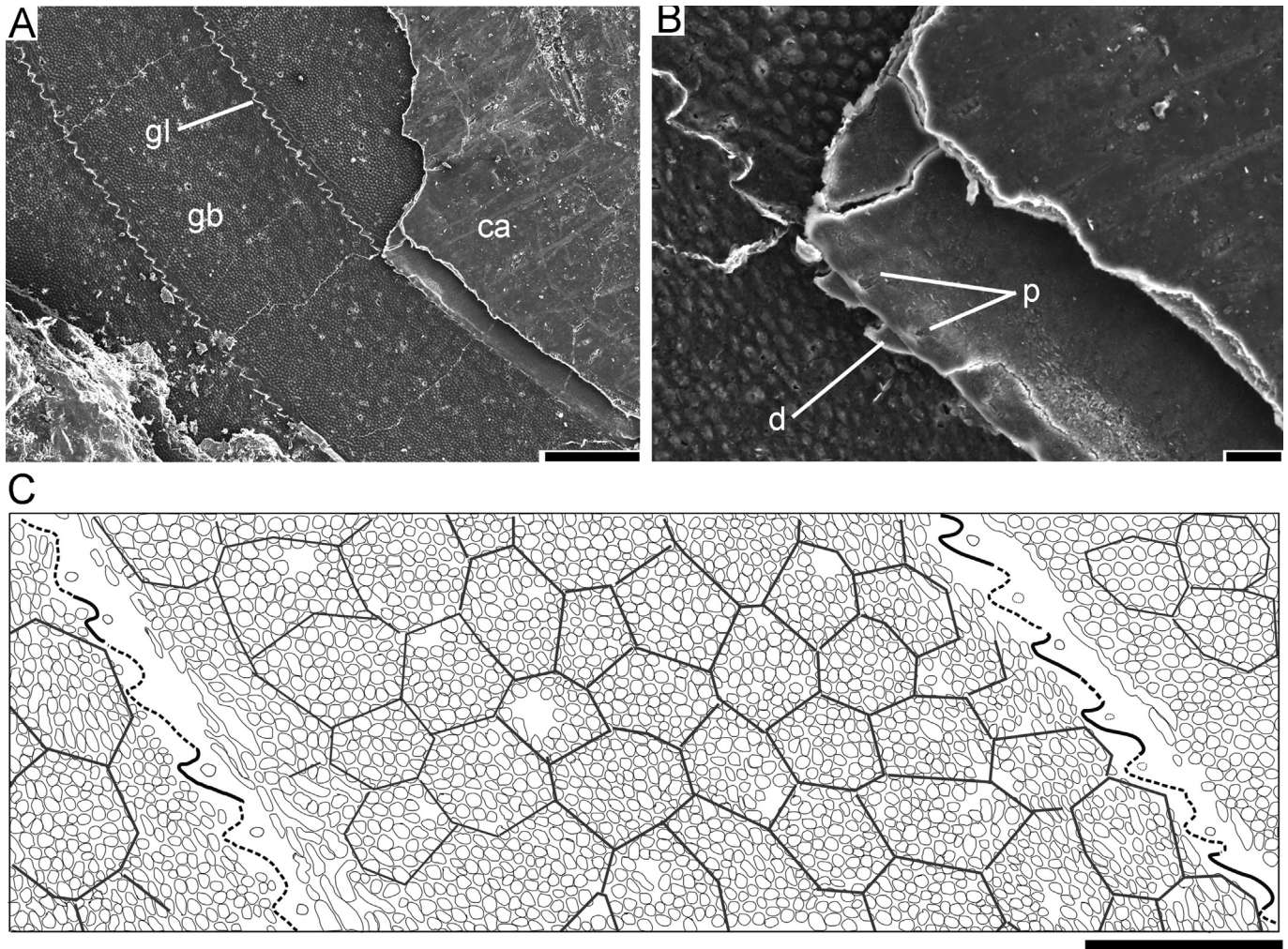
## 5.2. Comparisons to other genera and species

Some characters described in *Platystheria abaetensis*, such as oval elongate carapace (H/L ratio < 0.6) with long and straight hinge





**Fig. 3.** *Platyestheria abaetensis* comb. nov. IGC-P 0038 under SEM. A, right valve with several imbricated growth bands of the carapace. B, marginal reticular ornamentation within larger irregular polygons of distinct lamellae surfaces (see A for position). C, detail of B, showing the reticulation grading to posteriorly directed fringes. D, Schematic detail of the ornamentation based on IGC-P 0038 and other specimens. 1: alveoli of the external surface of the valve (preserved as cast); 2: fragment of the probable most internal preserved layer of the recorded fossil with the modified reticulation grading to posteriorly directed fringes; 3: layer showing reticular ornamentation and larger superimposed polygons; 4: third layer with similar reticular pattern and larger polygons. Scale bars: A = 1 mm; B = 20  $\mu$ m; C, D = 100  $\mu$ m.



**Fig. 4.** *Platystheria abaetensis* comb. nov. A, IGC-P 0037/1, detail of the anteroventral region of the left valve, showing the serrated growth line, reticular ornamentation composed of alveoli grouped into larger polygons on proximal region of growth bands. B, Detail of A, showing growth line with pits and sharply curved and pointed 'denticles'. Note that the alveoli are concentrically elongated below the growth line. C, Detailed drawing of the anteroventral region of a left valve with a serrate margin of growth bands characterized by sharply pointed and curved 'denticles' with pits. The growth bands present minute circular to concentrically elongated alveoli and superimposed larger and irregular polygons. Abbreviations: ca, carapace; d, 'denticle'; gb, growth band; gl, growth line; p, pits. Scale bars: A = 200  $\mu$ m; B = 20  $\mu$ m; C = 100  $\mu$ m.

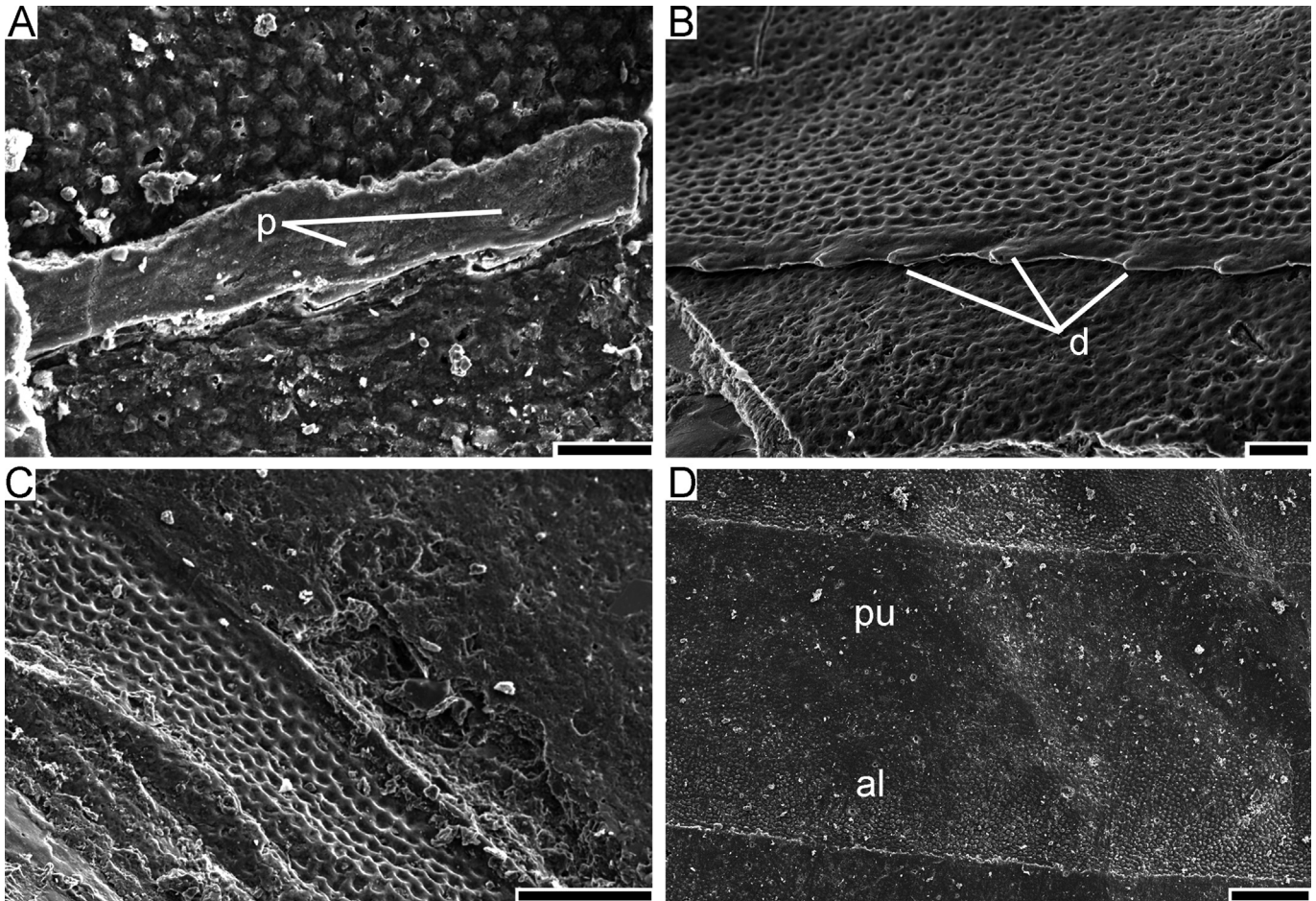
line and reticular ornamentation, have been variably noticed in several Cretaceous Spinicaudata taxa (e.g. *Nigerestheria*, '*Cyzicus*' *anomala*, *Tenuestheria*, *Pseudestherites*). Among those, the eosetheriid *Nigerestheria lamberti* (Defretin in Defretin et al., 1956) (Chen in Zhang et al., 1976; Chen and Shen, 1985; Shen, 2003) is similar in the long and straight hinge line and the posterior portion of the carapace higher than the anterior one. Yet, it differs significantly from *Pl. abaetensis* by its larger size (twice longer and proportionally longer than high), less numerous growth lines, supramarginal umbo, the predominance of the radial anastomosed ornamentation on the entire growth band, rather than the reticular type, which is restricted to the dorsal growth bands, and the presence small tubercles, not holes, on the outer face of the growth lines.

The holotype and only specimen of *Cyzicus* (*E.*) *anomala* (Jones, 1901), from the Early Cretaceous of South Africa (Tasch, 1987, pl 1, fig 3), is very similar to the largest carapaces of *Platystheria abaetensis*, except for its smaller size (less than half). The similarities include the H/L ratio, anterodorsal and posterodorsal curvatures, the anterior, submarginal umbo and the maximal height of the carapace at halfway the distance between the anterior and posterior extremities. Mild difference includes the smoother

posteroventral curvature of the *C. anomala* carapace. The ornamentation is described as close-packed granules, but these are not figured (Tasch, 1987). Further comparisons are hampered by unavailable ornamentation data.

Among species of *Tenuestheria*, *Platystheria abaetensis* is similar to *Tenuestheria canelonesensis* Gallego, Campos and Veroslavsky, 1999 (Castellanos Formation, Albion of Uruguay) (Gallego et al., 1999) in the H/L ratio of the carapace, the anterior position of the umbo, the maximal height in its midlength and, in part, the reticular ornamentation. On the other hand, the dorsal margin of *T. canelonesensis* carapace is relatively longer and its posterior margin is circular (i.e. dorsoventrally higher) rather than ellipsoid. Concerning the elongated shape of *Pl. abaetensis* and the relatively angular edge from the dorsal to the posterior margin, as well as some patterns of the ornamentation, this species is more similar to the type species *T. tenuis* Chen and Shen, 1977 from the Upper Cretaceous of China (Chen and Shen, 1977; Li et al., 2007; Li et al., 2010). The similarity in the ornamentation refers to the gradation from punctae to small alveoli observed on some growth bands (Fig. 5D) or, in proximal parts of some growth bands, the concentric elongation of the alveoli (Figs. 4, 5A). This concentric arrangement was the main characteristic used to advocate an





**Fig. 5.** *Platystheria abaetensis* comb. nov. A, IGC-P 0037/1C, detail of the growth band, showing the pits on growth line with curved 'denticles'. B, Isolated piece of carapace depicting the serration at the growth line and the reticular ornamentation. C, IGC-P 0037/2, marginal growth band with alveolar reticular ornamentation. D, IGC-P 0037/1, growth bands with graded punctae in the proximal region to alveoli in the distal regions of the growth bands. Abbreviation: al: alveoli zone; d, 'denticles'; p, pits; pu, punctae zone. Scale bars: A, B = 20  $\mu$ m; C = 50  $\mu$ m; D = 100  $\mu$ m.

emendation to the diagnosis of the genus proposed by Li et al. (2007). *T. canelonesensis* apparently lacks this elongated ornamentation (Gallego et al., 1999). On the other hand, the small alveoli of *T. tenuis* are not arranged in larger polygons, as is observed in *Pl. abaetensis* and in the loxomegalyptid *Shizhuetheria truncata* Shen and Chen, 1982, from the Middle Jurassic of the Sichuan Basin, in China (Li et al., 2009a).

The ornamentation of *Platystheria abaetensis* is also similar to that of the antronestheriid *Pseudestherites musacchioi* Gallego and Shen, 2004 from the Lower Cretaceous of the Neuquén Basin (Gallego and Shen, 2004). This includes the gradation from punctae to alveoli on the growth bands, as well as the oblique elongation of reticulation in distal regions of the carapace. However, the graded ornamentation is not present in all growth bands of *Pl. abaetensis*. In addition, the oblique fringes in *Pl. abaetensis* are less conspicuously anastomosed, and the alveoli may be encompassed by larger polygons. Other differences are the relatively longer valves of *Pl. abaetensis*, their straight dorsal margin and, particularly, the presence of serrated growth lines.

Serrated growth lines are not uncommon in spinicaudatans (Déperet and Mazeran, 1912; Cardoso, 1966; Chen and Hudson, 1991; Li and Batten, 2004a). The serrated morphology of *Pl. abaetensis* seems peculiar considering the curved, hook-like denticles with thickened bases (Figs. 4, 5A and B). These are different from the wavy, rounded to subtriangular shaped beads seen in assorted

families of spinicaudatans, including, for instance, the antronestheriid *Martinestheria*; the polygraptid *Dendrostracus lagarcitoensis* Prámparo, Ballent, Gallego and Milana, 2005; the afrograptid *Surreyestheria* Liao, Gallego, Shen, Jarzembowski and Huang, 2017; the fushunograptids *Qinghaiestheria* Wang, 1983 and some putative species of *Cratostracus* Huang (in Chen and Shen, 1977), *Orthestheria* Chen (in Zhang et al., 1976) and *Ordosestheria* Wang, 1984 (Li, 2004; Shen et al., 2004; Prámparo et al., 2005; Gallego et al., 2013; Boukhalfa et al., 2015; Li, 2017; Liao et al., 2017). One specimen of *Cratostracus? tunisiaensis* Boukhalfa et al., 2015 has apically pointed tooth-like serration on the ventral margin of the growth band (Boukhalfa et al., 2015, fig 5f). These differ from the denticles of *Pl. abaetensis* by being less curved and bearing wrinkles at their bases. Serrations are also seen in taxa from China, including *Cratostracus? cheni* Li and Batten, 2004a,b (Early Cretaceous), and the Turonian halysstheriids *Porostracus baichengensis* N. Chen (in Wang, 1980) and *Dictyestheria elongata* Chang and Chen, 1964 (Li and Batten, 2004a,b; Li et al., 2009b). The denticles observed in those species are diminutive, and do not match the morphology of *Pl. abaetensis*.

Besides the taxa discussed above, *Platystheria abaetensis* is also similar to *Euestheria sambaensis* Defrentin-Lefranc, 1967, from the Early Cretaceous of Congo Basin, and to *Nestoria pissovi* Krasinets, 1963, from the Early Cretaceous Dabeigou Formation in Inner Mongolia (Chen, 2008) in the anterior umbo, curvature of the anterodorsal and posterodorsal margins, maximal height at



midlength and large size (>9 mm). However, *Pl. abaetensis* has more elongated outline (not oval as the two species, with  $H/L > 0.6$ ) with different position of the umbo, longer dorsal margin and not large-mesh reticular ornamentation.

The comparisons presented herein indicate that the specimens described by Cardoso (1971) and those added in this paper indeed represent a distinct genus from the Lower Cretaceous of the San-franciscana Basin.

### 5.3. Affinities at superfamily and family rank

The taxonomy of spinicaudatans proposed by Zhang et al. (1976) and Chen and Shen (1985) distributed fossil and modern species into six (or perhaps five) superfamilies mainly based on the ornamentation on growth bands, position of umbo/larval carapace, relative number and density of growth lines, valve shape, and presence/nature of carinae or of 'spines' on the larval carapace (see review of Astrop and Hegna, 2015). Although some characteristics are not exclusive to a single superfamily, *Platyestheria abaetensis* fits best in Eoestherioidea Zhang and Chen (in Zhang et al., 1976), which has the following diagnosis (translation in Astrop and Hegna, 2015, p. 347): "Carapace valves of various shapes (predominantly cyziciform and cycladiform with some telliniform). Carapace small, unarmed and without preserved adductor muscle scar or carapace gland. No recurved growth lines or saw-toothed dorsal margin. Growth band smooth, or with a variety of indentations, as well as a mixed shaped decorative mesh network." This superfamily has a long geologic range, from Lower Devonian to Recent, and comprises several families, including the extant cosmopolitan Cyzicidae and Leptestheriidae (Astrop and Hegna, 2015).

With regard to the classification of *Platyestheria abaetensis* at family rank, similarities of this species with taxa of Antronestheriidae (i.e. *Pseudestherites*), Euestheriidae (i.e. *Tenuestheria*, *Euestheria*), and Loxomegaglyptidae (i.e. *Shizhuestheria*) have been noted. Such a range of possibilities may imply that unambiguous assignment of species to families of spinicaudatans is hampered by the lack of objective criteria for taxa recognition within clades. This is probably due to strong variation in the morphology of carapaces and the lack of character data sets for parsimony analysis. The available data in literature are still limited and heterogeneous. Most fossil spinicaudatans studies were based on the exposed external surface of the valve, not on multiple lamellae as provided by *Pl. abaetensis*. Inner portions of the carapace with elaborate and conspicuous ornamentation can be assigned to the procuticle and the larger secondary reticulate ornamentation was probably originated within the intracuticular space (between epicuticle and procuticle) of the carapace and suggest some degree of calcium-phosphate mineralization (Astrop, 2014).

The very fine alveoli grouped into larger and irregular polygons in *Platyestheria abaetensis* represent one of the peculiar characters of this species. This pattern resembles some species of the Asian endemic family Diestheriidae Zhang and Chen (in Zhang et al., 1976; e.g. *Neodiostheria dalaziensis* Chen revised by Li et al., 2016), but the large polygons of the species described here, where observable, are more tenuous, not forming large and strong transverse reticulation (see Astrop and Hegna, 2015). The family Diestheriidae has a probable close relationship to Loxomegaglyptidae, as discussed below.

Another family that deserves discussion is Euestheriidae Defretin-Lefranc, 1965, an extremely diverse and paraphyletic family, with species from the Middle Devonian to Cretaceous (Astrop and Hegna, 2015). The diagnosis in Zhang et al. (1976) includes "carapace outline variable, ranging from circular through triangular to trapezoidal (limnadiiform-cycladiform). Fine reticulate

**Table 1**  
Complete elemental data (C, O, F, Na, Mg, Al, Si, P, K, Ca, Ti, Fe) of all samples and of the different zones analyzed. All measurements are expressed as percentage weight (w/w %), n.d. = not detected.

Points	C	O	F	Na	Mg	Al	Si	P	S	K	Ca	Ti	Fe	Observations
A1	31.34	10.7	0.63	0.07	n.d.	0.04	0.64	12.52	0.66	0.26	42.86	n.d.	0.2	IGC-P 0038, outer lamella
A2	33.23	12.29	0.68	0.11	n.d.	0.44	2.64	11.68	0.71	0.85	36.24	n.d.	1.19	IGC-P 0038, below A1 (polygonal ornamentation)
A3	35.29	18.4	n.d.	n.d.	1.4	5.60	17.93	0.2	0.11	4.49	7.47	n.d.	9.09	IGC-P 0038, inner lamellae, possibly cast
A4	35.06	18.12	n.d.	n.d.	1.71	6.00	19.37	0.22	0.21	4.62	4.58	0.82	9.3	IGC-P 0038, rock matrix surrounding the specimen
B1	43.5	16.09	n.d.	0.14	n.d.	n.d.	0.43	10.01	0.59	n.d.	29.24	n.d.	n.d.	Isolated specimen 1 in cross-section, 'denticle'
B2	28.84	19.41	n.d.	0.38	n.d.	n.d.	0.35	13.47	0.84	n.d.	36.72	n.d.	n.d.	Isolated specimen 1 in cross-section, material between lamellae
C1	35.92	21.84	1.34	0.55	0.18	0.44	1.45	10.38	0.74	0.36	26.43	n.d.	0.36	Isolated specimen 2, alveolar ornamentation
C2	34.01	21.86	1.5	0.73	0.17	0.19	0.52	11.39	0.8	0.19	28.55	n.d.	0.07	Isolated specimen 2, cross section of inner lamella

ornamentation (0.01–0.02 mm) often containing granular ornament.” (translation of Astrop and Hegna, 2015, p. 348). Astrop and Hegna (2015) stated that the family comprises several carapace shapes (mainly telliniform), commonly (not necessarily) small and subovate, with small larval carapace positioned anteriorly and above the dorsal margin, dense growth lines and further ornamentation patterns as irregular reticulations or irregular lirae with much variation in each type. This variable set of characteristics may encompass combinations consistent with *Platyestheria abaetensis* (see comparisons to the euestheriid *Tenuestheria canelonesensis* above). However, considering the most typical morphotypes of the family (following Astrop and Hegna, 2015), *Pl. abaetensis* is larger, relatively longer, with sub-marginal, not supramarginal umbo, relatively loosely (not tightly) spaced growth lines and no irregular lirae as ornamentation.

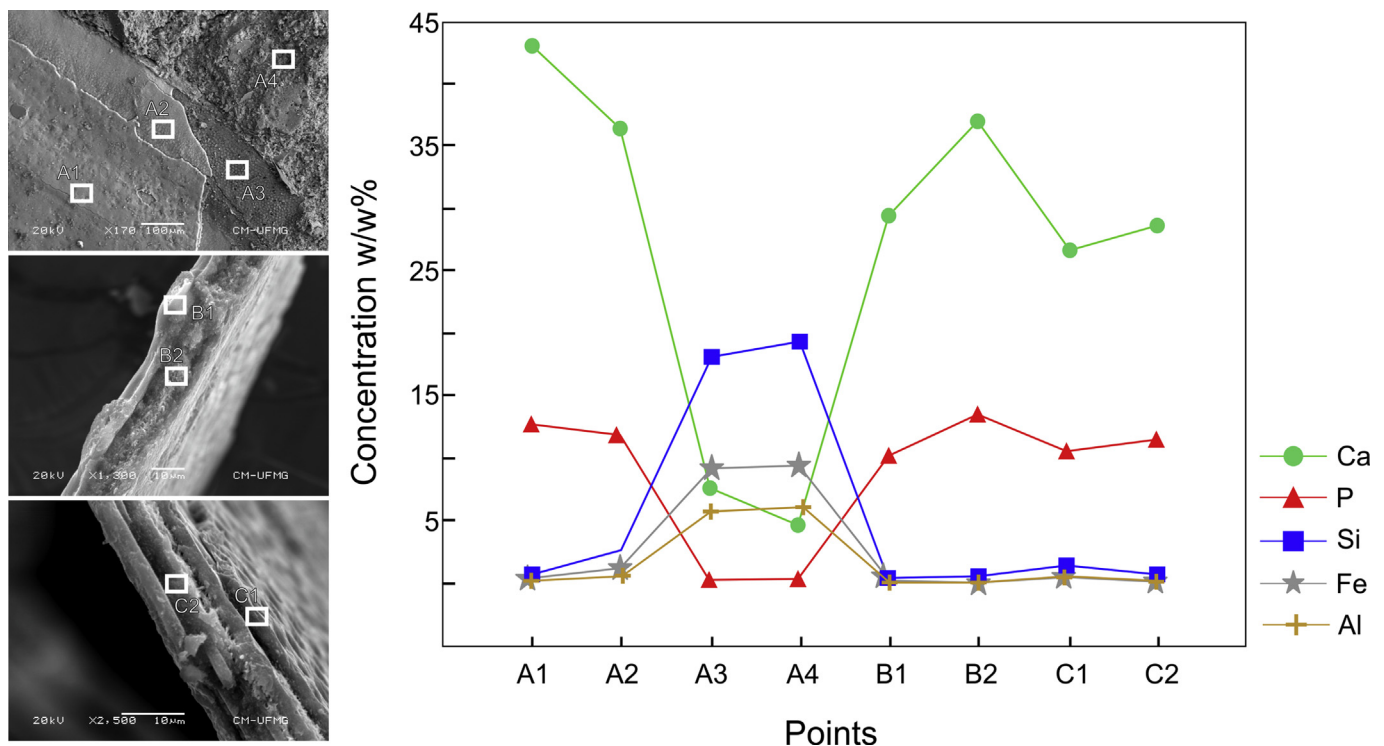
The shape of *Platyestheria abaetensis* and the general ornamentation pattern of growth bands fit relatively well into Loxomegaglyptidae Novojilov, 1958, considering its diagnosis (in Astrop and Hegna, 2015, p. 348, translated from Zhang et al., 1976): “growth bands wide and flat with large, irregular ‘mesh’ ornament, the walls of which are shallow and thin; ornament elongates transversely [i.e. concentrically] with ontogeny; generally with cyziciform-cycladiform carapace shapes”. In the discussion about the family, Astrop and Hegna (2015) also include a telliniform carapace shape (differing from the euestheriids due to a commonly more elongate outline) and mentioned that the large, irregular polygonal reticulation probably gave place to raised anastomizing ridges of modern Leptestheriidae and of the genus *Eocyclus*. The presence of reticular ornamentation (mesh diameter c. 5 µm) grouped into larger polygons of about 30–50 µm seen in *Pl. abaetensis* was also noticed in other loxomegaglyptids (e.g. *Shizhuestheria*, Li et al., 2009a). Due to the combination of features presented above, we provisionally assign *Pl. abaetensis* to

Loxomegaglyptidae, until further data on the taxonomy of Eoestherioidea is available.

#### 5.4. Possible other occurrences of *Platyestheria abaetensis*

Carvalho (1993) referred spinicaudatan carapaces from the Lower Cretaceous Santana Formation (Araripe Basin), Souza Formation (Uiraúna Basin) and ‘Itapecuru’ Formation (Parnaíba Basin) to ‘*Cyzicus*’ *abaetensis* based on the comparison with the type series described by Cardoso (1971) and the taxonomic review of Tasch (1987). In general, those specimens are poorly preserved, and detailed ornamentation data are lacking, which hampers comparison. We agree that the specimens from Parnaíba and Araripe basins are oval elongated with straight dorsal margin, similar to *Platyestheria abaetensis*. Yet, there are marked differences as the smaller size (less than 50%) and the posteroventral projection of the carapace of the Parnaíba specimens, and the convex, broad-sized growth bands with radial ornamentation of the carapace from Araripe (Carvalho and Viana, 1993). The specimen from Uiraúna Basin is articulated, but due to poor preservation, no diagnostic features of *Platyestheria abaetensis* were observed. In the light of the new anatomical information presented here, we consider the occurrence of ‘*Pseudestheria*’/‘*Cyzicus*’ *abaetensis* in those sedimentary basins as dubious.

In addition, Delicio et al. (1998) assigned a left valve collected in João Pinheiro to ?*Cyzicus*. This is similar to the carapaces of *Platyestheria abaetensis* in the H/L ratio, the number of growth lines and size of growth bands, and the curvature of the anterior and posterior margins. Yet, key characters such as the carapace dorsal margin, the position of umbo and the ornamentation could not be properly evaluated. Further data are required to confirm the occurrence of *Platyestheria abaetensis* in sites other than the type locality.



**Fig. 6.** Plot line graph of elemental composition from distinct points of three valves (A1–3, B1–2 and C1–2) of *Platyestheria abaetensis* carapace and the rock matrix (A4). Photomicrographs at left indicate the position of the analyzed points. Top image captured with backscattered electrons detector, thus the distinct shades of gray evidence differential chemical composition. See Table 1 for details (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).



## 6. EDSX results and taphonomic discussion

Chemical compositions of different parts of the fossil spinicaudatans and the rock matrix were obtained by EDSX analysis (Table 1). The analyzed points A1–A3 were taken on the ventral carapace zone in different layers and the point A4 gives the composition of the claystone adjacent to the fossil (Fig. 6). The points B1–B2 and C1–C2 correspond to cross sections of the whitish very fine layers of the fossil (Table 1).

Rock matrix EDSX analysis (A4) show low content of P and Ca, and significant higher proportions of Si, Fe and Al (Table 1; Fig. 6), suggesting a major silicate composition. Points measured on the whitish layers (A1–2, B1–2 and C1–2) exhibit principally high contents of P and Ca, being coherent with a predominantly calcium phosphate [ $\text{Ca}_3(\text{PO}_4)_2$ ] composition. The elemental profile (Table 1) is also compatible with a significant contribution of calcium carbonate, which is in accordance with the strong carbonatic cementation of the pelitic rocks of the Areado Group (Sgarbi et al., 1993). Minor elements [i.e., Mg, S, Al and Na] were also recorded. The composition at the point A3 (Fig. 6) is more similar to that of the rock matrix than to proportions determined for the whitish layers.

The figure 6 helps to visualize the chemical compositions according to the measured points and reinforces that almost all fossil layers (possible original lamellae) show similar proportions of chemical elements, except the point A3, which is more similar to the rock matrix.

The results presented above are consistent with previous works dealing with the composition the clam shrimp carapaces, which are mainly constructed with chitin, and predominantly mineralized with calcium phosphate (Astrop et al., 2015). This suggests that at least partially the mineral components of the carapace of *Platyestheria abaetensis* were preserved. Similar results were identified in *Carapacestheria disgregaris* (Tasch, 1987) from the Lower Jurassic of Antarctica, where a single valve showed internal layers preserved as silica substances and external layers preserved as calcium phosphate (Stigall et al., 2008). Scholze et al. (2015) emphasized that recent conchostracan shells are transparent to translucent or of light amber, brown to brownish-red, or yellow and, therefore, the white color of the fossil was probably caused by a diagenetic modification of the original chitinous substance.

The results indicate that the whitish layers in *Pl. abaetensis* (points A1–2, B1–2 and C1–2) represent calcium phosphate lamellae modified by the input of distinct elements from the sedimentary matrix during the diagenesis. They were peeled during the fossilization process and collection, exposing the sedimentary matrix at the point A3, a possible mold of the carapace with a composition similar to that of the rock matrix.

## 7. Conclusions

The morphology and taxonomy of ‘*Pseudestheria*’ *abaetensis* Cardoso, 1971, from the Lower Cretaceous Sanfranciscana Basin, southeast Brazil, is reassessed after the discovery of new material from its type locality. This is particularly important due to unknown whereabouts of the type series. In addition, the Sanfranciscana Basin is an extensive sedimentary deposit with massive potential for understanding the biota of the Western Gondwana prior to the opening of the Atlantic Ocean. This paper yields data for further biostratigraphic correlation.

We propose the new genus *Platyestheria* for this species due to a combination of peculiar characters of the carapace, as the shape, the serrated growth lines and the ornamentation pattern distinct from other genera of Spinicaudata. The new genus belongs to the Superfamily Eosestherioidea and we tentatively refer it to the Loxomegalyptidae, but other families cannot be completely ruled

out, because the taxonomy of spinicaudatans at family rank were defined by wide overlapping ranges of diagnostic characteristics and requires a deep review.

EDSX analysis of the studied material indicates that the multiple, whitish, thin layers of the fossil valves have a relatively high proportion of P and Ca, what suggests preservation, at least partially, of the original carapace. This result is corroborated by lower proportions of Ca and P and higher Si content in the sedimentary matrix.

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