ABSTRACT – Lioestheria codoensis Cardoso was described from materials originally collected from the Codó Formation (Lower Cretaceous, Parnaíba Basin, Piauí State), northeastern Brazil. Since its discovery L. codoensis has been assigned to different genera by different authors [as Estheriina (Nudusia) and Cyzicus (Lioestheria)]. In this paper, previous systematic assignments are reviewed and discussed in light of new scanning electron microscopy studies of new material. As a result of this research, the species is assigned to a new genus of the Family Antronestheriidae, and the study integrates palaeontological, biological and ecological approaches to provide a robust description for the species. Previous assignments to other genera (Estheriina, Lioestheria and Cyzicus) are also assessed and comparisons with other related genera of the Family Anthronestheriidae (Pseudestherites, Etmosestheria, Anthronestheria and Paleolepthestheria? chinensis) are made. Detailed stratigraphical (Codó, Santana, Itapecuru, Rio da Batateira and Missão Velha formations) and geographical (seven localities) records are compiled. Finally, the autecology and within-species morphological variation are also addressed.

Key words: Anthronestheriidae, Santana Formation, Early Cretaceous, Brazil.

INTRODUCTION

Lioestheria codoensis Cardoso, 1962 was originally defined by Cardoso (1962) from materials found within the Codó Formation (Lower Cretaceous, Aptian-Albian) from the Parnaiba Basin (Mendes & Borghi, 2004) or Grajaú Basin (Paz & Rossetti, 2005; Marchesini Santos & Carvalho, 2009), (Piauí State) northeastern Brazil. Tasch (1987) reassigned this taxon to the genus Estheriina (Nudusia). Later, Carvalho & Viana (1993) reported the presence of spinicaudatans in the Santana Formation (Lower Cretaceous, Araripe Basin), which they identified as Cyzicus cf. C. branchocarus Talent, 1965. Carvalho (1993) redescribed the specimens from the Santana Formation and identified them as Cyzicus (Lioestheria) codoensis. Carvalho et al. (1995) also noted additional occurrences of this species in the Aptian-Albian stages from the Parnaiba and Araripe basins and discussed its resemblance with other species from Brazil (Cyzicus L. florianensis Cardoso, C. mirandibensis Cardoso), Africa...
and Australia (*Cyzicus branchocharus* Tallent). Gallego & Caldas (1995, 2001) suggested that the species *C. codoensis* required detailed studies in order to provide a meaningful systematic position. Carvalho et al. (2001) reported the presence of *C. codoensis* in the Rio da Batateira Formation (Lower Cretaceous) from the Araripe Basin. Chiappe et al. (1998) tentatively reported the presence of a form named as *Cyzicus? codoensis* from the Lagarcito Formation (Aptian, San Luis Province) from Argentina. However, more recent studies of these specimens and new material from the same unit (San Juan Province) reinterpreted this occurrence as a new species (*Dendrostracus lagarcitoensis* Gallego in Prâmparo et al., 2005).

In the 1990’s E.B. Caldas (Geology Department, Universidade Federal de Ceará, Fortaleza, Brazil) collected samples from the Crato Member (Santana Formation), which were sent for identification. In this study it is investigated these specimens using new morphological evidence derived through the use of SEM microphotography, and is propose a reassignment of this species to the new genus *Martinsestheria*; it is also provide ecological inferences about the spinicaudatans from each locality.

### Geological setting

The renowned Santana Formation Lagerstätte has been studied extensively by many authors (*e.g.* Martill, 1993; Viana & Neumann, 1999) therefore not be considered here geological setting in extensive detail in this instance and refer readers to previous work. The Crato Member of the Santana Formation crops out around the northern, eastern and southeastern flanks of the Chapada do Araripe plateau that sits at the boundaries of southern Ceará, western Pernambuco and southeastern Piauí in northeastern Brazilian caatinga (Martill, 1993; Neumann & Cabrera, 1999). The Crato Member represents lacustrine facies associations that are mainly composed of carbonate units. These units are in turn composed of micritic, laminated limestones and clay-carbonate rhythmites with colours varying from light to dark brown and light to dark grey, which alternate with shales and fine sandstones. The clay-carbonate rhythmites always occur at the base of the carbonate units and are succeeded by the laminated limestones. Salt (halite) pseudomorphs are present alongside well-preserved fish, insects and plants within the laminated limestones (Viana & Neumann, 1999).

### Historical background

The earliest records of Cretaceous spinicaudatan faunas from South America date from the late 19th century (*i.e.* Jones, 1862, 1897a,b), and the first Cretaceous spinicaudatans from northern Brazil (*Estheriina expansa*, *E. astartoides* and *E. brasiliensis*) were described by Jones (1897a). Approximately 28 species have been described from the Jurassic-Cretaceous sedimentary rocks from Brazil and 31 Jurassic-Cretaceous species are known from the rest of South America (eight from Venezuela, one from Colombia, three from Uruguay and 19 from Argentina). The stratigraphical distribution of the Brazilian fauna ranges from the Middle Jurassic to the middle Upper Cretaceous (Rohn & Cavaleiro, 1996). Of the approximately 28 species from Brazil, 11 are assigned to the extant genus *Cyzicus* (and to the subgenus *Lioestheria*) all of them ornamented with striae, cross-bars and radial lirae. Some of them have been informally re-assigned to *C./Euestheria* by Carvalho (1993). All of these species are in need of systematic revision. Rohn et al. (2005) expressed that many genera are taxonomically “inflated” as taxa are assigned to groups to which they likely have no phylogenetic affinity. Unfortunately, until a dedicated revision of the taxonomic status of this fauna is undertaken, the stratigraphic application of this fossil Spinicaudata will be restricted to certain groups. A preliminary revision (Gallego & Martins-Neto, 2006; Gallego et al., 2010) of the Jurassic-Cretaceous fauna from Brazil presents evidence of high taxonomic diversity within this fauna and strengthens hypotheses of the relationships with Asian, central African and southern South American faunas.

This study presents a re-assignment of the typical Lower Cretaceous species *Lioestheria codoensis*. This species belongs to the Eosestherioidea-Anthronestheriidae group based on ornamentation consisting of few shallow elliptical cavities similar to other Early Cretaceous species (*Pseudosterites musacchioi* and *P. rivarolai*) from Argentina (Gallego & Shen, 2004; Prâmparo et al., 2005). New material assessed in this study allows interesting new interpretations of the paleogeographic, evolutionary and stratigraphical relationships of this problematic taxon while considering a wealth of previous research (*e.g.* Carvalho, 1993; Rohn & Cavaleiro, 1996; Cunha Lana & Carvalho, 2001, 2002; Rohn et al., 2005). This new assessment also sheds light on the relationships between Jurassic-Cretaceous faunas from Brazil, central Africa, northern and southern South America.

### MATERIAL AND METHODS

E.B. Caldas collected the material described in this paper during field trips in the 1990’s. The spinicaudatan bearing material is from two localities: Lameiro Village (LVC), Crato Municipality, and IBACIPE Caldas mine (ICMB), quarry near Barbalha, both from the Ceará State, northeastern Brazil (Figure 1) and they are stored in the Paleontological Collection, Universidad Nacional del Nordeste, Corrientes, Argentina (CTES-PZ); Departamento Geologia, Universidade Federal de Rio Janeiro (UFRJ) and the collection of the Facultad de Filosofia, Ciencias e Letras, Universidade de São Paulo (DGP-USP). Scanning electron micrographs taken using a JEOL JSM-5800LV Scanning Microscope (of the Secretaría General de Ciencia y Técnica-Universidad Nacional del Nordeste, Corrientes, Argentina) and light-microscope photographs (Olympus SZ50) provide detailed microscopic information of the morphologic characteristics. The taxonomy adopted here follows mainly that of Chen & Shen (1985), Chen & Hudson
GALLEGO ET AL. – REASSIGNMENT OF LIOESTHERIA CODOENSI S: SYSTEMATICS AND PALEOECOLOGY

Measurement abbreviations correspond to Tasch (1987). All statistics performed using PAST v1.25.

TAXONOMIC REVIEW

The genus Estheriina and its definition

“Estheriinids” are an interesting but problematic group as their diagnostic features (carapaces with two distinct areas, umbonal one convex with wide spacing growth lines and the flat marginal-ventral area with numerous close together growth lines) often vary depending on the type of preservation (Rohn & Cavalheiro, 1996). Jones (1897a, b) defined both the genus and three species (Estheriina brasiliensis Jones, 1897, E. astartoides Jones, 1897 and E. expansa Jones, 1897) from Brazilian material. Interestingly, it has been proposed that this group contains at least one brackish-water spinicaudatan: E. astartoides (Cunha Lana & Carvalho, 2001). Cardoso (1966) described the fourth member of this group (Notogrypta costai Cardoso), which was later assigned to the genus Estheriina by Tasch (1987) and Carvalho (1993).

The species “codoensis” was assigned by Tasch (1987) to the genus Estheriina (Nudusia?) Jones (Tasch & Jones, 1979) based their interpretation that of a notably swollen umbonal area lacked growth lines (sensu Tasch, 1987; Tasch & Jones, 1979). However, we propose that “codoensis” does not belong to Estheriina because it lacks the abrupt descent between the more convex umbonal area and the lower part of the valve and exhibits numerous close spaced growth lines in that region. Nevertheless, “codoensis” also has got lesser dimension than Estheriina species from Jones (1897) and Tasch (1987), its H/L ratio shows great values (0.73-0.94) than the Estheriina (0.57-0.78) and also itsumbo not raised above the dorsal margin. Furthermore, “codoensis” cannot be attributed to E. (Nudusia) because this species exhibits umbonal growth lines, whereas one of the diagnostic characteristics of the subgenus Nudusia is the absence of growth lines in the umbonal area.

The name Lioestheria definition and problems

The subgenus Lioestheria was defined by Depéret & Mazérán (1912) based on the presence of radial or punctate ornamentation pattern, thin, serrated growth lines and a smooth carapace. Estheria (Lioestheria) lallyensis is designated as the type species of the subgenus. Tasch (1969) transferred the subgenus to Cyzicus Audouin, as Cyzicus (Lioestheria). Kozur et al. (1981) restudied the type material of Lioestheria lallyensis and found that the umbonal area has a node and small rib. Both characters placed the type species and the genus in a different superfamily: Lioestharioidea Raymond, 1946 (or Lioestheriacea), previously known as Vertexioidea Kobayashi, 1954. This proposal was rejected by Tasch (1987) based on the absence of the ribbed structure on the umbonal region, but was accepted by Chen & Shen (1985). Due to the previous identification of these characters and the fact that our material lacks them; we infer that “codoensis” should not be included within Lioestheria.
The use of the name *Cyzicus* for fossil spinicaudatans

Audouin (1837) defined the genus *Cyzicus* based on the soft part anatomy of recent spinicaudatans and contemporary systematic work continues to use soft parts of extant genera to develop phylogenetic hypotheses (Olesen, 2007, 2009). The generalized application of the name *Cyzicus* to fossil spinicaudatans resembles the excessive usage of the name *Estheria* throughout the 19th century (Le Roux, 1960) (invalid by homonymy because the name is preoccupied by an extant insect). Shen (1994) recognized that the classification of living spinicaudatans is based mainly on soft part characters; hence the inherent difficulty in assigning fossil specimens confidently to any modern taxon. As the soft parts of branchiopod crustaceans are only lightly sclerotized, they are rarely preserved. Comparisons of fossilized soft parts, such as those of *Euestheria lanpingensis* Shen & Niu, 1990, from the Middle Jurassic of China, with those of recent *Cyzicus* reveals that the morphology of fossil forms was very different to the morphology of recent taxa (Zhang et al., 1990). In the absence of preserved soft parts, it becomes necessary to consider the morphology of the carapace alone. The palaeontological contributions mentioned previously give credence to the idea that it is inappropriate to identify fossil spinicaudatan taxa using extant spinicaudatan taxonomy below the subordinal taxonomic rank. Given this evidence, it seems that the use of extant taxonomic ranks in assigning fossil taxa is best avoided.

*Lioestheria codoensis* and its systematic position

Cardoso (1962) described *Lioestheria codoensis* from the Upper Jurassic Codó Formation in northern Brazil. In this contribution, Cardoso (1962) identified two geographical provenances for *L. codoensis*, the Piauí State (abstract, p. 26) and Maranhão State (p. 37, see Systematic Description for more details). Cardoso (1962) assigned the species "*codoensis*" to the genus *Lioestheria* Depéret & Mazérán (1912) based on the alveolar and crenulated ornamentation.

Gallego & Caldas (1995, 2001) revised the validity of the Family Afrograptidae and the "afrograptid"-like spinicaudatans from South America and included the species "*codoensis*" in this group based on the presence of beads on the growth lines. This assignment was based on the taxonomic principles discussed in works by Zhang et al. (1976) and Chen & Shen (1985). Later, Shen (2003) modified this proposal. Shen (2003) determined that "beads" were structural constraints rather than taxonomically informative characters and suggested that only the genera *Afrograpta, Camerunograptata, Graptoestheriella* and *Congestheriella* belong to the Superfamily Afrograptioidea and family Afrograptidae. Gallego & Martins-Neto (2006) analyzed the systematic position of *L. codoensis* and suggested a relationship with the "Eoosestherioidea-Anthonestheriidae group" due to its ornamentation constituted by scarce shallow elliptical cavities, similar to other Lower Cretaceous species (*Pseudesthesites musacchioi* and *P. rivarolai*) from Argentina (Gallego & Shen, 2004; Prâmparo et al., 2005). Martill et al. (2007, p. 136-137, fig. 10.2) also discussed scanning electron micrographs of the fossil spinicaudatans from the Crato Member and suggested that re-examination of *Cyzicus (Lioestheria) codoensis* was necessary to clarify its affinities. Furthermore, several authors (Carvalho, 1993, Rohn & Cavalheiro, 1996; Gallego & Martins-Neto, 2006; Gallego et al., 2010) have noted similarities between the Lower Cretaceous spinicaudatan faunas of northeast Brazil and those of Australia and West Africa.

**SYSTEMATIC DESCRIPTION**

Order DIPLOSTRACA Gerstaecker, 1866

Remarks. For more information about the use and meaning of the names “Conchostraca” and Diplostraca see recent contributions (e.g. Gallego, 2010; Tassi et al., in press), and consult the following references for fossil and extant forms (Fryer, 1987; Olesen, 1998; Stenderup et al., 2006; Martin & Davis, 2001; Shen, 2003, 2011; Shen et al., 2006; Shen & Huang, 2008). In this paper, the term “clam shrimp” provides a useful collective common name for fossil and extant laevicaudatans, spinicaudatans, leaiids and estheriellids (Shen, pers. comm. 2008). However, the term "conchostracan" is also used due to its extensive and frequent usage in both the technical and non-specialist literature.

Suborder SPINICAUDATA Linder, 1945

Superfamily EOSESTHERIOIDEA

Zhang & Chen (in Zhang et al., 1976)

Family ANTRONESTHERIIDAE Chen & Hudson, 1991

**Diagnosis emended.** Spinicaudatans with small to moderate carapace size (ranging from 1.0-9.5 mm length to 0.75-6.8 mm height; considering all known species of the family), elliptical to subovoidal, subtrigonal or circular in outline; numerous growth bands with cavernous sieve-like ornamentation; polygonal to elliptical fossae of small to large size with low or high density, simple or consisting of small punctae. Growth lines smooth or with beads.

**Biochron.** Middle Jurassic to Upper Cretaceous.


**Genus Martinsestheria** gen. nov.

**Type species.** *Lioestheria codoensis* Cardoso, 1962.

**Etymology.** Dedicated to Rafael G. Martins-Neto for his great contribution to the knowledge of the non-marine arthropod fauna from South America.

**Diagnosis.** Spinicaudatans with small carapace size (length: 1.0-4.50 mm, height: 0.75-3.20 mm), subovate to subtrigonal in outline (Figures 2, 7A), pronounced umbral region,
anterior umbo rises above dorsal margin, approximately 17-30 growth lines with festoon or garland (scallopc) beads (like “shark teeth” or triangular plates, Figures 3H, 4), growth bands ornamented by two ornamentation patterns, dorsally with polygonal ornamentation and in the medium-ventral growth bands with scarce shallow ovate cavities (45 to 90 μm) filled with minute punctae (2 to 3 μm) (Figures 3-4).

Remarks. Martinsestheria gen. nov. is placed within the Family Antronestheriidae based on the numerous growth bands with cavernous to shallow ovate cavities ornamentation. The new genus differs from other genera included within the Antronestheriidae in that Martinsestheria gen. nov. exhibits subovate to subtriangular outline, two ornamentation patterns – polygonal to shallow ovate cavities – and beads over the growth lines which are absent in other genera referred to that family. Ethmosestheria Stigall & Hartman, 2008 (Late Cretaceous, Madagascar) shares features with the new genus such as a moderately convex carapace and the umbo raised above dorsal margin, but differs in several features such as the elliptical outline, two distinct widths of growth bands (likely a paleoecological indicator rather than a reliable systematic character) and a highly dense sieve-like ornamentation. The taxa Anthronestheria, Pseudestherites and Paleolepthestheria? chinensis resemble the new genus in the cavernous ornamentation, mainly with Anthronestheria in the punctae filling the fossae and a row of cavities along the lower part of the growth band, not present in other genera. Also, Pseudolestherites musacchi and the genera Anthronestheria, Ethmosestheria and Martinsestheria gen. nov. share the low density of cavernous ornamentation (higher in the Chinese species of Pseustherites and P. rivarolai). Anthronestheria and Martinsestheria gen. nov. are both characterized by a row of crowded fossae, but in Anthronestheria they are along the upper margin of each growth band while in Martinsestheria gen. nov. they are placed in the lower third of the growth band. Thus, Martinsestheria gen. nov. exhibits several differences that distinguish it from other genera of the Family Antronestheriidae and justify the erection of a new genus.

Martinsestheria codoensis (Cardoso, 1962) comb. nov. (Figures 2-7, Table 1)

1962 Lioestheria codoensis Cardoso, p. 35-37, text-fig. 6, pl. II, fig. 5.
Figure 3. *Martinsestheria codoensis* (Cardoso) comb. nov. from Crato Member, Santana Formation, Brazil. Scanning electron micrographs. 

A, CTES-PZ 7288, paratype, subtriangular right valve; B-B’, CTES-PZ 7484, paratype, dorsal polygonal reticular ornamentation (B, umbonal ornamentation detail from B’); C, CTES-PZ 7484, paratype, medium striated/punctuated ornamentation (invert image function of the Adobe Photoshop); D, CTES-PZ 7484, paratype, medium ovate cavernous ornamentation; E, CTES-PZ 7483, paratype, ventral ovate cavernous ornamentation; F, CTES-PZ 7484, paratype, ventral ovate cavernous ornamentation, showing the minute punctae filling each one; G, CTES-PZ 7483, paratype, detail of the fossae and the punctae filling; H, CTES-PZ 7484, paratype, detail of the growth line showing the scalloped growth line and the elliptical holes above. Scale bars: A, B’ = 0.5 mm; B, F, D = 66 μm; C = 150 μm; E, G, H = 10 μm.
2001 *Cyzicus* (*Lioestheria*) *codoensis* Cardoso. Gallego & Caldas, p. 165-166, 169, pl. II, fig. i, pl. III, fig. c, d.

**Type material.** DGP-USP 7992 to 7995.

**Type locality.** After Cardoso (1962) and Marchesini Santos & Carvalho (2009), Imperatriz locality, gully of the Tocantins River (right margin), 18 km from Imperatriz (road to Montes Altos), 5 km to the south of Imperatriz city, Maranhão State, Brazil.


(ii) Codó locality, Santo Antônio, Porto Novo, margin of Gameleira stream, Cimento Nassau fabric (São Luís-Teresina road) and near Codó Municipality (04º30’S, 43º50’W), Maranhão State, Brazil, Codó Formation, Parnaiba Basin, Early Cretaceous. Associated fauna/flora: fossil plants, conifers, *Nymphaeites choffatti* (leaf and roots); ostracods and fish (*Vinctifer comptoni, Dastilbe elongates*);

(iii) Riacho da Batateira locality (after Carvalho et al., 2001), Crato Municipality, Ceará State, Brazil, Rio da Batateira Formation, Araripe Basin, Early Cretaceous;

(iv) Sitio Beleza locality after Carvalho (1993) and Carvalho & Viana (1993), Nova Olinda Municipality, Ceará State, Brazil, Santana Formation, Crato Member (four meters above the top of the laminated calcareous level), Araripe Basin, Early Cretaceous. Material sample B3-01, Departamento Geologia-UFRJ 15-Co;

(v) Caldas quarry locality after Carvalho (1993), IBACIPE, 12 km SW from Barbalha Municipality, Ceará State, Brazil, Santana Formation, Araripe Basin, Early Cretaceous. Material, Departamento Geologia-UFRJ 15-Co;
(vi) Casa Branca quarry locality after Carvalho (1993), Trindade - Ipubi Municipality, Pernambuco State, Brazil, Santana Formation, Ipubi Member (one meter above the gypsum level), Araripe Basin, Early Cretaceous. Material, Departamento Geologia-UFRJ 22-Co;

**Diagnosis emended.** Spinicaudatan with small carapace (length: 1.0-4.50 mm, height: 0.75-3.20 mm), subovate to subtriangular in outline, pronounced umbral region, anteriorumbo rises above dorsal margin, dorsal margin straight and inclined posteriorly (Figure 2), anterior margin less convex and larger than the posterior one, anterior margin in front of theumbo short and abruptly inclined, strongly convex ventral margin, approximatelty 17 to 30 growth lines with beads distally, growth bands ornamented by two patterns, dorsally near the convex umbral area with polygonal ornamentation (ranging 6.7 to 10 μm in diameter) and in the medium-ventral growth bands with the upper half of each growth band with scarce shallow ovate cavities, larger and more elongated than the space between growth lines contains irregularly distributed irregularly distributed and the exhibit ornamentation that looks oblique striate with minute punctations (3-5 μm) (Figures 3C-D). In the ventral-anterior area of the carapace, the space between growth lines contains irregularly distributed scarce shallow ovate cavities, larger and more elongated than the reticul ornametation (Figures 3E-G). The upper half of the growth band has fossae dimensions ranging from 7 to 12.6 μm filled with minute punctae 2 to 4 μm, the large cavities increase in size dorsally (Figure 3F). The lower half of each of the growth bands are ornamented with small fossae with dimensions ranging from 5.4 to 6.2 μm (Figures 3-4).

**Material examined.** CTES-PZ 7532-7536; SEM samples, 7288 (MEB 2), 7483 (MEB 16), 7484 (MEB 17).

**Locality of material examined.** Lameiro Village (LVC), Crato Municipality, and IBACIPE Mina Caldas (IMCB), quarry near Barbalha, Ceará State, northeastern Brazil.

**Stratigraphic provenance of material examined.** Araripe Basin, Santana Formation, Crato Member, from two levels, above and below (collection numbers LP-Mi C 001, 003, 005, 006, 100, 101, 200, 201) the laminated calcareous level (E.B. Caldas, pers. comm., 1990). Associated fauna: isolated fish scales and ostracods related to the genera Theryosinoecum ov/and Cypridea.

**Measurements.** (in mm, 25 individuals). L, 1.0-4.50, H, 0.75-3.20, H/L, 0.57-0.93, Ch, 0.60-2.25, Arr, 0.25-1.50, Av, 0.04-1.0, Cr, 0.30-1.90, a, 0.30-1.25, b, 0.40-1.60, c, 0.35-2.0.

**Description.** General details: small carapace with subovate (Figures 2B, C) to subtriangular (Figure 2A) outline, pronounced umbral region, umbo raised above dorsal margin toward anterior, maximal height at antero-medial region, dorsal margin straight and inclined posteriorly, slightly less than total length of the carapace, anterior margin less convex and larger than the posterior, anterior margin before of theumbo short and abruptly inclined, anterior and posterior margins joined continuously with ventral, strongly convex ventral margin, approximately 17 to 30 growth lines regularly spaced (Figures 2, 3A), growth bands in two incremental categories: younger stages, those in the medium-dorsal region (50-100 μm wide) and older stages those in the ventral area (25-75 μm wide; Figures 2A-C, 3A), some specimens present growth lines with a close spacing pattern (12-50 μm) in the ventro-medial area (middle stage) (Figures 2, 4C).

Microscopic details: growth bands ornamented by two kinds of cavernous ornamentation with varying space between each cavity (Figure 3). The first pattern appears in the dorsal area (umbo and first five growth bands) of the carapace, the cavities of the growth bands are regularly distributed with narrow space between them, the ornamentation appears as polygonal reticulation (6.7-10 μm) with minute punctuation filling the cavities (Figure 3B). The second pattern of cavernous ornamentation (12 μm width x 17.9 μm length) occurs in the medium-ventral area, the growth bands are irregularly distributed and the exhibit ornamentation that looks oblique striate with minute punctuations (3-5 μm) (Figures 3C-D). In the ventral-anterior area of the carapace, the space between growth lines contains irregularly distributed scarce shallow ovate cavities, larger and more elongated than the reticul ornamentation (Figures 3E-G). The upper half of the growth band has fossae dimensions ranging from 7 to 12.6 μm filled with minute punctae 2 to 4 μm, the large cavities increase in size dorsally (Figure 3F). The lower half of each of the growth bands are ornamented with small fossae with dimensions ranging from 5.4 to 6.2 μm (Figures 3-4).

Counter impression of the scallops (in damaged carapace areas) is expressed as a wavy line, the dimensions of which range from 1 to 10 μm at the base of bead (with an average of 100 per millimetre). Small elliptical holes (3.5 μm, two of them separated by 7.8 μm) in the upper margin of the growth line are present over each bead (distance between them 14.4 μm), these holes likely correspond to setae attachment sites (Figure 3H) similar to those seen in some modern spinicaudatans (*sensu* Shen, 2003).

**Discussion.** As mentioned above, *Martinsestheria codoensis* comb. nov. shares some features at the generic or specific level with other spinicaudatans (in general) and particularly with anthrasteriids, but it is characterized by other characters that justify the erection of a new genus and that also verify the validity of the species name *M. codoensis*...
comb. nov. Cardoso (1962) and Carvalho (1993) noted that *M. codoensis* comb. nov. shares features with *Lioestheria florianensis* (Motuca Formation, Paranaiba Basin, Permian or Late Triassic age) such as the general carapace outline with a prominent umbonal region and seems only to differ in the higher number of growth lines with crenulated borders in the former. It is important to remark that Cardoso (1962, p. 36) only mentioned the presence of beads (“fine crenulations around 75 per mm”) in the lower margin of the growth lines of *M. codoensis* comb. nov.; we consider this as one of the most important specific diagnostic character of this species. Carvalho (1993) compared “*codoensis*” with *Bairdestheria mirandibensis* (Cardoso, 1966; *Cyzicus* (Lioestheria) *mirandibensis* in Tasch, 1987) mainly for its general outline and only differs in the great umbonal convexity of the second species, but these Brazilian species clearly differ by the presence of “radial striated type marking” ornamentation. Furthermore, *Cyzicus brauni* and *C. pricei* can be differentiated based on their different gross morphological outline, the presence of striated ornamentation in the terminal growth bands in both *C. brauni* (radial striated type) and *C. pricei* (microalveolar), and also by the presence of beads over the growth lines in *M. codoensis* comb. nov..

Carvalho (1993, est. 37C-D) figured a specimen of *C. pricei* that shows in the SEM microphotograph crenulated or beaded growth lines, but this character has not been described yet for such species. The potential presence of beads in *C. pricei* suggests that it is necessary to engage in more studies with the Brazilian Cretaceous spinicaudatan faunas in order to elucidate their actual taxonomic affinities.

*Martinesstheria codoensis* comb. nov. shares with *Pseudestherites musacchioi* and *P. rivarolai* the presence of the cavernous sculpture on the carapace, but the outline and other features of the valve are quite different. The ornamentation of *P. rivarolai* resembles that of *M. codoensis* comb. nov. exhibiting scarce cavities and the smooth umbonal area, and *M. codoensis* comb. nov. shares with *P. musacchioi* the smooth upper half of growth bands. Both *M. codoensis* comb. nov. and *P. musacchioi* exhibit striae on the growth bands, these are transverse in *P. musacchioi* and straight in *M. codoensis* comb. nov. Stigall (pers. com., 2009) states that *M. codoensis* comb. nov. is similar to the *Ethmosestheria* in terms of overall carapace shape and the presence of the sieve-like ornament on the growth bands, and he also suggests that: “It could potentially fit in the same genus or a similar genus, but is definitely a different species”.

Finally, it is considered that the presence of beads (with morphological features such as the festoon or garland aspect and the holes above them, Figures 3-4) and the presence of the cavernous ornamentation (Figure 3), strong convexity of the umbonal region and the subovate to subtriangular outline (Figures 2-3A) are definitive diagnostic characteristics. This suite of characters differentiates *Martinesstheria codoensis* comb. nov. from other Jurassic or Cretaceous spinicaudatan from northeastern Brazil and also all other species of known Anthronestheriids.

**TAPHONOMY AND AUTECOLOGY**

**Carapace**

The exoskeleton of spinicaudatans consists of thin outer epicuticle and an internal procuticle. This procuticle is multilamellar parallel to the surface; often the exocuticle and endocuticle are divided into sublayers (Warth, 1969; Rieder et al., 1984; Vannier et al., 2003). These structures are clearly shown in SEM photographs for *Martinesstheria codoensis* comb. nov. (Figure 4) where the cuticle has been partly damaged during or after fossilization. The growth bands and growth lines are formed by successive layering through new generation of cuticle after each molt. In these specimens, we observed that there is one inner layer corresponding to the base of each growth band. Subsequent layers are supported on this lower layer to generate the structures for ornamentation. Growth lines are generated by beads and festoons situated on lower margin of each growth band. The last layers constitute the definitive carapace ornamentation (Figure 4).

Olępska (2004) published photographs detailing the construction of the growth bands in Triassic spinicaudatan from lacustrine claystone at Krasiejów in southwestern Poland. These spinicaudatan have the same general type of multilamellar shell structure as *Martinesstheria codoensis* comb. nov. in that it has lamellae of different thickness that make up the carapace.

Martill et al. (2007) reported two types of preservation that occur in Santana Formation spinicaudatan replacement in a dark-brown to orange-brown goethite (a hydrated iron oxide)
or as black, carbonaceous replicas with finely disseminated pyrite. Carvalho et al. (2001) observed calcified valves with three-dimensional preservation for “Cyzicus codoensis” that sometimes occur with sulfates in their shells. We observed the presence of thin pyrite layer covering the carapace of all spinicaudatan specimens examined that suggested an environment with anoxic conditions (high pH and cationic contents and restricted water circulation) similar to that documented by Gallego & Shen (2006) for Pseudestherites musacchioi from the Lower Cretaceous La Amarga Formation (Neuquen Basin, Argentina).

The spinicaudatan assemblages from both localities examined are monospecific. The number of specimens per square centimeter ranges from an average of 6.5 (complete specimens) and 9 (fragmentary ones) in the Lameiro Village locality (LVC) and 1.3 and 4 from IBACIPE Caldas mine locality (ICMB) respectively. The juvenile/adult ratio is 1:2.6-1:3.3 for LVC and 1:1-1:4 for ICMB localities. If elongate specimens are considered to represent males and subtriangular specimens represent females, the sex ratio is approximately 1.4:1 (male/female) for LVC and 1:4 (male/female) for ICMB. The low diversity/high density assemblage is typical of ephemeral waters with stressed conditions (wet/dry seasonal climate and pyroclastic deposits), this is also reflected in the anomalous sex ratios reported from either locality. These kinds of sex ratios are interpreted as a result of fluctuating environmental conditions, as noted in ecological studies of extant taxa (Belk, 1972; Machado et al., 1999; Popovic & Gottstein-Matoćec, 2007).

The presence of growth bands of variable widths in spinicaudatans and their biological (sex, growth rate, life span and senility) and ecological (food resources, environmental stability, permanent or ephemeral pools) controls have been discussed by various authors (Tasch, 1969; Webb, 1979; Frank, 1988). Weeks et al. (1997) and Stigall & Hartman (2008) suggested that these variable increments are linked to the onset of the sexual maturity and the transition between rapid juvenile growths to reproductive phase. The species studied here shows two categories of growth band, one in the younger growth stage and the other in the older stage, both with a set of wide to narrow growth bands. These variable growth increments could be interpreted to reflect changes in environmental conditions (food resources, mineral concentrations and other physical factors). However, they may reflect an accelerated life cycle to achieve reproductive maturity in the face of stressful environmental conditions. The examples studied here were probably generated by both factors: the younger narrow bands related to the juvenile-adult transition and the older ones, a dry season response to low food resources. On the other hand, several of the measured specimens show a ‘middle stage’ growth category with a close spacing pattern suggesting a change or fluctuation in some of the environmental or biological factors during the organisms’ life. Some of the studied specimens (five) present different patterns with wide spacing pattern in the ventral area (ranging from 100-225 μm), that probably also reflect another kind of change in these factors. This pattern is congruent with other observed parameters such as the sex ratios recorded from the IBACIPE Caldas mine and Lameiro Village localities.

**Morphometry**

Both linear and geometric morphometric measurements were analyzed in order to assess any variation in geometry in the samples of Martinsestheria codoensis comb. nov. examined in this study. The spinicaudatan carapace has been subjected to a variety of techniques in previous research to quantify the morphology of both living and fossil forms (Tintori & Brambilla, 1991; Stoyan et al., 1994; Zierold, 2007; Hethke et al., 2010; Astrop et al., 2012) yielding varying degrees of success. In this study, simple linear measurements are used to elucidate any geometric differences between individuals collected from different localities, while a more complex morphometric approach is applied to elucidate any trends in carapace shape change within _M. codoensis_ comb. nov. All statistics performed using PAST v1.25.

Linear measurements in the form of raw height and length measurements as well as height/length ratios were calculated and the locality of each specimen measured was noted. The distribution of individuals based on height and length measurements seen in Figure 5 suggests that there is
a significant difference [p=0.0232 (t-test based on H/L ratios for either locality)] between the Lameiro Village (LV) and IBACIPE Caldas mine (ICMB) localities (not enough samples from DGP-USP type material).

Well-preserved samples of Martinestheria codoensis comb. nov. were subjected to a standard eigenshape analysis following the protocol outlined in Astrop et al. (2012). Out of 28 available specimens, 15 were suitable for morphometric analysis. The remaining 13 samples were too poorly preserved to provide a reliable representation of carapace shape (incomplete carapaces/partially embedded in matrix). Eigenshape analysis (sensu MacLeod, 1999) is a contemporary method for the ordination of complex outlines and is a suitable technique where sample material lacks multiple, discreet homologous features (as is the case in the relatively character depauperate carapace of spinicaudatans) because only one point is needed across all specimens in which to “anchor” the outline for contiguous comparisons. The outlines of all 15 specimens were digitized using tpsDig2 (v.2.16) as 100 equidistant Cartesian x/y coordinates starting from the junction of the anterior and dorsal margins. These coordinates are compiled (using tpsUtil v.1.5) before being subjected to analysis. The eigenshape analysis in this study implemented modified versions of the mathematic notebooks, which are freely available via morpho-tools.net. The data set of x-y coordinates are transformed into a shape function as angular deviations (phi function: \( \phi \); Zahn & Roskies, 1972) from the previous step (coordinate) in order to describe the shape of the curve. These functions are then subjected to singular value decomposition in order to reduce the dimensionality of the data and expose sub-structure as trends in shape change. These new vectors should display any global changes in shape within the dataset in order of decreasing value.

Eigenshape analysis of the 15 viable specimens produced three (3) major principle components of shape variation accounting for nearly 50% of the variation within this dataset (Table 1). Trends in shape change captured by the first three eigenshape vectors are illustrated in Figure 5. The shape variation captured by the first two eigenshapes clearly displays changes in the length and shape of the dorsal margin while the third captures changes in the “roundedness” of the ventral margin. The less affine shape seen in the shapes above is likely due to the small size of the dataset. Cluster analysis (Wards method) of the 15 specimens using the first three eigenshapes produces two discrete clusters (Figure 7A). Long-branching is likely due to within-group shape variation resulting from preservational trends and small sample size.

Assuming these two groups are indeed morphologically distinct from each other (possible dimorphism) it is then possible to characterize the shape change responsible for this within-species variation in carapace shape. Deriving the mean carapace shape of these two groups reveals two very distinct morphotypes (Figure 7B). The first morphotype is highly elliptical with long dorsal and ventral margins; this morphotype shows little to no recognizable umbonal region. The second morphotype is ovate/triangular with pronounced umbonal region protruding the above dorsal margin, these mean shapes fit well with historical descriptions of species attributed to Martinestheria codoensis comb. nov. Plotting all 15 individuals on eigenshapes 1+2 reveals no overlap and little within-group variance (Figure 7B). The clarity of these results should be tempered with caution, as the sample size is relatively small. It is likely that the shape trends captured are real, but it would be unwise to derive further inference about the species from such a small sample size. Given these results it is likely that there are in fact two morphotypes of M. codoensis comb. nov., and given the known dimorphism in carapace-shape seen in other living and fossil taxa it is likely that these morphotypes correspond to male and female. However, better-preserved specimens would be needed to fully understand the mode and extent of dimorphism and to make any inferences about the sexual system employed by this taxon (see Astrop et al., 2012).

### FINAL COMMENTS

The Family Anthronestheriidae is one of the smallest and most interesting families within the late Mesozoic spinicaudatans. Antronestheriidae have been previously reported from the Middle Jurassic of Great Britain, China, and Thailand, the Early Cretaceous of China and Argentina (Chen & Hudson, 1991; Gallego & Shen, 2004) and the Late Cretaceous from Madagascar (Stigall & Hartman, 2008). The re-examination of Martinestheria codoensis comb. nov. represents the fourth record of this family from the Southern Hemisphere. As mentioned by Gallego & Martins-Neto (2006) and by Stigall & Hartman (2008), “...most spinicaudatan taxa described from Gondwana have only been illustrated using light microscopy (e.g. Tasch, 1987). Without SEM images, we are unable to diagnose the characteristics of the family in these specimens and thus cannot accurately determine taxonomic relationships without restudy...". Given the information assessed in this study, it likely that the Antronestheriidae were widely distributed throughout Gondwana, possibly globally.

Due to their morphologic features (mainly the ornamentation pattern, carapace outline and umbonal characteristic) the genera Anthronestheria, Pseudestherites,
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