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REASSIGNMENT OF *LIOESTHERIA CODOENSIS* CARDOSO (SPINICAUDATA, ANTHRONESTHERIIDAE) FROM THE LOWER CRETACEOUS OF BRAZIL: SYSTEMATICS AND PALEOECOLOGY

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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.

RESUMO – *Lioestheria codoensis* Cardoso foi descrita a partir de materiais originalmente coletados da Formação Codó (Cretáceo Inferior, bacia do Parnaíba, Estado do Piauí), nordeste do Brasil. Desde a sua descoberta *L. codoensis* tem sido atribuída a diferentes gêneros por diferentes autores, como *Estheriina* (*Nudusia*) e *Cyzicus* (*Lioestheria*). Neste trabalho, atribuições sistemáticas anteriores são revistas e discutidas à luz de novos estudos de microscopia eletrônica de varredura de novo material. Como resultado desta pesquisa, a espécie é atribuída a um novo gênero da Família Antronestheriidae, sendo que o estudo integrou abordagens paleontológicas, biológicas e ecológicas para fornecer uma descrição robusta para a espécie. Atribuições anteriores para outros gêneros (*Estheriina*, *Lioestheria* e *Cyzicus*) também são analisadas e comparadas com outros gêneros afins da Família Anthronestheriidae (*Pseudestherites*, *Etmosestheria*, *Anthronestheria* e *Paleolepthestheria*? *chinensis*). Registros estratigráficos (formações Codó, Santana, Itapecuru, Rio da Batateira e Missão Velha) e geográficos detalhados (sete localidades) são compilados nesta publicação. Finalmente, a autoecologia e a variação morfológica dentro da espécie também são abordadas.

Palavras-chave: Anthronestheriidae, Formação Santana, Cretáceo Inferior, Brasil.

INTRODUCTION

Lioestheria codoensis Cardoso, 1962 was originally defined by Cardoso (1962) from materials found within the Codó Formation (Lower Cretaceous, Aptian-Albian) from the Parnaíba Basin (Mendes & Borghi, 2004) or Grajaú Basin (Paz & Rossetti, 2005; Marchesini Santos & Carvalho, 2009), (Piauí State) northeasthern 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 Parnaíba and Araripe basins and discussed its resemblance with other species from Brazil (*Cyzicus L. florianensis* Cardoso, *C. mirandibensis* Cardoso), Africa and Australia (*Cyzicus branchocarus* 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 Prámparo *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 & Cavalheiro, 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 (*Pseudestherites musacchioi* and *P. rivarolai*) from Argentina (Gallego & Shen, 2004; Prámparo *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 & Cavalheiro, 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

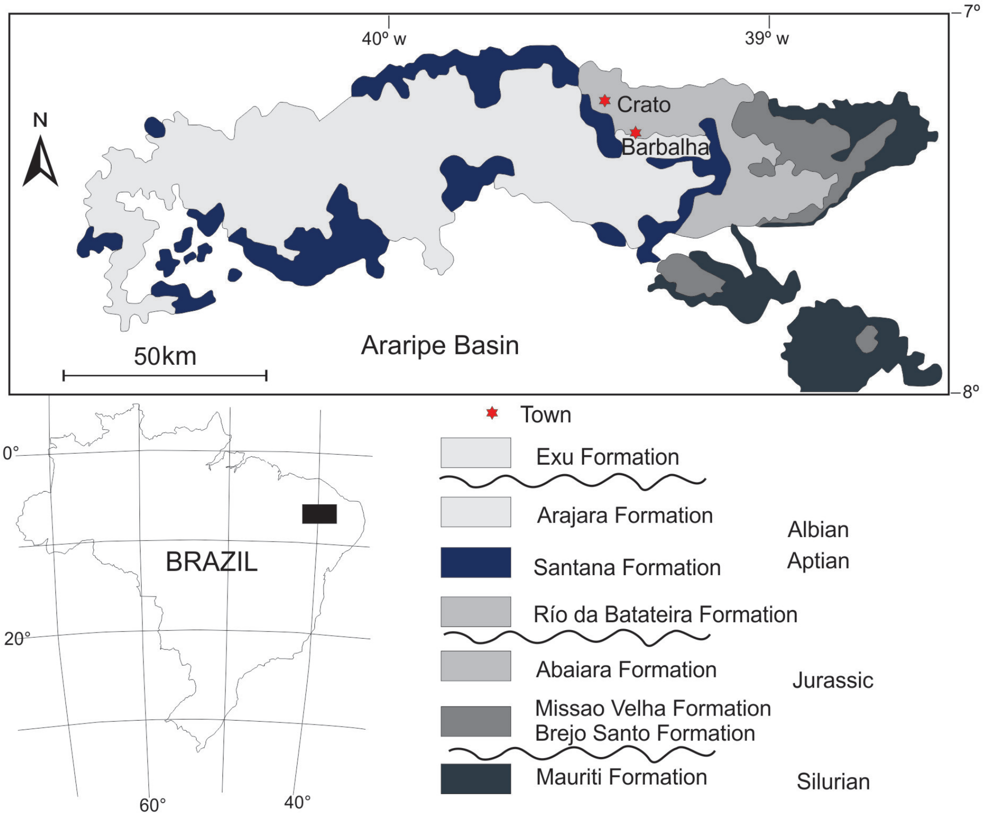

Figure 1. Location map of the fossiliferous localities within the Araripe Basin, northeasthern Brazil (modified from Viana & Neumann, 2002; Do Carmo *et al*., 2004).

(1991), Martin & Davies (2001) and Gallego & Shen (2004). 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 its umbo 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 & Mazerán (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: Lioestherioidea 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 luanpingensis* 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 & Mazerán (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*, *Camerunograpta*, *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 "Eosestherioidea-Anthronestheriidae group" due to its ornamentation constituted by scarce shallow elliptical cavities, similar to other Lower Cretaceous species (*Pseudestherites musacchioi* and *P. rivarolai*) from Argentina (Gallego & Shen, 2004; Prámparo *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 estherielliids (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, subovate, subtriangular or subcircular 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.

Includes the genera. *Anthronestheria* Chen & Hudson, 1991 (Middle Jurassic of Scotland), *Paleoleptestheria*? *chinensis* Chen, 1976 (*in* Zhang *et al*., 1976; Duan & Chen, 2000, Middle Jurassic of southwest China and Thailand), *Pseudestherites* Chen, 1976 (*in* Zhang *et al*., 1976, Early Cretaceous of northwest China and Argentina), *Ethmosestheria* Stigall & Hartman, 2008 (Late Cretaceous, Madagascar) and *Martinsestheria* gen. nov. (Early Cretaceous, Brazil).

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 subtriangular in outline (Figures 2, 7A), pronounced umbonal region, anterior umbo rises above dorsal margin, approximately 17-30 growth lines with festoon or garland (scallop) 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) filed 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, *Pseudestherites musacchioi* and the genera *Anthronestheria*, *Ethmosestheria* and *Martinsestheria* gen. nov. share the low density of cavernous ornamentation (higher in the Chinese species of *Pseudestherites* and *P. rivarolai*). *Antronestheria* and *Martinsestheria* gen. nov. are both characterized by a row of crowded fossae, but in *Antronestheria* 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 Anthronestheriidae 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.
1987 *Estheriina (Nudusia?) codoensis* Cardoso (*in* Tasch), p. 104.

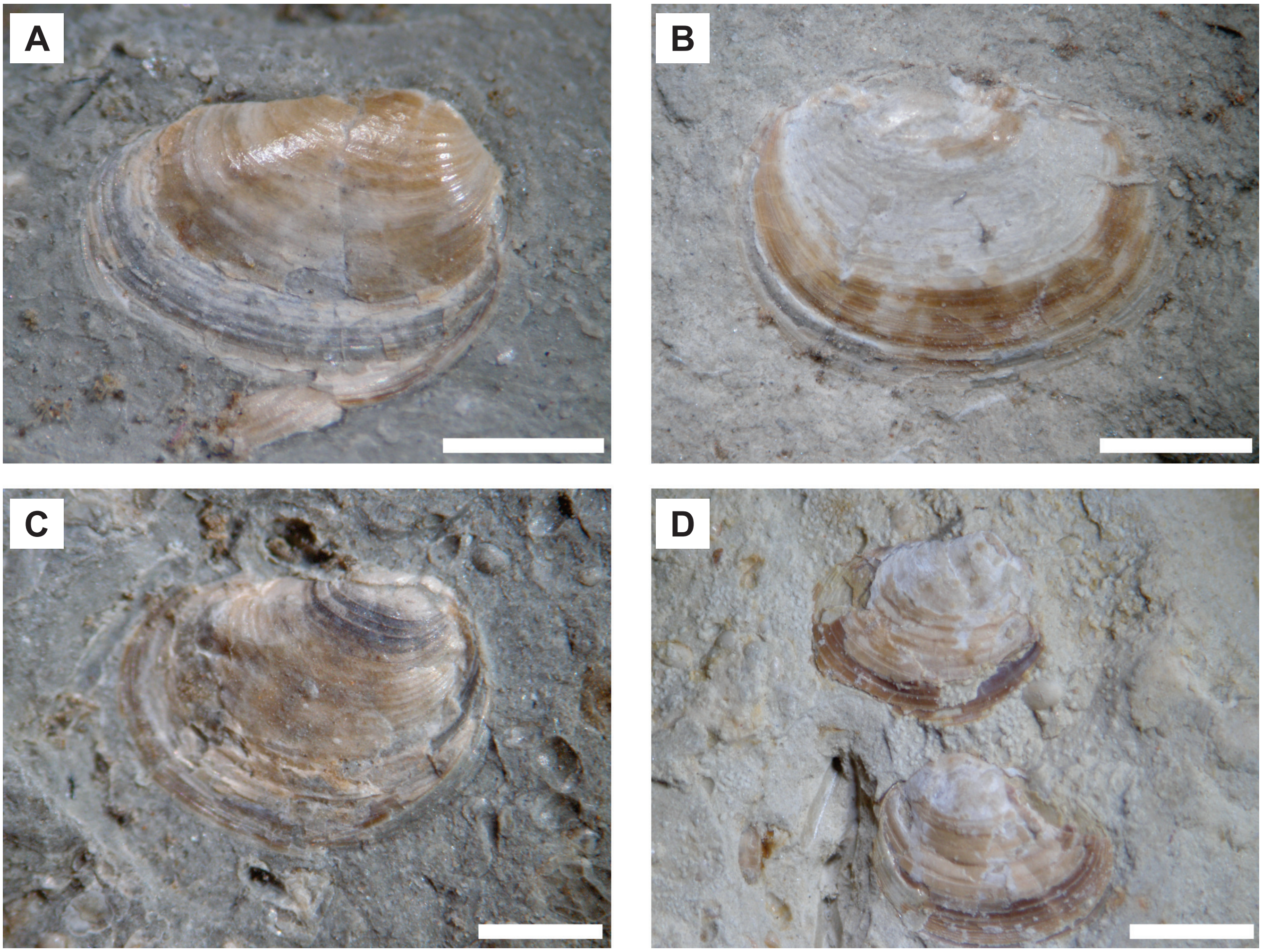

Figure 2. *Martinsestheria codoensis* (Cardoso) comb. nov. from Crato Member, Santana Formation, Brazil. Stereoscopic light pictures. **A**, CTES-PZ 7534, paratype, subtriangular right valve; **B**, CTES-PZ 7532b , paratype, subovate left valve; **C**, CTES-PZ 7535, paratype, subovate right valve; **D**, CTES-PZ 7533c, paratype, subtriangular right (top) and left (bottom) valves. Scale bars = 1 mm.

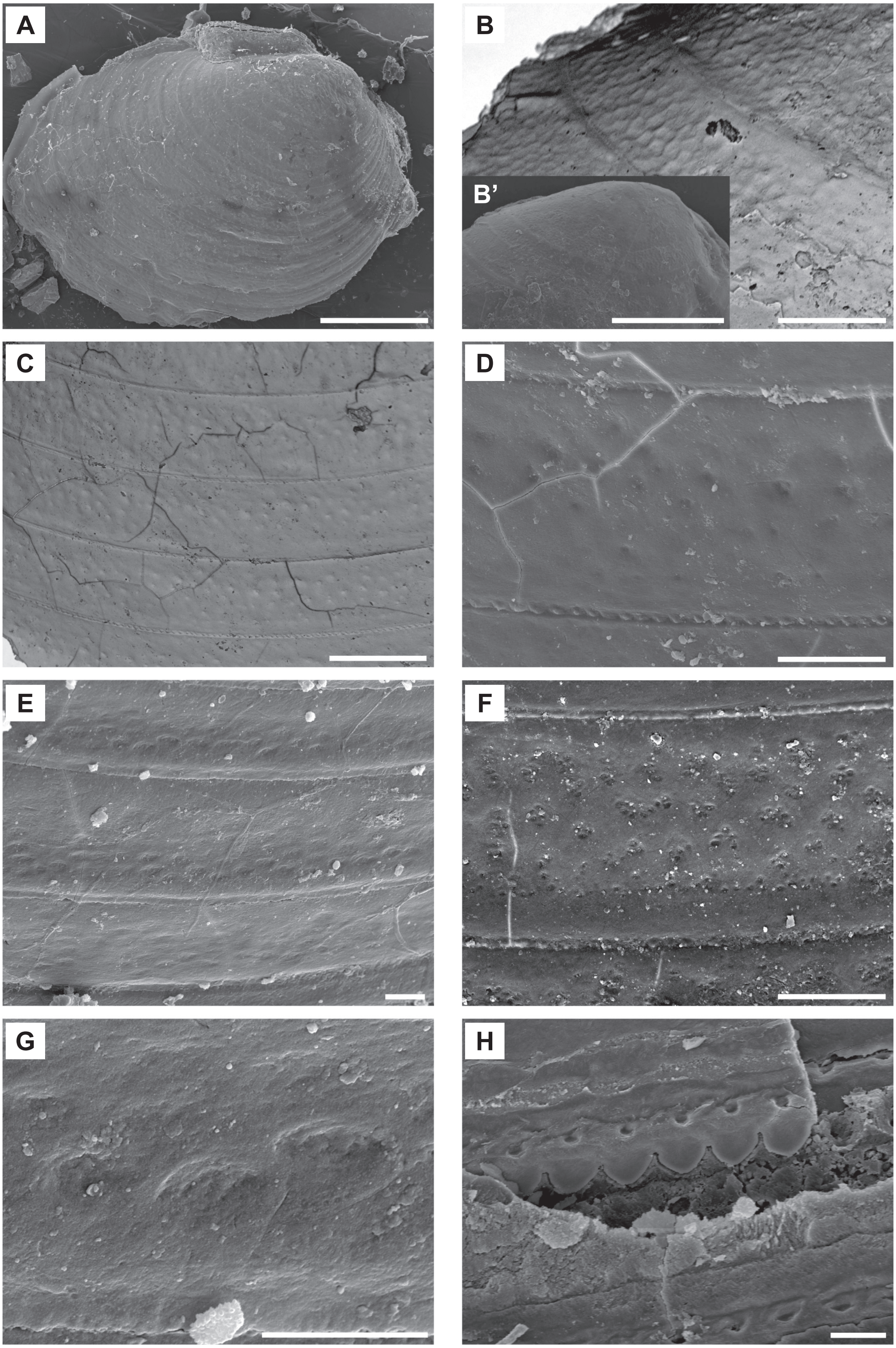

Figure 3. *Martinsestheria codoensis* (Cardoso) comb. nov. from Crato Member, Santana Formation, Brazil. Scanning electron micrographs. **A**, CTES-PZ 7288, paratype, subtriangular right valve; **B-B'**, CTES-PZ 7484, paratype, dorsal polygonal reticular ornamentation (B, umbonal ornamentation detail 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.

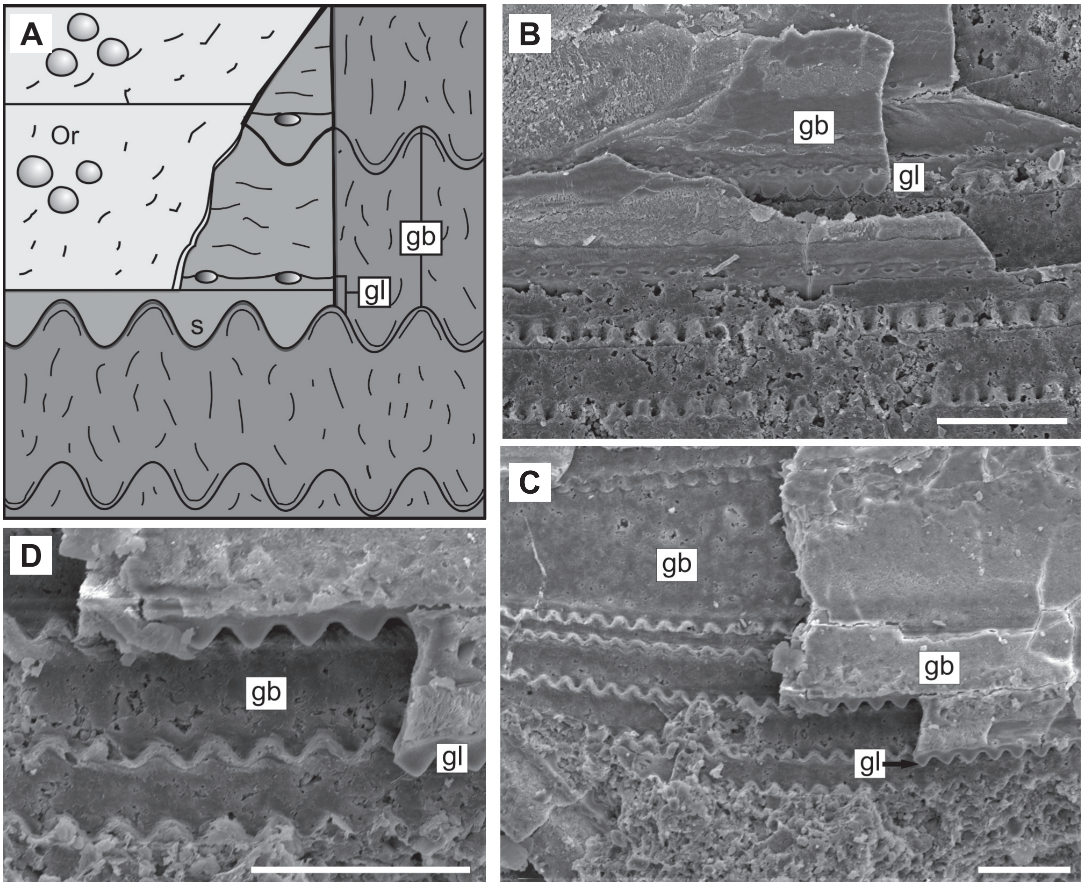

Figure 4. *Martinsestheria codoensis* (Cardoso) comb. nov. from Crato Member, Santana Formation, Brazil. Scanning electron micrographs shows growth band morphology and multilamellar cuticle. **A**, reconstruction of the growth band morphology; **B**, CTES-PZ 7484, detail of the triangular plate growth line morphology; **C**, CTES-PZ 7484, detail of the scallop/garland type of growth line morphology and the different growth bands spacing; **D**, detailed of C showing the festoon or "shark teeth" growth lines. **Abbreviations: gb**, growth band; **gl**, growth line; **s**, scallop, **or**, ornamentation. Scale bars = 60 µm.

1993 *Cyzicus* cf. *Cyzicus branchocarus* Tallent, 1965. Carvalho & Viana, p.184-186, est. I, A-B.

1993 *Cyzicus* (*Lioestheria*) *codoensis* Cardoso. Carvalho, p. 201-202, est. 44A, 45A-B, 46A-B, 47B, 57C-D, 58A-B, 59A-C.

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.

Stratigraphic section and age of the type locality. After Cardoso (1962) Codó Formation, Parnaíba Basin, Early Cretaceous (Aptian - Albian) - Early Cretaceous (*sensu* Marchesini Santos & Carvalho, 2009), palynological data indicate an Upper Alagoas (early Albian) age, by correlation with the Santana Formation; the laminated calcareous basal level is dated as Aptian. Associated flora/fauna: plants, fossil wood (conifers); invertebrates, ostracods (Marchesini Santos & Carvalho, 2009).

Other localities. After Marchesini Santos & Carvalho (2009):

(i) Jundiaí/Guariba locality, left margin of the Itapecuru river, north of Cantanhede, Itapecuru-Mirim Municipality, Maranhão State, Brazil; middle Itapecuru Formation, São Luís-Grajaú Basin, Cretaceous (early Albian-middle Albian). Associated fauna/flora: palynomorphs and plant remains, invertebrate ichnofossils *Skolithos*, anodontid bivalves, spinicaudatans (*Cyzicus*? *abaetensis*, *C. brauni*), fish (picnodontids teeth, *Mawsonia gigas* scales, teeth and vertebra), crocodylomorph teeth and theropod dinosaurs;

(ii) Codó locality, Santo Antônio, Porto Novo, margin of Gameleira stream, Cimento Nassau fabric (São Luis-Teresina road) and near Codó Municipality (04º30'S, 43º50'W), Maranhão State, Brazil, Codó Formation, Parnaíba 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;

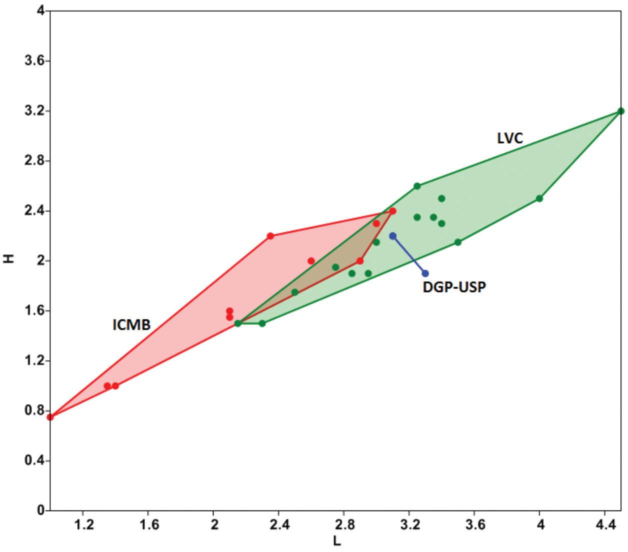

Figure 5. Height and length measurements of specimens from different localities. **Abbreviations: ICMB-IBACIPE**, Caldas mine, Barbalha; **DGP-USP**, Universidade de São Paulo; **LVC**, Lameiro Village, Crato.

(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;

(vii) Sitio Fundão locality after Carvalho (1993), Batateira River, Crato Municipality, Ceará State, Brazil, Missão Velha Formation, Barbalha Member, Araripe Basin, Early Cretaceous. Material AR-42-2 (Petrobrás).

Diagnosis emended. Spinicaudatan with small carapace (length: 1.0-4.50 mm, height: 0.75-3.20 mm), subovate to subtriangular in outline, pronounced umbonal region, anterior umbo 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 the umbo short and abruptly inclined, strongly convex ventral margin, approximately 17 to 30 growth lines with beads distally, growth bands ornamented by two patterns, dorsally near the convex umbonal 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 (ranging from 7 to 12.6 µm in length) filled with minute punctae (2 to 4 µm wide), lower half of growth bands 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).

Localities 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 LPMi 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* or/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 umbonal 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 the umbo 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 reticular 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 in width (Figures 3F-G). In the upper half of each growth band, small cavities (3.7-4.5 µm) appear aligned. Growth lines appear scalloped along the lower margin (like "shark teeth" or triangular plates) (Figures 3H, 4). The 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 anthronestheriids, 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*

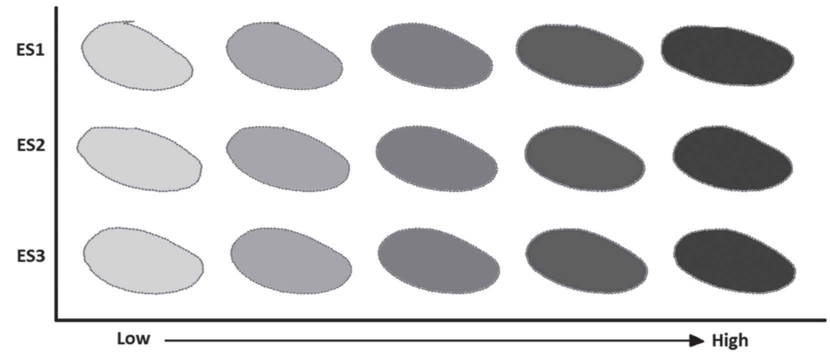

Figure 6. Trends in shape change captured by the first three eigenshape (ES) vectors, accounting for approximately 50% of the observed variation within the data set.

comb. nov. Cardoso (1962) and Carvalho (1993) noted that *M. codoensis* comb. nov. shares features with *Lioestheria florianensis* (Motuca Formation, Paranaíba 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.

Martinsestheria 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. musacchoi* exhibit striae on the growth bands, these are transverse in *P. musacchoi* 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 *Martinsestheria codoensis* comb. nov. from other Jurassic or Cretaceous spinicaudatans from northeasthern 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 *Martinsestheria 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).

Olempska (2004) published photographs detailing the construction of the growth bands in Triassic spinicaudatans from lacustrine claystone at Krasiejów in southwestern Poland. These spinicaudatans have the same general type of multilammellar shell structure as *Martinsestheria 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 spinicaudatans replacement in a dark-brown to orange-brown goethite (a hydrated iron oxide)

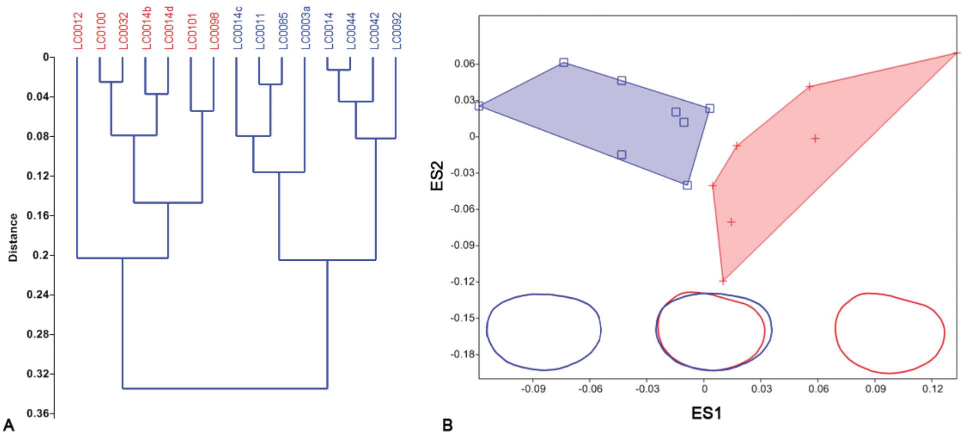

Figure 7. A, cluster analysis of all 15 specimens using Wards method, groups assigned using this information; **B**, distribution of all 15 specimens on eigenshape axes 1 and 2, mean shapes of both groups also shown separately and overlapping.

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-Matočec, 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

Table 1. The three major principle components of shape variation produced by an Eigenshape analysis of the 15 viable specimens.

	ES1	ES2	ES3
eigenvalues	0.048471	0.036888	0.026638
total variance (percent)	0.093393	0.071075	0.051326
cumulative variance (percent)	99.63342	99.7045	99.75582
adjusted total variance (percent)	20.30418	15.45216	11.15852
cumulative adjusted total variance (percent)	20.30418	35.75634	46.91485

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 *Martinsestheria 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: φ; 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 *Martinsestheria 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 *Martinsestheria 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 Anthronestheriidae 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*, *Ethmosestheria* and *Martinsestheria* gen. nov., are likely to be related phylogenetically. Some species of *Pseudestherites* and the form described here (as *P. rivarolai* and *M. codoensis* comb. nov.) have ornamentation with few shallow scarce cavities and large smooth umbonal area. While *P. musacchioi* and *M. codoensis* comb. nov. share a smooth upper half of the growth bands. Both *M. codoensis* comb. nov. and *P. musacchoi* exhibit striae on the growth bands, these are transverse in *P. musacchoi* and straight in *M. codoensis* comb. nov. With *E. mahajangaensis* and some species of extant *Cyzicus* (T. Astrop, pers. obs.) *M. codoensis* comb. nov. shares the presence of punctate ornamentation inside cavities and a sieve-like ornamentation with punctuations. According to Stigall & Hartman (2008), *Pseudestherites* has higher density of the cavernous ornamentation and is similar to the density seen in *Anthronestheria* and *Ethmosestheria.* Conversely, *M. codoensis* comb. nov. shows a lower density of the cavities, with large smooth areas around them. Finally, a definitively distinctive character of *M. codoensis* comb. nov. is the presence of beads on the lower margin of the growth lines.

Taphonomically, the portion of the cuticle that has been preserved is a multilamellar structure showing lamellae of different thicknesses. The high quality preservation seen in some of the specimens was likely achieved by the deposition of pyrite on the cuticle preventing the destruction of the carapace.

Several paleoecological observations can also be made using this material; *Martinsestheria codoensis* comb. nov. shows differences in size of the individuals between each locality. This likely represents different stages of maturity between populations or the stability of the ecosystem or environmental conditions that were prevalent at either locality. Environmental factors, such as population density, nutrient availability and habitat size often lead to the promotion, restriction and even cessation of growth in modern spinicaudatan species while cyclical fluctuations of environmental factors may also lead to irregular molting periods that result in the different widths of growth bands seen in both fossil and living spinicaudata (Astrop pers. obs.). Morphometric analyses confirm paleontological observations of two distinct morphotypes, the first being highly elliptical with long dorsal and ventral margins while the second is ovate/triangular with a pronounced umbonal region protruding the above dorsal margin. It is likely these morphotypes correspond to male and female sexes, respectively, given observed dimorphism in most living spinicaudatan and the recorded instances in fossil species.

The integrated approach used here in the systematic revision of *Martinsestheria codoensis* comb. nov. provides a template for future paleontological assessments of spinicaudatan clam shrimp that helps move the group toward a consistent taxonomic scheme and also provides a reference for the future identification and description of new species from South America.

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